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SPECIAL ISSUE

Body size of insular carnivores: evidence from the fossil record

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ABSTRACT

Aim Our goals here are to: (1) assess the generality of one aspect of the island rule – the progressive trend towards decrease in size in larger species – for fossil carnivores on islands; (2) offer causal explanations for this pattern and deviations from it – as far as fossil carnivores are concerned; and (3) estimate the speed of this trend.

Location Oceanic and oceanic-like islands world-wide.

Methods Body size estimates of fossil insular carnivores and of their phylogenetically closest mainland relative were obtained from our own data and the published literature. Our dataset consisted of 18 species from nine islands world-wide. These data were used to test whether the body size of fossil insular carnivores varies as a function of body size of the mainland species in combination with characteristics of the island ecosystem.

Results Dwarfism was observed in two canid species. Moderate decrease in body mass was observed in one hyena species. Gigantism was observed in one otter species. Moderate body mass increase was observed in two otter species, one galictine mustelid and perhaps one canid. Negligible or no change in body mass at all was observed in five otter species, three galictine mustelids and one genet. Size changes in teeth do not lag behind in comparison to skeletal elements in the dwarfed canids. The evolutionary speed of dwarfism in a canid lineage is low.

Main conclusions Size change in fossil terrestrial insular carnivores was constrained by certain ecological conditions, especially the availability of prey of appropriate body size. When such alternative prey was not available, the carnivores retained their mainland size. The impact of competitive carnivores seems negligible. The case of (semi-)aquatic carnivores is much less clear. The species that maintained their ancestral body mass may have changed their diet, as is evidenced by their dentition. Among the otters, one case of significant size increase was observed, perhaps best explained as being due to it entering the niche of an obligate aquatic otter. Dwarfism was not observed in otters. The island rule seems to apply to fossil carnivores, but with exceptions. The dependency of the island rule on resource availability is emphasized by the present study.

Keywords

Body size, carnivorous mammals, dwarfism, evolution, island biogeography, island rule, isolation, predator–prey relationships.

INTRODUCTION

Insular mammals often show remarkable and sometimes even bizarre adaptations, such as dwarfism and gigantism, the patterns of which are widely known as the island rule (Foster, 1964; Van Valen, 1973; Sondaar, 1977; Lomolino, 1983, 1985, 2005; Lomolino *et al.*, 2006; Whittaker & Fernández-Palacios, 2007). Understanding the underlying processes enables us to

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unravel the patterns of evolution on islands, or in fragmented habitats of the mainland. The best-known evolutionary response of large insular mammals to their isolated habitat is reduction in body size. This adaptation is spectacular in some cases, such as elephants and hippos with extreme body mass reductions up to 1 or 2% of their ancestral body mass – for example the Sicilian pygmy elephant *Elephas falconeri* (Roth, 1992; Weston & Lister, 2009). Lomolino (2005) suggested that this is a general property for all mammalian taxa, including carnivores. On the other hand, Meiri *et al.* (2004, 2006) stressed that insular carnivores form an exception to this. According to Meiri *et al.* (2008), size changes in island taxa do not follow the simple pattern of 'small things get larger and large things get smaller' and therefore more detailed, taxon-specific studies are needed. Discussions on the validity of the island rule regarding insular carnivores are based almost entirely on data from living carnivores. However, the majority of carnivores found today on islands are relatively recent Holocene isolated relicts from mainland faunas or culturally dependent introductions. This limitation was noted by Meiri *et al.* (2008), who added that size evolution perhaps expresses itself over longer periods of time than the datasets based on living species provide.

In this paper we present the fossil record of insular carnivores from islands with a considerable degree of isolation, both in time and distance, and that are inhabited by impoverished, disharmonic endemic faunas. Only a few carnivores managed to establish themselves on pre-Holocene islands and none of these endemic carnivores are referable to extant species. To test the general applicability of the island rule on these extinct insular carnivores, we assembled a dataset consisting of fossil terrestrial and semi-aquatic carnivores from eight islands world-wide in order to evaluate the quantitative prediction of the island rule in these cases. We assessed the applicability of various methods of estimating the body mass of fossil insular carnivores in order to test the accuracy of the method applied. For one lineage of three hypercarnivorous canids we were able to estimate the speed of evolution. Our dataset includes canids, a hyena, otters, galictine martens and a genet.

MATERIALS AND METHODS

The faunas and their taxa

Several types of fossil insular faunas are mentioned in the palaeontological literature, the most important of which are generally referred to as either balanced or unbalanced impoverished faunas. Only the latter may contain relatively large numbers of endemic taxa. Although the term impoverished is quite clear, meaning simply that taxonomic diversity is poor at the higher levels with many major groups absent (disharmonic), the term balanced needs some explanation. There is a difference in the usage of the term balanced between the subjects of palaeontology and ecology. Most palaeontologists use the term to mean that large carnivores are present and thus all major trophic niches are occupied. For ecologists, on the other hand, a balanced fauna means that it is ecologically stable, i.e. the trophic niches are not only occupied, but occupied in ratios that do not encourage transitions. Here we follow the palaeontological use of the term.

For this study we used insular fossil species from islands that were significantly isolated from the mainland and evolved over hundreds of thousands of years, without any gene flow from the mainland and as part of an associated mammalian fauna considerably different from that of the mainland in terms of composition (impoverished, unbalanced and endemic). Local extinctions were not balanced by new colonizations.

Canidae

The best-known fossil insular canid is the Sardinian dog (*Cynotherium sardous*) from the latest early Pleistocene–late Pleistocene of Sardinia and Corsica (Malatesta, 1970; Abbazzi *et al.*, 2005; Lyras & van der Geer, 2006). The species derived from the mainland *Xenocyon lycaonoides* (Lyras *et al.*, 2006) (Fig. 1). There is a very good fossil record for this insular species, consisting of several post-cranials and skulls from various localities of different age, including a practically complete skeleton from Corbeddu Cave, Sardinia, dated to 11,350 ± 100 years ago (Klein Hofmeijer, 1997). In total, the species remained in isolation for about 800,000 years. During that time, the Sardinia–Corsica block was always separated from the mainland of Italy and can be considered a true island (Klein Hofmeijer, 1997). The fauna of this period was endemic and impoverished, with the dog and several otters as the only carnivores. The elements of this fauna arrived from Italy via sweepstake dispersal with a few exceptions such as lagomorphs, which evolved from ancestors belonging to an earlier biozone. Possible prey species consisted of lagomorphs (giant pikas) and rodents. No competitors have been identified in the rich fossil record of the island (Abbazzi *et al.*, 2004), except for birds of prey, which might have competed to some extent with the canids for micromammals.

Fossil canids have also been reported from Java [late Early Pleistocene (Jetis fauna), *Megacyon merriami*; Middle Pleistocene (Trinil fauna), *Mececyon trinilensis*] as part of the Javanese Siwalik faunas, which are impoverished but balanced mainland faunas. *Megacyon merriami* is similar to the European continental species *Xenocyon lycaonoides* (Schütt, 1973), especially in size. It differs from *Cuon* (to which genus *Mececyon* is often incorrectly attributed) by a series of characters, the most typical of which are the presence of a lower third molar and the lesser degree of specialization in the lower first molar's talonid (it retains a connecting cristid to the hypoconid and a less reduced endoconid). The Javanese faunas arrived through filter dispersal from the Malay Peninsula via Sumatra (van der Geer *et al.*, in press). Possible prey species of *Megacyon* consisted of deer, bovids and (young?) stegodons. Possible prey species of *Mececyon* consisted of rodents and small deer. Competitors in both cases were large tigers (*Panthera tigris*), and maybe also sabre-toothed cats, but their stratigraphical positions are unresolved.

