Sondaar, P.Y., Van der Geer, A.A.E. 2002. Plio-Pleistocene terrestrial vertebrate faunal evolution on Mediterranean islands, compared to that of the Palearctic mainland. Annales Géologiques des Pays Helléniques 1e Série 39, A: 165-180.

Plio-Pleistocene terrestrial vertebrate faunal evolution on Mediterranean islands, compared to that of the Palearctic mainland

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Summary

In the Mediterranean two types of Plio-Pleistocene islands are recognized: continent islands like Sardinia/Corsica, and ocean-like islands like Crete and Cyprus. The origin of the fauna of the first type is a Pliocene mainland fauna, while the second type is colonized by overseas sweepstake dispersal.

In both cases there is a fast adaptation to the island environment followed by a stasis, or long-lasting equilibrium. Arrival of humans caused dramatic faunal changes on Sardinia, from the Middle Pleistocene, and on Cyprus from the Early Neolithic.

The pattern of faunal changes on islands is essentially different from the faunal evolution of Plio/Pleistocene Palearctic mainland, where many faunal turnovers took place, mainly triggered by global climatological events. These events had little impact on the faunal evolution on islands.

Introduction

The Late Pliocene fauna of Vatera (Lesvos, Greece) has a mainland stamp and, based on faunal content, it can be placed in the St. Vallier Faunal Unit (MN 17) in the Palearctic faunal succession. The geographic isolation of Lesvos from the mainland is a recent geological event, mainly caused by eustatic rise of sea level in the Holocene. Lesvos is therefore a clear example of a continental island.

It is evident that the composition of an island fauna greatly depends on which landvertebrates could reach the islands and at what time, thus it is necessary to know the geologic history of the islands. Zoogeographically two types of islands can be recognized (Darlington, 1957): a) Continental islands which became isolated from the mainland through subsidence of the isthmus of a peninsula. In this case, the ancestral fauna of the island is a mainland fauna; b) Oceanic islands are assumed to have arisen beneath the sea. In this case the most obvious obstacle to reach the islands for landvertebrates is water, like channels, straits or open seas. Land vertebrates could reach these islands by sweepstake dispersal, which was defined by Simpson (1965) as follows: 'spread is impossible for the most and very improbable for some, but does occur accidentally'. If an

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island becomes populated by sweepstake dispersal, only very few taxa will reach the island. Among the ungulates, it are only those with good swimming or floating capacities. The endemic Pliocene/Pleistocene insular faunas show that especially elephants, hippos and deer were successfull in reaching the islands.

The paleogeography of the Mediterranean islands is complex. For example, Crete was part of the mainland during the Miocene, submerged in the Pliocene, and got its present shape in the Pleistocene. Other islands have a different paleogeographic history, but in general it can be said that the Plio-Pleistocene terrestrial faunas of these islands are impoverished and show characteristic features. The composition of these endemic faunas suggests that the colonizing population came overseas. Alcover *et al*. (1998) call these islands oceanic-like islands, and give the following definition: oceanic islands have always been isolated, while oceanic-like islands have been at times connected to the continents.

The composition of the fauna depends on which animals could reach the islands (sweepstake dispersal). The frequency of elephants, deer and hippos on islands can be explained by their shared characters: they can swim very well and their digestive system produces gasses which add to the floating capacity. In addition, the trunk of an elephant serves as a snorkel device, which enhances their potential to survive for longer periods in the water. Finally, these animals live and swim in herds. Carnivores, too, can swim, but they do not have the above described floating capacity. Further, if they reach the island, it will not be in a herd, and therefore the founder population may be too small to establish a viable population. The lack of predators and the restricted territory both lead to unique evolutionary changes, for example, the dwarfing of the herbivores and endemism of rodents. Though each island has its own geologic history and in consequence its own evolutionary history in respect to vertebrates and prehistory, they share evolutionary patterns that clearly set them apart from the mainland (Sondaar & Boekschoten, 1967; Sondaar, 1977). However, not all Mediterranean islands can be classified as oceanic-like islands. Sardinia for example, is considered a continental island.

