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The effect of area and isolation on insular dwarf proboscideans

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Abstract

Aim We investigated the hypothesis that insular body size of fossil elephants is directly related to isolation and surface area of the focal islands. **Location** Palaeo-islands worldwide. **Methods** We assembled data on the geographical characteristics (area and isolation) of islands and body size evolution of palaeo-insular species for 22 insular species of fossil elephants across 17 islands. **Results** Our results support the generality of the island rule in the sense that all but one of the elephants experienced dwarfism on islands. The smallest islands generally harbour the smallest elephants. We found no support for the hypothesis that body size of elephants declines with island isolation. Body size is weakly and positively correlated with island area for proboscideans as a whole, but more strongly correlated for Stegodontidae when considered separately. Average body size decrease is much higher when competitors are present. **Main conclusions** Body size in insular elephants is not significantly correlated with the isolation of an island. Surface area, however, is a significant predictor of body size. The correlation is positive but relatively weak; c. 23% of the variation is explained by surface area. Body size variation seems most strongly influenced by ecological interactions with competitors, possibly followed by time in isolation. Elephants exhibited far more extreme cases of dwarfism than extant insular mammals, which is consistent with the substantially more extended period of deep geological time that the selective pressures could act on these insular populations.

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THE EFFECT OF AREA AND ISOLATION ON INSULAR DWARF PROBOSCIDEANS

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ABSTRACT

Aim We investigated the hypothesis that insular body size of fossil elephants is directly related to isolation and surface area of the focal islands.

Location Palaeo-islands worldwide.

Methods We assembled data on geographic characteristics (area and isolation) of islands and body size evolution of palaeo-insular species for 22 insular species of fossil elephants across 17 islands.

Results Our results support the generality of the island rule in the sense that all but one of the elephants experienced dwarfism on islands. The smallest islands generally harbour the smallest elephants. We found no support for the hypothesis that body size of elephants declines with island isolation. Body size is weakly and positively correlated with island area for proboscideans as a whole, but more strongly correlated for Stegodontidae when considered separately. Average body size decrease is much higher when competitors are present.

Main conclusions Body size in insular elephants is not significantly correlated with the isolation of an island. Surface area, however, is a significant predictor of body size. The correlation is positive but relatively weak; about 23% of the variation is explained by surface area. Body size variation seems most strongly influenced by ecological interactions with competitors, possibly followed by by time in isolation. Elephants exhibited far more extreme cases of dwarfism than extant insular mammals, which is consistent with the substantially more extended period of deep geological time that the selective pressures could act on these insular populations.

KEYWORDS

Elephas, fossil record, insularity, island biogeography, island rule, *Palaeoloxodon*, Pleistocene, *Stegodon*

INTRODUCTION

Vertebrates on islands generally follow a body size trend from gigantism in small species to dwarfism in large species, a trend coined “the Island Rule” by Van Valen (1973) and subsequent authors. The many deviations from this pattern have given rise to considerable criticism regarding generality and causality of the rule: see, for example, Meiri *et al*. (2004, 2006, 2008a) for mammalian carnivores (but see Lyras *et al*. 2010), Meiri (2007) for lizards, Meiri *et al*. (2011) for birds and lizards (though they found weak support for mammals), and Itescu *et al*. (2014) for insular tortoises worldwide. A large study has investigated the generality of the island rule (Lomolino *et al*., 2013), which, by analysing both extant and extinct mammals (including very large mammals such as elephants in the dataset), includes the important factor deep geological time under which species evolved in isolation. Context (ecological interactions, isolation, area, climate etc.) appears to be of crucial importance and differences herein can explain differences in observed body size evolution between populations of the same species (Lomolino *et al*., 2012). The various contextual factors do not contribute equally to the eventual body mass outcome, for example, the presence of ecologically relevant competitors appears to have a higher impact than ancestral body mass and climatic variability (Sondaar, 1977; Lomolino, 1985; Raia & Meiri, 2006; Palombo, 2007, 2009; Lomolino *et al*., 2012; van der Geer *et al*., 2013; *inter alia* Itescu *et al*., 2014). For example, insular elephants have been shown to have maintained a larger body mass in the presence of deer and hippo, likely because the presence of smaller-bodied intra-guild competitors prevented elephants from reaching a similar size class (Palombo, 2007).

Taxa such as murids and deer are well represented in both the fossil as well as the extant insular record. Whereas very large-bodied taxa such as elephants and hippos are extremely limited in the extant record despite being common, not to say typical, elements of island faunas worldwide during the Pleistocene. Elephants provide some of the most spectacular cases of body size evolution in palaeo-insular mammals (Fig. 1). For example, the elephant (*Palaeoloxodon falconeri*) from Spinagallo Cave (Siracuse, Sicily; Middle Pleistocene) dwarfed to just 2% of the size (body mass) of its mainland ancestor (*Palaeoloxodon antiquus*) (Ambrosetti, 1968; Palombo & Ferretti, 2005; Lomolino *et al*., 2013).