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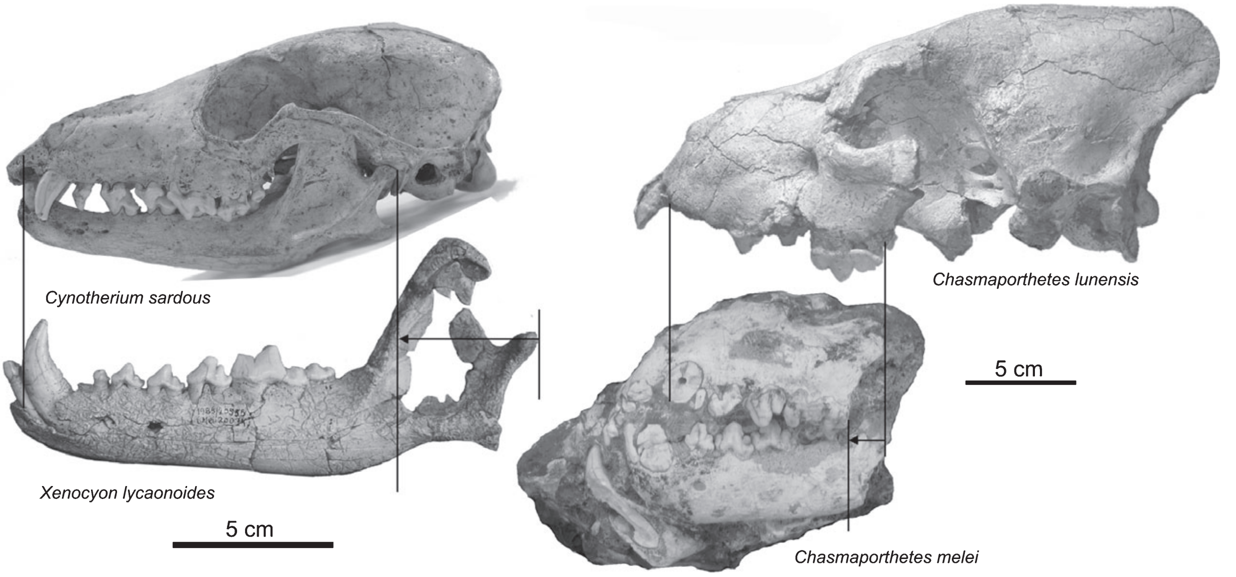

Figure 1 Cranial elements of two fossil endemic terrestrial carnivores compared with their mainland relatives. *Cynotherium sardous* evolved from *Xenocyon lycaonoides* and *Chasmaporthetes melei* from *C. lunensis*. Skull of *Cynotherium sardous* and *Chasmaporthetes melei* from Soprintendenza Archeologica Sassari e Nuoro (Nuoro, Italy), mandible of *X. lycaonoides* from Forschungsstation für Quartärpaläontologie (Weimar, Germany) and skull of *Chasmaporthetes lunensis* from Antón *et al.* (2006).

Hyaenidae

The only fossil insular hyena known so far is the Sardinian hunting hyena (*Chasmaporthetes melei*) from the Early Pleistocene of Sardinia. The species is known from a single partial skull. It is related to the mainland *Chasmaporthetes lunensis* (Rook *et al.*, 2004) (Fig. 1). There is no temporal overlap with the above-mentioned Sardinian dog. The associated fauna was the result of vicariance and was impoverished and endemic. Possible prey species consisted of several goat-sized bovids, a species of small pig and a species of macaque. No competitors were present.

On Java, remains of a short-snouted hyena (*Hyaena brevirostris*) were found (Middle Pleistocene; Kedung Brubus fauna) as part of the Javanese Siwalik faunas. This species is considered continental because no endemic features have been described. Over time, more elements reached Java, and the Kedung Brubus fauna is therefore balanced and only slightly impoverished, in contrast to the older Trinil and Jetis stages, to which respectively *Mececyon trinilensis* and *Megacyon merriami* belong (van den Bergh *et al.*, 1996). This is further confirmed by dental measurements of the Javanese *Hyaena brevirostris*, which are 22.9–24.1 mm for the length of the lower third pre-molar and 14.5 mm for the width of the lower carnassial (Brongersma, 1937), and thus fall within the range of continental Middle Pleistocene specimens for the same teeth, which are 22.7–26.3 mm and 13.7–17.0 mm, respectively (Kurtén & Garevski, 1989).

Viverridae

The only fossil insular viverrid known is *Genetta plesictoides* from the terminal Pleistocene or Early Holocene of Cyprus (Bate, 1903; Simmons and Associates, 1999; Theodorou *et al.*, 2007). The best-preserved specimen is a complete skull from Aghia Napa. The species is considered to be a descendant of the common genet (*Genetta genetta*). The time of its arrival is unknown, but its introduction could have been culturally dependent (Morales, 1994; Reese, 1995; Simmons and Associates, 1999). Possible prey species consisted initially of lizards and invertebrates. The fauna was extremely unbalanced and strongly endemic, practically consisting of only pygmy hippos and pygmy elephants and lacking micromammals. At the same time as, or perhaps shortly after, the arrival of the genet the first micromammals (*Crocidura suaveolens praecypria* and *Mus* spp.) were introduced to Cyprus, but in the beginning their populations were probably too low to be hunted systematically by the genet. Competitors were absent.

Mustelidae

Fossil insular otters have been reported from Crete (Late Pleistocene, *Lutrogale cretensis*), Malta (Middle or Late Pleistocene, *Lutra euxena*), Sicily (Middle or Late Pleistocene, *Lutra trinacriae*), Sardinia and Corsica (Middle Pleistocene, *Cyrnolutra castiglionis*; Late Pleistocene, *Sardolutra ichnusae*, *Algarolutra majori*, *Megalenhydris barbaricina*), Gargano (Late Miocene, *Paralutra garganensis*), Tuscany (Miocene, *Tyrrhenolutra helbingi*, *Paludolutra maremmana*, *Paludolutra campanii*) and Java (Middle Pleistocene, *Lutrogale robusta*, *Lutrogale palaeoleptonyx*). From the Late Pleistocene of the Californian Channel Islands a few fossils of a further undescribed sea otter (labelled as *Enhydra lutris*) are known. As the ancestry of the otters from Tuscany and Java is insufficiently known, they are not included in the study.