The Plio-Pleistocene continental island Sardinia-Corsica

The presence of a hyaenid in association with a diverse terrestrial mammal fauna, Early Pleistocene in age (Ginesu & Cordy, 1997) means that during the Plio/Pleistocene Sardinia was not colonized overseas, and therefore cannot be considered an oceanic-like island in that time (Sondaar, 2000). The fauna is endemic, yet balanced. If we take into account the evolution of the Tyrrhenian sea which opened in the Early Pliocene, Sardinia must be considered a continental island which became separated in the Early Pliocene from the mainland. The ancestral fauna of the endemic Plio/Pleistocene fauna must therefore be an Early Pliocene mainland fauna. This is confirmed by the murid *Rhagapodemus minor* (type locality Mandriola, Pliocene), as it is not strongly derived as the insular *Rhagamys orthodon* (Late Pleistocene), but is similar to the mainland *Rhagapodemus* (Martin Suarez & Mein, 1998). The taxa found at the Mandriola site are also present in the Early Pleistocene fauna of the Orosei fissure deposits.

The Plio/Early Pleistocene fauna is characterized by *Rhagapodemus minor*. During this period the mainland is characterized by several faunal turnovers (MN 14 to MQ 4), whereas there is a stasis in the fauna of Sardinia. In the Early Middle Pleistocene, however, there is a dramatic faunal turnover, with extinctions and new arrivals, followed by three more faunal turnovers (fig. 1).

Altogether five different faunal units can be recognized during the Pliocene-Holocene of Sardinia and Corsica (Ginesu & Cordy, 1997; Sondaar, 1987,1998, 2000; Vigne, 1998; Van der Made, 1999). These are, from oldest to youngest (fig. 2):

1) the *Rhagapodemus* - caprid fauna,
2) the *Tyrrhenicola* - *Nesogoral* - *Homo* fauna,
3) the *Tyrrhenicola* - *Megaloceros* - *Homo* fauna,
4) the Mesolithic *Tyrrhenicola* - *Prolagus* fauna,
5) the Early Neolithic fauna.

The third fauna is the best known of all these fossil associations. It is supposed to range from the Late Middle Pleistocene to the Lower Holocene. Although it is clearly endemic and exhibits a cervid as do so many other island faunas, it is quite original in several aspects. The deer *Megaloceros* is not a dwarf; a fox-sized canid *Cynotherium* is present, as well as a rabbit-like mammal *Prolagus*. The *Tyrrhenicola* - *Megaloceros* fauna is represented by large bone accumulations in cave deposits at Dragonara and Corbeddu (Malatesta, 1970; Caloi & Malatesta, 1974; Klein Hofmeijer, 1996; Sondaar *et al*., 1984). The Mesolithic fauna (nr. 4) is mainly known from Corsica (Vigne, 1998). The Early Neolithic fauna (nr. 5) is characterized by the introduction of pig, sheep and goat.
In all the Pleistocene and Early Neolithic faunas, *Prolagus* is abundant.

The stasis in faunal evolution from Early Pliocene till Early Middle Pleistocene on Sardinia, followed by four dramatic faunal turnovers, is difficult to understand if we don’t take the impact of human colonization into account. Human presence on the Pleistocene island is attested by archaeological complexes and human fossils.

On Sardinia, there are more than ten Paleolithic sites, which are placed in three different complexes (Martini, 1992). The two oldest complexes are compared with complexes called "Early Clactonian" and "Late Clactonian" from the continent. Their age is based on geomorphologic and pedologic studies of the sediment as well as on the technological and typological features of the lithic artefacts themselves. The oldest (Coa de sa Mua, Perfugas) is interpreted as Middle Pleistocene. The subsequent (Sa Pedrosa-Pantallino, Sassari) is older than the last glaciation (Arca *et al*., 1982; Bini *et al*. 1993; Martini, 1992). There is a hiatus in the archaeological record till the upper part of the Late Pleistocene from Corbeddu cave, Oliena, where a lithic complex is found of siliceous limestone, dated 14.000-12.000 BP (Martini, 1992; Sondaar *et al*., 1991). This industry is characterized by a very particular elementary and undifferentiated technology. Tools characterizing Upper Paleolithic complexes of the continent are lacking. In addition, human fossils with endemic characters (Spoor & Sondaar, 1986) have also been discovered in this cave (breccia layer 2; Klein Hofmeijer, 1996). The endemic lithic industry and endemic human fossils are found in association with the typical Late Pleistocene Sardinian/Corsican *Tyrrhenicola- Megaloceros* fauna.