Here, we expand the dataset for insular proboscideans as given in Lomolino *et al*. (2013) and further evaluate insular size trends of these very large insular mammals which are lacking in basically extant insular faunas. The dataset is limited to North America and Eurasia as no fossil proboscideans have been discovered from islands of Africa, South America or Antarctica.

In the conceptual model as proposed by Lomolino *et al*. (2012), the principal selection force for (very) large mammals is ecological release. Ecological release, however, is more important on smaller islands (where there are fewer competitors/predators), which would indirectly introduce an effect of area on elephant body size. The number of ecologically relevant competitors / predators is also related to isolation, as the chance of successful dispersal is inversely related to isolation. This means that both area and isolation are expected to have an indirect effect on the degree of dwarfism of elephants through ecological release.

The effect of factors associated with thermoregulation (e.g. island latitude, temperature and seasonality) is potentially relevant, but will not be tested here as the variation in climatic variables, especially lowest winter temperature and rainfall, across the focal palaeo-islands and the different geological periods (including glacials, interglacials, and spanning the entire Pleistocene) cannot be estimated reliably.

The testable predictions of the ecological model of body size evolution (Lomolino *et al.*, 2012) for palaeo-insular proboscideans are as follows.

1) Proboscideans should exhibit dwarfism on islands, following the general “Island Rule” prediction that large mammals become smaller;

2) Body size in proboscideans should be positively correlated with island area but negatively correlated with isolation. The rationale here is that both area and isolation are correlated with the presence and number of ecologically relevant competitors and predators: the first as a function of carrying capacity, the second as a function of dispersal chances.

3) The degree of dwarfism should be highest in the absence of ecologically interacting taxa. The presence of large to medium-sized competing herbivores and/or of predators is expected to prevent dwarfism to avoid competition and/or escape predation, respectively.

MATERIALS AND METHODS

Estimation of body size and relative size index (S_i)

As is detailed within Table 1, the dataset comprises 22 insular proboscidean species. Because this study includes fossilised individuals, preservation is inconsistent. Therefore, and of necessity, different methods for estimating body size and relative size index were applied. The calculated relative size index (S_i or size ratio) for each pair of insular proboscidean and its mainland ancestral species was obtained by dividing the estimated body mass of the focal species by that of the ancestral species (=SR in Meiri *et al*., 2008a). Body size (or mass) of insular fossil species and their mainland ancestors was either estimated using taxon-specific equations for estimating body masses developed by Christiansen (2004) for living elephants, or taken from published sources (see Appendix S1 for details and references). The alternative method of calculating ratios based on linear measurements and applying the cubic law instead of indirectly via body mass has been demonstrated to work equally well (Meiri *et al*., 2006, 2008a), but we preferred the indirect method enabling inclusion of data from the literature and thereby increasing our sample size. Parameters that were used in this study to estimate body mass were the lengths of appendicular bones (humerus, femur, tibia) that provided the most reliable regression results in the study by Christiansen (2004). For each species, we calculated body masses based on the average lengths for each element (or one or two of these elements, if not all three were available, again in order to increase our S_i sample size). We then took the average of the mass estimates based on different appendicular bones, assuming dependency between the different elements by absence of evidence that the 'bauplan' of insular elephants had changed drastically. We found that estimations of S_i based on a single element versus based on all three elements produced similar results (see Appendix S1 following Table S3). We also based our body-weight estimates on length measurements only (as opposed to minimum circumferences of long bone diaphyses) because it has been observed that stegodonts had comparatively sturdy long bones as compared to modern elephants (Hooijer, 1955).

For species for which no suitable postcranial elements were available, S_i was calculated as the ratio of the cubed linear dimensions of the lower third molar following Lomolino (2005). The problem with only using dental elements, however, is that on geological time scales, molar dimensions have been found to lag behind in the initial stages of dwarfism (Lister, 1989, 1996). This also applies to palaeoloxodontine dwarf elephants, where decrease in humerus length (as a proxy for body size) and molar width (as a proxy for dental size) have initially different scaling rates (see Appendix S1).

For *Stegodon* species of which no suitable postcranial was available, but adult mandibles instead, a new regression was established (see Appendix S1 Table S3). This regression is derived from femur/tibia/humerus lengths against mandibular width of other *Stegodon* species, for which both long bones and (fragments of) mandibles of full-grown individuals could be measured (see Appendix S1).

The resulting dataset comprises 22 island-mainland pairs of fossil proboscideans and their calculated size indices (S_i values) on 17 islands worldwide (Fig. 2).

Estimation of island area and isolation

Island area and isolation were estimated with Global Mapper v.15 software based on published data on palaeogeography, geodynamics, sea level changes, extension of tectonically undisturbed marine deposits, and offshore bathymetry. For most of the islands in the Wallacea region we used the map of Hanebuth *et al.* (2011) representing the palaeogeography at 12.7 kyr BP, when the sea level was 60 m below present. This can be considered as the ‘mean’ sea-level that prevailed for the longest periods of time during the Quaternary (calculated from Pleistocene sea-levels as given in Bintanja *et al*., 2005). A sea level of -60 m also applies to the Mediterranean, following Lambeck & Chappell (2001) for the late Pleistocene. We assume here that body mass evolution in proboscideans takes a considerable time, and thus likely depends more on mean surface area rather than on the relatively short-lived extreme values. We infer this from the observation that Holocene endemics did not reach the same drastic body size decrease as Pleistocene endemics did (Lomolino *et al*., 2013).

