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Why are there no giants at the dwarves feet? Insular micromammals in the eastern Mediterranean



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ABSTRACT

The eastern Mediterranean has yielded some textbook examples of insular evolution among large mammals such as the world's smallest hippopotamus and mammoth. By contrast, gigantism among small mammals is limited, with the exception of the early Pleistocene murid *Kritimys* from Crete. The large body size of insular rodents can be related to an energetically advantageous position at the slow end of the mammalian fast–slow continuum. In order to test the hypothesis that the development of gigantism was hampered by the harsher climatic conditions of the middle and late Pleistocene, we constructed a dataset of endemic murids and cricetids from islands all over the world. Upto the middle Pleistocene, giant rodents can be found all over the world. However, in the later part of the Pleistocene and Holocene, these are only found at lower latitudes, suggesting that indeed the harsher conditions of the north no longer allowed insular rodents to develop the slow life-strategy that previously could still be achieved at these latitudes.

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1. Introduction

The Pleistocene faunas from the eastern Mediterranean have yielded some remarkable examples of insular evolution. Paramount in these are the examples of dwarfed hippopotami, such as *Hippopotamus minor*, the smallest hippo that ever lived (Forsyth Major, 1902; Bate, 1906; Boekschoten and Sondaar, 1972). Other large mammals follow suit, with the world's smallest mammoth *Mammuthus creticus* appearing on Crete (early Pleistocene; Herridge and Lister, 2012), dwarf elephants on, e.g., Cyprus, Naxos and Tilos (*Palaeoloxodon cypriotes*, *P. lomolinoi*, *P. tiliensis*; late Pleistocene; Bate, 1903, 1904, 1905; Theodorou et al., 2007; Sen et al., 2014; Van der Geer et al., 2014; Athanassiou et al., 2015; Mitsopoulou et al., 2015) and a radiation of the endemic deer *Candiacervus* with eight species on Crete (De Vos, 1979). These islands were not connected to the mainland at any time during the geological period considered here (Marra, 2005), and were colonised by the focal taxa by sweepstake (chance) dispersal (Van der

Geer et al., 2015). Tilos and Crete were connected to the mainland in a deeper past, but our taxa do not originate from that remote period in time. Islands that are colonised in this way are expected to show the highest level of endemism.

Whereas from a large mammal perspective, the eastern Mediterranean islands provide a wealth of textbook examples of island evolution, the situation is much less spectacular when we consider the small mammals of the region. Here, we would expect gigantism as a usual response to insular condition (see for an explanation, below). Indeed, a clear example of this is the Cretan early Pleistocene endemic murid *Kritimys* (Mayhew, 1977; Van der Geer et al., 2013). However, in the middle and early Pleistocene faunas of the island, we find another endemic murid lineage, which shows far less modifications to the point that it is still included in the mainland genus *Mus*, albeit clearly enlarged compared to similar mainland species (Mayhew, 1977). Both in *Kritimys* and the Cretan *Mus* lineage chronospecies are recognised. However, there is no sign of radiation, which, considering that deer did radiate on the island, is somewhat remarkable.

Cyprus also has an endemic species of *Mus*, *M. cypriacus*. The presence of this species was only discovered quite recently, when DNA analysis indicated that what was previously believed to be an

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island population of *M. musculus* was, in fact, a species of its own, which, indeed, also showed minor morphological differences (Cucchi et al., 2006). However, the Cyprus *Mus* hardly shows any sign of body mass increase. Molecular clock dating provided an estimated age of separation from the mainland species around 600 ky, i.e., in the middle Pleistocene. Even more remarkable is the find of *Apodemus* on Naxos. This population was tentatively attributed to a mainland species and classified as *A. cf. mystacinus* (Van der Geer et al., 2014). These authors even pointed out that the Naxos assemblage has characters that link it to the western subspecies *A. m. epimelas*. Nevertheless, the Naxos murid was found together with a proboscidean that showed clear insular characteristics, the dwarfed elephant *Palaeoloxodon lomoloini* (Van der Geer et al., 2014). Therefore, we must assume isolation for the mammal faunas of Naxos. This, however, did not lead to any morphological differentiation in the dentition of the murid from the mainland species.

The limited size increase in the Cretan and Cyprus *Mus*, and the lack of any form of gigantism in the Naxos murid is remarkable, considering that large mammals of all these islands do show significant or even spectacular size adaptations in being smaller than their mainland ancestor. This paper seeks an explanation for the lack of gigantism in the late Pleistocene insular faunas of the eastern Mediterranean.

1.1. Insular gigantism

There is no simple single factor to explain insular gigantism (Lomolino, 2005; Lomolino et al., 2012). Instead, changes in body size seemed to be caused by a combination of factors. Lomolino (2005) considered gigantism of small mammals and dwarfism as part of a single phenomenon. Documenting size change in insular population/species in relation to the size of the mainland ancestor, the S_i -index, he found a statistically significant relation between the size of the ancestor and the S_i . As the regression line passes through $S_i = 1$ (i.e., no size difference between mainland and island species), this feeds the notion that species converge to the 'ideal size' from an energetic point of view. This idea behind this ideal size for insular mammals is that on the mainland, the need to outgrow predators (large mammals) or to be able to hide from them (small mammals) as well as presence of many competitors keeps mainland mammals to obtain the most energetic dimensions. The release of competition and predation on islands, however, makes it a far more important factor. Lomolino pointed out that this 'ideal size' would not be the same for all mammals. For rodents, for instance, the regression line crosses $S_i = 1$ around 260 g.

