ORIGINAL ARTICLE

Body size evolution of palaeo-insular mammals: temporal variations and interspecific interactions

Alexandra A. van der Geer[1]*, Georgios A. Lyras[2], Mark V. Lomolino[3], Maria Rita Palombo[4] and Dov F. Sax[5]

[1]*Naturalis Biodiversity Center, Department of Geology, Leiden, The Netherlands,* [2]*National and Kapodistrian University of Athens, Department of Geology and Geoenvironment, 15784, Zografos, Greece,* [3]*State University of New York, College of Environmental Science and Forestry, Syracuse, NY, 13210, USA,* [4]*Dipartimento di Scienze della Terra, Università di Roma 'La Sapienza' and CNR, Istituto di Geologia ambientale e Geoingegneria, 00185, Roma, Italy,* [5]*Department of Ecology and Evolutionary Biology, Brown University, Providence, RI, 02912, USA*

ABSTRACT

Aim We investigated the hypothesis that body size evolution of mammals is strongly influenced by ecological interactions, resulting in evolutionary divergence in body size in species-rich (e.g. mainland) biotas, and convergence on the size of intermediate but absent species in species-poor (e.g. insular) biotas.

Location Mediterranean palaeo-islands.

Methods We assembled data on temporal variation in body size of palaeo-insular mammals and associated variation in ecological characteristics (colonization or extirpation of mammalian competitors and predators) for 19 species of fossil, non-volant mammals across four large (> 3640 km^2) islands ranging between the late Miocene and Holocene. These are the only fossil species for which fine-detailed time series are available at present.

Results Our results are consistent with predictions based on an ecological interactions hypothesis of body size evolution. Following colonization (or first appearance in the insular fossil record) small mammals (such as mice, shrews and pikas) tended to increase in body size. These trends, however, ceased or were reversed following colonization of the focal islands by mammalian predators or competitors.

Main conclusions While body size evolution is likely to be influenced by a variety of characteristics of the focal islands (e.g. climate, area, isolation and habitat diversity) and species (e.g. diet, resource requirements and dispersal abilities), temporal trends for palaeo-insular mammals indicated that the observed trends for any particular species, island and climatic regime may be strongly influenced by interactions among species. Ultimately, invasion of a competitor often leads to the extinction of the native, insular species.

Keywords
Biological invasions, body size fluctuations, competition, extinct species, fossil record, island evolution, island rule, mammals, Mediterranean palaeo-islands, predation.

*Correspondence: Alexandra van der Geer, Naturalis Biodiversity Center, P.O. Box 9517, 2300 RA Leiden, The Netherlands.
E-mail: alexandra.vandergeer@naturalis.nl

INTRODUCTION

The island rule, a term coined by Van Valen (1973), describes a graded trend in populations of insular vertebrates from gigantism in small species to dwarfism in large species (e.g. Heaney, 1978; Lomolino, 1985, 2000, 2005; Whittaker & Fernández-Palacios, 2007; Lomolino *et al.*, 2012). Although the considerable scatter about this graded trend has generated much debate over the generality of the pattern (see, e.g. Palkovacs, 2003; Meiri *et al.*, 2004a,b, 2008; Köhler *et al.*,

2008; Raia *et al.*, 2010), such variation is both expected and informative as it may provide key insights into the factors and processes influencing body size evolution on islands (see Fooden & Albrecht, 1993; Lomolino *et al.*, 2012).

Earlier papers attributed observed trends of insular body size to a variety of factors, including characteristics of the islands (e.g. area or isolation) and species (resource requirements, trophic strategy, dispersal abilities and bauplan), but also to release from ecological pressures of competition and predation on islands, which tend to be species-poor with

regard to mammals that often dominate mainland communities (see, e.g. Case, 1978; Heaney, 1978; Lomolino, 1985, 2000, 2005; Brown *et al.*, 1993; Fooden & Albrecht, 1993; Simberloff *et al.*, 2000; Grant & Grant, 2006; Millien, 2006; Meiri *et al.*, 2011). That is, in species-rich systems, competition and predation are hypothesized to result in ecological displacement and diversification among resident species, e.g. predatory pressures resulting in small prey becoming smaller and large prey becoming larger. In species-poor communities, release from the pressures of these ecological interactions reverses these trends and the few or sole resident species converge on intermediate body sizes. In a recent and comprehensive investigation of the causality of the island rule in extant mammals, Lomolino *et al.* (2012) found further support for the contextual and multifactoral nature of processes influencing body size evolution. The patterns observed for extant insular mammals are consistent with the hypothesis that body size evolution is influenced by selective forces whose importance and nature of influence varied in a predictable manner with characteristics of the species (in particular, their ancestral body size and diet) and the islands (area, isolation and climate), and with ecological interactions among mammals.

Despite some exceptions, body size variation among palaeo-insular mammals is generally consistent with the graded trend of the island rule (see e.g. Sondaar, 1977; Lister, 1989, 1996; Roth, 1992; van den Bergh *et al.*, 1996; Palombo, 2004, 2007, 2009; Palombo & Giovinazzo, 2005; Millien, 2006; Raia & Meiri, 2006; Bromham & Cardillo, 2007; de Vos *et al.*, 2007; van der Geer, 2008; Lyras *et al.*, 2008, 2010; Weston & Lister, 2009). Palaeo-insular mammals, however, exhibit much more extreme cases of gigantism and dwarfism than living species (examples in van der Geer *et al.*, 2010).

Nonetheless, several cases were noted among small mammals where body size evolution in palaeo-insular taxa is not constant or unidirectional (Freudenthal, 1976, 1985; Mayhew, 1977; Butler, 1980; Angelone, 2007; Boldrini, 2008; Rinaldo & Masini, 2009; Melis *et al.*, 2012). In fact, in these cases, trends opposite to those predicted (small mammals getting smaller again) are observed during some time spans. Generally, these temporal fluctuations are explained as being due to climatic changes (e.g. McFarlane *et al.*, 1998, for *Amblyrhiza*), but colonizations by mammalian competitors or predators may play a substantial role as well (Bover & Alcover, 2008).

The fossil record and, in particular, time-sequenced series of body size variation within insular lineages provides a potentially powerful insight into the causality of body size evolution on islands and an ecological hypothesis of body size evolution which asserts that body size evolution is strongly influenced by ecological interactions. The purpose of this paper is to further evaluate this hypothesis – by testing the following predictions.

1. Following colonization of islands lacking mammalian competitors and predators, small mammals will increase in body size (we define 'small' as mainland, ancestral mammals of less than *c*. 3 kg body mass; see Lomolino *et al.*, 2012).

2. The observed trend in temporal variation predicted above should cease or be reversed when the focal island is colonized by mammalian predators or competitors. Studies of extant taxa indicate that invading species may alter the evolutionary pathway of native species by competition, niche displacement, predation, and ultimately extinction (Mooney & Cleland, 2001), although available evidence suggests that extinction is much more likely to be driven by predation than by competition (Sax & Gaines, 2008). We expect that these patterns will apply to the fossil record as well.