Initially, dwarfism may evolve rapidly (in a few thousand years), but is then followed by a second stage of slower, but ultimately much more pronounced size change (Lister, 1989, 1996; van der Geer *et al*., 2013). We are aware that -60 m may be somewhat arbitrary, but since we apply this level to all islands, the results are biased in the same direction, and remain the same when comparing islands mutually.

Sumba and Timor are exceptional cases, because their late Pleistocene uplift far exceeded the eustatic sea level fluctuations. The strong recent tectonic uplift of Sumba has a rate of 0.2–0.5 m/kyr, as evidenced by dated raised coral terraces (Bard *et al*., 1996). We have taken the 500 m contour level (the highest coral terrace is 475 m above present-day sea level) to calculate the palaeo-surface area. Timor has also been strongly uplifted, at least 700 m during the last 200,000 kyr (de Smet *et al.*, 1990), and therefore we have taken the 500 m contour as a rough estimate of the middle Pleistocene coastline of Timor. Flores in contrast, appears not to have been uplifted in such a dramatic way as Timor and Sumba were. The recent uplift of Flores is much less substantial, as indicated by the flat lying terrestrial sediments of early and middle Pleistocene age now occurring at an elevation of around 350 m above present sea level (Brumm *et al*., 2010), unlike the highly uplifted Pleistocene marine coralline sediments of similar ages on Timor-Sumba. We therefore have estimated the area and isolation for Flores in a similar way as for most other islands, at -60 m sea level.

The following islands have alternative values for either area or isolation (for details, see Appendix S1). Crete in the early Pleistocene may have still consisted of two islands as it did at the end of the Pliocene (van Hinsbergen & Meulenkamp, 2006), or alternatively, was already merged due to the uplift into a single island as suggesed by the presence of *Kritimys* in both parts. The uncertainty is caused by the uncertain age of the Cretan dwarf mammoth (Herridge & Lister, 2012). Flores (Pleistocene) was isolated from the mainland via Komodo, Sumbawa and Lombok or alternatively, via Sulawesi and the Philippines, based on ocean currents and the fossil record (Morwood & Jungers, 2009; Dennell *et al*., 2014). Luzon (late Pleistocene) was part of the palaeo-island Greater Luzon (Heaney *et al*., 2005) or alternatively, its northern part (where the fossils come from) constituted a separate island during much of the Pleistocene, separated from the southern part by a NW-SE trending fault zone (Defant & Ragland, 1988) at present bordered to the south by the low lying Central Valley. Luzon (late Pleistocene) was isolated from the mainland via Mindoro and Palawan or alternatively, via Mindoro, Palawan and Borneo, assuming that Palawan was not connected to Borneo. Sicily (early Middle Pleistocene) still consisted of two palaeo-islands, or alternatively of one larger, merged island (see palaeo-maps in Bonfiglio *et al*., 2002; partially based on endemism of the fauna, implying a potential circularity), which influences the estimated values for both area and isolation. Furthermore, a connection between Sicily and Malta is unproven (Herridge, 2010), and if a connecting ridge was ever exposed, it likely was merely a series of stepping stones (van der Geer *et al*., 2010) as exposure of a continuous land bridge would require a drop in sea level of at least 120 to 150 m. Because of these uncertainties we have not included the Maltese material attributed to *P. falconeri* into our analysis. South-western Sulawesi during the early Pleistocene still constituted a separate palaeo-island or alternatively, may have been already merged with the other parts of Sulawesi rather than at some stage during the middle or late Pleistocene (van den Bergh, 1999).

Taxonomic and phylogenetic framework

Here, we use the generic name *Palaeoloxodon* instead of *Elephas* for the Mediterranean insular and mainland straight-tusked elephants (following Shoshani *et al.*, 2007; Todd, 2010). *Palaeoloxodon* “*mnaidriensis*”, referred to as *Palaeoloxodon* nov. sp. in Herridge (2010), still awaits revision. The “large-sized *Elephas*” from Sulawesi (*Palaeoloxodon* sp., Tanrung Formation) is here considered conspecific with, or at least identical in size to *P. namadicus* (following van den Bergh, 1999).

Ancestral taxa for each insular species are based on the literature (van den Bergh, 1999; Palombo, 2001; Herridge, 2010; Herridge & Lister, 2012; Roth, 1982; van der Geer *et al*., 2010). For mainland *Palaeoloxodon*, we use specimens from Italy and Greece, that are considered ancestral to the insular populations. In case an insular species was derived from a mainland taxon that must have migrated via an intermediate island (Flores, Timor, Sumba), we calculated body size index relative to the mainland ancestor, and not relative to the dwarfed taxon from the intermediate island. Most likely, the ancestral species from the intermediate island did not disperse to the island farther away following drastic reduction in body size on the intermediate island, but more likely this happened relatively soon after colonization when it was still large-bodied. This inference is considered the most likely scenario, because smaller body size for swimming elephants would signify reduce dispersal probability due to more restricted fasting endurance and reduced buoyancy (pneumatic bone tissue is lost in dwarf elephants) (Sondaar, 1977).