Other fossil insular mustelids that have been reported so far belong to the group of galictine martens, and are *Pannonictis* sp. from Sardinia (Early Pleistocene), *Enhydrictis galictoides* from Sardinia and Corsica (Middle–Late Pleistocene), *Mustelercta arzilla* from Sicily (Early Pleistocene) and *Oriensictis nipponica* from Japan (Middle Pleistocene). The marten from Japan was previously attributed to *Lutra* (Naora, 1968) but was moved to the galictine mustelids on the grounds of, amongst other things, the characteristically long and straight upper canines with vertical, deep grooves (Ogino & Otsuka, 2008), which are distinct from the ungrooved canines of otters. The genus *Enhydrictis* was proposed by Forsyth-Major (1901) for material from the Late Pleistocene of Sardinia, with the specific name *E. galictoides*. The taxonomic position of this genus in the European fossil record has been long debated (see Ficcarelli & Torre, 1967; García *et al.*, 2008). New unpublished material from the Middle to Late Pleistocene of Sardinia (mentioned by Abbazzi *et al.*, 2004) will form the basis for clarifying the taxonomic status and evolutionary history of this genus endemic to Sardinia. In this paper, we follow García *et al.* (2008) and combine the data for *Pannonictis nestii* and *Pannonictis pilgrimi*. The diet of insular otters probably included fish, shell-fish and gastropods, whereas that of insular martens probably included small terrestrial vertebrates such as lizards and rodents, eggs and insects, and perhaps also shell-fish and gastropods. Competitors of the martens are birds of prey, often barn owls (*Tyto*).

Felidae

Fossil felids are restricted to Java (Middle–Late Pleistocene, *Panthera tigris*, *Felis bengalensis*), Japan (Middle Pleistocene, *Panthera tigris*) and the Ryukyu Islands (Late Pleistocene, *Felis* sp.). The Japanese remains are insufficiently described and the stratigraphical context is unclear. Data from Java on the other hand are well documented, and changes in body mass through time of the Javanese tigers are reported by Hertler & Volmer (2008). However, the range per site is very large and the changes between faunal units are not straightforward. Furthermore, tigers may have repeatedly colonized Java because they are competent swimmers. For these reasons the Javanese tigers are not included in our study. Subfossil tiger remains have been reported from Borneo, Sumatra and the Philippines (all Holocene, *Panthera tigris*). The degree of endemism of these subfossil tigers is unclear. In addition, the subfossils were found in archaeological contexts and might have been used as amulets or otherwise valuable objects imported from the mainland. The sabre-toothed cats (*Megantereon* sp., *Homotherium ultimum*, *Hemimachairodus zwierzyckii*) of the Pleistocene of Java lack stratigraphical context (van den Bergh, 1999). Felids are thus excluded from this study.

Body mass changes

The accuracy of predicting the body mass of extinct animals depends greatly upon the functional relationship between body size and the skeletal elements used (Kaufman & Smith, 2002). Various methods to predict the body mass of extinct carnivores are described in the literature, based either on cranial and dental measurements (e.g. Van Valkenburgh, 1990) or on post-cranial elements (e.g. Anyonge, 1993; Egi, 2001; Andersson, 2004; Anyonge & Roman, 2006).

Estimating changes in body mass in fossil insular carnivores in comparison with their mainland relatives is hampered by the nature of the fossil findings, which in most cases consist of nothing more than isolated fragmentary skulls or dental remains. This excludes the use of most methods for estimating body size. This limitation applies to both the insular carnivore itself and also its closest mainland relative. For example, *Cynotherium* is a very well-represented taxon (Malatesta, 1970), whereas its mainland ancestor, *Xenocyon,* is known only by isolated teeth, mandibles and a few post-cranial fragments (Sotnikova, 2001; Martínez-Navarro & Rook, 2003; Tedford *et al.*, 2009). The same applies to most insular otters. Some of them are known by a nearly complete skeleton, but this is certainly not the case for their mainland ancestor, *Lutra simplicidens* (Willemsen, 1992).

As a direct result, the availability of elements for estimating relative body mass of insular species is rather limited. For this reason, we use two different approaches. The first produces only relative designations such as smaller, equal or larger as compared with their mainland relative. To indicate the degree of body size change, we provide measurements where available. The second approach produces a quantitative estimation of the body mass based on the length of the lower first molar. This element is the best-represented element in our mainland–insular pairs.

The use of teeth in estimating body mass of insular mammals has been criticized as being inaccurate, because island mammals are not simply geometrically scaled models of their mainland relatives (Sondaar, 1977; Weston & Lister, 2009). For example, many insular mammals have shorter legs relative to their mainland ancestor, and therefore equations based on limb length or proportions underestimate the actual mass of the animal. Furthermore, the teeth of phyletic dwarfs (in the sense of Weston & Lister, 2009) or anagenetic dwarfs are claimed to be usually relatively larger and, as a result, equations based on tooth measurements may overestimate their mass (see Köhler & Moyà-Solà, 2004, for a further discussion). The methods developed for estimating body mass in mainland species therefore might not be applicable directly to insular species. To date, however, such a limitation remains undocumented by quantitative data for fossil insular carnivores. Therefore, in order to evaluate the various methods we estimate the body mass of fossil carnivores that are known from a complete or partial skeleton belonging to a single individual. Five species are available for which body mass can be estimated on the basis of different elements. In this way: (1) we assess the validity of the method used for the other, incompletely preserved, insular carnivores; and (2) we check whether changes in the size of carnivore teeth lag behind in insular evolution or not.

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Finally, in order to estimate the rate of body size change on the island, we plot the estimated body mass of two well-dated specimens of the Sardinian dog, *Cynotherium sardous*, as a function of time. This species is the only fossil insular carnivore that is available for a reliable evaluation. The rest of the fossil island–mainland pairs lack sufficient geochronologically dated specimens. The earliest known specimens of the genus *Cynotherium* are from Capo Figari [minimum electron spin resonance (ESR) age 366.950 ± 73.390 ka for Capo Figari II; ESR is a radiometric dating technique based on radioactive decay products], Santa Lucia (ESR age 450 ± 90 ka) and Monte Tuttavista (earliest? Middle Pleistocene, undated) (van der Made & Palombo, 2006) and are described as *Cynotherium* sp. The Capo Figari material is a mixture, and also includes fossils with an ESR age of 1807.5 ± 361.5 ka (Capo Figari I). However, the accepted time of arrival of *Cynotherium* is during the first important glaciations around the Early to Middle Pleistocene transition (van der Made & Palombo, 2006); in addition, *Cynotherium* is found together with *Megaloceros* and *Microtus* (*Tyrrhenicola*), both lineages of the Middle–Late Pleistocene, and not with *Nesogoral*, the lineage of the Early Pleistocene. We therefore take the age of Capo Figari II as the most likely minimum age for the oldest *Cynotherium*. The geologically youngest specimens are from Corbeddu Cave, dated at 11,350 ± 100 yr BP or 11,199–11,405 cal. yr BP (Klein Hofmeijer, 1997). Only Dragonara Cave is known for a large accumulation of *C. sardous* fossils; they are not dated more precisely than Late Pleistocene (maximum age *c.* 126 ka). Its most closely related mainland relative is *X. lycaonoides*. The latter has been found, amongst others, at the late Early Pleistocene sites of Untermassfeld, Germany, dated to approximately 1.05 Ma (Kahlke, 2001) and Stranska Skala, Czech Republic, estimated to slightly younger than 1 Ma, based on stratigraphy (Martínez-Navarro & Rook, 2003). Body mass estimations for the *Xenocyon–Cynotherium* lineage are based on the circumference of the trochlea of the humerus, using the method developed by Andersson (2004) (see Appendix S1 in Supporting Information). In addition, we provide the greatest distal width of the humerus as well. The speed of evolution is measured in Darwins with the following formula: $r = (\ln X_2 - \ln X_1)/\Delta t$, where X_1 and X_2 are the initial and final body masses (here in kg) and Δt is the time span in millions of years.