MATERIALS AND METHODS

Selected taxa

Our data include only taxa that are represented by a time series that includes populations of the ancestral form, one or more intermediate stages, and at least one moment in time where a change in the ecological assemblage was recorded and that were recovered from sites where all relevant contemporaneous taxa occur as well so that co-existence is proven. Large mammals are not included in our data set because their fossil record lacks sufficient time series with multiple stages and colonization or extinction of mammalian competitors or predators. Fossils of small mammals, for the majority preserved as teeth in owl pellets, are much more numerous and often found throughout a stratigraphical succession. Even so, extensive time series for small mammals are extremely rare because of the limited chronological range of continuous sedimentary sequences exposed in the fossiliferous sites on most palaeo-islands.

We have also included the criterion that each time series should be limited to periods during which the physiographic features of the islands were relatively constant, thus controlling for some factors extrinsic to our ecological hypothesis of body size evolution. However, because climatic conditions sometimes varied substantially during the time periods included in our study, and body size is often correlated with climatic conditions, especially temperature (Bergmann, 1847; Rensch, 1938; Mayr, 1956; Smith *et al.*, 1995; Smith & Betancourt, 2003; Millien *et al.*, 2006; Lomolino *et al.*, 2012), we also present data on temperature variation where available.

Limited by these criteria, our data included temporal variation for 19 late Miocene to Holocene species belonging to eight insular lineages across four palaeo-islands (see Appendix S1 in Supporting Information; nomenclature follows van der Geer *et al.*, 2010). This set comprises all available time series that meet the required conditions as given above (Fig. 1).

Biochronology

Biochronology is used here as a means of ordering the sites due to the scantiness of firm geochronological contraints and reliable absolute datings and the lack of continuous strati-
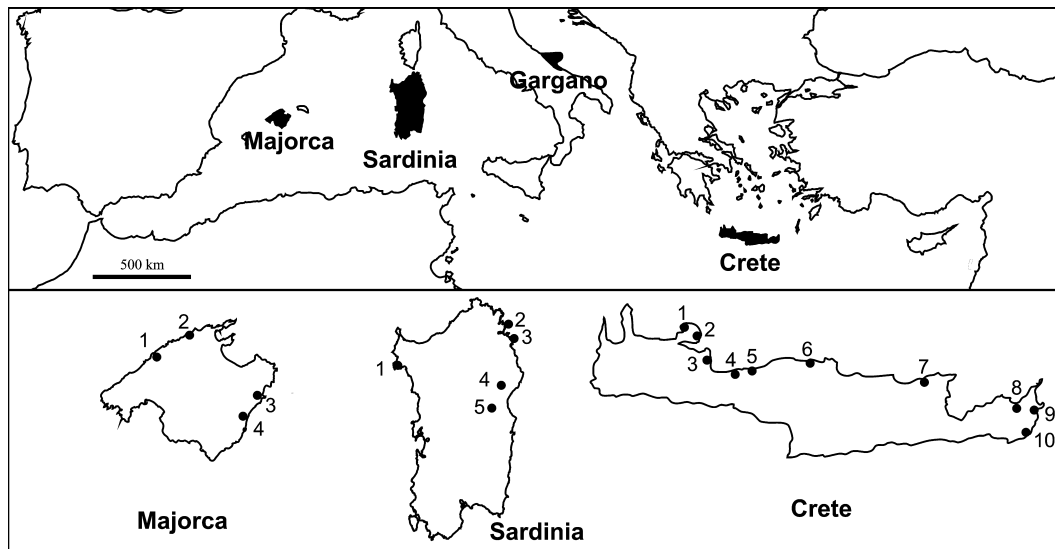
Figure 1 (Top) Location of four Mediterranean islands with a record of fossil mammals sufficient to analyse body size evolution through time. (Below) Fossil sites mentioned in the text or the figures. Note that the islands are not drawn to the same scale. Majorca: 1, Son Muleta; 2, Cova Estreta; 3, Caló den Rafelino; 4, Son Bauza. Sardinia: 1, Dragonara; 2, Tavolara; 3, Capo Figari; 4, Monte Tuttavista; 5, Corbeddu. Crete: 1, Stavros; 2, Cape Meleka; 3, Liko; 4, Gerani; 5, Koumpes; 6, Bali; 7, Milatos; 8, Siteia; 9, Karoumbes; 10, Xeros.

graphic sequences. Biochronological principles include first and last appearances, associations of taxa recognized as being peculiar to a biochron and evolutionary trends in phyletic lineages, in this case mainly tooth morphology. Perhaps the most debated assumption of biochronology is the principle of irreversibility, in particular the loss of complex characters (part of 'Dollo's law'; Dollo, 1893). Many recent studies (see Appendix S1 for evaluation) found violations of this law, claiming loss and subsequent recovery of functionalities and/ or elements, including even wings and digits. However, Goldberg & Igic (2008) have shown that the methods used in these studies are flawed. That means that at the present stage of knowledge, there is no hard evidence that the loss of complex character states would be reversible. As long as this issue remains unresolved, we consider the evolution of complex character states to be irreversible. In addition, our case is strengthened because we would have to assume the simultaneous reversal of two independent characters (body size plus molar size or morphology). Reverse evolution is rarely possible but falls even further in likelihood as the complexity of adaptation increases (Tan *et al.*, 2011), where we consider a combination of characters a case of increased complexity. In addition, for Majorca, Crete and Gargano, the chronology is not based on the target species only but also on co-occurring taxa (see Appendix S1 for details), which further adds to the robustness of our biochronology. The weakest chronology is that for the *Kritimys catreus* zone of Crete, as it was established practically only on molar size. Only the geologically first and last sites with *Kritimys* are firmly established, whereas the ordering of the other sites is weak.

Ongoing dating work may eventually alter some of the sequences presented here, but even though some age order-ing is not robust, the basic conclusions are, because the most relevant part of the sequences is the moment when an interfering taxon appears for the first time in the fossil record. The timing of these arrivals is supported by the biostratigraphy, and for Majorca also by absolute datings. For a detailed account of the biochronology per site, see Appendix S1.

Body size index

Our analyses were based on relative size (S_i), which is defined as mass of insular form divided by that of its ancestor – values greater than 1.0 indicate a trend towards gigantism, and those less than 1.0 indicate a trend towards dwarfism. Body size of insular fossil species and their mainland ancestors were calculated using taxon-specific equations for estimating body masses (see Appendix S1 for details and references) based on data measured directly from specimens in museum collections or given in the literature.

Ecological assemblages

Data on the presence of competitors and predators included species of mammals most likely to directly interact with the focal insular species, present in the same locality (Table 1; for details, see Table S15 in Appendix S1). Ecological interactions with reptilian predators and competitors, although potentially interesting, were not taken into account as we are assuming that (1) ecological interactions, especially competition, is more intense between more closely related species, (2) in comparison to birds and reptiles, the occurrence of mammals on the focal islands was more variable over space and time, thus forming the primary treatment variable in

Table 1 List of mammalian competitors and predators that are most likely to have interacted with the focal insular taxa to illustrate the extent of potential ecological release. The competitors and predators are found together with the target species in the same locality and horizon in all cases, except for *Lutrogale cretensis* and *Paralutra garganensis*. These otters are found only in one or two localities (Liko and Fina/Gervasio, respectively) and their presence throughout the biozone is conservatively assumed on the ground of lack of evidence for faunal turnovers. For complete fossil fauna lists, see Table S15 in Appendix S1.