The *S. trigonocephalus* sample (Java) includes various subspecies of different sizes. We here only use the Trinil H.K. material, which forms a homogenous sample from a single layer estimated to 0.9 Ma (van den Bergh, 1999; but 0.54–0.43 Ma in Joordens *et al*., 2014), when Java constituted an island, based on the endemic character of the fauna from this site (van den Bergh, 1999). The alternative scenario is that Java was connected through a filtered corridor with the mainland (Larick *et al*., 2000; see for an extensive discussion of pros and contras, Meijaard [2004]). Evidence for at least a partial isolation is provided by the presence of the following endemic taxa at Trinil H.K.: *Axis lydekkeri*, *Bibos palaesondaicus*, *Bubalus palaeokerabau*, *Duboisia santeng*, *Mececyon trinilensis* (=*Cuon* in Louys, 2014; here, we follow Lyras *et al*. 2010, awaiting a revision of the Javanese canids), and *Sus brachygnathus*.

Palaeoloxodon leonardi (Sicily) and *P*. sp. (Delos) are excluded because their stratigraphic positions remain unresolved. This also applies to the significantly larger elephant species (*P. xylophagou*) of Cyprus (Athanassiou *et al*., 2014; Athanassiou *et al*., 2015). The indeterminate Proboscidea and *E*. or *P. beyeri* from Luzon (de Vos & Bautista, 2003) are omitted because their ancestry, chronology and context are insufficiently known.

Ecological assemblages

The number of competitors and predators most likely to have directly interacted with the focal insular species are based on published fauna lists (van den Bergh, 1999; van der Geer *et al*., 2010) for local faunal assemblages containing the focal species. Judgement on the likelihood of competition or predation were based on consultation of references on the diet and habitats of those species in order to determine which ones were likely to be significant competitors or predators of the focal insular species. Reptiles were not considered as potential interacting taxa because of their low energetic demands.

Late middle to late Pleistocene Sicily, however, poses a problem. The dwarf elephant belongs to two successive faunal units or complexes (*P. mnaidriensis* FC and San Teodoro FC) (Bonfiglio *et al*., 2000). The elephant sample we use here is from

Puntali Cave, dated either late middle Pleistocene (c. 180 ka) or late Pleistocene, comparable to that of San Teodoro (c. 32 ka) (Ferretti, 2008). We here tentatively include faunal elements from both FC's, with the exception of the lion, which we omit as it is restricted to San Ciro cave and Canita. Elements not retrieved from Puntali Cave itself are indicated with a question mark.

Statistical analyses

We first tested for the normality of our data (body mass index, area, isolation) by using the Shapiro-Wilk test (Shapiro & Wilk, 1965). Then we used 2-tailed Pearson's test to check for correlations between the variables (significance level alpha=0.05). For significantly correlated variables, a simple linear regression analysis (parametric) was used to test for the goodness of fit (r^2; proportion of variability in the response) of the correlation. We used an independent-samples' t-test to compare the insular body size evolution of the various genera. Statistical analyses were performed using IBM SPSS Statistics for Windows, Version 21. A 1-step ANOVA was used to test the effect of the presence of competitors on body size evolution.

For the development of a regression to estimate body size with mandibular width measurements, a reduced major axis regression on log-transformed (base 10) data was used.

RESULTS

As illustrated in Table 1 and consistent with Prediction 1, body size variation among insular proboscideans matches previously reported patterns for extant mammals and other vertebrates and was entirely consistent with the island rule. That is, all proboscidean species except one had a smaller body size than the respective mainland ancestral species (n=23; mean S_i=0.28, SD=0.24). The most pronounced case of size reduction is exhibited by *P. falconeri* (Sicily; S_i=0.02) and *P. cypriotes* (Cyprus; S_i=0.02) for *Palaeoloxodon*, *M. creticus* (Crete; S_i=0.04) for *Mammuthus* and *S. sumbaensis* (Sumba; S_i=0.08) for *Stegodon*. No size reduction is observed in the large *Elephas* species from Sulawesi. Limited size reduction is seen in *S. trigonocephalus* (Java, Trinil) (S_i=0.65). On a whole, *Stegodon* species (n=10) show a lesser body size reduction (or higher S_i) than *Palaeoloxodon* (n=8), with a respective mean S_i = 0.33 (SD=0.19) and S_i=0.16 (SD=0.13). This difference is significant (t (16) =-2.20, p=0.04). The number of *Mammuthus* species (n=4) is too low to be included in the t-test.

The log-transformed (base 10) variables of surface area, alternative surface area and untransformed minimal isolation were normally distributed, but maximal isolation is not (for SPSS output, see Appendix S1, after Table S4). However, the normality of maximal isolation is only minimally violated, and we proceed with it as if normally distributed.