The occurrence on Sardinia of two lithic complexes similar to the mainland Early Clactonian and Late Clactonian led Martini (1992) to the hypothesis of two human migration waves, one in the Early Middle Pleistocene and the second in the Early Late Pleistocene. This hypothesis fits very well with the dramatic faunal turnovers, which could have been caused, at least in part, by human arrivals.

The third endemic industry, dated at Late Pleistocene (14.000-12.000 BP), points to a long occupation of the island (Martini, 1992). A human phalanx dated at 20.000 BP, and two skull fragments dated at 8.750 ± 140 BP were found in the breccia layer 2 at Corbeddu (Sondaar *et al*., 1995; Spoor & Sondaar, 1986; Klein Hofmeijer, 1996; Klein Hofmeijer *et al*., 1987). The skull fragments show endemic characters which may point, just as the endemic industry (Martini, 1992) to a longer isolation. Thus, the entire picture is more consistent with a long human occupation rather than with 'occasional visits' (Cherry, 1990, 1992). Although this picture may hopefully be corroborated by further findings in the future (Kra, 1998), there is absolutely no reason to speak of 'erratic human bones' (Vigne, 1996) when referring to the fossils found and excavated from breccia layer 2 of Hall 2.

Faunal turnovers

It appears that the transition between the different Pleistocene fauna’s is not gradual, but punctuated instead. The changes are characterized by an extinction of large herbivores/omnivores, and an arrival of new herbivores from the mainland. On the whole, after each transition, or faunal turnover, there is a loss in total number of large herbivores.

There are four dramatic faunal turnovers, with extinctions and arrivals of herbivores, in some cases in association with archaeological complexes (fig. 3). The boundaries between the faunal units are sharp, characterized by extinctions which point to a catastrophic event. There are two faunal turnovers in the Pleistocene and two in the Holocene.

1) In the Early Middle Pleistocene between the *Rhagapodemus* - caprid and the *Tyrrhenicola* - *Nesogoral* fauna: eight taxa (> 50%) become extinct, among which the large herbivores and the hyaenid *Chasmaporthetes* (Ginesu & Cordy, 1997). New arrivals are the ancestors of *Tyrrhenicola* and *Nesogoral,* and possibly also *Homo erectus* arrived (Sondaar, 1998, 2000).

2) In the Late Pleistocene between the *Tyrrhenicola* - *Nesogoral* and the *Tyrrhenicola* - *Megaloceros* fauna: *Nesogoral* and *Macaca* become extinct. New arrivals are *Megaloceros* and probably an archaic *Homo* "*sapiens*".

3) In the Early Holocene between the *Tyrrhenicola - Megaloceros* and the *Tyrrhenicola - Prolagus* fauna.

4) In the Holocene between *Tyrrhenicola - Prolagus* and the recent fauna, with the arrival Neolithic modern humans.

Extinction of more than one taxon at the same time suggests a kind of event. MacPhee & Marx (1997) stress the importance of diseases as cause for extinction. At the Pleistocene site Mavro Mouri (Rethymnon, Crete), many of the excavated fossils of the endemic deer *Candiacervus* were affected by a severe bone disease. Yet this disease did not result in the extinction of the Cretan deer (Sondaar, 1977). In this case the disease was not even responsible for the extinction of one taxon only.

Natural disasters could lead to the extinction of an endemic terrestrial island fauna. A clear example of such an event is Late Pleistocene Ibiza. Nearly all endemic land vertebrates became extinct. The only land vertebrate found in the Late Pleistocene fauna, besides birds and bats, was *Podarcis pytyusensis* (Alcover *et al*., 1994; Sondaar *et al*., 1995). The nature of the natural disaster is not yet clear, but it affected all land vertebrates.

In the case of Pleistocene Sardinia, it were only the larger herbivores that became extinct. Diseases or natural disasters can therefore not have been the cause, nor did global climatological changes affect island environments directly. The more the faunal turnovers can be correlated with a change in archaeological complex, the best they can be explained by a human colonization wave.

