

# ALLOMETRIC TRENDS IN DWARFING IN THE EXTINCT PLEISTOCENE CHANNEL ISLANDS PYGMY MAMMOTH, *MAMMUTHUS EXILIS*

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**Abstract**—Large mammals on islands, especially proboscideans, hippos, and rhinos, often show a trend toward dwarfing during their isolation. This may be due to limited resources, lack of competition, or lack of predators. How do these animals change their proportions as they become dwarfed? We looked at a large sample of the extinct Pleistocene pygmy mammoths *Mammuthus exilis* from the Channel Islands, and compared the slope of their limb growth from young juveniles to the slopes of size reduction of their limbs from their ancestor, *M. columbi* (Columbian mammoth). The first surprise is that neither the pygmy mammoths nor the living African elephants show growth slopes that are as robust as expected for a huge graviportal mammal. Instead, the humerus, femur, and tibia change isometrically as they grow, and only the ulna tends to grow more robust as the mass increases rapidly. Previous studies have shown that dwarfed hippos and rhinos tended to develop more robust limbs as they became dwarfed. However, the pygmy mammoths only showed more robustness in the shrinking proportions of the ulna, but the humerus, femur, and tibia became reduced in size isometrically. Thus, these expectations of much greater robustness as proboscideans grow huge, or as they reduce in size, is not matched by most of the limbs we examined.

## INTRODUCTION

Many animals on islands show a striking tendency toward body size change with respect to their mainland ancestors. In most cases, smaller species become larger, while large species are dwarfed. It is such a common phenomenon that it has been called the “island rule”, “island effect”, or “Foster’s rule” (Foster, 1964). Very large animals are particularly consistent in their tendency to become dwarfed (Sondaar, 1977; Heaney, 1978; Case, 1978; Wassersug et al., 1979; Prothero and Sereno, 1982; Sondaar et al., 2005; Van de Bergh et al., 2008; Raia and Meiri, 2006; Van der Geer et al., 2010). This is thought to be due to the limited resource base of many islands, decreased competition, changes in reproductive strategies, and the lack of large predators (Sondaar, 1977; Case, 1978; Van de Bergh et al., 2001, 2008; Raia and Meiri, 2006, 2011; Van der Geer et al., 2010).

Dozens of examples of dwarfing have been documented in island non-avian dinosaurs and birds, squamates, sloths, carnivorans, bovids, cervids, and primates (including the controversial “hobbits” or “Flores man”). But insular dwarfism is particularly striking in the largest megamammal groups: proboscideans, rhinoceroses, and hippopotamuses. At least 19 examples of extinct dwarfed proboscideans are known from islands all over the world, including Crete, Sardinia, Malta, Cyprus, Naxos, Rhodes, Japan, the Flores Islands, Java, Mindanao, Sulawesi, Sumba, Timor, and others (Aziz et al., 1995; Van der Geer et al., 2010). The Cretan dwarfed mammoth was only about 1 m high at the shoulder and weighed only about 180 kg (Herridge and Lister, 2012; Larramendi, 2016), a remarkable size reduction from the largest land mammals of the Pleistocene, the mammoths. At least six islands produced dwarfed hippos, including Madagascar, Crete, Malta, Cyprus, Sicily, and Bumaiyu (Aziz and Van de Bergh, 1995; Van der Geer et al., 2010). There are also three instances of dwarfed rhinoceroses known, two from the Miocene of Texas (Prothero and Sereno, 1982), and one from the Pleistocene of the

Philippines (Renema, 2007).

Previous studies have shown that island dwarfs often end up with more robust limbs than their mainland counterparts (Prothero and Sereno, 1982). But how do they acquire these limb proportions? Is it possible to see allometric trends for growth from juvenile to adult? Do large mammals acquire their limb proportions while dwarfing with the same rate of change as they grew those limbs in non-dwarfed relatives?