Neither minimal nor maximal isolation is statistically correlated with insular body size index (Pearson R=-0.09 and -0.05, respectively, with p=0.69 and p=0.84). Surprisingly, some islands within visual range (12 km) have very small elephants ($S_i \leq 0.20$). There is no trend (p=0.08) for increased dwarfism on islands further away than 48 km (the maximum reported distance covered by swimming for Asian elephants in Johnson [1980]).

Log surface and log surface alternative are very strongly correlated with each other (Pearson R=0.96, p<0.01) and with S_i (Pearson R=0.48, p<0.05 and 0.53, p<0.05, respectively). Based on this result, we proceeded with the first only, because this is considered the most reliably estimated value for any given island. The correlation between island area and body size index is positive but weak, with area explaining only 23% of the total variance ($r^2=0.23$, $p=0.02$). The residuals show no correlation with latitude ($r^2=0.02$, $p=0.52$). The residuals for *Stegodon* only, however, show a single outlier: *S. aurorae* from Japan. The difference from the predicted value is -0.26 compared to -0.17–0.09 for the other species. *Stegodon aurorae* occurred at a much higher latitude as compared to all other *Stegodon* species. Considering the three genera separately, the correlation is stronger and more significant for *Stegodon* ($r^2=0.83$, $p<0.01$; with the tentative exclusion of the Japanese stegodont based on latitude) than for all taxa taken together.

The effect of competition (Table 2) on body size variation of proboscideans is limited (on average, $S_i=0.41$ with competitors against $S_i=0.17$ without competitors) but significant ($p<0.01$). Within the group lacking competitors, there is one less size-reduced species (*S. florensis florensis*, S_i =0.51). This species is a 700 kyr older chronosubspecies of the much smaller form (*S. florensis insularis*, $S_i=0.17$).

The effect of predation remains unclear. Given the lack of large terrestrial predators on the focal islands (except for three or five islands, depending on whether hominins can be considered as effective predators; Table 2), we were unable to assess the potential effect of predation on body size variation of these very large mammals. However, between species that occur on the same island but during a different time period, the species with predators show a smaller size reduction than the species without predators. This is shown by *P. mnaidriensis* versus *P. falconeri* and perhaps by *S. florensis* versus *S. sondaari*. Admittedly, a different geological period likely implies different vegetation, area, isolation etc. as well, so the interpretation of this observation is tentative.

DISCUSSION

Temporal variation in body size of proboscideans

Fossil proboscideans exhibit much more extreme cases of dwarfism than living species (less than 5% the body mass of their ancestors; Fig. 1). One plausible explanation is that these differences in degrees of body size evolution between extant mammals and those studied here is simply a function of the much more extended geological period over which the evolutionary change could be analysed in the fossil record, rather than the comparatively short time span of ~ 15 kyr since the last sea-level rise during which size reduction occurred in most extant mammals occurring on continental islands, as was also suggested by Lomolino *et al.* (2013).

Factors associated with body size variation in proboscideans

Body size reduction in proboscideans appears to be most pronounced for the species occurring on the most isolated palaeo-island: *P. falconeri* of south-eastern Sicily, whether its isolation is 100 km or 200 km. Yet, when considering all species together, no significant correlation was found between isolation and the degree of body size reduction. A possible explanation for the lack of a correlation may be that isolation per se is not a good estimator for accessibility. For example, despite the great distance, Sulawesi appears to have been comparatively “easy” to colonize, if we take into account the comparatively large number of terrestrial immigrants that were able to cross Makassar Strait: apart from murine rodents, also squirrels, bovids, suids, macaques, and hominins reached Sulawesi at some stage prior to the late Pleistocene (de Bruyn *et al*., 2014; G.D. van den Bergh *et al*., in press). These are all clades that are not typical island taxa. It is likely that prevailing oceanic currents are a major factor in determining island accessibility (Ali & Huber, 2010), but these are difficult to incorporate into a generalized isolation index. Similarly, despite the relatively small distance between Flores and the mainland (one or two crossings with visibility of the target island) the strong Indonesian through-flow currents (Sprintall *et al.*, 2014) that pass through these gaps may have significantly undermined overseas dispersal to Flores.

Body size appears positively but weakly correlated with island area for proboscideans as a whole. The relation is much more robust for *Stegodon*, if we exclude the most northern species (*S. aurorae*), which appears much smaller than would be predicted, and the earlier chronosubspecies of Flores (*S. florensis florensis*).