RESULTS

Table 1 lists the relative size of insular carnivores in comparison with their most likely mainland ancestors. The table is limited to measurements of elements that are common in both the insular and the mainland form. The relative size changes, given as smaller, larger or equal, are based solely on these measurements.

Most insular otters appear to have retained their ancestral body size. This applies to *Lutrogale cretensis*, *Lutra euxena*, *Sardolutra ichnusae* and *Paralutra garganensis*. A body mass increase is seen in *Cyrnolutra castiglionis*, *Algarolutra majori* and perhaps in *Lutra trinacriae*. One endemic aquatic otter (*Megalenhydris barbaricina*) became truly gigantic. Some island otters (*Paralutra garganensis*, *A. majori* and *Lutrogale cretensis*) developed a more robust dentition, apart from a body size change.

The galictine martens and the genet (*Oriensictis nipponica*, *Mustelercta arzilla*, *Enhydrictis galictoides* and *Genetta plesictoides*) maintained a body mass comparable to their phylogenetically closest relatives. An exception is provided by *Pannonictis* sp., which is larger than its mainland relative.

The Sardinian hunting hyena (*Chasmaporthetes melei*) is smaller than its mainland relative. The Sardinian dog (*Cynotherium sardous*) on the other hand, was a dwarf in comparison to the mainland *Xenocyon*, its ancestor. The two Javanese canids each evolved in an opposite direction: the stratigraphically older Merriam's dog (*Megacyon merriami*) became larger whereas the younger Trinil dog (*Mececyon trinilensis*) became smaller.

Table 2 shows the body mass estimations of species that are known from a skeleton (partial or complete) of one individual. These are one canid (*C. sardous*) and three otters (*Sardolutra ichnusae*, *Lutra trinacriae* and *Lutrogale cretensis*). Body masses are given per element, using equations given in the literature for each carnivore group. Estimations based on molar, skull and body length measurements of *S. ichnusae* and *Lutra trinacriae* yield comparable results. The molar length of *Lutrogale cretensis* results in a higher estimated body mass than do the skull and body length, but this is probably related to the fact that this animal has a more robust dentition. The same applies to *C. sardous*. Body length of the latter cannot be used because the vertebral column is incomplete. All other elements give comparable results.

Figure 2 (see also Appendix S1) plots the ratio between insular body size and mainland body size against mainland carnivore body size, as estimated from the length of the first lower molar. The plot shows two distinct groups. The first group includes species that show a significant size change (*C. sardous*, *Mececyon trinilensis* and *Megalenhydris barbaricina*). The second and largest group includes species that show a moderate change or no change at all (*Megacyon merriami*, *Pannonictis* sp., *Lutra trinacriae*, *Lutra euxena*, *Lutrogale cretensis*, *S. ichnusae*, *Mustelercta arzilla*, *E. galictoides*, *A. majori* and *Cyrnolutra castiglionis*). *Chasmaporthetes melei* is omitted because no equation to estimate the body mass of this genus is available; *Chasmaporthetes* differs too much from extant hyenas to use equations for hyenas. *Genetta plesictoides* is omitted because no equation could be found to estimate its body mass based on the available data.

Figure 3 gives an idea of the possible rate of change of size within the *Xenocyon–Cynotherium* lineage of Sardinia. In a time span of about 0.8 Myr, the body mass of this canid dropped from about 30 to 10 kg, resulting in an evolutionary speed of 1.38 Darwins (a Darwin reflects changes in body mass per million years on a natural logarithmic scale). The speed on the trajectory between Capo Figari and Corbeddu is 1.31 Darwins.

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Table 1 List of fossil insular carnivores, compared with their phylogenetically closest mainland relative, including a listing of known materials. Data are from our own measurements and from the literature.

Island and stratigraphic position	Insular species	Mainland relative	Linear measurements (mm)	Relative size
	Hyaenidae			
Sardinia (Italy) Early Pleistocene	*Chasmaporthetes melei*[1]	*Chasmaporthetes lunensis*[a]	Length of P4: *C. melei*: 29.17 (*n* = 1)[a] *C. lunensis*: 32.7–34.8 (*n* = 10)[a] Length of p4: *C. melei*: 20.05 (*n* = 1)[a] *C. lunensis*: 21.0–26.3 (*n* = 14)[a]	Smaller
	Canidae			
Sardinia and Corsica (Italy and France) Middle–Late Pleistocene	*Cynotherium sardous*[2]	*Xenocyon lycaonoides*[b]	Length of m1: *C. sardous*: 17.8–20.5 (*n* = 14)[c] *X. lycaonoides*: 26.5–30.2 (*n* = 17)[d] Length of mandible: *C. sardous*: 108.2–130 (*n* = 10)[e] *X. lycaonoides*: 210 (*n* = 1)[e] Width of the humerus at the midshaft: *C. sardous*: 9.9 (*n* = 1)[e] *X. lycaonoides*: 17.2–17.8 (*n* = 2)[d]	Smaller
Java (Indonesia) Early Pleistocene	*Megacyon merriami*[3]	*Xenocyon lycaonoides*[e]	Length of m1: *M. merriami*: 32.2 (*n* = 1)[f] *X. lycaonoides*: 27.7–30.2 (*n* = 3)[d]	Larger
Java (Indonesia) Middle Pleistocene	*Mececyon trinilensis*[4]	*Xenocyon lycaonoides*[e] Probably chronospecies of *Megacyon merriami*[e]	Length of m1: *M. trinilensis*: 17 (*n* = 1)[f] *X. lycaonoides*: 27.7–30.2 (*n* = 3)[d]	Smaller
	Viverridae			
Cyprus late Late Pleistocene	*Genetta plesictoides*[5]	*Genetta genetta*[g]	Length of P4: *G. plesictoides*: 10.05 (*n* = 1)[h] *G. genetta*: 7.0–8.5 (*n* = 4)[e] Condylobasal length of skull: *G. plesictoides*: 86 (*n* = 1)[h] *G. genetta*: 86–95 (*n* = 18)[i]	Equal
	Mustelidae			
Crete (Greece) Late Pleistocene	*Lutrogale cretensis*[6]	*Lutrogale perspicillata*[j]	Length of m1: *L. cretensis:* 15.6–16.5 (*n* = 3)[j] *L. perspicillata*: 15.2–15.4 (*n* = 2)[j] Length of P4: *L. cretensis*: 14.6 (*n* = 1)[j] *L. perspicillata*: 12.9–14.8 (*n* = 6)[j] Condylobasal length of skull: *L. cretensis*:120 (*n* = 1)[k] *L. perspicillata*: 115–128 (*n* = 16)[l]	Equal
Malta late Middle Pleistocene	*Lutra euxena*[7]	*Lutra* sp., perhaps *Lutra simplicidens*[j]	Width of proximal epiphysis of radius: *L. euxena*: 9.6 (*n* = 1)[d] *L. simplicidens*: 9.2–10.2 (*n* = 2)[j]	Equal