Terminal species of insular lineage	Palaeo-island	Competitors	Predators
Lagomorpha			
Prolagus sardus	Sardinia	*Microtus (Tyrrhenicola), Rhagamys orthodon*	*Cynotherium sardous, Enhydrictis galictoides*; during the early Pleistocene perhaps also *Pannonictis* and *Mustela*
Rodentia			
Hypnomys morpheus	Majorca	Only during Holocene *Eliomys quercinus*	None
Kritimys catreus	Crete	Just before extinction *Mus batei*	None; just before extinction perhaps *Lutrogale cretensis*
Mus minotaurus	Crete	*Kritimys* for the earliest species (*Mus batei*), *Mus musculus* just before extinction; in between none	*Lutrogale cretensis*; just before extinction perhaps *Meles meles* and *Marten foina*
Mikrotia (three lineages)	Gargano	*Stertomys* and other *Mikrotia*; in the earlier part also *Hattomys*	*Paralutra garganensis*
Hattomys gargantua	Gargano	*Stertomys, Mikrotia*	*Paralutra garganensis*
Insectivora			
Nesiotites hidalgo	Majorca	Only during Holocene *Eliomys quercinus* and *Apodemus sylvaticus*	None
Crocidura zimmermanni	Crete	None during the Pleistocene; during the Holocene *Crocidura suaveolens* and *Suncus etruscus*	None during *Kritimys* faunal complex, *Lutrogale cretensis* during *Mus* faunal complex; during the Holocene *Meles meles* and *Marten foina*

this study, and (3) the degree to which our assumptions are wrong would only add to unexplained error or produce results counter to our preditions. In addition, large reptiles such as varanids that exert signifcant predatory pressure on mammals did not occur on our islands during the relevant time range. The reptilian predators are limited to snakes and lizards.

Possible mammalian predators and competitors were identified by consulting the lists of species found in local faunal assemblages to which the focal species belongs. A few remarks are, however, needed. We consider *Mus* a competitor for *Kritimys* as they are both Murinae sharing basic dental features. For *Hypnomys*, one of the Holocene competitors was the garden dormouse (*Eliomys*), which is closely related to the ancestral form of *Hypnomys*. The other Holocene competitor, perhaps to an even greater extent, was the wood mouse (*Apodemus*), as *Hypnomys* had a semi-fossorial (Bover *et al.*, 2010) or terrestrial lifestyle (Hautier *et al.*, 2009) in comparison to the more arboreal habitats of *Eliomys*. *Hypnomys morpheus* had shifted its ecological niche towards a more omnivorous and abrasive diet (Hautier *et al.*, 2009), probably increasing niche overlap with murids (*Apodemus* in this case). The same garden dormouse also competed with *Nesiotites*, because *Eliomys quercinus* is partly insectivorous and a predator of molluscs and insect larvae (Ognev, 1963) and as such is a likely competitor of a large shrew. The early Pliocene hamster *Tragomys macpheei* is not considered a competitor for the earliest *Hypnomys* or *Nesiotites* because it has a high-crowned, selenodont dentition, very unlike that of dormice and shrews. The murid *Rhagamys*, with its specialized high-crowned dentition, might theoretically have been a partial competitor for *Prolagus*. Also, the field mouse (*Microtus*) is tentatively considered a competitor during the late early Pleistocene–Holocene for *Prolagus* as it eats grasses and maybe sedges as do pikas (tentatively, because their size difference is considerable). During the early Pleistocene, *Pannonictis* and *Mustela* may have caused some additional predation pressure on *Prolagus* for an unknown time span. For *Prolagus* during the Holocene, direct competition was perhaps not the case, but possibly the combined effect of rats, (wood) mice, dormice and for a while *Microtus* that survived until the Bronze Age was significant. Humans exerted a predation pressure to some extent, because burnt *Prolagus* bones are a common finding in archeological contexts.

Statistical analysis

Given the limited nature of the fossil record, statistical analyses are limited to binomial tests (calculating cumulative probabilities, with a priori probability of success = 0.5; Microsoft Excel 2007) of our two primary predictions: (1) that on islands lacking mammalian competitors and predators, focal species of small mammals exhibit temporal trends of increasing body size (i.e. more instances of increases than we would expect by chance), and (2) that the tendency

towards increases in body size is lower (closer to random expectations) once an island has been colonized by mammalian competitors or predators. The null predictions are thus of equal frequencies of increases and decreases, whether mammalian predators and competitors are absent or present.

RESULTS

Temporal trends in body size of focal species were consistent with predictions of the ecological hypothesis of body size evolution (see Figs 2–5 and Tables S13 & S14 in Appendix S1). When tabulated over all time periods, species and islands, we recorded twelve cases of increased and four cases of decreased body size when mammalian predators and competitors were absent ($P = 0.0384$, binomial test; see Table S13 for details about the recorded intervals matching with the graphs in Figs 2–4). In contrast, the trend towards gigantism was much less pronounced when mammalian predators or competitors were present (27 increases and 20 declines in body size; $P = 0.1908$). Removal of the two species with the highest occurrence (Mikrotia and Mus) did not alter results for when predators and competitors were absent, but did result in seven increases and nine declines in body size in the

presence of predators and competitors (again, a non-significant trend, $P = 0.4018$).

Species accounts

Crete

Kritimys – The body size of the Cretan rat (Kritimys), represented by the chronospecies Kritimys aff. K. kiridus, K. kiridus and K. catreus (from old to young; Fig. 2, Table S1 in Appendix S1) gradually increased with a slight decrease at the level of Karoumpes 4 (where molars from an embedded breccia boulder – base – are larger than those of the younger, surrounding deposits – top; Mayhew, 1977), and a peak at the level of Bali. After colonization by Mus, and just before its extinction, Kritimys exhibited a significant decrease in size.

Mus – The mouse Mus bateae increased in size and evolved into the large Mus minotaurus. It attained its largest size at the level of Milatos 2, after which its size decreased again as evidenced by Liko B (Fig. 2, Table S2 in Appendix S1). Minor fluctuations within Liko Cave (Table S3 in Appendix S1) were already noted by Mayhew (1977), who observed two opposite trends: one in a stratigraphic section at the front of the cave
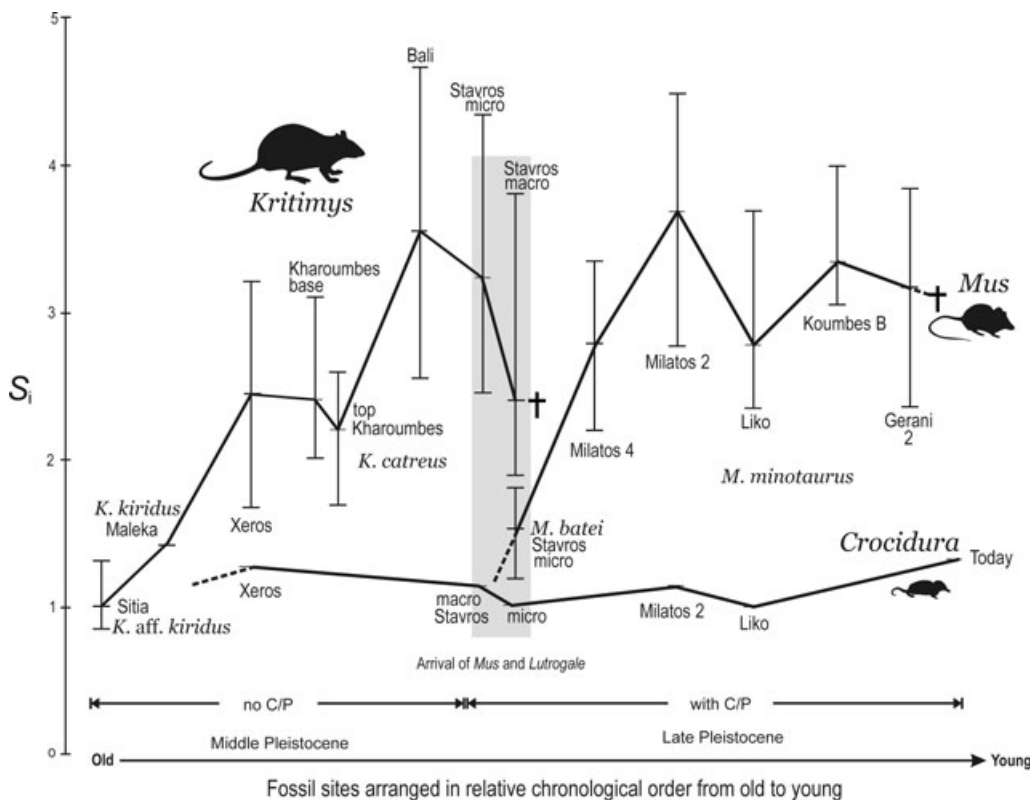