Such research is usually limited because we have few or no juveniles of the dwarfed island species to estimate how they grew to adulthood. However, juvenile specimens along with fully-grown individuals of the Channel Islands pygmy mammoth, *Mammuthus exilis* (Stock and Furlong, 1928; Agenbroad, 2001, 2002, 2005, 2009, 2010, 2012; Agenbroad and Morris, 1999; Agenbroad et al., 1999) are common enough in the collections of the Santa Barbara Museum of Natural History (Fig. 1), and the Natural History Museum of Los Angeles County to determine their ontogenetic growth patterns. Although preliminary comparison between *M. exilis* and *M. columbi* limb lengths have been made previously (Roth, 1982; Agenbroad, 2002), continued collecting efforts have provided a more robust sample across age groups. These specimens allow us to look at how the adults *M. exilis* became dwarfed from their ancestors, the Columbian mammoths (*M. columbi*) of the mainland.

## METHODS

We measured as many complete unbroken limb elements (humerus, ulna, femur, tibia) of *M. exilis* as we could find in the collections of the Santa Barbara Museum of Natural History and the Natural History Museum of Los Angeles County. Sample sizes are given in Table 1. The ulna is the main weight-bearing element of the distal forelimb in the proboscideans, so it was measured instead of the radius. To make all the data comparable with the measurements of growing mammalian limbs made by Kilbourne and Makovicky (2012), we used a flexible metric tape measure to find the circumference of the midshaft and the



FIGURE 1. A growth series of humeri of *Mammuthus exilis* compared to the adult humerus of *M. columbi* (bone on extreme left), on display at the Santa Barbara Museum of Natural History.

TABLE 1. Humerus data of various mammals. **CI** = slope confidence interval limits; **L.S.SLOPE** = least squares slope; **RMA** = reduced major axis slope. **(G)** = gracile; **(I)** = isometric; **(R)** = robust. *Loxodonta africana* data from Kilbourne and Makovicky (2012). Mammoth dwarfing slope estimated in two ways: RMA analysis of the pooled data from adult *M. exilis* and *M. columbi*; and the slope of the line connecting the means of adult *M. exilis* and *M. columbi* (thus, not mixing intraspecific and interspecific variation)

TAXON	N	L.S.SLOPE	Y-INTERCEPT	R <sup>2</sup>	CI	RMA
<b>Humerus</b>						
<i>M. exilis</i> growth	14	1.06	0.452	0.940	0.94,1.27	1.09(I)
<i>L. africana</i> growth	11		1.63	0.945	0.62,1.03	0.90 (I)
Mammoth dwarfing RMA	30	0.754	1.68	0.900	0.78,1.12	0.93 (I)
Mammoth dwarfing means	2	0.757	1.58			
<b>Ulna</b>						
<i>M. exilis</i> growth	11	1.06	0.452	0.879	0.70,1.17	0.91(I)
<i>L. africana</i> growth	7		1.85	0.984	0.63,0.95	0.86 (R)
Mammoth dwarfing RMA	12	0.538	1.06	0.947	0.72,0.91	0.81 (R)
Mammoth dwarfing means	2	0.583	2.16			
<b>Femur</b>						
<i>M. exilis</i> growth	8	0.947	1.16	0.879	0.67,1.84	1.11(I)
<i>L. africana</i> growth	11		1.56	0.972	0.70,1.06	0.95 (I)
Mammoth dwarfing RMA	35	0.888	1.38	0.961	0.81,1.05	0.92 (I)
Mammoth dwarfing means	2	0.998	0.72			
<b>Tibia</b>						
<i>M. exilis</i> growth	30	0.778	1.15	0.753	0.74,1.08	0.89(I)
<i>L. africana</i> growth	10		1.74	0.940	0.59,1.09	0.97(I)
Mammoth dwarfing RMA	41	0.888	1.38	0.896	0.88,1.14	1.00 (I)
Mammoth dwarfing means	2	1.111	3.38			

