

THE ISLAND RULE IN LARGE MAMMALS: PALEONTOLOGY MEETS ECOLOGY

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Abstract.—The island rule is the phenomenon of the miniaturization of large animals and the gigantism of small animals on islands, with mammals providing the classic case studies. Several explanations for this pattern have been suggested, and departures from the predictions of this rule are common among mammals of differing body size, trophic habits, and phylogenetic affinities. Here we offer a new explanation for the evolution of body size of large insular mammals, using evidence from both living and fossil island faunal assemblages. We demonstrate that the extent of dwarfism in ungulates depends on the existence of competitors and, to a lesser extent, on the presence of predators. In contrast, competition and predation have little or no effect on insular carnivore body size, which is influenced by the nature of the resource base. We suggest dwarfism in large herbivores is an outcome of the fitness increase resulting from the acceleration of reproduction in low-mortality environments. Carnivore size is dependent on the abundance and size of their prey. Size evolution of large mammals in different trophic levels has different underlying mechanisms, resulting in different patterns. Absolute body size may be only an indirect predictor of size evolution, with ecological interactions playing a major role.

Key words.—Body size, character displacement, competition, island rule, predation, resource base, sexual size dimorphism.

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Vertebrates on islands undergo considerable body size changes over short evolutionary times (Lister 1989). In mammals, large species seem to dwarf on islands while small species increase in size. This well-known phenomenon (Foster 1964; Lomolino 1985) was named “the Island Rule” (Van Valen 1973). The rule has many exceptions, with some large mammals getting even larger on islands (e.g., the Kodiak bear *Ursus arctos middendorffi*, and the extinct Crete deer *Cervus major*) and some small mammals getting smaller (e.g., *Mastomys huberti* [Ganem et al. 1995], *Sundamys muelleri* [Nor 1996], *Parantechinus apicalis* [Mills et al. 2004]). Further, Meiri et al. (2004, 2006) found no predictable trend for carnivores. Nevertheless, the island rule continues to be a major theme in island biogeography (Clegg and Owens 2002; Boback and Guyer 2003; Lomolino 2005; Lomolino et al. 2005).

Many hypotheses have been advanced to explain this rule (Hooijer 1949; Foster 1964; Case 1978; Heaney 1978; Lomolino 1985; Roth 1992). Reduced insular species richness can drive the pattern through rarity of predators and competitors (Dayan and Simberloff 1998). Accordingly, Boekschoten and Sondaar (1966) and Sondaar (1977) suggested that the reduced (often absent) predation pressure on islands allows large species to attain smaller sizes because large size is a means to counteract predation (e.g., Sinclair et al. 2003). Smith (1992) argued that in the absence of mammalian predators small herbivores grow large to facilitate more effective digestion. Other authors suggested that smaller size is a way of coping with resource shortages on small islands (Heaney 1978; Lomolino 1985; Angerbjörn 1986; Roth 1992; Burness et al. 2001). However, Meiri et al. (2005a,b; 2006) have shown that neither island area nor isolation have a consistent effect on carnivore body size. A third group of hypotheses explains the island rule in terms of selective advantage of

body size alteration via life-history traits (Melton 1982; Brown et al. 1993; Marquet and Taper 1998; Palkovacs 2003; Raia et al. 2003).

The above hypotheses are not mutually exclusive. Many factors probably govern body size evolution on different islands (Dayan and Simberloff 1998). In a recent review, Lomolino (2005) claimed that the island rule is a general emergent attribute at different phylogenetic scales and advanced the existence of taxon-specific “fundamental” body sizes (Brown et al. 1993) functioning as evolutionary attractors. Here we offer a new explanation for the island rule that includes both ecological interactions and resources as factors, and we show that different mechanisms affect the sizes of herbivores and carnivores.

Many spectacular examples of body size evolution on islands come from fossil faunas in the Mediterranean (Ambrosetti 1968; Malatesta 1980; Lister 1996; Sondaar 1977; Bover and Alcover 2000; Vos 2000), where there appear to have been several forms of minute elephants and hippopotamuses (Caloi and Palombo 1983; Lister 1993). No wild ungulates survived human colonization on any of these islands. However, most of these faunas have been intensively studied for more than a century, and detailed stratigraphic and paleoecologic reconstructions are available for some (Vos 2000; Abbazzi et al. 2004; Marra 2005). These examples afford the unique opportunity to study the island rule in large ungulates. Size changes in insular carnivores are usually not as drastic as they are in herbivores. This may be because other selective forces affect the sizes of animals in those trophic levels. Although data on fossil carnivores are insufficient to allow statistical testing, a large, global dataset of recent insular carnivores, compiled by Meiri et al. (2004, 2005b) offers the possibility of comparing patterns and processes in these two trophic groups.

The Theoretical Framework

We predict that ecological interactions affect carnivores and herbivores differently, with dwarfing being more common and more drastic in herbivores, because of dietary differences and the peculiarity of intraguild killing in carnivores. Size reduction in mammals often entails an increase in lifetime offspring production (Calder 1996, p. 248). Offspring number, however, is negatively correlated with average viability, with large litters facing increased mortality (Promislow and Harvey 1990). Thus, life history remains a matter of strategy (Roff 2002), and no size confers an a priori advantage (Blackburn and Gaston 1996, Kozłowski and Teriokhin 1999). Raia et al. (2003) suggested that size reduction of large insular mammals depends on selection for greater reproductive investment under condition of reduced external mortality. Raia and colleagues argued that at the individual level organ growth and repair compete with reproductive effort (Holliday 1989; Mangel and Stamps 2001). As a consequence, increased energy allocation toward reproduction occurs at the expense of growth. Impressively high numbers of juveniles seem to point to intense reproductive effort in insular dwarf fossil mammals both in the absence (e.g., Malatesta 1980; Raia et al. 2003) and presence (Abbazzi et al. 2004) of predators. Unfortunately, data are generally too scarce to be tested statistically, but it seems that herbivores that actively defend themselves and their calves from predators (e.g., elephants) retain their ancestral size if carnivores are present. Competition similarly affects offspring mortality because competitors reduce resource availability. Poulakakis et al. (2002) and Raia et al. (2003) suggested that different levels of dwarfism in Pleistocene elephants on Mediterranean islands depended on the presence of smaller species with overlapping diets. Raia et al. (2003) specifically advocated the incumbency of smaller competitors in the same niche (Rosenzweig and McCord 1991) and predation to explain differential dwarfism in the straight-tusked elephant *Elephas antiquus* in fossil assemblages on Sicily. In carnivores, intraguild predation and interference competition could severely counterbalance any fitness advantage accrued by size reduction. Large carnivores often kill smaller ones (see, e.g., Palomares and Caro 1999; Creel and Creel 2002). Often this results in smaller carnivores living in peripheral sink populations that are relatively predator free (Mills and Gorman 1997; Creel and Creel 2002). Intraguild predation may be even more influential on islands, where predator-free space is scarce and sink populations are not viable (Rosenzweig 1995).