***Prolagus*, the natural food resource for Paleolithic colonization**

On Corsica, which was connected with Sardinia during stages of low sea level, a Late Pleistocene Paleolithic occupation is recognized (Bonifay, 1994). Moreover, between the Paleolithic and the Neolithic, a so-called Preneolithic, now called Mesolithic, has well been established by a series of sites (Vigne, 1998; Lanfranchi, 1998). This Mesolithic is characterized by the absence of pottery and domesticated animals, while *Megaloceros*, so characteristic for the Late Paleolithic on Sardinia/Corsica, must have been extinct, in contrast to *Prolagus*, which was the dominant mammal and still present on the island. This ochotonid weighing about 800 grams is a giant compared to its extant relative *Ochotona* (140 grams). Artefactual material consists of idiosyncratic lithics from local quartz and rhyolithe, without the obsidian that marks the beginning of the Early Neolithic (Vigne, 1998).

The chronological position of the Corsican Mesolithic sites, occupied by permanent hunter-gatherer groups, covers the Middle and the second half of the 9th millennium, and probably also part of the 8th millennium BP (Vigne, 1998). This is confirmed by the discovery of a female human skeleton with modern morphology, by Lanfranchi in the Mesolithic of the abri d'Araguina-Sennola, dated to 8520 ± 150 BP (Lanfranchi *et al*.

1973; Duday 1975; Lanfranchi, 1998). Thus, the Mesolithic of Corsica might cover a time span of a millennium (Lanfranchi, 1998; Vigne, 1998).

Proportions of the weights of edible matter from sea-shells, fishes, birds, rodents and *Prolagus* from five Mesolithic sites on Corsica are calculated by Vigne (1998) on the basis of Minimal Number of Individuals (MNI) and (zoological group specific) average individual weight of edible matter. The percentages of *Prolagus* appear to vary between 78 and 95-98%. This indicates that for about a millennium, more than 80% of edible resources for the Sardinian/Corsica Mesolithic people was obtained from *Prolagus* hunting (fig. 4).

If we calculate the *Prolagus* MNI needed to cover the metabolic costs of humans, we get the following results (Sondaar & Van der Geer, 2000). A *Prolagus* of 800 g yields 0,8 x 530 x 8 = 3392 kJ, and 128 g proteins, using the nutritional data of the wild rabbit *Oryctolagus cuniculus*. Present day men of 70 kilos, ages 20 to 35, and medium activity need 70 g protein at 12,1 MJ, whereas pregnant and breast feeding women of 60 kilos, ages 20 to 35, and medium activity need 75 g proteins at 11,6 MJ. Thus, these humans need only two ochotonids in three days to cover their protein needs, or four to cover their caloric need also. Most calories, however, will come from non-animal sources like fruits, grains, roots and bulbs. A group of forty persons, consisting of, for example, twenty of the above high-energy-cost persons, and twenty ‘three-quarters’, will need 20 ochotonids a day (or 7300 a year) to cover their protein needs, if we assume that the flora contains no proteins, which is highly improbable. Most edible plants contain about at least 1,4 gram protein per 100 gram. If *Prolagus* females had 20 young a year, that is an average of 10 per individual, the population needs to consist of at least 730 individuals if the human hunters could not find any other protein source. In conclusion, it is highly probable that a human group can survive on *Prolagus* or similar animals, especially if we take into consideration that earlier humans were smaller, and had access to other food sources as well. Thus, it may be safely stated that the Sardinian/Corsican *Prolagus* population could support, without danger of becoming exhausted, a viable human population over a long period of time.

In conclusion it can be said that:

1) Plio/Pleistocene Sardinia is a continental island that became isolated from the mainland in the Early Pliocene. There was probably a rapid adaptation of the Early Pliocene mainland fauna, which resulted in the *Rhagapodemus* - caprid fauna with the hyenid *Chasmaporthetes*. There was a stasis in faunal evolution from Early Pliocene to Early Middle Pleistocene.

2) different archaeological complexes indicate human presence on the island from the Middle Pleistocene on Sardinia.

3) four different dramatic faunal turnovers can be recognized in the Pleistocene faunal succession of Sardinia with extinctions of endemic large herbivores.

4) four different archaeological complexes can be recognized, which corroborate in time sequence with the faunal turnovers.

5) a possible explanation might be that the faunal turnovers are related to different human colonization waves. These humans introduced new hunting techniques which appeared to be fatal for the endemic large herbivores through overkill.

6) crucial for a successful colonization of Sardinia/Corsica was the presence of *Prolagus* in the local fauna. A *Prolagus* population could support, without danger of exhaustion, a viable human population.

7) *Prolagus* is present in the Early Pleistocene fauna and survives the four different faunal turnovers.