Table 1 Continued

Island and stratigraphic position	Insular species	Mainland relative	Linear measurements (mm)	Relative size
Sicily (Italy) late Middle Pleistocene	*Lutra trinacriae*[8]	*Lutra* sp., perhaps *Lutra simplicidens*[j]	Length of m1: *L. trinacriae*: 13.1 ($n = 1$)[j] *L. simplicidens*: 12.5 – 12.95 ($n = 4$)[j] Minimum width of humerus shaft: *L. trinacriae*: 7.8 ($n = 1$)[j] *L simplicidens*: 6.4 – 8.0 ($n = 4$)[j] Breadth of distal epiphysis of radius: *L. trinacriae*: 14 ($n = 1$)[j] *L. simplicidens*: 10.6–13.2 ($n = 4$)[j]	Larger?
Sardinia (Italy) Late Pleistocene	*Sardolutra ichnusae*[9]	*Lutra* sp., perhaps *Lutra simplicidens*[j]	Length of m1: *S. ichnusae*: 12.9 ($n = 1$)[j] *L. simplicidens*: 12.5 – 12.95 ($n = 4$)[j] Minimum width of humerus shaft: *S. ichnusae*: 6.5 ($n = 1$)[j] *L. simplicidens*: 6.4 – 8.0 ($n = 2$)[j]	Equal
Corsica (France) late Middle Pleistocene	*Cyrnolutra castiglionis*[10]	*Lutra* sp., perhaps *Lutra simplicidens*[m]	Length of m1: *C. castiglionis*: 13.4 ($n = 1$)[n] *L. simplicidens*: 12.5 – 12.95 ($n = 4$)[j] Minimum width of humerus shaft: *C. castiglionis*: 6.5 ($n = 1$)[m] *L. simplicidens*: 6.4 – 8.0 ($n = 2$)[j] Anteroposterior breadth of proximal epiphysis of radius: *C. castiglionis*: 7.2 ($n = 1$)[n] *L. simplicidens*: 6.3 ($n = 2$)[j]	Larger
Sardinia (Italy) Late Pleistocene	*Megalenhydris barbaricina*[11]	*Lutra* sp., perhaps *Lutra simplicidens*[m] Phylogenetically related to *Cyrnolutra castiglionis* and *Sardolutra ichnusae*[m]	Length of m1: *M. barbaricina*: 17.1 ($n = 1$)[j] *C. castiglionis*: 13.4 ($n = 1$)[q] *S. ichnusae*: 12.9 ($n = 1$)[d] *L. simplicidens*: 12.5–12.95 ($n = 4$)[j]	Larger
Sardinia and Corsica (Italy and France) Late Pleistocene	*Algarolutra majori*[12]	*Lutra* sp., perhaps *Lutra simplicidens*[j]	Length of m1: *A. majori*: 14.2 ($n = 1$)[j] *L. simplicidens*: 12.5 – 12.95 ($n = 4$)[j]	Larger
Gargano (Italy) Late Miocene	*Paralutra garganensis*[13]	*Paralutra jaegeri*[o]	Length of P4: *P. garganensis*: 12.6 ($n = 1$)[o] *P. jaegeri*: 10.9 – 12.8 ($n = 2$)[o]	Equal
Kyushu (Japan)	*Oriensictis nipponica*[14]	*Oriensictis melina*[p]	Length of m1: *O. nipponica*: 13.23 ($n = 1$)[p] *O. melina*: 12.3 – 14 ($n = 4$)[p]	Equal
Sardinia (Italy) Early Pleistocene	*Pannonictis* sp.[15]	*Pannonictis nestii*	Length of P4: *Pannonictis* sp.: 11.1 ($n = 1$)[e] *P. nestii*: 10.45 – 10.50 ($n = 2$)[q,r] Length of m1: *Pannonictis* sp.: 13.6 ($n = 1$)[e] *P. nesti*: 11.50 – 12.6 ($n = 7$)[q,r]	Larger

Table 1 Continued

Island and stratigraphic position	Insular species	Mainland relative	Linear measurements (mm)	Relative size
Sardinia (Italy) late Early–Late Pleistocene	*Enhydrictis galictoides*[16]	*Pannonictis nestii*[q]	Length of P4: *E. galictoides*: 10.10–10.86 (n = 10)[e] *P. nestii*: 10.45–10.50 (n = 2)[q,r] Length of m1: *E. galictoides*: 12.11–13.71 (n = 12)[e] *P. nestii*: 11.5–12.6 (n = 7)[q,r]	Larger?
Sicily (Italy) Early Pleistocene	*Mustelercta arzilla*[17]	*Pannonictis nestii*[r]	Length of P4: *M. arzilla*: 10.5 (n = 1)[q] *P. nestii*: 10.45–10.50 (n = 2)[q,r] Length of m1: *M. arzilla*: 12 (n = 1)[q] *P. nestii*: 11.5–12.6 (n = 7)[q,r]	Equal

P4, upper fourth premolar; p4, lower fourth premolar; m1, lower first molar.

Known material: [1]A partial skull, preserving I1-P4 and i3-p4 (Abbazzi *et al.*, 2004). [2]Large collection of cranial and post-cranial materials, including an associated skeleton (Lyras *et al.*, 2006; Malatesta, 1970). [3]Part of a mandible and an isolated M1 (Schütt, 1973). [4]Two mandible fragments and three isolated molars (Schütt, 1973). [5]A nearly complete skull and a mandible (Theodorou *et al.*, 2007). [6]An almost complete skeleton, one mandible, two isolated molars and a femur (Willemsen, 1992). [7]One incisor, one canine and a few post-cranial elements (Willemsen, 1992). [8]An almost complete skeleton (Willemsen, 1992). [9]A complete skeleton (Willemsen, 1992). [10]Partial skeleton (Willemsen, 1992). [11]A mandible, part of the axial skeleton and a humerus (Willemsen & Malatesta, 1987). [12]Two pre-molars (P4) and four molars (m1 and M1) (Willemsen, 1992). [13]A maxillary fragment, preserving P4-M1 and a calcaneum (Willemsen, 1983). [14]Two partial maxillae, preserving P3-M1 and P4-M1, and a mandible (Ogino & Otsuka, 2008). [15]Two skulls (Abbazzi *et al.*, 2004). [16]A skull, a mandible and several undescribed specimens (Abbazzi *et al.*, 2004). [17]A partial skull, preserving C-P4, a mandible and some post-cranial fragments (Burgio & Fiore, 1997).

Related species suggested by and measurements from: [a]Rook *et al.* (2004), [b]Lyras *et al.* (2006), [c]Malatesta (1970), [d]Sotnikova (2001), [e]own data, [f]Schütt (1973), [g]Bate (1903), [h]Theodorou *et al.* (2007), [i]Larivière & Calzada (2001), [j]Willemsen (1992), [k]Symeonides & Sondaar (1975), [l]Hwang & Larivière (2005), [m]Willemsen (2006), [n]Pereira & Salotti (2000), [o]Willemsen (1983), [p]Ogino & Otsuka (2008), [q]Burgio & Fiore (1997), [r]Rook (1995).