Size differences have been claimed to promote coexistence in herbivores (Bell 1971; McNaughton and Georgiadis 1986). Large herbivores can access low-quality food because at least up to about rhino size, gut retention time scales positively with body size (Demment and Van Soest 1985; Illius and Gordon 1992; Clauss and Hummel 2005). Thus, in classical "grazing chains" (Bell 1971), larger species feed on the low quality forage, permitting smaller species to exploit the higher quality parts of the plants. This coexistence mechanism should accrue to island herbivores as well.

In carnivores, the presence of similar-sized or larger competitors could impede the onset of dwarfism by increasing

the risk of intraguild predation. Moreover, prey size is of crucial importance to carnivores, because carnivores need to be large enough to subdue their prey. Therefore, even in the absence of competitors, size reduction may not be adaptive, unless large prey is absent (Jessop et al. 2006). Furthermore, islands often offer extremely abundant resources in the form of carcasses, fishes, and marine bird nests (Case and Schwaner 1993; Goltsman et al. 2005). Thus, resource abundance should be much more frequently important to carnivores, and size would evolve accordingly.

We therefore predict different evolutionary trajectories for carnivores and herbivores with the most remarkable cases of size reduction occurring in the latter. We predict herbivore size will be related to the prevailing competition and predation pressures. We expect carnivores to evolve to be smaller or larger on islands primarily in relation to the relative size and abundance of their prey. We do not expect ancestral body size to be a major predictor of size change, except through its influence on the above factors. Four predictions arise from our theory.

The biological interaction effect hypothesis (fossil ungulates).—If competition and predation drive the extent of size decrease, we would expect different degrees of size reduction for the same species depending on the presence and the size of competitors and on the presence of predators. Because smaller competitors can prevent size decrease (Dayan et al. 1989), we expect the degree of dwarfism to be higher in the absence of smaller competitors.

Overdispersion hypothesis (fossil ungulates).—If competition is important, body size should be overdispersed in multispecies assemblages (i.e., size ratios between species should be more equal than expected by chance; Dayan and Simberloff 2005). Late colonizing/new species should remain large if smaller competitors are present because of niche incumbency (Rosenzweig and McCord 1991). In our data there is only one case where this prediction is testable (Crete fossil deer).

Carnivore resource-competition hypothesis (extant carnivores).—We expect body size change in insular carnivores to depend on the presence of potential predators, smaller and larger competitors, dietary preferences, and the nature of the resource base. Size is predicted to evolve toward that of missing competitors, decrease in the absence of predators, and correlate positively with the size and abundance of available prey.

Sexual size dimorphism hypothesis (extant carnivores only because fossils cannot be accurately sexed).—A greater investment in reproduction should be paralleled by increased sexual size dimorphism (SSD). This could occur because males gain less than females from size reduction. Large size is often an effective mean of displacing rival males at mating, and reproduction is less costly for males. We therefore predict females of insular dwarves will decrease more in size relative to males of the same populations, thereby increasing SSD on islands.

MATERIALS AND METHODS

Pleistocene Ungulates of the Mediterranean Islands

We gathered data on large mammals of Plio-Pleistocene assemblages of different Mediterranean islands from the lit-

TABLE 1. Fossil ungulate guilds on islands with more than one faunal complex included in this study.

Island	Herbivores	Carnivores	Age
Crete	<i>Cervus dorotheoensis</i>	absent	late Pleistocene
	<i>Cervus major</i>		
	<i>Cervus rethymnensis</i>		
	<i>Elephas creutzburgi</i>		
	<i>Hippopothamus creutzburgi</i>		
	<i>Praemegaceros cretensis</i>		
Crete	<i>Praemegaceros ropalophorus</i>	absent	early Pleistocene
	<i>Mammuthus creticus</i>		
Sardinia	<i>Sus sondaari</i>	<i>Chasmaportetes meleii</i> , <i>Cynotherium</i> sp.	late Pliocene—early Pleistocene
	<i>Nesogoral</i> sp.		
	Caprinae indeterminate		
Sardinia	<i>Praemegaceros</i> sp.	<i>Cynotherium</i> sp.	middle Pleistocene
	Caprinae indeterminate		
Sardinia	<i>Mammuthus lamarmorae</i>	<i>Cynotherium sardous</i>	late Pleistocene
Sicily	<i>Praemegaceros cazioti</i>	<i>Crocota crocuta</i> , <i>Ursus arctos</i> , <i>Panthera leo</i> , <i>Canis lupus</i>	middle to late Pleistocene
	<i>Bison priscus sicilii</i>		
	<i>Bos primigenius sicilii</i>		
	<i>Cervus elaphus sicilii</i>		
	<i>Dama carburangelensis</i>		
	<i>Elephas mnaidriensis</i>		
	<i>Equus hydruntinus</i>		
	<i>Hippopotamus pentlandi</i>		
	<i>Sus scrofa</i>		
Sicily	<i>Elephas falconeri</i>	absent	early Pleistocene
Cyprus	<i>Elephas cypriotes</i>	absent	middle Pleistocene
	<i>Phanourios minor</i>		
Corse	<i>Praemegaceros cazioti</i>	absent	late Pleistocene
Corse	<i>Praemegaceros cazioti</i>	<i>Cynotherium sardous</i> , <i>Canis</i> sp.	middle Pleistocene
	<i>Cervus elaphus rossii</i>		