The oceanic-like island Cyprus

Once an endemic island fauna is established, it remains more or less stable in composition and morphology, and is not affected by global climatic changes. For example, the *Myotragus* fauna from Mallorca did not change in composition, nor did *Myotragus* itself change much in morphology from the Early Pliocene until colonization of the islands by humans took place (Alcover *et al*., 1994; Alcover *et al*., 1998; Sondaar *et al*., 1995).

The Pleistocene fauna of Cyprus contains two large herbivores: the dwarf elephant *Elephas cypriotes* and the dwarf hippo *Phanourios minutes* (Bate, 1906; Boekschoten & Sondaar,1972; Houtekamer & Sondaar, 1979; Spaan, 1996). More than 90% of the fossils belong to the hippo and were found at more than ten sites, which means that the environment must have been quite favorable for *Phanourios minutes.* This dwarf hippo was well adapted to walking on rocky soil and also to climbing, but it never evolved a better cursorial locomotion than its ancestor from the mainland. Its dentition was lophodont, indicating an adaptation to browsing, which is unique in the family Hippopotamidae. Accordingly, the Pleistocene Cyprus must have been forested or at least covered with shrubs.

As on other oceanic-like islands, the established endemic mammal fauna from Cyprus did not change much through time. Fossil hippos from localities that differ in age, are quite similar in morphology and do not show different evolutionary stages on which a relative age could be based. Moreover, there are no clear stratigraphical sections in which a faunal succession could be studied (Boekschoten & Sondaar, 1972; Houtekamer & Sondaar 1979). As the morphology of the molars of *Elephas cypriotes* suggests an ancestry from the Pliocene/Early Pleistocene *Mammuthus meridionales* from the mainland, the minimum age for the endemic *Phanourios minutes - Elephas cypriotes* fauna might be Early Pleistocene (see also dates given by Reese, 1996).

The discovery of the Akrotiri Aetokremnos site (Cyprus), in which the Pleistocene endemic dwarf hippos and dwarf elephants are found together with a lithic industry (Mandel & Simmons, 1997; Simmons, 1988, 1999) brought not only new insight on the extinction of these endemics, but also on the exploitation of food resources by the earliest humans on a Mediterranean island. In this site, a large deposit of fossils of Pleistocene endemic fauna, mainly consisting of dwarf hippos, is associated with artefactual material and burnt bones and shells dating to the mid ninth millennium BC. The main strata (stratum 2 and 4) differ considerably in their faunal content. In the older stratum 4, the bulk of the remains belongs to the hippo (>98%), whereas this percentage is less than 20% in the younger stratum 2 (Reese, 1996) (fig. 5). This suggests that the human consumption of hippos eventually resulted in a decline in their number (Simmons, 1996; Reese, 1996).

Although C14 dating is available for both strata, they cannot be compared as such, as the samples from the stratigraphically older bone accumulation of stratum 4 were taken from dwarf hippo bones, while those of the younger stratum 2 were taken from shells and charcoal. The different C14 ages are 10.640 ± 30 BP for stratum 2 and 9.835 ± 70 BP for stratum 4 (Simmons & Wigand, 1994). Bunimowitz & Barkai (1996) consider this an "interesting case of reversed stratigraphy", and use these datings to cast doubt on the interpretations of Simmons (1988). In general, it may be said that for C14 dating, mammal remains yield ages that are closer to the real age than charcoal. This is due to the longevity of trees and the fact that it never can be verified if the charcoal from fires originates from burnt fresh wood or collected dead wood. Therefore, dating based on the hippo bones from stratum 4 probably comes closer to the real age, than the charcoal ages from stratum 2.

We agree with Simmons (1996) that there might be only a small difference in age between stratum 4 and 2. In other words, the sharp decline in the population of hippos took place in the time span between stratum 4 and stratum 2, which must have been of a short duration. Furthermore, if we look at the percentage of shellfish, we see that it is only about 1% in stratum 4 against more than 70% in stratum 2. The percentage of bird fossils is negligible in stratum 4 , while it rises to 10 % in stratum 2. The great bustard, *Otis tardus*, and the goose, *Anser anser*, are dominant in this avifauna (Reese, 1996).The above percentages clearly show an increase in shellfish collecting and bird hunting. This evident change in food customs of the Akrotiri people might very well have been caused by a sharp decline in the hippo population due to overkill.