Figure 2 Temporal variation in body size (S_i) of small mammal lineages of Crete during the Pleistocene. The grey area indicates the periods of major faunal turnover and coexistence of Mus and Kritimys. Ordering of sites is based on current biostratigraphic understanding (see Appendix S1) and is liable to modification in the future; uncertainties are concentrated in parts of the sequence without change in associated fauna. The Kritimys fauna is likely to have arrived early in the Pleistocene (Mayhew, 1977; Reumer, 1986) and the second dispersal (with Mus) to have taken place in the middle of the middle Pleistocene (Kuss, 1970) [see van der Geer et al. (2010) for other possible scenarios]. For a list of likely mammalian competitors and predators (= C/P on horizontal axis), see Table 1.
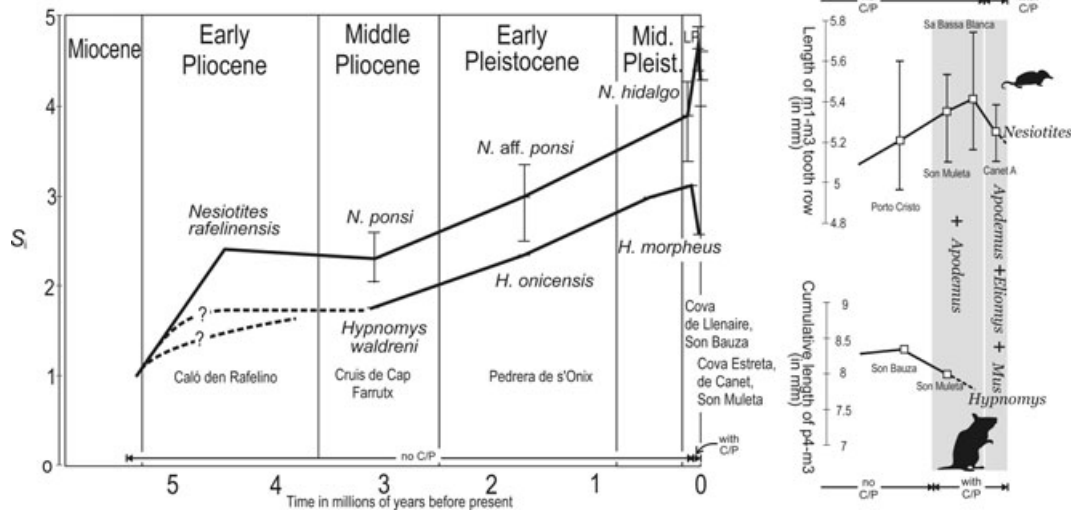
Figure 3 Temporal variation in body size (S_i) of small mammal lineages of Majorca during the Plio-Pleistocene. The fossil sites on the right are set in an exact geochronological place but those on the left are listed in a simple chronological order because absolute dates are missing here. The order is based on the evolutionary stage of all three endemic lineages (*Nesiotites*, *Hypnomys*, *Myotragus*) per site; sites with only one taxon were excluded. The diagrams to the right are a detailed representation of the terminal part of the fossil record of the endemic dormouse and shrew. Grey areas indicate the arrival of alien species and the period of coexistence with the endemic species within the same site. For a list of likely mammalian competitors and predators (= C/P on horizontal axis), see Table 1.
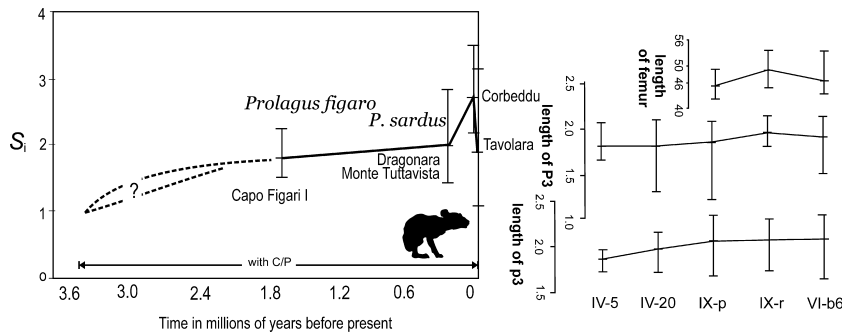

Figure 4 Temporal variation in size (S_i, molar and femur length) of the ochotonid *Prolagus* of Sardinia–Corsica during the Pleistocene. For Corbeddu and Capo Figari, absolute datings are available; the young age of Tavolara is based on archaeological remains and the other two sites are placed relatively based on biochronological data. The Dragonara fossiliferous layer forms part of a stratigraphic succession (see Appendix S1). The diagram on the right side represents a detailed account of body size changes as recorded in fissures of Monte Tuttavista. Body mass indices (S_i) are not given here because the lower third premolar is not suitable for body mass estimations in insular *Prolagus*, contrary to mainland lagomorphs. Insular *Prolagus* species have generally relatively larger lower third premolars than their mainland relatives (Angelone, 2007), and thus would easily lead to overestimations of body mass. The ordering of the sites within Monte Tuttavista is primarily based on fauna lists but is confirmed based on evolutionary stages of molar patterns for *Prolagus*, *Rhagamys* and *Microtus* (see Appendix S1), co-occurring in the same fissures. For a list of likely mammalian competitors and predators (= C/P on horizontal axis), see Table 1.

and another at the back of the cave. The changes between specimens coming from the two Liko sections are considerably smaller than the general size changes of *M. minotaurus* between the sites. At the level of Koumbes B, *M. minotaurus* is again large, but not as large as at the Milatos 2 level. After Koumbes, the size of *Mus* decreases once more.