erature, supplemented by measurement of Sicilian species and *Cervus elaphus thyrrenicus* taken by P. Raia (Table 1; Appendix 1 available online only at <http://dx.doi.org/10.1554/05-664.1.s1>). We excluded small mammals because of their patchy fossil record (Damuth 1982). We did not test for the effects of island area on fossil ungulate size as Pleistocene island areas are not reliable. We include island area as a predictor when analyzing carnivore sizes. We used the length of the third lower molar (M_3) as an index of size, because this measurement is well correlated with body size in many mammalian families (Damuth and McFadden 1990). When this was not reported we used the length of the lower molar row or the third upper molar. A separate size index was derived from long bone measurements: we used metatarsal lengths, and when these were unavailable either tibiae or metacarpal lengths. Teeth and bone measurements other than third molars and metapodials lengths can admittedly be better predictors of body size (Janis 1990; Scott 1990). Yet, M_3 is the most morphologically distinctive tooth and could be easily recognized (and measured) in both ruminants and proboscideans (the third molar of elephants has distinctive shape because, being the last to erupt, it is not pushed forward by any other tooth; thus, its rear part is elongated). Similarly, metapodials are easily recognized and often distinctive among ruminants and are more abundant in fossil samples than any other long bone. The choice of these measurements therefore maximizes both the number of species included and sample size for each species. Measurements of mainland species were preferentially taken from Mediterranean populations (Italy, Greece, Spain, and southern France). The same

mainland population was used as a reference to calculate size reduction indices (SR; size on island/size on the mainland) in all insular descendants (Appendix 2, available online only at <http://dx.doi.org/10.1554/05-664.1.s2>; and Appendix 3, available online only at <http://dx.doi.org/10.1554/05-664.1.s3>).

Some islands had more than one faunal complex (i.e., chronologically distinct fossil assemblages): Sardinia, Sicily, and Crete had four each. In these islands there were cases of in situ speciation (deer in Crete, a caprine in Sardinia). Some colonization events were recurrent: dwarfism of the straight-tusked elephant *E. antiquus* occurred on Tilos, Crete, Sicily (twice), Malta (twice), Rhodos, Cyprus, Naxos, Delos, and Favignana. Similarly, the megacerine deer *Praemegaceros verticornis* colonized Sardinia, Corsica, Crete, Kasos, and Karpathos. Red deer (*Cervus elaphus*) inhabited Crete, Corsica, Capri, Malta, and Sicily. Hippos inhabited Cyprus, Crete, Malta, and Sicily. Large carnivores include the running hyena, *Chasmaportetes meleii*, and the canid, *Cynotherium sardous*, on Sardinia and cave hyena *Crocota crocuta*, wolf (*Canis lupus*), brown bear (*Ursus arctos*), and lion (*Panthera leo*) on Sicily. We followed the biostratigraphic accounts of Dermitzakis and Vos (1987; Crete), Kotsakis (1990; other East Mediterranean islands), Abbazzi et al. (2004; Sardinia), and Marra (2005; Sicily). The species we included date from the earliest Pleistocene (oldest faunal complex in Sardinia with *C. meleii*) to the latest Pleistocene (Crete largest deer in Simonelli Cave, $32,500 \pm 20\%$ years before present [BP]; Karpathos deer, $14,320 \pm 20\%$ years BP; Reese et al. 1996) and mid-Holocene (one record, pigmy Tilos elephant, 4390

± 600 years BP; Reese et al. 1996). Middle Pleistocene faunas include Crete hippos and the smallest elephant (Reese et al. 1996), Sicilian *E. falconeri* (550,000 \pm 25–30% years BP; Belluomini and Bada 1985) and Sardinia faunal complexes with deer and mammoth; Abbazzi et al. 2004). Late Pleistocene faunas also include the Sardinian larger mammoth (Palombo et al. 2004); younger Sicilian faunas with *E. mnaidriensis* plus carnivores, hippo, deer, auroch, and bison (whose absolute dating ranges between 200,000 and 88,000 years ago; Bada et al. 1991).

Species with uncertain biostratigraphic position or of unclear descent (e.g., Balearic *Myotragus* spp., Sardinian *Nesogoral* spp.) were excluded (online Appendix 1). We also excluded all island fossil assemblages either known or suspected to belong to a phase of connection between the island and the mainland.

Modern Carnivore Faunas

We measured crania of medium to large (larger than marten-sized, >2 kg) carnivores in museum collections (see Acknowledgments), using condylo-basal length (CBL) as an index of size. CBL was chosen because it is invariant in adults, has low intrapopulation variability, low measurement error (Dayan et al. 2002; Meiri et al. 2005c), and does not change with time since collection as do some skin measurements (Winker 1993). We used only specimens with complete closure of the dorsal sutures and treated males and females as separate morphospecies. We compared only population pairs from which we had at least three specimens of a given morphospecies on both the island and the mainland.

Analyses

The biological interaction effect hypothesis

We tested this hypothesis by comparing sizes of extinct insular species with those of their likely mainland ancestors, taken from the recent paleontological literature (online Appendix 1). A size ratio (SR; size on island/size on mainland) was computed by taking the ratio of linear measurements, chosen to maximize sample size. We calculated SR using the same measurement for all descendants of a common ancestor. Size ratio implies scaling is isometric. However, many (but by no means all) insular dwarfed ungulates have often been noted for their comparatively large teeth and short metapodials (Gould 1975; Sondaar 1977). Thus, size ratios calculated using teeth have higher SR values (i.e., a lesser degree of dwarfism) than values based on metapodials. Consequently, we performed separate tests for long bones and teeth. We tested for the influence of predation, competition, and ancestral body mass on SR. Most of the effects of predation and competition depend on population densities, which is unknown for fossils. Thus, we tried to model predation and competition independently of density effects, by categorizing whether any degree of predation is likely to have prevailed. Predation was categorized by distinguishing three predation levels (PLs) of increasing intensity: (1) no predator known to be present, (2) mammalian predators not larger than 1/10 the size of the species in question and/or large birds of prey known to be present, (3) mammalian predators larger