In Sondaar (2000: fig. 2) the percentages of identified specimens of different taxa are given for stratum 2 and 4 of Aetokremnos on Cyprus (after Reese, 1996) and of Araguina on Corsica (after Vigne, 1998). The diagrams for Aetokremnos stratum 4 and Corsica are remarkably similar, with as only difference the fact that for the Aetokremnos stratum 4 hunter the hippo was the main source of food, while it was *Prolagus* for the Mesolithic hunter of Corsica. In contrast to the dwarf hippo, the *Prolagus* population was not reduced in number by overkill, most likely because of its high reproduction rate and way of life, that is, storing large amounts of dried food in huge hay stacks for scanty times. If we compare the small game of the Corsica Mesolithic with the Aetokremnos hunters, than it becomes evident that there is no ecological counterpart for *Prolagus* in the Cypriot assemblage.

The animal exploitation pattern of the Aetokremnos hunters from stratum 2 differs completely from that of stratum 4. They collected more shells and hunted birds. The dramatic decrease in the exploitation of hippo and an increase in the consumption of shellfish and birds is difficult to explain other than by a reduction in number of the slow moving endemic dwarf hippo population, caused by overkill. There is a gap of a millennium between the occupation of the Aetokremnos site and the site of Shillourokambos, which yielded Preceramic Neolithic assemblages (Vigne, 1998; Roonen, 1995; Guilaine *et al*., 1995). This might be explained as caused by a paucity of natural food resources and a subsequent dramatic drop in the human population, or even the disappearance of humans from the island. Birds and shellfish probably were not sufficient to support a viable human population over a long period of time after the extinction of the dwarf hippo.

Concluding it can be said that:

1) Cyprus was colonized by a mainland elephant and hippo in the Late Pliocene - Early Pleistocene. They arrived on an oceanic-like island by sweepstake dispersal. After punctuated evolutionary processes they obtained the typical island adaptation. There was a stasis in the faunal evolution till the arrival of humans in the Late Pleistocene - Early Holocene.

2) the Cypriot Aetokremnos taphonomy is much more easy explained by an overkill of the hippos.

3) the human hunters might well have been responsible for the extinction of the slow moving dwarf hippo (Simmons, 1988; Reese, 1996).

4) the data presented by Vigne (1998) on the taphonomy of the Mesolithic Corsican sites suggests that the *Prolagus* population, through its high reproduction rate, could support a viable human hunter population over a longer period, without becoming exhausted.

Discussion and conclusion

At least four faunal turnovers can be recognized in the Plio/Pleistocene of the Palearctic mainland, in a time span of around 4.5 million years from MN 14-17 (Pliocene) to MQ 4 (Pleistocene). These successive faunal units are characterized by new arrivals, extinctions and local evolution. A relation between the faunal turnovers and global climatological changes is in many cases clear. However, from the faunal evolution on the islands a completely different picture arises.

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Two types of Plio/Pleistocene Mediterranean islands can be recognized: continental and oceanic-like islands. Though the origin of these faunas are completely different, the faunal evolutionary pattern is similar. Oceanic-like islands, Crete, Cyprus and the like, are colonized overseas by sweepstake dispersal, while the ancestral fauna of a continental island as Sardinia was an Early Pliocene mainland fauna. In both cases a fast evolutionary change can be recognized, which can be explained as an adaptation to the restricted island environment. On the oceanic-like islands, without large predators, dwarf herbivores evolve. On Sardinia this change includes a loss of diversity, extinction of Proboscidae, equids, rhinos and the like, but at the same time evolution of endemic bovids. The hyena *Chasmaporthetes* survives. In both cases, continental and ocean-like islands, there is a stasis in the faunal evolution, after the endemic insular fauna is established.

This stasis is dramatically disturbed by human colonizations on the islands, which take place in the Middle Pleistocene on the continental island Sardinia and in the Holocene on the oceanic-like islands like Cyprus and Crete. From archaeological complexes it can be learned that Sardinia was colonized by humans as early as the Middle Pleistocene, whereas the colonization of the Mediterranean took place no sooner than the Early Neolithic. The reason for this early succesful colonization can be found in the presence of the ochotonid *Prolagus* on this continental island. The taphonomy of the Mesolithic Corsican sites is suggestive for the explanation that the *Prolagus* population, through its high reproductive rate, could support a viable human hunter-gatherer population over a longer period, without becoming exhausted. On the other hand, the colonization of oceanic-like islands by Paleolithic / Mesolithic hunter-gatherer societies must have led to a dramatic reduction of the dwarf herbivores. Furthermore, the lack of ecological alternatives on the Pleistocene oceanic-like islands made Preneolithic human colonization unsuccessful. Cyprus provides such an example.