The idea of having an ideal insular size is tempting, particularly since the economic use of available resources, and hence energy reduction, is an important factor in insular evolution. Nevertheless, as Lomolino et al. (2012) made a strong case that insular evolution should be regarded in an ecological context, there seem to be more tangible explanations for size change. One of these factors is the difference in possibilities for different groups to reach far away islands (Lomolino, 2005). Ungulates are more often than not absent on islands, which leaves the niche of the middle-sized herbivores open. Palombo (2007) noted that proboscideans showed a lesser degree of size reduction on Mediterranean islands in which also ruminants were present (i.e., Sardinia, Sicily and Crete), suggesting that elephants competed for this niche. On the other hand, the vacant niche of middle-sized plant eaters can also be filled by large rodents (e.g., giant caviomorphs in the West Indies; e.g., Hansford et al., 2012), lagomorphs (e.g., the giant *Nuralagus rex* on Majorca; Quintana et al., 2011) or primates (e.g., giant, now extinct lemurs on Madagascar) and is on some islands even taken over by birds (Lomolino, 2005). Especially on remote oceanic islands such as New

Zealand and Hawaii that lack native non-volant mammals, birds may take over the role of megaherbivores (James and Burney, 1997; Wood et al., 2008, 2012). Thus, the convergence to a single body size may in part be attributed to filling the middle-sized niches, and gigantism and dwarfism are not necessarily linked to a single explanation. We will therefore consider gigantism in this paper as a process by itself.

It is, of course, clear that any expression of insular evolution is linked to the ecological circumstances typical for insular environments. The three main factors linked to gigantism and dwarfism are competitive release, predation release and resource limitations. Above we already discussed the effects of competitive release, as the absence or paucity of middle-sized herbivores led to other vertebrates taking over that niche. It has to be noted, however, that the niche for small-sized herbivores is also available, and that on some islands (e.g., Gargano, Flores; Locatelli et al., 2015) part of the rodent fauna retains a size similar to mainland species. In addition, apart from body size changes, we often see other morphological changes, that are best explained as adaptation to the local environment (Van der Geer et al., 2014). Here, though, we limit ourselves to body size changes as this is most reliably measured.

Because of the typical absence of mammalian predators on islands, there is no need for herbivores to outgrow potential hunters, allowing for size reduction in middle- and large-sized mammals. Small mammals on the other hand, no longer need to resort to hiding, and can afford to obtain a larger body size. Whereas the argument is straightforward for larger mammals, there is a catch for the smaller ones. Rodents and other small mammals are not only hunted by mammalian predators, but also to a large degree by birds of prey. And these can also be found in insular environments. In part, gigantism could be explained by an attempt to outgrow avian predators, and particularly owls. Thus, the presence of large-sized owls and long-legged terrestrial owls on islands, such as *Tyto gigantea* on Gargano (late Miocene; Ballmann, 1973), *Ornimegalonyx* on Cuba (late Pleistocene; Brodkorb, 1961), *Athene cretensis* on Crete (late Pleistocene; Weesie, 1982) and *Athene trinacriae* on Sicily (middle Pleistocene; Pavia and Mourer-Chauviré, 2002) results for co-evolution prompted by the increased size of rodents on these islands in combination with the lack of terrestrial predators.

The importance of resource limitations becomes apparent, when one considers that adaptations for energy conservations are not only limited to a change in size. The flightlessness or increased terrestriality in many insular birds (McNab, 1994, 2002), low-gear locomotion in island ungulates (Van der Geer, 2005, 2008; Rozzi and Palombo, 2014) and perhaps the reduction of brain size (Köhler and Moyà-Solà, 2004; Palombo et al., 2008; Lyras et al., 2009; Weston and Lister, 2009) are all adaptations that save energy. Whereas the absence of predators allows these adaptations without repercussions, the driving force lies in the limited resources. In this respect, a simple explanation for gigantism are the energetic advantages of a larger body, such as thermoregulation. However, a large body size is correlated with a range of life-history traits, which place larger species more to the slow end of the fast–slow continuum in mammal life strategies (Oli, 2004), or in other terms, towards more K-select. More K-select species are typical for surroundings with low extrinsic mortality, which again ties in the absence or paucity of predators on islands. MacArthur and Wilson (1967) pointed out that r-selected species, with a large amount of offspring, would quickly overcrowd an island leading to starvation. Therefore, insular environment would favour those individuals that can at least reproduce themselves, i.e., the more K-select. Whereas body size is an important factor, there are many other characteristics which determine the position of a mammal species in the fast–slow continuum (e.g., Oli, 2004; Bielby

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