Crocidura – The shrew *Crocidura zimmermanni* exhibited only minor changes in body size (Table S6 in Appendix S1). After an initial increase, its body size decreased slightly during the middle Pleistocene as recorded in Stavros macro, reaching a lowest level coinciding with the arrival of new-

comers and the smallest *Kritimys kiridus*, after which it steadily but marginally increased during the late Pleistocene with, again, reversals at the level of Liko Cave. The currently extant *C. zimmermanni* has attained the same large size ($S_i = 1.26$) as it had at the level of Xeros ($S_i = 1.27$; middle Pleistocene).

Balearic Islands

Hypnomys – The body size of the dormouse *Hypnomys*, represented by the chronospecies *Hypnomys waldreni*, *Hypnomys*
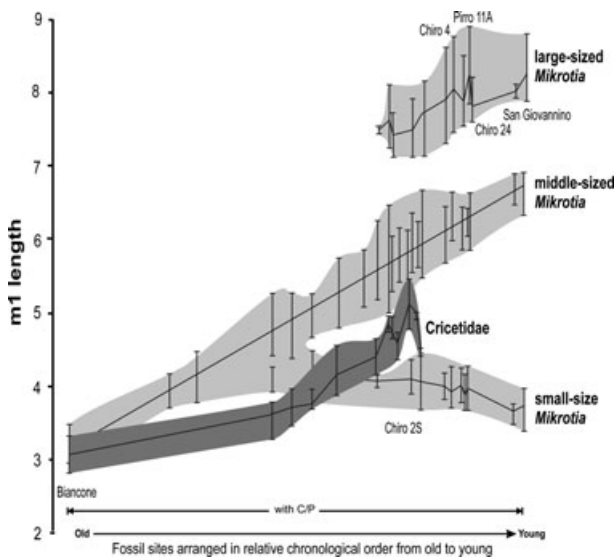
Figure 5 Temporal variation in the size of the first upper molar of the three murid lineages (*Mikrotia*) and of the cricetid lineage (*Hattomys*) of the Gargano palaeo-island (late Miocene; Freudenthal & Martín-Suárez, 2010). Molar length is indicated on the vertical scale in tenths of millimetres. The vertical lines represent the ranges of the molar lengths in the various populations. The non-fluctuating, straight line for the middle-sized *Mikrotia* is artificial; this is how Freudenthal reconstructed the biochronology: larger specimens were considered younger. Rinaldo & Masini (2009) re-ordered the fissures based on dental morphology of relevant taxa and found only minor deviations from the pattern represented here (see Appendix S1). Redrawn from Freudenthal (1976, Fig. 4).

onicensis and *Hypnomys morpheus*, increased gradually (Fig. 3, Tables S4 & S5 in Appendix S1) [the yet undescribed earliest form from Caló den Rafelino (Rofes *et al.*, 2012) has not been included]. The largest specimens of *Hypnomys* (S_i = 3.13; Cala Blanes) in our data set occurred during the late Pleistocene, after which it decreased slightly in size but never reached the size of its immediate preceding chronospecies. At some point after its decline in size, *Hypnomys* went extinct.

By the end of the late Pleistocene, alien rodents entered the Balearics. *Hypnomys* is found together with the field mouse *Apodemus sylvaticus* (in Canet; Reumer, 1980) and with *Eliomys quercinus* [in Cova des Moro, dated 13,500–11,800 BC (calibrated); Bover & Alcover, 2008]. The last occurrence of *H. morpheus* is 4840–4690 BC (calibrated) in Cova de sa Tossa Alta (Bover & Alcover, 2008).

Nesiotites – Body size of the shrew *Nesiotites*, represented by the chronoseries *Nesiotites rafelinensis*, *Nesiotites ponsi*, *Nesiotites* aff. *ponsi* and *Nesiotites hidalgo*, shows an overall trend of increase through time (Fig. 3, Tables S7 & S8 in Appendix S1). The initial body size increase was large, but this trend soon attenuated, with perhaps even a slight reversal at the level of the second chronospecies, *N. ponsi*. After reaching a maximum size (S_i = 4.68) at the end of the Pleistocene, *Nesiotites* underwent a slight decrease in size just before its extinction, sometime after the first appearance of *Mus* and *Eliomys*. The last

occurrence of *Nesiotites* is 3030–2690 BC (calibrated) in Cova des Garrover (Bover & Alcover, 2008).

Sardinia

Prolagus – *Prolagus figaro*, which evolved from mainland *Prolagus michauxi*, and the larger *Prolagus sardus* (Fig. 4; Table S10 in Appendix S1) are clearly identifiable by their dental morphology (Angelone *et al.*, 2008), and probably constitute chronospecies, based amongst others on the very limited overseas dispersal ability of lagomorphs.

Prolagus sardus (max S_i = 2.75) exhibited small-scale fluctuations in the lengths of the third premolars and the femur (Fig. 5; Table S12 in Appendix S1) during the time period represented by the Monte Tuttavista fissure fillings. The two youngest samples show a small inversion of the size trend. S_i values cannot be calculated here due to the lack of reliable equations based on third premolars, while data on the femur of the putative ancestor are not available. Although the species was commonly found in archaeological sites and persisted on the island until historical time, its size variation during the Holocene (if any) has not been studied. Our Holocene sample is limited to one site where the endemic small mammals co-occurred with newcomers (*Apodemus*, *Rattus*, *Eliomys* and *Mus*). The body size of *Prolagus* here is smaller than in any late Pleistocene site.

Gargano

Mikrotia, Hattomys – A steady increase in body size of both murids (*Mikrotia*) and hamsters (*Hattomys*) is seen in the lower part of the stratigraphy, but just before the extinction of the hamsters an even larger murid and a smaller murid lineage appear in the fossil record (Fig. 5). The hamster lineage seems to slightly decrease in size just before its extinction. At the last appearance of the hamsters, a full size range is present in the murid record with three distinct morphotypes, including the giant *Mikrotia magna*. Size fluctuations are observed in all lineages, except for the middle-sized lineage in which the lack of fluctuation is an artefact of the biostratigraphical method applied (see caption of Fig. 5). The extinction of *Mikrotia* does not coincide with new arrivals but is entirely due to submergence of the entire island.

DISCUSSION

The temporal trends in body size of insular mammals from the fossil record conform to predictions of our hypothesis of ecological release as a mechanism for the island rule, with small mammals evolving towards larger size when no mammalian competitors or predators are present. This trend is much less pronounced and is sometimes reversed when the islands are colonized by mammalian competitors or predators.

Such shifts in evolutionary trends probably reflect reversals in selective pressures (*sensu* Lomolino, 2010). The five cases

of body size shifts in response to reversals in ecological pressures studied here include the Cretan *Kritimys* (newcomer: *Mus musculus*) in the middle Pleistocene, the Balearic *Hypnomys* and *Nesiotites* (newcomers: *Eliomys quercinus* and *Apodemus sylvaticus*) and the Cretan *Mus minotaurus* (newcomers: *Mus musculus* with Neolithic settlers) at the end of the Pleistocene and *Prolagus sardus* (newcomers: *Mus*, *Rattus*, *Apodemus* and *Eliomys* with Neolithic settlers) in the early Holocene. Interestingly, and perhaps significantly, these endemic species all went extinct following their size decrease. Consistent with what we report here, others have noted earlier that body size changes of insular fossil proboscideans is not as extreme when they co-occur with competitors or predators (including humans; Sondaar, 1977; van den Bergh *et al.*, 1996, 2008; Sondaar & van der Geer, 2005; Palombo, 2007, 2009).