length of the diaphysis (shaft of the limb elements) excluding the epiphyseal caps. These are often missing in juvenile limb elements, since they are still cartilage or only poorly ossified and weakly attached to the growth surface of the diaphysis. Roth (1982, 1984) demonstrated the considerable variability in limb bone fusion sequences in modern elephants: intramembral (i.e., distal versus proximal epiphyses of the same bone), intermembral (e.g., femur versus humerus), and interspecific (e.g., *Elephas maximus* versus *Loxodonta africana*). However, limb bone growth ceases with fusion so that complete fusion signifies a physically mature element (Nilsson and Baron, 2004). We noted complete fusion in the measured *M. exilis* specimens to identify developmentally mature adults, although we acknowledge that the unfused specimens are not all developmentally equivalent (Roth, 1982, 1984; Herridge, 2010). The completely fused specimens were used to assess interspecific static adult allometry of dwarfing between *M. columbi* and *M. exilis*. We also compared the ontogenetic allometry between unfused and completely fused *M. exilis* specimens, generally expecting isometric growth (Herridge, 2010). The widely varying sizes of completely fused *M. exilis* limb bones obfuscate the growth series and subsequently make ontogenetic scaling indistinguishable from geometric scaling (Roth, 1982, 1984, 1990).

Our data for adult Columbian mammoths comes from a variety of museums, including the Denver Museum of Nature and Science, Denver, Colorado, the Mammoth Site of Hot Springs, South Dakota (Agenbroad, 1994), the Waco Mammoth National Monument in Waco, Texas, and numerous other specimens in the following museums: the La Brea Tar Pits and Museum (formerly the George C. Page Museum of La Brea Discoveries), Los Angeles, California; the Natural History Museum of Los Angeles County; the Western Science Center, Hemet, California; and the Sternberg Museum in Hays, Kansas.

Following the conventions of most allometric studies, raw data were converted to natural logs and plotted in log-log graphs, so that the exponential slope of allometry would give a simple linear slope. We used Excel to calculate the simple least-squares regression of the data. Since there is no dependent or

independent variable in this study (an assumption of the least-squares regression method), we adopted the more commonly used Reduced Major Axis (RMA) method of correlation to determine the slope between the two variables (calculated using the R program “smatr”)(Warton et al., 2007, 2012).

We followed the conventions of Kilbourne and Makovicky (2012) in plotting length on the Y axis vs. circumference on the X axis, which should give an isometric slope in log-log space of approximately 1.0 (linear dimension vs. linear dimension), and allometric slopes greater than 1.0 if the limb becomes more gracile (positive allometry), and less than 1.0 if the limb becomes more robust with increasing size (negative allometry). This allowed us to compare our results to the data of living mammals examined by Kilbourne and Makovicky (2012).

## RESULTS

Results of our analysis are shown in Table 1 and in Figure 2. Despite expectations, the modern African elephant (*Loxodonta africana*) does not show particularly robust limb growth through ontogeny. The prevailing wisdom is that as an elephant grows from a relatively small calf to a huge adult, its limbs should grow progressively stouter and more robust compared to the increase in length. Christiansen (2007) claimed significant negative allometry and increasing robustness in his analyses of the growth of the two large species of living elephants, *Loxodonta africana* and *Elephas maximus* (Asian elephant) but isometry could not be ruled out given the error limits of his analysis. In contrast, Kilbourne and Makovicky (2012) found that three of the four limbs (humerus, femur, tibia) in *Loxodonta africana* show isometric growth, with slopes of 0.90, 0.95, and 0.97 for the humerus, femur, and tibia respectively, all within the confidence limits that include the isometric slope of 1.0. Only the ulna (slope = 0.86) was significantly more robust. Kilbourne and Makovicky (2012) suggested that the difference of their results with previous studies might be because they had a greater size range in their sample than did Christiansen (2007). To test this, they removed the smallest specimen from their sample and obtained negative allometric slopes comparable to those