DISCUSSION

Otters form by far the majority of the fossil insular carnivores. Larger vertebrate carnivores are generally lacking from endemic insular faunas, due to their poor overseas dispersal abilities combined with their dependency on a minimal availability of prey animals and often solitary lifestyle. These restrictions pose no problems for otters for obvious reasons, and that is why they form a regular part of most endemic insular faunas. Otters are not only excellent swimmers but also depend mainly, or for the greater part, on fish, crustaceans and other invertebrates for their diet, which are widely available along the coasts of islands and in freshwater bodies. The same is valid for the insular galictine martens (*Enhydrictis galictoides*, *Pannonictis* sp., *Mustelercta arzilla* and *Oriensictis nipponica*), all good swimmers and probably preferring a habitat near rivers and wetlands, where they fed on birds, eggs, fish, insects and small vertebrates, as they would do on the mainland. The insular species were probably more aquatic than the living galictine martens (Rook, 1995). The nature of their diet, habitat and lifestyle apparently prevents insular mustelids from changing their body size. Lomolino (2005) noted that values for fundamental size, or size where species tend to exhibit no size change, tend to be much higher for species with aquatic prey, such as otters and galictine martens. He explains this as a lesser dependency on the limited terrestrial resource of islands. Our results confirm this observation.

The single insular otter that shows a dramatic increase in size is the Sardinian *Megalenhydris barbaricina.* The body mass of *Megalenhydris* is estimated to about 17 kg (see Appendix S1) when the length of the lower first molar is taken into account. However, its skeletal remains (a mandible, part of the axial skeleton and a humerus) indicate that this animal was much larger than the living giant otter *Pteronura brasiliensis* (Willemsen & Malatesta, 1987), a species with a maximal weight up to 28 kg (Rosas *et al.*, 2009). It is therefore likely that *Megalenhydris* was much heavier than the estimated weight of 17 kg. This size increase remains unexplained, but might be due to niche expansion towards that of an obligatory aquatic otter as evidenced by the tail (which is much flattened right from the tail root) and by the flexible backbone.

Three otter species (*Lutrogale cretensis*, *Lutra trinacriae*, *Cyrnolutra castiglionis*) show a moderate increase in the length of the lower first molar without a detectable change in other linear measurements (Table 1); one otter species shows a similar increase (*Algarolutra majori*), but other measurements are lacking here. The enlargement of the first molar in these three or four species might be an indication of size increase, but may equally well be explained as a dietary adaptation. In the case of *Lutrogale cretensis*, this was previously highlighted

Table 2 Body mass estimations for fossil insular carnivores that are known from a complete or partial skeleton of a single individual. The estimations are based on measurements of different elements.

Taxa and method based upon measurements of	Reduced major axis for estimating body mass (BM) and standard error of estimate (PE)	Measurement	Log(BM)	Body mass (kg)
Cynotherium sardous				
Skull condylobasal length (SKL)[a]	log(BM) = 2.86log(SKL) – 5.21 (PE, 21%)	SKL: 15.4 cm	1.046	*c.* 11 (±2.1)
First lower molar length (Lm1)[a]	log(BM) = 1.82log(Lm1) – 1.22 (PE, 27%)	Lm1: 18 mm	1.064	*c.* 11.5 (±2.2)
Proximodistal length of the femur (F)[b]	log(BM) = 2.92log(F) – 5.27 (PE, 20%)	F: 141 mm	1.005	*c.* 10 (±1.8)
Circumference of the femur at the midshaft (cF)[b]	log(BM) = 2.88log(cF) – 3.40 (PE, 18%)	cF: 35 mm	1.047	*c.* 11 (±1.8)
Proximodistal length of humerus (H)[b]	log(BM) = 1.64log(H) – 2.38 (PE, 21%)	H: 132 mm	1.097	*c.* 12.5 (±2.3)
Circumference of the humerus at the midshaft (cH)[b]	log(BM) = 1.86log(cH) – 1.75 (PE, 16%)	cH: 34 mm	1.098	*c.* 12.5 (±1.8)
Humerus trochlea circumference (TC)[c]	log(BM) = 2.252(±0.192)log(TC) – 0.586 (BM in g)	TC: 7.9 mm	4.016	*c.* 10
Sardolutra ichnusae				
Skull condylobasal length (SKL)[a]	log(BM) = 3.39log(SKL) – 6.03 (PE, 40%)	SKL: 102 mm	0.779	*c.* 6 (±2)
First lower molar length (Lm1)[a]	log(BM) = 3.48log(Lm1) – 3.04 (PE, 45%)	Lm1: 12.9 mm	0.824	*c.* 6 (±2.5)
Head–body length (HBL)[a]	log(BM) = 2.81log(HBL) – 7.08 (PE, 48%)	HBL: 632 mm	0.790	*c.* 6 (±2.5)
Lutra trinacriae				
Skull condylobasal length (SKL)[a]	log(BM) = 3.39log(SKL) – 6.03 (PE, 40%)	SKL: 114 mm	0.942	*c.* 8.5 (±3)
First lower molar length (Lm1)[a]	log(BM) = 3.48log(Lm1) – 3.04 (PE, 45%)	Lm1: 13.1 mm	0.848	*c.* 7 (±2.6)
Head-body length (HBL)[a]	log(BM) = 2.81log(HBL) – 7.08 (PE, 48%)	HBL: 680[d] mm	0.879	*c.* 7.5 (±2.8)
Lutrogale cretensis				
Skull condylobasal length (SKL)[a]	log(BM) = 3.39log(SKL) – 6.03 (PE, 40%)	SKL: 120 mm	1.018	*c.* 10 (±3.5)
First lower molar length (Lm1)[a]	log(BM) = 3.48log(Lm1) – 3.04 (PE, 45%)	Lm1: 16.05 mm	1.155	*c.* 14 (±5.4)
Head–body length (HBL)[a]	log(BM) = 2.81log(HBL) – 7.08 (PE, 48%)	HBL: 725 mm	0.957	*c.* 9 (±3.6)

[a]Van Valkenburgh (1990), [b]Anyonge (1993), [c]Andersson (2004), [d]estimated from a mounted skeleton.

by Willemsen (1996) when pointing out its relatively robust dentition with enlarged talon on the fourth premolar. This is also reflected in the diet of the single extant species, the smooth-coated otter (*Lutrogale perspicillata*), which is a shellfish-eater rather than a fish-eater. A shellfish diet has also been proposed for the giant Sardinian otter (*M. barbaricina*), as inferred from its teeth, which resemble those of the extant clawless otter (*Aonyx*). The latter genus is, like *Lutrogale*, characterized by a large talon on its last pre-molar (Willemsen & Malatesta, 1987). The same is observed in the Miocene genus *Paralutra*. The endemic form from Gargano bears an even larger talon than the type species (*Paralutra jaegeri*), on the basis of which it is assumed that it consumed more shellfish than its ancestor (Willemsen, 1983). Most insular otters do not differ much from the mainland species but apparently some of them shifted towards a diet containing a larger portion of shellfish.

The teeth of one Sardinian galictine marten increased in size. This indicates either an increase in body size, perhaps in relation to an abundance of murids, or a shift in diet comparable to what is observed in the otters. As far as the genet is concerned, the material is scanty and the variation unknown. Tooth measurements from the adult skull from Aghia Napa (Theodorou *et al.*, 2007) and from the juvenile dentary from Aetokremnos (Simmons and Associates, 1999) indicate a slight increase in size. In addition, Theodorou *et al.* (2007) observed an increased cutting function of its cheek teeth, in comparison with the common genet. Furthermore, the second upper molar is either missing or diminutive. It seems that instead of a change in body size, a shift in diet took place as in some otters. This might be explained by the total lack of raptor birds on Cyprus during the entire Pleistocene as a direct result of the absence of micromammals. The genet, which was probably introduced by humans in the Early Holocene, or later for pest control, as in the rest of Europe (Morales, 1994; Gaubert *et al.*, 2009), found itself the dominant carnivore here. This is certainly not the case for the other martens, as their islands also harboured birds of prey, often barn owls (*Tyto*). These occupy the same dietary niche as the martens and thus constitute possible competitors.