than 1/10 the size of the focal species present. The lower limit for the inclusion of predators in our dataset was 2 kg. Carnivores can subdue prey as much as five times larger than themselves, and even 10 times larger in the case of group-hunting lions (Radloff and Du Toit 2004). Our size limit of 1/10 the size of the focal prey was decided accordingly. Category 2 is meant to indicate occasional predation at best. Small predators may be important to dwarfing herbivores: wolves or hyenas were probably not a serious threat to mainland straight-tusked elephants, but might have preyed on juveniles and even on adults of the most dwarfed insular forms. Thus, for example, the Sicilian elephant *E. mnaidriensis* (some 30% the mass of its mainland ancestor) was ascribed to predation category 2 given the presence of cave lion, wolf, and cave hyena. Category 3 indicates more severe predation pressure, being restricted to assemblages with carnivores large enough to prey on the focal herbivores.

Guilds were defined by feeding habits (ascertained by comparison with living relatives, see Nowak 1999) and phylogenetic criteria as follows: deer were considered to be mixed feeders because large deer can tolerate low-quality food (Geist 1998), and most insular deer originated from mixed-feeding red and fallow deer. Elephants were also considered mixed feeders. *Bos*, *Bison*, and *Equus* species were considered to be grazers. Suids were considered to be omnivores, and hippos were classified in a unique dietary group because of their peculiar niche.

We recognize three competition levels (CLs): (1) no competitor present; (2) competing species of a different guild present or a smaller competitor in the same guild and no species in other guilds; (3) smaller competitors in the same guild (more than half the size of the focal species) and at least one other species, irrespective of guild, present. Category 1 includes the species freed from competition at the onset of size reduction. Category 2 includes species that faced diffuse competition from species of different guilds exploiting overlapping resources (e.g., grasses for both mixed feeders and grazers), or have just one species in the same guild but are free to exploit resources in other guilds. Category 3 was intended to test our assumption that smaller species in the same guild decrease little in size when available free niche space in other guilds is scarce. For example, if the fossil assemblage includes both an elephant and a hippopotamus, competition was set at level 1 for both. If there were an elephant and deer, competition was set at level 2 for both. If there were two bovids and a deer intermediate in size between these bovids, competition was set at level 3 for the larger bovid, level 1 for the smaller, and level 2 for the deer.

We performed two separate analyses of covariance (ANCOVAs) on SRs with competition and predation levels as factors, and log-transformed estimates of ancestral mass (online Appendix 2) as a covariate to test whether mass, rather than faunal composition, is a predictor of size change, as predicted by the island rule (Lomolino 1985, 2005). Our SR estimates are conservative because our samples may comprise some individuals that were fossilized before the dwarfing reached its final (and presumably greatest) extent. Furthermore, Capasso Barbato and Gliozzi (1997) suggested there was gene flow between mainland red deer and Capri *Cervus elaphus thyrrenicus*, and Palombo et al. (2004) argued that

TABLE 2. Data on metatarsus length used for testing size overdispersion. ML, mean metatarsus length.

Capasso Barbato 1988					
Species	Locality	<i>n</i>	ML (mm)	Log ML	Interval length
<i>Praemegaceros ropalophorus</i>	Simonelli and Bate caves	135	127.567	2.11	0.135
<i>P. cretensis</i>	Liko	3	174	2.24	0.120
<i>Cervus rethymnensis</i>	Rethymnon, Mavro Mouri	2	229.25	2.36	0.119
<i>C. dorotheoensis</i>	Bate Cave	2	301.2	2.48	0.130
<i>C. major</i>	Bate Cave	1	406	2.61	
De Vos 1979					
Species	Locality	ML (mm)	Log ML	Interval length	
<i>Praemegaceros ropalophorus</i>	Gerani 4	121.6	2.08	0.056	
<i>Praemegaceros</i> sp.	Liko	138.4	2.14	0.114	
<i>Praemegaceros cretensis</i>	Liko 2637	180	2.26	0.128	
<i>C. cretensis</i>	Li 2388	241.5	2.38	0.010	
<i>C. dorotheoensis</i>	Bate	304	2.48	0.126	

mainland *Mammuthus meridionalis* invaded Sardinia when the dwarfed *M. lamarmorae* was already present there.

Finally, we tested whether size change is size dependent. Lomolino (1985, 2005) suggested that a regression of island size versus mainland size should have a slope lower than one. We regressed third lower molar lengths of island fossil species on that of their mainland ancestor after partitioning island species by their CLs. We repeated the analyses using humeri lengths as the size index. We avoided using metatarsal lengths because the metatarsals of most artiodactyls are different from those of elephants and hippos: in ruminant artiodactyls only metatarsals 3 and 4 remain, fused into a single elongated “cannon bone,” whereas in elephants and hippos these bones are unfused, short, and compact. Differential scaling of bone length among large herbivores (Biewener 1989; Bertram and Biewener 1990) could affect the results: elephant columnar limbs are disproportionately long and slender compared with those of hippos and rhinos (Christiansen 1999). Since the stance of elephants is an adaptation to large body mass, it is conceivable that elephant bones become greatly changed in proportions (to save structural energy expenditure) at dwarfing. Thus, our regression of long bone lengths could have an artificially low slope.

Overdispersion hypothesis

Because of uncertainty in the taxonomy of Crete deer we tested for overdispersion using both the taxonomy of Capasso Barbato (1988, 1990; five species) and that of Vos (1979; six species). For each species, mean metatarsus length was taken from the literature (Table 2). We tested for overdispersion using the Barton-David test (Barton and David 1956; Simberloff and Boecklen 1981) on metapodial lengths. A similar analysis for carnivores will be reported elsewhere (S. Meiri, T. Dayan, and D. Simberloff, unpubl. ms.).