Our results provide only limited support for a direct influence of predation on body size of insular proboscideans (but see Meiri's *et al.*'s [2008b] account of dwarfism in extant, large mammals, which may have been associated with reduced predator pressures of Borneo). This may stem at least in part from the limited variability in predator assemblages on the islands we studied. Nevertheless, temporal variation in ecological assemblages on Flores reveals the lack of a significant effect of predators on body size evolution of native stegodonts in the long run. Here, a geologically older pygmy stegodont (*Stegodon sondaari*) was replaced by a larger stegodont (*S. florensis*), coinciding with the arrival of a hominin. The latter apparently had access to carcasses as attested by cut marks on stegodont bones in the site Liang Bua (van den Bergh *et al*., 2009). Yet, even with this putative predator around, the larger *Stegodon* decreased in size between the middle Pleistocene (Soa Basin; subspecies *florensis*) and the latest Pleistocene (Liang Bua; subspecies *insularis*) (van den Bergh *et al.*, 2008), and eventually its degree of dwarfism practically rivalled that of *S. sondaari* (S_i=0.17 and 0.15 respectively). It seems, thus, that the effect of predation on proboscideans was either modest or, perhaps more likely, a function of the diversity and intensity of predators. After all, a single, hominin predator is likely not as significant as an assemblage of large felids and other mega-carnivores as present in mainland settings. In addition, *Stegodon* predation by hominins on Flores may have been a relatively late development, since there are no indications for active hunting or butchering of stegodont remains in the various middle Pleistocene assemblages from the So'a Basin (van den Bergh *et al.*, 2014).

The presence of other large herbivores on the other hand has a significant influence on the degree of dwarfism of insular elephants. Species with other proboscideans as a competitor all show a less dramatic size reduction than species with other competitors or no competitors at all. The strong influence of competition on body size evolution is in line with the model of Lomolino *et al*. (2012), and was also noticed for Mediterranean elephants by Palombo (2009).

CONCLUSIONS

This study provides further support for the applicability of the island rule to the largest terrestrial mammalian herbivorous taxa (see Benton *et al.* [2010] and Stein *et al*. [2010] for intriguing indications that very large herbivorous dinosaurs such as titanosaurian sauropods may have also followed the predicted pattern).

The patterns discussed here for body size variation of proboscideans over space and time do not support a significant relation between isolation and body size decrease for proboscideans. Islands relatively close to the mainland may harbour extremely size-reduced proboscideans as well as normal-sized species. Islands further away than 48 km (the maximum reported distance an Asian elephant can swim) do not harbour the smallest species.

The correlation between area and body size is positive but weak with much scatter around the trend for all proboscideans but more robust for *Stegodon* from low latitude islands. Our observations support an ecological hypothesis of body size evolution, inferred from the significant influence of competition on body size evolution (see also Palombo, 2009). On the mainland and on relatively balanced and ecologically rich palaeo-islands such as Sulawesi, interaction with ecologically relevant species resulted in a (relatively) large body size. On islands with more depauperate assemblages, however, release from these ecological interactions appears to have resulted in a smaller body size. In the absence of competitors, body size tends to trend towards a size positively correlated with island area, provided that deep geological time was available to allow the dwarfing process to proceed beyond the initial phases.

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SUPPORTING INFORMATION

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

Appendix S1 Body mass estimations of palaeo-species, palaeo-island characteristics and statistical analyses.

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*. Her current research focuses on evolutionary processes on islands, including body size evolution and morphological changes in the skeleton. Author contributions: A.V.G., G.A.L., G.v.d.B conceived the ideas, planned the analysis and analysed the data; G.A.L., G.v.d..B., U.W., R.D.A., E.S. collected the data; G.A.L. prepared the figures; and A.V.G. led the writing assisted by G.A.L., G.v.d..B., U.W., R.D.A., E.S. and H.D.

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TABLES AND FIGURE CAPTIONS

Table 1 Variation in body mass indices (**S**$_i$ as a proportion of ancestral body size) of insular proboscideans in alphabetical order of species name. Body mass estimations were based on postcranial elements (humerus, femur, tibia) using the equations of Christiansen (2004) for *Mammuthus, Palaeoloxodon* and for *Stegodon* species for which these elements were available. For *Stegodon* species of which only (fragments of) adult mandibles were available, body mass estimates were based on a regression between log-transformed postcranial-based average body mass estimates and average mandibular width measurements of adult specimens (M18 of van den Bergh, 1999; only mandibles were used in which the last molar was in function), with body mass as the 'dependent' variable. This method was developed based on *Stegodon* species for which both variables were available based on averages of more than 1 specimen (Appendix S1). Indices based on the lower third molar (M_3) are calculated as the ratio of the cubed linear dimensions, following Lomolino (2005). Although this method likely overestimates body size of large-sized insular forms, it appears reliable in small-sized phylogenetic dwarfs (see for a discussion on teeth and body size reduction of phylogenetic dwarfs in Lister, 1996 and Appendix S1). The species indicated with an asterisk is an older chronospecies preceding the smaller form. Sources for *S*$_i$: 1=van den Bergh, 1999; 2= Lomolino *et al.*, 2013; 3= this study, based on M=mandible, P=postcranial, or T=third molar (see Appendix S1 for specimens, method and details); 4 = van der Geer *et al.*, 2014. The "large-sized *Elephas*" from Sulawesi (Tanrung Formation) might be *P. namadicus*. No complete long bones or third molars were found, but according to van den Bergh (1999) the size of a molar fragment falls within the size range of *P. namadicus*, hence its body size index is tentatively taken here to be 1.0. This may be an over-estimation in case size decrease had just begun. For calculation of area and isolation at sea level 60 m below present, see Appendix S1. Geological age: EP=early Pleistocene, MP=middle Pleistocene, LP=late Pleistocene, H=Holocene.