An opposite effect of the introduction of a competitor on body size evolution seems to be observed in the Cretan shrew *Crocidura zimmermanni* during the Holocene. This shrew increased in size after the introduction of two competitive shrews (*Crocidura suaveolens* and *Suncus etruscus*). Reumer (1986) explains this as ecological displacement away from its earlier, lowland distribution towards higher regions where size increase may be an adaptation for lower temperatures (see Smith *et al.*, 1995; Smith & Betancourt, 2003).

In six or seven (see below) other cases, however, body size appeared to fluctuate without any contemporaneous change in ecological assemblage. These include *Mus minotaurus* (late Pleistocene), *Crocidura zimmermanni* (middle–late Pleistocene), and possibly, with some restriction due to less robust chronologies, *Kritimys* and *Prolagus sardus* (middle Pleistocene), *Mikrotia* and *Hattomys* (late Miocene), and *Nesiotites* (Pliocene). These seemingly anomalous fluctuations might be explained by climate oscillations. Warming environmental conditions are expected to promote smaller body sizes (Bergmann's rule; Bergmann, 1847; Smith *et al.*, 1995; Smith & Betancourt, 2003; Millien *et al.*, 2006) and thus reverse the island rule trend predicted for small mammals (see also Lomolino *et al.*, 2012). Mayhew (1977) has previously suggested that the size fluctuations of *Mus minotaurus* might be related to the periodically changing climatic conditions of the late Pleistocene. This is supported by data on temperature, because the Liko Cave specimens [marine isotope stage (MIS) 5c; corresponding to a considerably warmer period than Koumpes Cave specimens] are smaller than Koumpes Cave specimens (MIS 3). Co-occurring *Crocidura zimmermanni* show a comparable size difference and direction of difference. Within Liko Cave, the minor size fluctuations of *Mus* may match the climate fluctuations where the largest specimens occurred during the intermediate cold and dry phase of the period 105,000–87,000 years ago (Caron *et al.*, 2009).

Fluctuations in climate may have also influenced body size evolution of *Kritimys* and *Prolagus sardus*, but no absolute data are available to confirm this. Preliminary results of an analysis on $\delta^{18}O$ values obtained from the teeth and bones

of *P. sardus* tentatively suggest that a positive correlation exists between femur dimensions and temperature (Boldrini & Palombo, 2010) and thus, *inter alia,* between body mass and temperature. As far as *Nesiotites* is concerned, the temporary break during the middle Pliocene in its trend towards gigantism is suggested to be due to the same crisis that led to the extinction of practically all mammalian lineages except for *Nesiotites*, *Myotragus* and *Hypnomys* (Rofes *et al.*, 2012).

We note that short-term climatic fluctuations may indeed influence body mass, but in a variety of ways that are generally inconsistent with our predictions. Warming trends may be associated with increased fat tissue and, thus, an increase in live body mass during boom (warm) phases of boom-or-bust fluctuations. The estimated body size we use here, however, is not based on fat tissue and live body mass, but on skeletal measurements. Alternatively, one might speculate that colonizations of competitors or predators may have been associated with cooling trends – that is, coincident with reduced sea levels and exposure of land bridges during glacial periods. According to the spatial and temporal trends associated with Bergmann's rule (Smith *et al.*, 1995; Smith & Betancourt, 2003), however, body size (live and skeletal) is expected to increase during glacial periods, while the arrival of competitors or predators is predicted to have the opposite effect in the species we study here.

One especially important insight from these and other studies of the insular, fossil record is that the impact of the arrival of alien competitors and predators (including ancient as well as recent hominids) may not be restricted to altering initial trends in body size evolution, but might sometimes coincide with the eventual extinction of the resident species (Bover & Alcover, 2008). Of the six extinctions we noted here [*Kritimys catreus*, *Mus minotaurus*, *Nesiotites hidalgo*, *Hypnomys morpheus*, *Prolagus sardus,* omitting the one due to flooding (*Mikrotia*)], all except for *Hattomys* were subsequent to the arrival of a mammalian competitor.

Taken together, the dynamic patterns discussed here are consistent with those described in Wilson's theory of taxon cycles (Wilson, 1959, 1961), and, in particular, with the adaptation of this theory proposed by Roughgarden & Pacala (1989) to explain body size dynamics in *Anolis* lizards of the Lesser Antilles. According to their model, the first colonist and sole resident *Anolis* species evolves towards an optimum or characteristic body size and more specialized niche, only to be displaced and ultimately extirpated when a second *Anolis* colonizes the island and reinitiates the cycle.

CONCLUSIONS

Despite the challenges of reconstructing the abiotic and ecological characteristics of ancient environments, the patterns discussed here for body size variation of palaeo-insular mammals over time strongly support the ecological hypothesis of body size evolution. As is generally known, on the mainland and on relatively balanced and ecologically rich palaeo-islands, interacting lineages of mammals are subject to

ecological character displacement – resulting in divergence in body size. On islands with depauperate and unbalanced assemblages, however, release from these ecological interactions appears to have resulted in adaptive radiations of some lineages, and body size dynamics consistent with the island rule (i.e. convergence on the size of intermediate but absent species) in others. However, after colonization by ecologically significant mammals, these trends were often reversed because 'natives' may have become entrained in ecological and evolutionary taxon cycles, ultimately punctuated by extinction of the native species.

ACKNOWLEDGEMENTS

REFERENCES

Angelone, C. (2007) Messinian *Prolagus* (Ochotonidae, Lagomorpha) of Italy. *Geobios*, **40**, 407–421.

Angelone, C., Tuveri, C., Arca, M., López Martínez, N. & Kotsakis, T. (2008) Evolution of *Prolagus sardus* (Ochotonidae, Lagomorpha) in the Quaternary of Sardinia Island (Italy). *Quaternary International*, **182**, 109–115.

van den Bergh, G.D., Sondaar, P.Y., de Vos, J. & Aziz, F. (1996) The proboscideans of Southeast Asian islands. *The Proboscidea: evolution and palaeoecology of elephants and their relatives* (ed. by J. Shoshani and P. Tassy), pp. 240–248. Oxford University Press, Oxford.

van den Bergh, G.D., Awe, R.D., Morwood, M.J., Sutikna, T., Jatmiko, P. & Wahyu Saptomo, E. (2008) The youngest *Stegodon* remains in Southeast Asia from the Late Pleistocene archaeological site Liang Bua, Flores, Indonesia. *Quaternary International*, **181**, 16–48.

Bergmann, C. (1847) Ueber die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse. *Göttinger Studien*, **3**, 595–708.

Boldrini, R. (2008) *Microtus* (*Tyrrhenicola*) *henseli* (Major, 1905) di Grotta dei Fiori (Sardegna Sudoccidentale): caratteri evolutivi e interpretazione biocronologica. *Geologica Romana*, **41**, 55–64.

Boldrini, R. & Palombo, M.R. (2010) Did temperature regulates limb length in the Sardinian endemic ochotonid *Prolagus sardus*? *Convegno in memoria di Alberto Malatesta*

(1915–2007), *geologo e paleontologo*. Abstracts, 12–13. Università Roma Tre, Rome.

Bover, P. & Alcover, J.A. (2008) Extinction of the autochtonous small mammals of Mallorca (Gymnesic Islands, Western Mediterranean) and its ecological consequences. *Journal of Biogeography*, **35**, 1112–1122.