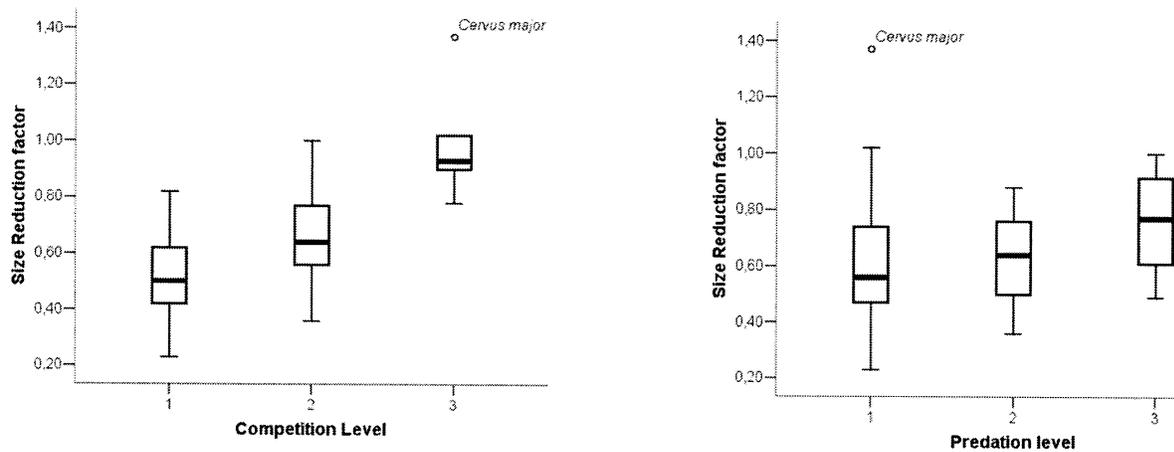
Carnivore resource-competition hypothesis and sexual size dimorphism hypothesis

Dietary preferences were taken from the literature (Meiri et al. 2005c). The presence or absence of competitor species from islands was determined from data in Meiri et al. (2005b).

Absence of potential predators was taken from reports of interspecific killings in carnivores (e.g., Palomares and Caro 1999) or was determined from faunal composition. Resource base characteristics were determined on the basis of island-mainland differences in faunal composition and published sources (e.g., the observation that where brown bears are absent black bears can exploit salmon [Jacoby et al. 1999]; and the absence of rabbits [*Sylvilagus*], an important prey of mainland grey foxes [Fritzell and Haroldson 1982] from the California Channel Islands). We quantified these attributes as follows: Diet: (1) <50% animal matter; (2) >50% invertebrates; (3) >50% nonmammalian vertebrates; (4) 50–90% mammals; (5) >90% mammalian prey. Resource base was ranked as (–2): lower on the island relative to the mainland, (–1): probably lower on the island, (0): similar on island and mainland, (1): better on the island. Predation was ranked as either lower on the island (–2), possibly lower on the island (–1) and similar on both island and mainland (0). Absence from an island of a smaller competitor was ranked (–2), that of a smaller species that may be a competitor was ranked (–1). The presence of a similar smaller competitor was ranked (0), and presence of a smaller competitor on an island that is larger than the mainland smaller competitor (one case, Java leopard as competitor of tiger) was ranked (1). Similarly, the absence of a larger competitor was ranked (2), the absence from an island of a larger species that may be competing with the focal species was given a score of (1), similar larger species composition was ranked (0), and if a larger competitor was present on an island but not on the mainland it was ranked (–1). We also computed a combined competition vector by adding the latter two indices to produce a common competition index (which with our data scales from –2 to 2).

We simultaneously analyzed the effects of all these factors (once treating larger and smaller competitors separately and once with the combined index) using a backwards stepwise multiple regression procedure. We included ancestral body mass (S. Meiri, unpubl. data) and island area (log transformed, data from Meiri et al. [2005a, 2005b]) as additional predictors.

A



B

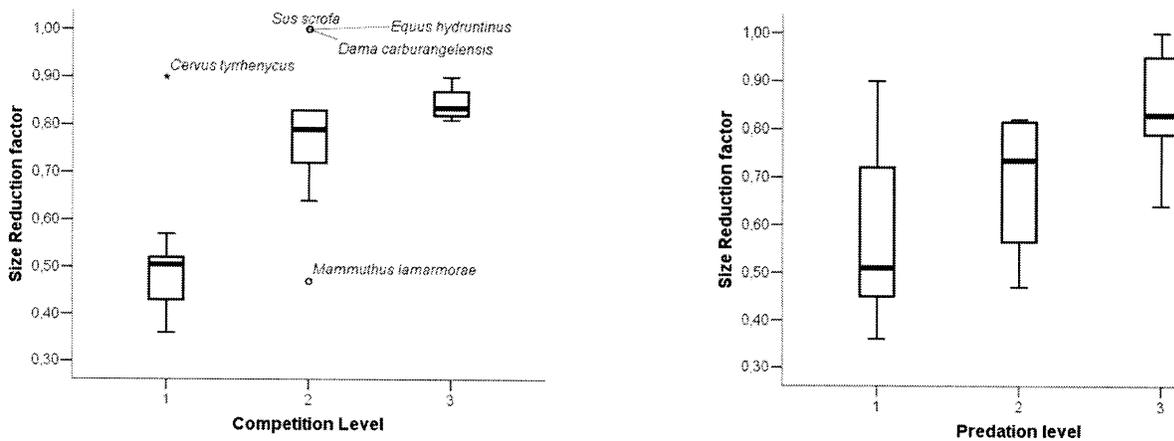


FIG. 1. Size change (SR) across competition and predation levels in analysis of long bones (A) and teeth (B) of fossil Mediterranean ungulates. Displayed are medians (black line), interquartile ranges (box), confidence intervals (error bars), and outliers (open circles).