Palaeo-island	**Species**	**Mainland ancestor**	**S_i**	**Source**	**Area (km2) / isolation (km)**	**Geological age**
Crete	*Mammuthus creticus*	*M. meridionalis*	0.04	2	(4175 or 8350) / 90	EP
Santa Rosae	*Mammuthus exilis*	*M. columbi*	0.17	2	2200 / 10	LP
Sardinia	*Mammuthus lamarmorai*	*M. meridionalis*	0.08	2	26343 / 50	LP
Wrangel	*Mammuthus primigenius*	*M. primigenius*	0.47	2	7600 / 140	H
Sicily	*Palaeoloxodon ‘mnaidriensis’*	*P. antiquus*	0.17	2	23000 / (1 or 4)	late MP-early LP
Crete	*Palaeoloxodon creutzburgi*	*P. antiquus*	0.38	2	9460 / 90	LP
Kassos	*Palaeoloxodon 'creutzburgi'*	*P. antiquus*	0.30	3 (T)	600 / 50	LP
Cyprus	*Palaeoloxodon cypriotes*	*P. antiquus*	0.02	4	9234 / 69	LP
Sicily	*Palaeoloxodon falconeri*	*P. antiquus*	0.02	2	(2200 / 200) or (11600 / 100)	early MP
Naxos	*Palaeoloxodon lomolinoi*	*P. antiquus*	0.08	4	1226 / 30	LP
Rhodos	*Palaeoloxodon* sp.	*P. antiquus*	0.19	4	1660 / 15	LP?
Sulawesi	*Palaeoloxodon* sp. ("large-sized *Elephas*")	*P. namadicus*	~1.00	1	174600 / 50	MP
Tilos	*Palaeoloxodon tiliensis*	*P. antiquus*	0.09	2	116 / 15	LP
Japan	*Stegodon aurorae*	*S. zdanskyi*	0.25	3 (P)	263237 / 20	EP
Flores	*Stegodon florensis florensis**	*S. ganesa*	0.51	3 (P)	21910 / (45 or 225)	MP
Flores (Liang Bua)	*Stegodon florensis insularis*	*S. ganesa*	0.17	3 (P)	21910 / (45 or 225)	LP
Luzon	*Stegodon luzonensis*	*S. ganesa*	0.39	3 (T)	(157000 or 59250) / (45 or 65)	LP
Sulawesi	*Stegodon sompoensis*	*S. ganesa*	0.32	3 (M)	(174600 or 24020) / 50	EP

Flores (So’a Basin)	*Stegodon sondaari*	*S. elephantoides*	0.15	3 (P)	21910 / (45 or 225)	EP
Sulawesi	*Stegodon* sp. B	*S. ganesa*	0.57	3 (T)	174600 / 50	MP
Sumba	*Stegodon sumbaensis*	*S. ganesa*	0.08	3 (M)	3250 / 119	MP–LP
Timor	*Stegodon timorensis*	*S. ganesa*	0.23	3 (M)	10560 / 78	MP
Java (Trinil H.K.)	*Stegodon trigonocephalus*	*S. ganesa*	0.65	3 (P)	138794 / (1 or 4)	late EP

Table 2 Presence of ecologically relevant competitors and predators for the insular species mentioned in Table 1. Predators less than c. 15 kg (e.g. otters, foxes) are not considered potentially relevant for proboscideans and omitted here. EP = early Pleistocene, MP = middle Pleistocene, LP = late Pleistocene, P = Pleistocene (no further stratigraphical evidence), H = Holocene.

Species	**Palaeo-island**	**Geological time**	**Competitors**	**Predators**
E. sp.	Sulawesi	MP	Elephant (*Stegodon* sp. B), bovid? (*Bubalus depressicornis*), suid? (*Celebochoerus* sp.)	-
M. creticus	Crete	EP	-	-
M. exilis	Santa Rosae	LP	-	-
M. lamarmorai	Sardinia	LP	Deer (*Praemegaceros cazioti*)	-
P. creutzburgi	Crete	LP	Deer (*Candiacervus* spp.)	-
P. aff. *creutzburgi*	Kassos	LP	Deer ("*Candiacervus*" sp.)	-
Palaeoloxodon cypriotes	Cyprus	LP	-	-
P. falconeri	Sicily	early MP	-	-
P. ‘mnaidriensis’	Sicily	late MP–LP	Deer (*Cervus elaphus, Dama carburangelensis?*), bovids (*Bos primigenius, Bison priscus*)	Hyena (*Crocuta crocuta*), wolf (*Canis lupus*)?
P. sp.	Rhodos	LP?	-	-
P. lomolinoi	Naxos	LP	-	-
P. tiliensis	Tilos	LP–H	-	-
S. aurorae	Japan	EP	Deer (*Elaphurus* spp., *Cervus* sp.), rhino (*Rhinoceros* sp.)	wolf (*Xenocyon falconeri*)
S. florensis florensis	Flores	MP	-	hominin (*Homo floresiensis*)?
S. florensis insularis	Flores	LP	-	hominin (*Homo floresiensis*)?