Acknowledgments

The authors are indepted to the organizers of the Workshop, who gave us the opportunity to discuss the models, and to compare it with processes that take place on the mainland. Especially Dr de Lanfranchi (Corsica), Dr Vera Eisenmann (Paris), Dr Reese (Chicago), and M. Arca, C. Tuvieri, M. Sanges (Sardinia) are thanked for their help and contribution, resulting in the present article.

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Figures

Fig. 1. Fauna list of Pleistocene - Holocene mammals on Sardinia/Corsica.

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	Pleistocene			Holocene	
	Early	Middle	Upper	Mesolithic	Early Neolithic
	Cava 6 15 species 8 extinctions	Cava 10 9 species 2 arrivals 2 extinctions	Cava 7, Corbeddu 2, 3 6 species 1 arrivals	Araguina	Corbeddu
Macaca majori	x	x			
Talpa tyrrhenica	x	x			
Nesiotites similis	x	x	x	x	
Prolagus sp.	x	x	x	x	x
Leporoid	x				
Tyrrhenicola sp.		x			
Tyrrhenicola henseli			x	x	x
Rhagamys minor	x	x			
Rhagamys orthodon			x	x	x
Glirid	?	?			
Chasmaporthetes	x				
Mustelid sp. 1	x				
Mustelid sp. 2	x	x			
Cynotherium sp.	x	x?			
Cynotherium sardous			x		
Nesogoral melonii		x			
Nesogoral sp. 2		x			
Sus nanus	x				
Caprine sp. nov.	x				
Megaloceros cazioti			x		
Domestic animals					x

Fig. 2. Relation different human colonization waves and extinction/arrival of island herbivores. After each new colonization there is an extiction event of large endemic herbivores, which are replaced by new arrivals. However, there is a loss in total number of herbivore taxa after each colonization event. Probably after the arrival of modern Mesolithic *Homo sapiens* the last large herbivore *Megaloceros cazioti* became extinct.

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	Pleistocene			**Holocene**	
	Early	Middle and Late		Mesolithic	Early Neolithic
Faunal unit	*Rhagapodemus* caprid	*Tyrrhenicola* *Nesogoral*	*Tyrrhenicola* *Megaloceros*	*Tyrrhenicola* *Prolagus*	Cattle *Prolagus*
Homo erectus?		x			
Homo sapiens archaic			x		
Homo sapiens modern				x	x
Macaca	x	x			
Nesogoral 1		x			
Nesogoral 2		x			
Leporoid	x				
Sus nanus	x				
Sus sp.	x				
Caprine sp. nov.	x				
Megaloceros			x		
Sheep					x
Goat					x
Pig					x
Prolagus	x	x	x	x	x

Fig. 3. The impact of human colonization waves on Pleistocene - Holocene Sardinia/Corsica. Four archaeological complexes and four dramatic faunal turnovers can be recognized. These events might indicate four different human colonization waves. A Late Pleistocene endemic archaeological complex and *H. sapiens* might be explained as an adaptation to the island environment.

Fig. 4. The proportion of *Prolagus* in weight of edible matter in five Mesolithic sites on Corsica (after Vigne, 1998). *Prolagus,* with its high reproduction rate, did supply enough food to support a viable human hunter population, without getting exhausted, for about a millenium. The sites cover the middle and second half of the 9th and probably the 8th millennium BP.

Fig. 5. Proportions of number of collected specimen from the Araguina Mesolithic site on Corsica (Vigne, 1998) and Akrotiri Cyprus (Reese, 1996), which might be considered as food remains (burnt bones and shells). The pattern from Araguina and Akrotiri stratum 4 are strikingly alike for the land mammals dwarf hippo for the Akrotiri hunters, and *Prolagus* for the Mesolithic people from Corsica. The figure shows a the dramatic drop in number of hippo remains in stratum 2, not much younger in age. Probably the available food resources shellfish, vipers and birds were not enough to support a viable human population. There is a gap of a millennium in the archaeological record when the aceramic Neolithic people colonize Cyprus.