RESULTS

The Biological Interaction Effect Hypothesis: Plio-Pleistocene Ungulate Size

ANCOVA on long bone data reveals a significant increase in dwarfing with diminishing levels of competition (long bones, $df = 2$, $F = 7.924$, $P = 0.002$). A post-hoc Tukey honest significant difference test indicates competition level 3 (smaller intraguild competitors present) had size reduction index (SR, mean = 0.934) significantly higher than both competition level 1 (SR difference = 0.44, $P < 0.001$) and 2 (SR difference = 0.28, $P = 0.006$). Although SR values were smallest at competition level 1 (mean SR = 48.6% of the size on the mainland), the difference between levels 1 and 2 is not significant (SR difference = 0.17, $P = 0.106$). Predation does not influence dwarfism ($df = 2$, $F = 0.044$, $P =$

0.957; Fig. 1A). Body mass of ancestral species was not a significant predictor of dwarfism ($df = 2$, $F = 0.803$, $P = 0.378$).

The analysis on teeth supports the data on long bones for competition ($df = 2$, $F = 3.868$, $P = 0.038$). Post-hoc Tukey HSD indicates that dwarfing is most pronounced at competition level 1 (no competitors present, mean SR = 0.515) compared to both competition level 2 (SR difference = 0.27, $P < 0.001$) and 3 (SR difference = 0.34, $P = 0.001$). SR difference between groups 2 and 3 is nonsignificant (SR difference = 0.05, $P = 0.739$). This is because some taxa in category 3 are known by postcranial bones only. Again, predation does not influence SR ($df = 2$, $F = 0.540$, $P = 0.948$; Fig. 1B). The effect of body mass of ancestral species was non-significant ($df = 2$, $F = 3.340$, $P = 0.079$).

The identity of the ancestral species did not have a sig-

TABLE 3. Results of regression analyses of insular M₃ length (upper) and humerus length (lower) on the respective mainland lengths. Species were partitioned per competition level (CL).

CL		Coefficients slope	95% CI		F	R ²	P
			lower bound	upper bound			
CL1	intercept	-0.002	-0.347	0.343	148.867	0.955	<0.001
	mainland M ₃ lengths	0.863	0.696	1.030			
CL2	intercept	-0.083	-0.305	0.139	365.687	0.976	<0.001
	mainland M ₃ lengths	0.966	0.852	1.080			
CL3	intercept	0.165	-9.627	9.956	3.065	0.714	0.330
	mainland M ₃ lengths	0.853	-5.338	7.045			

Dependent variable: island M₃ lengths

CL		Coefficients B	95% CI for B		F	R ²	P
			lower bound	upper bound			
CL1	intercept	0.939	-0.468	2.346	6.849	0.494	0.047
	mainland radius lengths	0.527	0.009	1.045			
CL2	intercept	0.313	-0.808	1.433	23.726	0.795	0.003
	mainland radius lengths	0.814	0.405	1.222			

Dependent variable: island humerus lengths.

nificant effect when SRs were compared at the same competition level (CL) for long bones (CL1: df = 2, F = 3.158, P = 0.150; CL2: df = 3, F = 1.757, P = 0.242; CL3: df = 2, F = 0.233, P = 0.802). Ancestral species identity significantly affects SR at predation level (PL) 1 (df = 2, F = 11.431 P = 0.002), but this result is not significant after the gigantic Crete deer *C. dorotheoensis* and *C. major* are removed. At PL3 (df = 2, F = 4.363 P = 0.100) ancestry is not a significant factor. We did not analyze ancestral effects at PL2 because of a small sample size. No significant effect of ancestry was found when we analyzed tooth sizes at different competition (CL1: df = 3, F = 15.961, P = 0.059; CL2: df = 4, F = 0.295, P = 0.868; CL3: df = 2, F = 0.056, P = 0.949) and predation levels (PL1: df = 3, F = 0.563, P = 0.659; PL2: df = 2, F = 0.158, P = 0.872, PL3: df = 2, F = 0.952, P = 0.479). Guild membership does not affect SR for either long bones (df = 1, F = 1.135, P = 0.367) or teeth (df = 1, F = 1.230, P = 0.334).

Regressing M₃ lengths of insular species on those of main-

land populations (both log transformed) gives a slope not significantly different from one (intercept = 0.016; slope = 0.898, 95% CI = 0.795–1.001). The slope of the regression of humeri lengths is significantly lower than one (intercept = 0.624; slope = 0.679, 95% CI = 0.385–0.973). Within competition levels, however, regression of SR on mass using either M₃ or humerus lengths had slopes not different from one (Table 3). Similar patterns are obtained regardless of the metric used to calculate SR (Appendix 4 available online only at <http://dx.doi.org/10.1554/05-664.1.s4>).

Size Overdispersion Hypothesis

Irrespective of which taxonomy we adopted, Barton-David tests indicate that the body sizes of deer on Crete were overdispersed: data from Capasso Barbato (1988); G₁₄ = 0.88, P < 0.001; G₁₃ = 0.91, P = 0.0032; G₂₄ = 0.89, P = 0.0068. Data from Vos (1979); G₁₄ = 0.44, P < 0.01; G₁₃ = 0.44, P = 0.07; G₂₄ = 0.783, P = 0.003.

Carnivore Resource-Competition Hypothesis

Data on localities, sample sizes, sex, and CBL of 131 island/mainland population pairs of modern carnivores, as well as diets and the relative size, predation pressures, interspecific competition, and resource base attributes are listed in Appendix 5 (available online only at <http://dx.doi.org/10.1554/05-664.1.s5>). Because the categories we use are not continuous (e.g., category 2 of larger competitor does not imply twice as strong a competition force as category 1), we urge the reader to view our results as qualitative rather than quantitative. Resource base is the sole significant factor and is positively correlated with size change (n = 130, β = 0.550, P < 0.0001, Fig. 2). Other factors are not significant (sex, β = 0.072, P = 0.16; mass, β = 0.02, P = 0.83; diet, β = 0.013, P = 0.87; predation, β = -0.110, P = 0.29; smaller competitor, β = 0.058, P = 0.52; larger competitor β = -0.140, P = 0.16; area, β = 0.052, P = 0.59). Combining the smaller and larger competitor categories to form a unified competition vector results in the resource base being the sole significant predictor (β = 0.569, P < 0.0001), and it is the