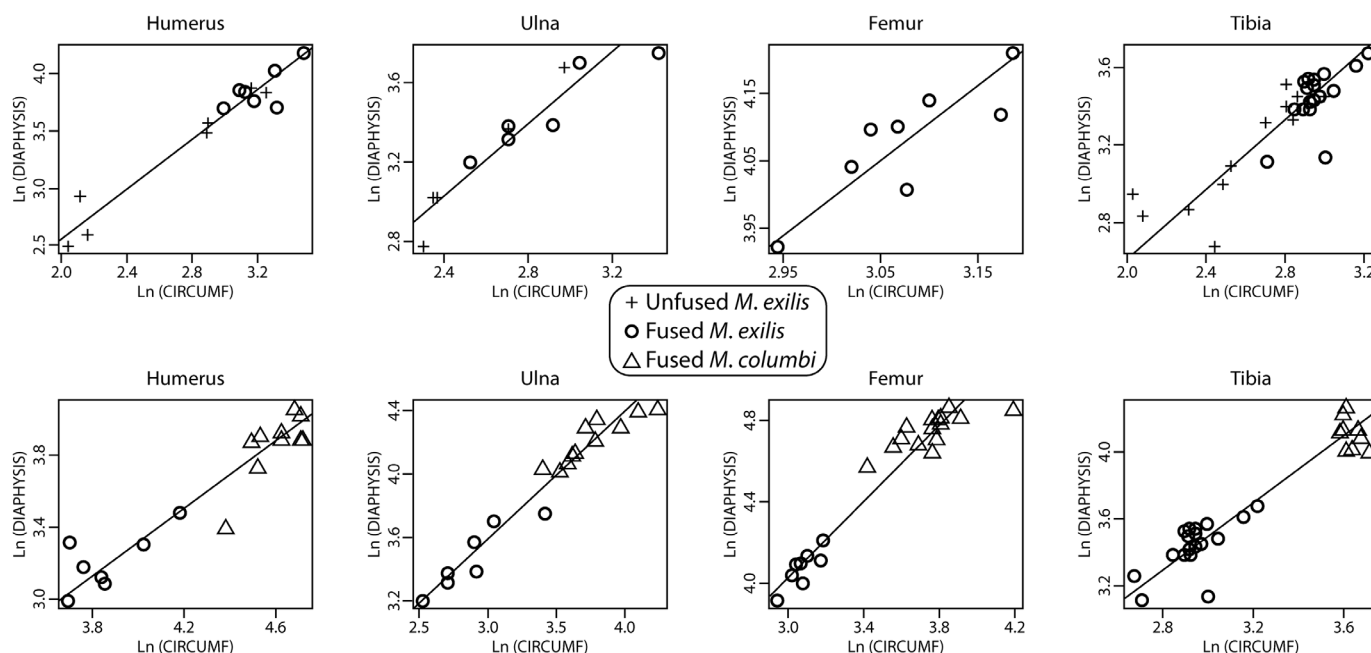


FIGURE 2. Bivariate log-log plots of the data with the circumference on the x-axis and the length on the y-axis, with the line of the RMA slope shown. In the top row is the growth data of the pygmy mammoth, *M. exilis*. In the bottom row is the comparison of the adults of the pygmy mammoth (open circles) with adults of their presumed ancestor, the Columbian mammoth (triangles).

found by Christiansen (2007). In fact, several previous studies (Johnson and Buss, 1965; Laws, 1966; Laws et al., 1975; Roth, 1982, 1984, 1990; Raia et al., 2001) have shown isometric growth in proboscidean limbs, so the outdated expectation that they should grow more robust has been long refuted.

Kilbourne and Makovicky (2012) also suggested that there may be two growth trajectories in these living proboscideans, with a more isometric trend in the younger juveniles changing to a negative allometric trend later in ontogeny, but their sample of juveniles is too small to determine this. In fact, this change of growth trajectory has already been demonstrated in proboscideans (Herridge, 2010).

Growth of *M. exilis* from juveniles to adults follows a similar trend (Table 1, Fig. 2) to that of Kilbourne and Makovicky (2012), and in contrast with the results of Christiansen (2007). The growth slopes of the humerus, femur, and tibia were 1.09, 1.11, and 0.89, respectively, all which were not significantly different from 1.0 given their confidence intervals. In the case of the pygmy mammoth, even the slope of the ulna was 0.91, not significantly different from isometry. Thus, all four limbs in the pygmy mammoth show isometric rather than allometric growth, as expected from previous studies on dwarf mammoths (Roth, 1982, 1984, 1990; Herridge, 2010).