S. luzonensis	Luzon	P	Elephants (Proboscidea indet., *Elephas beyeri*), deer (*Cervus* sp.), rhino (*Rhinoceros luzonensis*)	-
S. sompoensis	Sulawesi	EP	Elephant (*Stegoloxodon celebensis*), suid (*Celebochoerus heekereni*)	-
S. sondaari	Flores	EP	-	-
S. timorensis	Timor	MP	-	-
S. sp. B	Sulawesi	MP	Elephant (*Elephas* sp.), bovid? (*Bubalus depressicornis*), suid? (*Celebochoerus* sp.)	-
S. trigonocephalus	Trinil (Java)	late EP	Deer (*Axis lydekkeri*, *Rusa timorensis*), large bovids (*Bubalus palaeokerabau*, *Epileptobos groeneveldti*, *Bibos palaesondaicus*), elephant (*E. hysudricus*), rhino (*Rhinoceros sondaicus*)	Tiger (*Panthera tigris*), hyena (*Pachycrocuta brevirostris*), hominin (*Homo erectus*)?
S. sumbaensis	Sumba	MP–LP	-	-

Figure 1 Reconstruction of four insular dwarf proboscideans with their respective mainland ancestors . Mainland proboscideans: 1, *Palaeoloxodon antiquus*; 2, *Mammuthus columbi*; 3, *Stegodon zdanskyi*. Insular proboscideans: 4, *Palaeoloxodon* ‘*mnaidriensis*’; 5, *Palaeoloxodon falconeri*; 6, *Mammuthus exilis*; 7, *Stegodon aurorae*. Based on skeletons at Museo di Paleontología, University of Rome, Italy (1), American Museum of Natural History, New York (2), Taylor Made Fossils, U.S. (3), Museo di Paleontología e Geología G.G. Gemmellaro, Palermo, Italy (4), Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt, Germany (5), Santa Barbara Museum of Natural History, Santa Barbara, U.S. (6), Taga Town Museum, Honshu, Japan (7). Photos 1–2, 4–7 George Lyras, photo 3 courtesy of TaylorMadeFossils.com, reproduced here with permission.

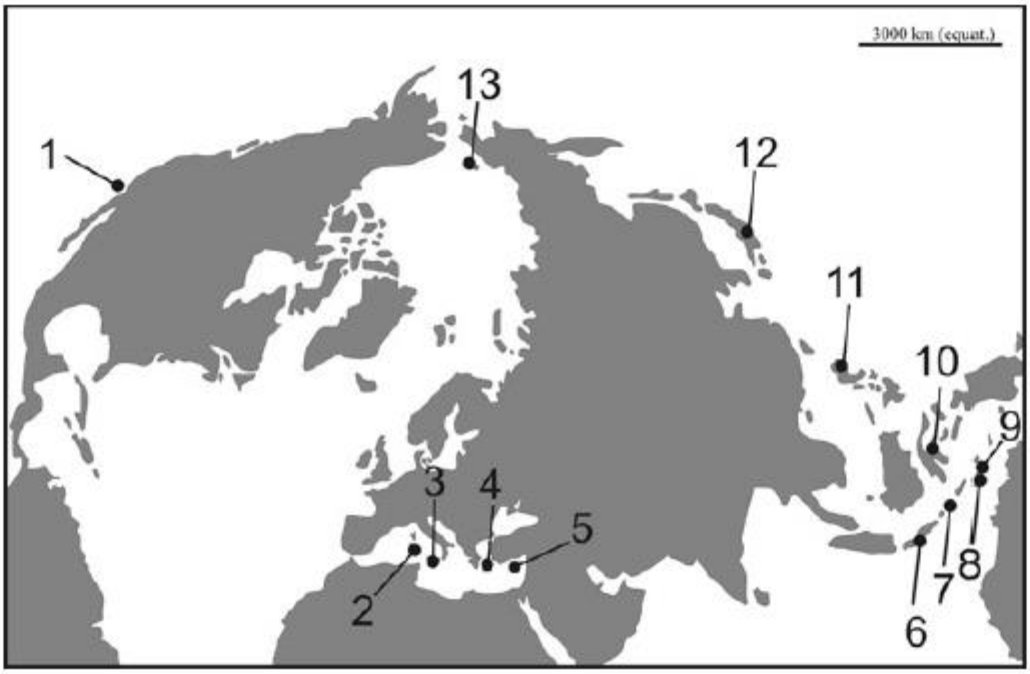

Figure 2 Simplified map showing the geographical position of the islands with insular Proboscidea used in this study. 1, California Channel Islands; 2, Sardinia; 3, Sicily; 4, Islands of the Aegean (Crete, Karpathos, Palaeo-Cyclades, Rhodos); 5, Cyprus; 6, Java; 7, Flores; 8, Sumba; 9, Timor; 10, Sulawesi; 11, Philippines; 12, mainland Japan and the Ryukyu Islands; 13, Wrangel. The coastline is based on a map from d-maps.com.