Mele's hunting hyena (*Chasmaporthetes melei*) and the Sardinian dog (*Cynotherium sardous*) both originated from large carnivores (Fig. 1) that preyed on animals larger than themselves. They were the dominant carnivores in their insular ecosystem, in the sense that they controlled, at the species level, the largest proportion of a limited resource of prey. In addition, they both persisted for a prolonged time (thousands of years) in isolation from the mainland. They both evolved towards smaller sizes. *Chasmaporthetes melei* is only moderately smaller than the mainland form. It was an active

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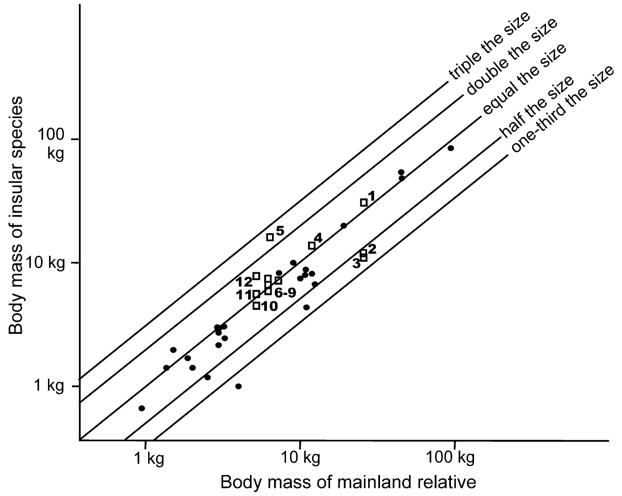

Figure 2 Plot of the body mass of insular carnivores versus the body mass of their mainland phylogenetic relatives. Filled circles represent carnivores living today on islands. Open squares represent fossil insular carnivores. The data for the living carnivores are from Meiri *et al.* (2006, their supplement 1). The estimation of the body mass of the fossil carnivores is based on the length of the lower first molar (see Appendix S1). 1, *Megacyon merriami*; 2, *Cynotherium sardous*; 3, *Mececyon trinilensis*; 4, *Lutrogale cretensis*; 5, *Megalenhydris barbaricina*; 6, *Oriensictis nipponica*; 7, *Lutra trinacriae*; 8, *Sardolutra ichnusae*; 9, *Cyrnolutra castiglioni*; 10, *Enhydrictis galictoides*; 11, *Mustelercta arzilla*; 12, *Pannonictis* sp.

predator, able to bring down large prey and crush their bones, much like its mainland relative (Rook *et al.*, 2004). *Cynotherium sardous*, on the other hand, was a dwarf in comparison with mainland *Xenocyon*, and had reached about half the original size. The reason for this great size reduction is that it shifted from hunting large prey to hunting small prey, such as the abundantly present lagomorphs (Lyras *et al.*, 2006). This latter feeding strategy requires relatively low hunting costs but it cannot sustain a large body mass (Carbone *et al.*, 1999, 2007), therefore the species evolved towards dwarf size (Lyras & van der Geer, 2006). The same did not apply to the hyena of the previous period, because even the smallest available prey (goat-antelope-like bovids and pigs) was not only still rather large, but also strong and massive. It is probable that this prevented the hyena from becoming a dwarf.

The Trinil dog (*Mececyon trinilensis*) provides a similar case of dwarfing in a large hypercarnivorous canid. The Javanese dogs shared the position of top predator with tigers, but these tigers were probably bound to a different habitat. In addition, tigers are obligatory solitary hunters whereas wolves and dogs are pack hunters, which implies a totally different prey spectrum for equal body mass. This is also concluded by Hertler & Volmer (2008), who suggested a prey-species range of 5–10 kg for *Mececyon*. The dwarfism of *Mececyon* is even more spectacular because it originates from the late Early Pleistocene *Megacyon merriami*. The latter species is a large *Xenocyon*, perhaps even larger than the mainland forms, as

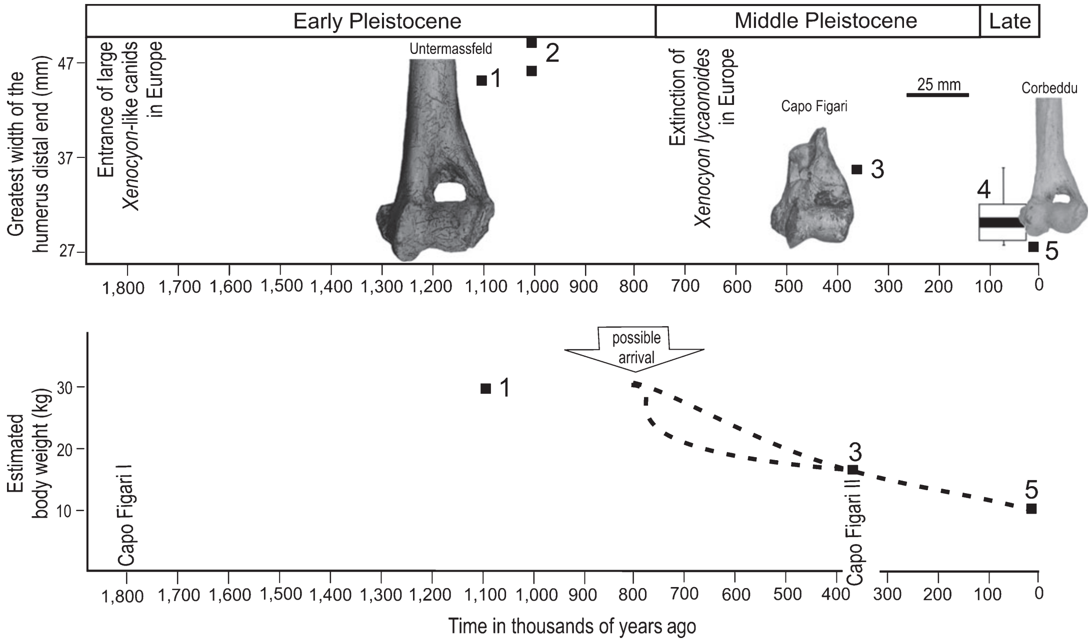

Figure 3 Speed of the size reduction of *Cynotherium*. The upper diagram shows the width of the humerus at the distal end versus the geochronological time of the specimens. The lower diagram shows the estimated body mass as calculated from the circumference of the humerus trochlea. 1, *Xenocyon lycaonoides* from Untermassfeld, Germany. 2, *X. lycaonoides* from Stránská Skála, Czech (measurements from Sotnikova, 2001). 3, *Cynotherium* sp. from Capo Figari (measurement from van der Made, 1999). 4, Average and range of *C. sardous* from Dragonara Cave (data from Malatesta, 1970). 5, *C. sardous* from Corbeddu Cave (measurement from Lyras & van der Geer, 2006). For the body mass estimations, see Appendix S1.

inferred from its first lower molar, whereas the Middle Pleistocene *Mececyon trinilensis* is a dwarf of similar size to *C. sardous* or even somewhat smaller.