The main question, however, is whether the slope of size *decrease* due to dwarfing shows the same values as the slopes of size *increase* due to ontogenetic growth? Previous studies (Prothero and Sereno, 1982) found that dwarfed versions of hippos and rhinos tended to have slightly more robust limb proportions compared to their larger counterparts. There are two ways to calculate these slopes. One way would be to pool all the data from the adult *M. columbi* and adult *M. exilis*, and calculate an RMA slope through the entire combined data set (Fig. 2). In this instance (Table 1), we find that the dwarfing slope of the humerus was 0.93, and for the ulna was 0.81, with the ulna significantly more robust than expected for isometric growth, while the humerus shows isometry within the error limits of the slope. The slope for the femur (0.92) and tibia (1.00) calculated this way do not depart significantly from isometry, so the robustness trends occurs only in the forelimb. Thus, we found isometry in three out of four limbs; only the ulna was significantly more robust. By contrast, Herridge (2010) found isometry in all four limbs in the Mediterranean dwarf elephants and mammoths.

However, as Prothero and Sereno (1982) pointed out, mixing the data for two species this way can lead to problems. If one species has a much larger sample size than the other, it will dictate the slope and could give a spurious result. Many previous studies made this mistake of mixing intraspecific variation with interspecific variation. To address the problem, Prothero and Sereno (1982) calculated a slope between the mean of one species and the mean of another. These results are also shown in Table 1. The slope calculated by this method gives essentially the same result (probably because the sample sizes of both species are roughly comparable). The slope for the ulna (0.58) is similar to the slopes calculated by determining the RMA of the pooled samples of both species, but the slope for the humerus (0.75) is significantly more robust than the slope obtained by the other method (0.93). The ulna slope is significantly more robust than expected compared to the confidence intervals around the growth slope of *M. exilis*. Thus, the ulna shows a robust slope of change during dwarfing, whether the slope is calculated using an RMA of the pooled sample, or by calculating the slope of the means of the two species and avoiding mixing intraspecific and interspecific variability. Likewise, the slopes for the hind limb are isometric using the method of calculating the slope between the means of the two species. The slopes for the femur was 0.99 and for the tibia 1.11, both essentially isometric size reduction slopes, and not significantly different from the slope calculated

by doing a RMA fit of the pooled sample of both species.

This isometric reduction of humerus, femora and tibiae is at odds with previous estimates that showed that *M. exilis* femora were proportionately longer than the other limb bones (Agenbroad et al., 1999). However, Agenbroad's analysis only quantified length and had considerably smaller samples sizes. By contrast, this study measured 11 ulnae and 30 tibiae, while Agenbroad et al. (1999) had only 5 ulnae and 1 tibia. Further, the isometric reduction of *M. exilis* humerus and hindlimbs in this study is comparable to the isometric reduction seen in the hindlimbs of the Mediterranean dwarf *Palaeoloxodon falconeri* (Herridge, 2010).

## CONCLUSION

The previous literature on growth of graviportal mammals predicted that both living and extinct proboscideans should show increased robustness as their masses increased by a power of three during growth (Christiansen, 2007). Instead, the living African elephant shows isometric growth in three limbs (humerus, femur, tibia) and is only more robust in growth in the ulna. Our data indicate that the growth of the Channel Islands pygmy mammoth exhibited isometry in all four limbs.

How do the slopes of growth of pygmy mammoths compare to the slope of their size decrease from their full-sized ancestor? From previous literature, it would be expected that the limbs of the dwarfs would be more robust than their ancestors. We found that on of the forelimb segments (humerus) was isometric, but the other (ulna) was robust, while the hindlimb segments (femur, tibia) were isometric in their size reduction, just as in their growth. Thus, the simplistic predictions based on models of graviportal growth, and of size reduction, are not borne out when real examples are studied. The reasons for this are not immediately clear, but perhaps the Channel Island pygmy mammoths needed "low-gear locomotion" to handle the steep mountainous island terrain, as suggested by Sondaar (1977) for the dwarfed proboscideans of Mediterranean islands. Alternatively, the negative allometry of the ulna may reflect the increased load of a disproportionately large skull (Herridge, 2010).