Bover, P., Alcover, J.A., Michaux, J.J., Hautier, L. & Hutterer, R. (2010) Body shape and life style of the extinct Balearic dormouse *Hypnomys* (Rodentia, Gliridae): new evidence from the study of associated skeletons. *PLoS ONE*, **5**, e15817.

Bromham, L. & Cardillo, M. (2007) Primates follow the "island rule": implications for interpreting *Homo floresiensis*. *Biology Letters*, **3**, 398–400.

Brown, J.H., Marquet, P.A. & Taper, M.L. (1993) Evolution of body size: consequences of an energetic definition of fitness. *The American Naturalist*, **142**, 573–84.

Butler, P.M. (1980) The giant erinaceid insectivore *Deinogalerix* Freudenthal from the Upper Miocene of the Gargano, Italy. *Scripta Geologica*, **57**, 1–72.

Caron, V., Bernier, P. & Mahieux, G. (2009) Record of Late Pleistocene (Oxygen Isotopic Stage 5) climate changes during episodes of karst development on the Northern coast of Crete: sequence stratigraphic implications. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **277**, 246–264.

Case, T.J. (1978) A general explanation for insular body size trends in terrestrial vertebrates. *Ecology*, **59**, 1–18.

Dollo, L. (1893) Les lois de l'évolution. *Bulletin de la Société Belge de Géologie de Paléontologie et d'Hydrologie*, **7**, 164–166.

Fooden, J. & Albrecht, G.H. (1993) Latitudinal and insular variation of skull size in crab-eating macaques (Primates, Cercopithecidae: *Macaca fascicularis*). *American Journal of Physical Anthropology*, **92**, 521–538.

Freudenthal, M. (1976) Rodent stratigraphy of some Miocene fissure fillings in Gargano (prov. Foggia, Italy). *Scripta Geologica*, **37**, 1–23.

Freudenthal, M. (1985) Cricetidae (Rodentia) from the Neogene of Gargano (Prov. of Foggia, Italy). *Scripta Geologica*, **77**, 29–74.

Freudenthal, M. & Martín-Suárez, E. (2010) The age of immigration of the vertebrate faunas found at Gargano (Apulia, Italy) and Scontrone (l'Aquila, Italy). *Comptes Rendus Palevol*, **9**, 95–100.

van der Geer, A. (2008) The effect of insularity on the Eastern Mediterranean early cervoid *Hoplitomeryx*: the study of the forelimb. *Quaternary International*, **182**, 145–159.

van der Geer, A., Lyras, G., de Vos, J. & Dermitzakis, M. (2010) *Evolution of island mammals: adaptation and extinction of placental mammals on islands*. Wiley-Blackwell, Oxford.

Goldberg, E.E. & Igic, B. (2008) On phylogenetic tests of irreversible evolution. *Evolution*, **62**, 2727–2741.

Grant, P.R. & Grant, R. (2006) Evolution of character displacement in Darwin's finches. *Science*, **313**, 224–226.

Hautier, L., Bover, P., Alcover, J.A. & Michaux, J. (2009) Mandible morphometrics, dental microwear pattern, and

palaeobiology of the extinct Balearic Dormouse *Hypnomys morpheus*. *Acta Paleontologica Polonica*, **54**, 181–194.

Heaney, L.R. (1978) Island area and body size of insular mammals: evidence from the tri-colored squirrel (*Callosciurus prevosti*) of Southeast Asia. *Evolution*, **32**, 29–44.

Köhler, M., Moyà-Solà, S. & Wrangham, R.W. (2008) Island rules cannot be broken. *Trends in Ecology and Evolution*, **23**, 6–7.

Kuss, S.E. (1970) Abfolge und Alter der pleistozänen Säuge-tierfaunen der Insel Kreta (Griechenland). *Berichte der Naturforschenden Gesellschaft zu Freiburg im Breisgau*, **59**, 137–168.

Lister, A.M. (1989) Rapid dwarfing of red deer on Jersey in the Last Interglacial. *Nature*, **342**, 539–542.

Lister, A.M. (1996) Dwarfing in island elephants and deer: processes in relation to time of isolation. *Symposia of the Zoological Society of London*, **69**, 277–292.

Lomolino, M.V. (1985) Body size of mammals on islands: the island rule reexamined. *The American Naturalist*, **125**, 310–316.

Lomolino, M.V. (2000) Ecology's most general, yet protean pattern: the species–area relationship. *Journal of Biogeography*, **27**, 17–26.

Lomolino, M.V. (2005) Body size evolution in insular verte-brates: generality of the island rule. *Journal of Biogeography*, **32**, 1683–1699.

Lomolino, M.V. (2010) Four Darwinian themes on the origin, evolution and preservation of island life. *Journal of Biogeography*, **37**, 985–994.

Lomolino, M.V., Sax, D.F., Palombo, M.R. & van der Geer, A.A. (2012) Of mice and mammoths: evaluations of causal explanations for body size evolution in insular mammals. *Journal of Biogeography*, **39**, 842–854.

Lyras, G.A., Dermitzakis, M.D., van der Geer, A.A.E., van der Geer, S.B. & de Vos, J. (2008) The origin of *Homo floresiensis* and its relation to evolutionary processes under isolation. *Anthropological Science*, **117**, 33–43.

Lyras, G.A., van der Geer, A. & Rook, L. (2010) Body size of insular carnivores: evidence from the fossil record. *Journal of Biogeography*, **37**, 1007–1021.

Mayhew, D.F. (1977) The endemic Pleistocene murids of Crete I-II. *Proceedings of the Koninklijke Akademie van Wetenschappen (Series B)*, **80**, 182–214.

Mayr, E. (1956) Geographical character gradients and climatic adaptation. *Evolution*, **10**, 105–108.

McFarlane, D.A., MacPhee, R.D.E. & Ford, D.C. (1998) Body size variability and a Sangamonian extinction model for *Amblyrhiza*, a West Indian megafaunal rodent. *Quaternary Research*, **50**, 80–89.

Meiri, S., Dayan, T. & Simberloff, D. (2004a) Carnivores, biases and Bergmann's rule. *Biological Journal of the Linnean Society of London*, **81**, 579–598.

Meiri, S., Dayan, T. & Simberloff, D. (2004b) Body size of insular carnivores: little support for the island rule. *The American Naturalist*, **163**, 469–479.

Meiri, S., Meijaard, E., Wich, S.A., Groves, C.P. & Helgen, K.M. (2008) Mammals of Borneo – small size on a large island. *Journal of Biogeography*, **35**, 1087–1094.

Meiri, S., Simberloff, D. & Dayan, T. (2011) Community-wide character displacement in the presence of clines: a test of Holarctic weasel guilds. *Journal of Animal Ecology*, **80**, 824–834.

Melis, R.T., Ghabel, B., Boldrini, R. & Palombo, M.R. (2012) The Grotta dei Fiori (Sardinia, Italy) stratigraphical suc-cessions: a key for inferring palaeoenvironment evolution and updating the biochronology of the Pleistocene mam-malian fauna from Sardinia. *Quaternary International*, **288**, 81–96.

Millien, V. (2006) Morphological evolution is accelerated among island mammals. *PLoS Biology*, **4**, e321.