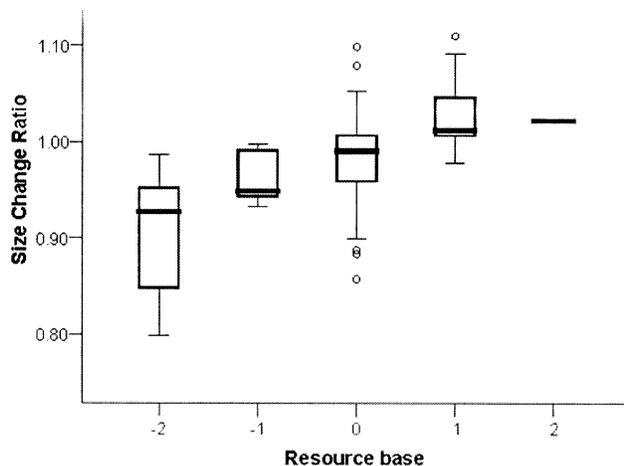


FIG. 2. Size change (SR) across resource base categories in crania of extant insular carnivores. Displayed are medians (bold black line), interquartile ranges (box), confidence intervals (error bars), and outliers (open circles).

only variable retained in the model using stepwise backwards regression ($\beta = 0.585$, $P < 0.0001$).

Taken separately, the resource base is significantly and positively correlated with size change (Spearman $r = 0.527$, $P < 0.0001$), and so is the presence of a smaller competitor (Spearman $r = 0.172$, $P = 0.050$), whereas other variables are not (mass, $r = 0.097$, $P = 0.27$; diet, $r = -0.085$, $P = 0.33$; predation, $r = 0.046$, $P = 0.60$; larger competitor, $r = -0.058$, $P = 0.51$, combined competition index, $r = 0.106$, $P = 0.23$; area, $r = 0.05$, $P = 0.59$).

Thus, the resource base, even with the crude estimate we employ, explains a significant portion of the variance in carnivore size, whereas sex, diet, island area and the presence of predators, and competitors small and large, seem to play little or no role in affecting carnivore size evolution.

Sexual Size Dimorphism Hypothesis

Using only island mainland pairs for which we had data for both males and females of the same species, we tested for differences between insular and mainland SSD (calculated as male CBL/female CBL), and whether such differences are male or female driven. There are no differences between males and females in the pattern of size change on islands (calculated as insular CBL/mainland CBL. Paired t -test, $n = 48$, $t = 1.32$, $P = 0.19$). In fact, the patterns for males and females are highly correlated (product moment correlation, $r = 0.798$, $P < 0.0001$). Insular SSD is not different from mainland SSD (paired t -test, $n = 48$, $t = 1.27$, $P = 0.21$). The difference between mainland and insular SSD is negatively correlated with female body mass ($r = -0.38$, $P = 0.007$), mainly because large carnivores are less dimorphic on islands. The difference between mainland and insular SSD is positively correlated with predation level (Spearman $r = 0.29$, $r = 0.045$). Island SSD is significantly lower than mainland SSD for predation category -2 (predation pressure lower on islands), than they are for categories -1 (predation pressure possibly lower on islands) and 0 (predation pressure similar on islands and mainlands) (Fisher least significant difference post-hoc test, differences between categories -2 and 0 , $P = 0.024$, between -2 and -1 , $P = 0.043$, between categories -1 and 0 , $P = 0.715$). Other variables are not correlated with the difference between insular and mainland SSD (diet, Spearman $r = 0.01$, $P = 0.94$; resource base, Spearman $r = -0.16$, $P = 0.29$; presence of smaller competitors, Spearman $r = 0.18$, $P = 0.21$; presence of larger competitors, Spearman $r = -0.07$, $P = 0.62$; combined competition index, Spearman $r = 0.11$, $P = 0.46$). Because our hypothesis predicts enhanced insular SSD in dwarf populations only, we compared the difference between SSD of insular dwarves (mean SR for males and females < 1) with that of insular giants. Insular dwarves are as dimorphic as their near-mainland conspecifics (mean SSD 0.2% higher on islands, $n = 30$ population pairs), whereas insular giants are slightly less dimorphic than their near-mainland conspecifics (mean SSD 2.1% higher on the mainland, $n = 18$ population pairs). The difference between these groups is marginally nonsignificant (Mann-Whitney U -test, $U = 186$, $P = 0.074$). SR of females in the 30 population of insular dwarves (mean: 95.4%) is not significantly different than that of males in the

same populations (mean 95.6%, Wilcoxon matched pairs, $T = 221$, $P = 0.81$).

DISCUSSION

We suggest that different selective forces drive size evolution in large insular herbivores and carnivores. Our results lend strong support to two of our hypotheses: herbivore size decreases in the absence of competitors and predators, and decreases to a lesser extent when some competitors and predators are present (biological interaction effect hypothesis). Sizes of Crete deer were overdispersed, with size ratios between adjacent-sized species tending toward equality (overdispersion hypothesis). Carnivore size patterns support our assumption that the nature of the resource base is an important determinant of body size, but refute our prediction that competition, predation, and diet will also be important (carnivore resource-competition hypothesis). Carnivores do not exhibit increased sexual size dimorphism on islands, refuting our SSD hypothesis.

Size of large fossil ungulates was significantly affected by the presence of smaller guild members, and by predators. Competition appears to be more important than predation: some dwarfing occurred even when large predators were present. For instance, some four distinct faunal complexes settled in Sicily (Bonfiglio et al. 2002; Marra 2005). The oldest includes *Elephas falconeri*, a diminutive (some 23% the size of its mainland ancestor in linear dimensions), dimorphic and paedomorphic elephant (Palombo 2001; Raia et al. 2003), and no carnivores. Later faunal complexes were rich in both carnivores and ungulates, and dwarfism occurs in six of eight large ungulates, but to a lesser degree (SR = 0.64–1.00). The four Sardinian complexes always feature at least one carnivore, and dwarfism is limited (online Appendix 1). Three observations are particularly relevant, as they are at odds with models suggesting that island area, island isolation, and ancestral size are the major determinants of body size evolution on islands (Van Valen 1973; Heaney 1978; Lomolino 1985, 2005).