Schütt (1973) noted that *Mececyon*, *Xenocyon* and perhaps *Cynotherium* belong to one genus, based on shared adaptational features in their dentition and the presence of a lower third molar (missing in *Cuon*). Each island therefore harbours its own genus. This situation is undesirable from a phylogenetic point of view, and a single genus should be retained for the various *Xenocyon* lineages, which, following rules of priority should be either *Cynotherium* (in line with Lyras *et al.*, 2006) or *Lycaon* (in line with Martínez-Navarro & Rook, 2003). However, a taxonomical revision, regardless of its biogeographic importance, is beyond the scope of this paper.

With regard to the evidence from Sardinia and Java, it seems that *Xenocyon* had better dispersal abilities than other canids. On Java, it perhaps dwarfed because of the simultaneous presence of large cats, forcing it to change prey and expand its niche to feed mainly on rodents. On Sardinia and Corsica, however, no such competitor was present, but a change in prey took place nonetheless, implying that interspecific competition is not an important factor for canids derived from *Xenocyon*. In these cases, no restrictions were present because foxes are missing in both faunas.

The Sardinian dog *Cynotherium* is of particular interest for two more reasons. It is the only fossil insular carnivore that gives us the opportunity to: (1) investigate whether the teeth lag behind during dwarfism, and (2) estimate the speed of its size reduction. The results of estimations of body mass based on various elements of one individual (Table 2) indicate that the direct application of the methodologies developed for mainland species also seems to work in the case of this dwarfed canid. An important implication of this observation is that it is probable that these methodologies can thus be applied to other insular canids, as Lomolino (2005) and Meiri *et al.* (2004, 2005, 2008) have done. Apparently, the teeth of this dwarf canid do not lag behind in evolution.

The gradual decrease in size of *Cynotherium* has been noted previously, because fossils from stratigraphically older sites are larger than those from younger sites (Abbazzi *et al.*, 2005; Lyras & van der Geer, 2006). The results of the estimation of the evolutionary rate (Fig. 3) indicate that the speed of this size decrease is rather slow for this lineage. Whether an early fast evolutionary trend took place or not is unclear. Figure 3 shows the two possible extremes, which have different implications for the overall pattern of the evolutionary speed of this feature. At the present stage of knowledge, neither of the two can be excluded. Millien (2006) shows that morphological evolution is accelerated among island mammals and that an initial period of fast change is followed by a period with smaller rates of change, as described previously by Sondaar (1977), although not quantitatively. This means that in the longer term the calculated speed of evolution of any island species is much lower than during the initial stage. In other words, the longer the period of isolation, the lower the expected rate of change. If this initial acceleration is also valid for canids, the lower of the two dotted lines is the most likely. To validate this, more fossils from older localities are needed.

How do our data from the fossil record compare with the situation seen on present-day islands? Meiri *et al.* (2004) noted that the majority of insular carnivores today inhabit continental shelf islands and are relicts of mainland populations that became isolated. Only a minority live on what they consider oceanic islands, but which are better referred to as oceanic-like in the sense of Alcover & McMinn (1994), which means that although they originated from continental plates, their fauna and flora are similar to those of oceanic islands. This minority represents insular carnivores that reached the island after crossing a substantial sea barrier and evolved thereafter in isolation. Meiri *et al.* (2004) report the following: the eupleurid carnivores of Madagascar, the Sulawesi palm civet (*Macrogalidia musschenbroekii*), the recently extinct Falkland Islands wolf (*Dusicyon australis*) and the Channel Islands fox (*Urocyon littoralis*). These species appear to be the only recent carnivores that resemble the fossil species described in this paper with regard to faunal composition and degree of isolation, but not in all cases regarding the method of dispersal. Present-day islands, such as Vancouver Island, despite the fact that geographically they can be called islands, do not have the same ecological conditions as Pleistocene Crete or Cyprus. A problem for a better understanding of the evolutionary history of the above-mentioned recent insular carnivores is that a close mainland relative can be safely assigned to only two of them. These are the Channel Islands fox (*U. littoralis*) and the Falkland Islands wolf (*D. australis*). The former is a descendant of the North American *Urocyon cinereoargenteu*s and most linear measurements are 25% smaller than those of its mainland ancestral species (Moore & Collins, 1995) (Fig. 4). The latter is phylogenetically related to the South American fossil species *Dusicyon avus* (Berta, 1988) and had a similar size (Rodrigues *et al.*, 2004; Prevosti *et al.*, 2009). Unfortunately, not much is known about the Falkland Islands wolf as it became extinct in the 19th century. What is known, however, is that it preyed on birds, such as geese and penguins, and on seals (Nowak, 1999). *Dusicyon* was the only terrestrial mammal on the islands. Whereas the Channel Islands fox evolved a smaller body size, the Falkland Islands wolf maintained its ancestral size. It seems that the total absence of small mammals

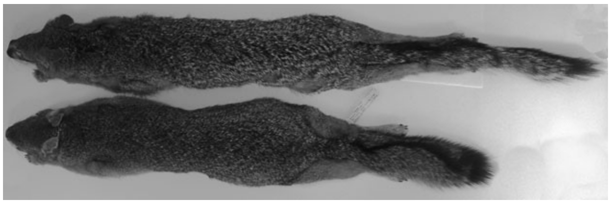

Figure 4 Comparison of the Channel Islands fox, *Urocyon littoralis* (bottom), with its mainland ancestor, the grey fox, *Urocyon cinereoagenteus* (top). Both specimens are from the Field Museum of Natural History, Chicago.

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from the Falklands prevented the size decrease of *Dusicyon*, simply because it had to remain large in order to hunt big prey. Carnivore size on islands is closely related to the relative abundance and size spectrum of available resources (Meiri *et al.*, 2006; Raia & Meiri, 2006). But this statement requires some adjustment, because the size reduction of both the Sardinian dog and the Trinil dog suggests that where an alternative, small prey is available, carnivore body size tends to decrease even if larger prey is available at the same time. Those two carnivores became smaller while medium-sized bovids and deer were available in sufficient quantities. Where no alternative prey is available, ancestral body size is retained. An optimal body size therefore seems not to exist for carnivores, as noted by Meiri *et al.* (2005), and cases of dwarfism as well as gigantism do exist.

CONCLUSIONS

Two fossil insular canids and one otter underwent significant changes in body mass once isolated, compared with their phylogenetically closest relatives from the adjacent mainland. The rate of this evolution is slow (1.38 Darwin) for one of these canids. The other carnivores studied (one canid, four martens, six otters, one genet) show a moderate change or no change at all. Size decrease in insular carnivores seems constrained by certain ecological conditions, specifically by the availability of a prey that befits their smaller size. When this alternative prey is not available, they retain their mainland size, as in the case of *D. australis*, or evolve at most a moderately smaller size, as in the case of *Chasmaporthetes melei*. When alternative prey is available, they may evolve towards dwarfism, as in the case of *Cynotherium* and *Mececyon*. This change in prey seems unaffected by the presence of competitors. Size increase is very rare, and might coincide with a niche expansion. The island rule thus seems to apply to (originally) large and medium-sized terrestrial carnivores, as Lomolino (1985, 2005) suggested. However, we also agree with Meiri *et al.* (2004, 2008), who suggested that many factors influence mammalian body size and detailed studies are often needed for every individual case. The dependency of the island rule on resource availability (McNab, 2002) is emphasized by the present study.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Body mass estimations for some insular carnivores and their mainland relatives.

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