Millien, V., Lyons, S.K., Olson, L., Smith, F.A., Wilson, A.B. & Yom-Tov, Y. (2006) Ecotypic variation in the context of global climate change: revisiting the rules. *Ecology Letters*, **9**, 853–869.

Mooney, H.H. & Cleland, A.A. (2001) The evolutionary impact of invasive species. *Proceedings of the National Academy of Sciences USA*, **98**, 5446–5451.

Ognev, S. (1963) *Mammals of the U.S.S.R. and adjacent coun-tries, Vol. 6, Rodents*. Israel Program for Scientific Transla-tions, Jerusalem.

Palkovacs, E.P. (2003) Explaining adaptive shifts in body size on islands: a life history approach. *Oikos*, **103**, 37–44.

Palombo, M.R. (2004) Dwarfing in insular mammals: the endemic elephants of Mediterranean islands. *Miscelánea en homenaje a Emiliano Aguirre, Vol. 2, Paleontología* (ed. by E. Baquedano Pérez and S. Rubio Jara), pp. 355–371. Mu-seo Arqueológico Regional, Madrid.

Palombo, M.R. (2007) How can endemic proboscideans help us understand the "island rule"? A case study of Mediter-ranean islands. *Quaternary International*, **169–170**, 105–124.

Palombo, M.R. (2009) Body size structure of the Pleistocene mammalian communities from Mediterranean Islands: what support for the "island rule"? *Integrative Zoology*, **4**, 341–356.

Palombo, M.R. & Giovinazzo, C. (2005) *Elephas falconeri* from Spinagallo Cave (South-Eastern Sicily, Hyblean Plateau, Siracusa): brain to body weight comparison. *Pro-ceedings of the International Symposium "Insular Vertebrate Evolution: the Palaeontological Approach"* (ed. by J.A. Alcover and P. Bover). Monografies de la Societat d'Història Natural de les Balears, **12**, 255–264.

Raia, P. & Meiri, S. (2006) The island rule in large mammals: paleontology meets ecology. *Evolution*, **60**, 1731–1742.

Raia, P., Carotenuto, F. & Meiri, S. (2010) One size does not fit all: no evidence for an optimal body size on islands. *Global Ecology and Biogeography*, **19**, 475–484.

Rensch, B. (1938) Some problems of geographical variation and species-formation. *Proceedings of the Linnean Society of London*, **150**, 275–285.

Reumer, J.W.F. (1980) Micromamals from the Holocene of Canet Cave (Majorca) and their biostratigraphical implication. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen (Series B)*, **83**, 335–360.

Reumer, J.W.F. (1986) Notes on the Soricidae (Insectivora, Mammalia) from Crete. I. The Pleistocene species *Crocidura zimmermanni*. *Bonner Zoologische Beiträge*, **37**, 161–171.

Rinaldo, P.M. & Masini, F. (2009) New data on the taxonomy of the endemic Myomiminae (Gliridae, Rodentia) from the Late Miocene–Early Pliocene of Gargano (southern Italy) with the description of the new species *Stertomys degiulii*. *Bollettino della Società Paleontologica Italiana*, **48**, 189–233.

Rofes, J., Bover, P., Cuenca-Bescós, G. & Alcover, J.A. (2012) *Nesiotites rafelinensis* sp. nov., the earliest shrew (Mammalia, Soricidae) from the Balearic Islands, Spain. *Palaeontologica Electronica*, **15.1.8A**, 1–12.

Roth, V.L. (1992) Inferences from allometry and fossils: dwarfing of elephants on islands. *Oxford Surveys in Evolutionary Biology*, **8**, 259–288.

Roughgarden, J. & Pacala, S. (1989) Taxon cycle among *Anolis* lizard populations: review of evidence. *Speciation and its consequenses* (ed. by D. Otte and J. Jendler), pp. 403–432. Sinauer Associates, Sunderland, MA.

Sax, D.F. & Gaines, S.D. (2008) Species invasions and extinction: the future of native biodiversity on islands. *Proceedings of the National Academy of Sciences USA*, **105**, 11490–11497.

Simberloff, D., Dayan, T., Jones, C. & Ogura, G. (2000) Character displacement and release in the small Indian mongoose, *Herpestes javanicus*. *Ecology*, **81**, 2086–2099.

Smith, F.A. & Betancourt, J.L. (2003) The effect of Holocene fluctuations on the evolution and ecology of *Neotoma* (woodrats) in Idaho and northwestern Utah. *Quaternary Research*, **59**, 160–171.

Smith, F.A., Betancourt, L. & Brown, J.H. (1995) Evolution of body size in the woodrat over the past 25,000 years of climate change. *Science*, **270**, 2012–2014.

Sondaar, P.Y. (1977) Insularity and its effect on mammal evolution. *Major patterns in vertebrate evolution* (ed. by M.N. Hecht and P.L. Goody), 671–707. Plenum, New York.

Sondaar, P.Y. & van der Geer, A.A.E. (2005) Evolution and Extinction of Plio-Pleistocene island ungulates. *Les ongulés holarctiques du Pliocène et du Pléistocène* (ed. by E. Crégut-Bonnoure), pp. 241–256. Quaternaire, International Journal of the French Quaternary Association, hors-série 2005, 2. Maison de la Géologie, Paris.

Tan, L., Serene, S., Chao, H.X. & Gore, J. (2011) Hidden randomness between fitness landscapes limits reverse evolution. *Physical Review Letters*, **106**, 198102.

Van Valen, L. (1973) Pattern and the balance of nature. *Evolutionary Theory*, **1**, 31–49.

de Vos, J., van den Hoek Ostende, L.W. & van den Bergh, G. (2007) Patterns in insular evolution of mammals: a key to island palaeogeography. *Biogeography, time, and place: distributions, barriers, and islands* (ed. by W. Renema), 315–345. Springer, Dordrecht.

Weston, E. & Lister, A.M. (2009) Insular dwarfism in hippos and a model for brain size reduction in *Homo floresiensis*. *Nature*, **459**, 85–88.

Whittaker, R.J. & Fernández-Palacios, J.M. (2007) *Island biogeography: ecology, evolution, and conservation*, 2nd edn. Oxford University Press, Oxford.

Wilson, E.O. (1959) Adaptive shift and dispersal in a tropical ant fauna. *Evolution*, **13**, 122–144.

Wilson, E.O. (1961) The nature of the taxon cycle in the Melanesian ant fauna. *The American Naturalist*, **95**, 169–193.

SUPPORTING INFORMATION

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

Appendix S1 Body mass estimations, dental and postcranial linear measurements and body mass indices (S_i) of palaeospecies throughout time.

BIOSKETCH

Alexandra A.E. van der Geer is a palaeontologist and first author of *Evolution of island mammals: adaptation and extinction of placental mammals on islands*. She is interested in evolutionary processes on islands with an emphasis on artiodactyls. Processes of speciation within a monophyletic lineage have her particular interest. Her other field of research involves the role of animals in human culture, especially in South Asia.

Author contributions: A.V.G., G.A.L., M.V.L. and M.R.P. conceived the ideas and planned the analyses; G.A.L. and A.V.G. collected and analysed the data; G.A.L. prepared the figures and tables; and A.V.G. led the writing assisted by M.V.L., M.R.P. and D.F.S.

Editor: Judith Masters