First, in cases of repeated colonization of the same species in different islands, size change follows the competition/predation regime regardless of phylogeny. Second, island identity and hence its area, isolation, and, arguably, total resources are not significant predictors of ungulate size evolution. Admittedly, we did not test explicitly for the effect of island area and isolation in fossil ungulates because these data are not available in most cases. Yet, it is worth noting that elephants from Crete (8300 km²), Cyprus (9200 km²), Rhodos (1400 km²), Sicily (25,700 km²), and Tylos (61 km²) were of comparable size although these islands are (and certainly were) different in area by more than two orders of magnitude. In addition, the two youngest Crete deer, living along with at least four other deer species, were larger than their mainland counterparts, although inhabiting a relatively small island.

Third, the body sizes of mainland ancestors/conspecifics do not affect the magnitude of size evolution after controlling for the effect of competition (in herbivores). An intriguing observation concerns Crete deer. In Crete, the smallest species were the oldest (Reese et al. 1996; Vos 2000). Yet, they

later cohabited with new species evolving in situ (Vos 1996, 2000). Depending on whether one recognizes one or two colonization events, either four or three deer species originated on this island (Capasso Barbato 1988, 1990; Vos 1996, 2000). The three largest, and stratigraphically younger (*Cervus rethymnensis*, *C. dorothoensis*, and *C. major*), were as large as or even larger (much larger in the case of *C. major*; online Appendix 1) than mainland red deer. The size of younger Crete deer contradicts the common rule for large mammals (i.e., dwarfism, Lomolino 2005) but is expected according to our hypothesis. The overdispersion of Crete deer sizes (which is robust irrespective of the taxonomy one applies) further indicates the importance of competition among them. The regression of M_3 lengths in island-mainland pairs had a slope not statistically different from one, indicating that the degree of dwarfism is independent of ancestor size. This is striking given that our dataset is disproportionately rich in islands where elephants were the only large herbivores (and therefore reducing the most in size relative to their mainland ancestors, according to our expectations).

Our results suggest that carnivore sizes are influenced by resources and little else. However, whether it is resource biomass available or prey size or both that are important is unclear. Carnivore size is affected neither by ancestral body size per se (Meiri et al. 2004, 2006; this study); nor by island area, isolation, diet, and phylogenetic affinities (Goltsman et al. 2005; Meiri et al. 2004, 2005a, 2006; this study); nor by most within-guild interspecific interactions (this study). Although modal prey size may differ between males and females of the same species (e.g., Loy et al. 2004; Radloff and Du Toit 2004), the effect of the nature of the resource base is shared among the sexes, and SSD does not increase on islands. Unfortunately, we cannot test for SSD in fossil ungulates (except for a few deer populations) because of the difficulties in sexing fossils. Thus, the claims of large SSD (and paedomorphosis) in island fossil ungulates remain anecdotal (e.g., Ambrosetti 1968; Malatesta 1980; Capasso Barbato 1988; but see Palombo 2001; Raia et al. 2003). Nevertheless, we predict that increased SSD is likely to occur in ungulates because they are not constrained by the need to remain large in order to subdue prey. We could not quantify resource availability for fossil ungulates; yet, the highly significant effects of competition and predation indicate that resource limitations could not have been very important. Primary productivity seems to have little influence on energy flow in island ecosystems (Schoener 1989).

Another class of explanation of size evolution rests on optimal body size hypothesis (Brown et al. 1993; Damuth 1993; Marquet and Taper 1998; cf. Blackburn and Gaston 1996; Kozlowski and Teriokhin 1999; Roy et al. 2000; Meiri et al. 2004, 2005b). Lomolino (2005) distinguished different optima for different taxa (or underlying bauplans). Our data suggest that body size on islands evolves according to prevailing ecological conditions. In Pleistocene Mediterranean islands, there were several cases of a mainland species repeatedly colonizing islands. SR varied from 0.23 to 0.82 in *E. antiquus*, from 0.6 to 1.35 for the *C. elaphus*, from 0.47 to 0.91 for *Praemegaceros verticornis*, and so on. Similarly, SR often varies in carnivores on different islands (e.g., in *Paradoxurus hermaphroditus* it ranges from 1.1 to 0.88). The

direction of this variation agrees with the influence of biological interaction—mainly competition in the case of ungulates and resource base in the case of carnivores—and contradicts the notion of an optimal size. Instead, smaller sizes may be selected for in insular ungulates because resources that are no longer needed for antipredator behavior and interspecific competition can be safely reallocated to reproduction (Brown 1995; Raia et al. 2003; Lomolino 2005), resulting in lower adult body mass (Roff 2000; Stearns et al. 2000; Charnov 2001). However, once the smallest size classes were occupied, new species evolved larger body size. This should be not viewed as maladaptive. We argue that species arriving later simply faced different conditions, for which the size they attained was probably adaptive (Case 1978). Indeed, larger size allows the inclusion of new (lower quality but often superabundant) resources, at least in herbivores (Demment and Van Soest 1985; Illius and Gordon 1992; Clauss and Hummel 2005). Competition with smaller species is thus reduced. The only clear disadvantage of larger-sized ungulates seems to be an extended growth period. In carnivores, body size seems mainly related to the ability to acquire resources. Superabundant, energetically rich foods (e.g., salmon runs), will promote gigantism (Case and Schwaner 1993; Goltsman et al. 2005), but prey size is also a major factor: in the absence of large prey, carnivores can dwarf (e.g., island foxes, *Urocyon littoralis* dwarf in the absence of rabbits, see also Jessop et al. 2006), but when large prey is available carnivores remain large.

In summation, we believe size evolution on islands is not directly dependent on abiotic attributes such as area and isolation. Such factors can have an indirect effect on animal body sizes because they influence the numbers and identities of species that occur on islands. However, we emphasize that species are real interacting entities, not merely numbers to be added. Size of insular mammals probably depends on the peculiar biotic characteristics of a given island in a given time, and on the biological attributes of resident species. These attributes may be weakly correlated with absolute body size, but a better understanding of the autecological characteristics of a given insular population is the key to predicting the direction of magnitude of size evolution on islands and elsewhere.

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