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## REFERENCES

- Agenbroad, L.D., 1994, Taxonomy of North American *Mammuthus* and biometrics of the Hot Springs mammoths; in Agenbroad, L.D., and Mead, J. I., eds., The Hot Springs Mammoth Site: The Mammoth Site of South Dakota, Hot Springs, SD, p. 158-207.
- Agenbroad, L.D., 2001, Channel Islands (USA) pygmy mammoths (*Mammuthus exilis*) compared and contrasted with *M. columbi*, their continental ancestral stock. La terra degli Elefanti: Atti del 1st Congresso Internazionale (The World of Elephants: Proceedings of the 1st International Congress). Rome: Consiglio Nazionale delle Ricerche, p. 473-475.
- Agenbroad, L.D., 2002, New localities, chronology, and comparisons for the pygmy mammoth (*Mammuthus exilis*): 1994-1998; in Browne, D., Mitchell, K. and Chaney, H., eds., Proceedings of the Fifth California Islands Symposium: USDI Minerals Management Service and The Santa Barbara Museum of Natural History, Santa

- Barbara, p. 518–524.
- Agenbroad, L.D., 2005, North American proboscideans: Mammoths: The state of knowledge, 2003. *Quaternary International*, v. 126–128, p. 73–92.
- Agenbroad, L.D., 2009, *Mammuthus exilis* from the Channel Islands: height, mass, and geologic age; in Damiani C.C. and Garcelon D.K., eds., *Symposium Proceedings of the Seventh California Islands: Institute for Wildlife Studies, Arcata*, p. 15–19.
- Agenbroad, L.D., 2010, *Mammuthus exilis* from the Channel Islands: height, mass, and geologic age; in Damiani C.C. and Garcelon D.K., eds., *Symposium Proceedings of the 7th California Islands Symposium: Institute for Wildlife Studies, Arcata*, p. 17.
- Agenbroad, L.D., 2012, Giants and pygmies: Mammoths of Santa Rosa Island, California (USA): *Quaternary International*, v. 255, p. 2–8.
- Agenbroad, L.D., and Morris, D.P., 1999, Giant island/pygmy mammoths: The Late Pleistocene prehistory of Channel Islands National Park: National Park Service Paleontological Research, v. 4, p. 35–39.
- Agenbroad, L.D., Morris, D.P., and Roth, V.L., 1999, Pygmy mammoths *Mammuthus exilis* from Channel Islands National Park, California (USA); in Haynes, G., Klimowicz, J., and Reumer, J.W.F., eds., *Mammoths and the Mammoth Fauna: Studies of an Extinct Ecosystem: Deinsea*, v. 6, p. 80–102.
- Aziz, F., and Van den Bergh, G.D., 1995, A dwarf *Stegodon* from Sambungmacan (Central Java, Indonesia). *Proceedings of the Koninklijke Nederlandse Akademie Wetensch.*, v. 98, p. 229–241.
- Case, T.J., 1978, A general explanation for insular body size trends in terrestrial vertebrates: *Ecology*, v. 59, p. 1–18.
- Christiansen, P., 2007, Long-bone geometry of columnar-limbed animals: Allometry of the proboscidean appendicular skeleton: *Zoological Journal of the Linnean Society*, v. 149, p. 423–436.
- Foster, J.B., 1964, The evolution of mammals on islands: *Nature*, v. 202, p. 234–235.
- Heaney, L.R., 1978, Island area and body size of insular mammals: Evidence from the tricolored squirrel (*Callosciurus prevosti*) of Southeast Asia: *Evolution*, v. 32, p. 29–44.
- Herridge, V.L., 2010, Dwarf elephants on Mediterranean islands: A natural experiment in parallel evolution [Ph.D. dissertation]: University College London, London, UK; accessible online at [http://discovery.ucl.ac.uk/133456/2/133456\\_Vol.2.pdf](http://discovery.ucl.ac.uk/133456/2/133456_Vol.2.pdf)
- Herridge, V.L., and Lister, A.M., 2012, Extreme insular dwarfism evolved in a mammoth: *Proceedings of the Royal Society B: Biological Sciences*, v. 279, p. 3193.
- Johnson, O.W., and Buss, I.O., 1965, Molariform teeth of male African elephants in relation to age, body dimensions, and growth: *Journal of Mammalogy*, v. 46, p. 373–384.
- Kilbourne, B.M., and Makovicky, P.J., 2012, Postnatal long bone growth in terrestrial placental mammals: Allometry, life history, and organismal traits: *Journal of Morphology*, v. 273, p. 1111–1126.
- Larramendi, A., 2016, Shoulder height, body mass, and shape of proboscideans: *Acta Palaeontologica Polonica*, v. 61, p. 537–574.
- Laws, R.M., 1966, Age criteria for the African elephant *Loxodonta a. africana*: *East African Wildlife Journal*, v. 4, p. 1–37.
- Laws, R.M., Parker, I.S.C., and Johnstone, R.C.B., 1975, Elephants and their Habitats: The Ecology of Elephants in North Bunyoro, Uganda: Clarendon Press, Oxford, UK, p. 1–376.
- Nilsson, O., and Baron, J., 2004, Fundamental limits on longitudinal bone growth: Growth plate senescence and epiphyseal fusion: *Trends in Endocrinology and Metabolism*, v. 15, p. 370–374.
- Prothero, D.R., and Sereno, P.C., 1982, Allometry and paleoecology of medial Miocene dwarf rhinoceroses from the Texas Gulf Coastal Plain: *Paleobiology*, v. 8, p. 16–30.
- Raia, P., and Meiri, S., 2006, The island rule in large mammals: Paleontology meets ecology: *Evolution*, v. 60, p. 1731–1742.
- Raia, P., and Meiri, S., 2011, The tempo and mode of evolution: Body sizes of island mammals: *Evolution*, v. 65, p. 1927–1934.
- Renema, W., 2007, *Biogeography, Time and Place: Distribution, Barriers, and Islands*: Springer Verlag, Berlin
- Roth, V.L., 1982, Dwarf mammoths from the Santa Barbara, California, Channel Islands: size, shape, development, and evolution [Ph.D. dissertation]: Yale University, New Haven, CT.
- Roth, V.L., 1984, How elephants grow: Heterochrony and the calibration of developmental stages in some fossil and living species: *Journal of Vertebrate Paleontology*, v. 4, p. 126–145.
- Roth, V.L., 1990, Insular dwarf elephants—a case study in body mass estimation and ecological inference; in Damuth, J., and MacFadden, B.J., eds., *Body Size in Mammalian Paleobiology: Estimation and Biological Implications*: Cambridge University Press, Cambridge, UK, p. 151–180.
- Sondaar, P.Y., 1977, Insularity and its effect on mammal evolution; in Hecht, M. K., Goody, P. C., and Hecht, B. M., eds., *Major Patterns of Vertebrate Evolution*: Plenum Press; New York, p. 671–707.
- Sondaar, P.Y., and van der Geer, A.A.E., 2005, Evolution and extinction of Plio-Pleistocene island ungulates: *International Journal of the French Quaternary Association*, v. 2, p. 241–256.
- Stock, C., and E.L. Furlong, 1928, The Pleistocene elephants of Santa Rosa Island, California: *Science*, v. 68, p. 140–141
- Van Den Bergh, G.D., Rokhus Due Awe, Morwood, M.J., Sutikna, T., Jatmiko, W., Saptomo, E., 2008, The youngest *Stegodon* remains in Southeast Asia from the Late Pleistocene archeological site Liang Bua, Flores, Indonesia: *Quaternary International*,
- Van Der Geer, A., G. Lyras, J. de Vos, and Dermitzakis, M., 2010, Evolution of island mammals: adaptation and extinction of placental mammals on islands. Wiley-Blackwell, Chichester, West Sussex, U.
- Van der Geer, A., Lyras, G., de Vos, J., and Dermitzakis, M., 2010, Evolution of Island Mammals: Adaptation and Extinction of Placental Mammals on Islands: Wiley-Blackwell, Chichester, UK.
- Warton, D.I., Wright, I.J., Falster, D.S., and Westoby, M., 2007, Bivariate line-fitting methods for allometry: *Biological Reviews*, v. 81, p. 259–291.
- Warton, D.I., Duursman, R., Falster, D.S., and Taskinen, S., 2012, SMATR 3—an R package for estimation and inference about allometric lines: *Methods in Ecology and Evolution*, v. 2, p. 257–259.
- Wassersug, R.J., Yang, H., Sepkoski, J., and Raup, D.M., 1979, The evolution of body size on islands: A computer simulation: *American Naturalist*, v. 114, p. 287–295.

