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Revisiting the Intricacies and Theories of the Island Rule: Understanding the Trends of Insular Body Size Evolution

Bao Lam (Peter)

Abstract

The Island Rule is the observed tendency for island isolated animals to either grow or shrink in size compared to their mainland counterparts. Though the phenomenon was initially observed to only occur in a handful of taxa (carnivores, artiodactyls, rodents, and lagomorphs), it was expanded to include 2 major trends: 1) Large animals from the mainland tend to shrink on islands, and 2) Small animals from the mainland tend to grow. The mechanisms attributed to those two trends generally involved factors that include resource availability, ecological release, niche expansion, predation, competition, and life history traits. Other theories were also proposed, but each had their own caveats that did not apply as a general rule. The study of the island rule, and island biogeography in general, allows a simplified view of dynamics that may possibly be reflected on mainlands. An example of this includes ecological release and niche expansion in the case of mammals following the Cretaceous/Tertiary extinction event. Following the collapse of dinosaurian prevalence, the relatively small mammals were given the opportunity to grow and speciate accordingly.

However, upon further observation, the island rule in its generality did not encompass all fauna, and exceptions were found for the insular trend. Bergmann's rule of latitudinal differentiation for body sizes, as well as general climate change, have been found to potentially influence body size shifts as well. As a result, some have chosen to strip the Island Rule of its status as a virtual law, and instead explain the trend as being a

phenomenon greatly affected by both biotic and abiotic components to determine insular body size. Regardless of the specific definition, it is maintained that a strong understanding of island processes may lend a better understanding of mainland developmental ecology and evolution.

Introduction

The field of island biogeography made its first appearance in the academic world under the guidance of Robert MacArthur and E. O. Wilson. Their book, *The Theory of Island Biogeography*, outlined the fundamentals of the new subdiscipline of biology (Quammen, 1996). Though originally directed toward the study of species number and ecology on literal islands, island biogeography has expanded to include mainland “islands” where sections of land are isolated. Specifically, the isolative quality of islands has afforded ecologists the ability to study on a small scale the patterns of acquired niche recognition in novel species (Case, 1978). Islands, whether literal or virtual, represent much simpler systems due to their having less complicated and stronger selective pressures compared to mainland dynamics. An example of the usefulness of islands in biogeography can be seen in Wilson’s experiment in which he fumigates a mangrove island to observe the population of a newly uninhabited ecosystem. As it was defined by David Quammen, author of the book, *Song of the Dodo*, “...biogeography does more than ask *Which species?* and *Where*. It also asks *Why?* and, what is sometimes more crucial, *Why not?*” (Quammen, 1996).

Early in the history of island biogeography there was a trend observed for insular fauna to differ in size from mainland counterparts. Specifically, dwarfism seemed to be exhibited by insular carnivores, artiodactyls (hoofed animals), and lagomorphs



Figure 1. Artist's representation of the Island Rule effect taking place on deer. The smallest deer measures 55-65 cm at shoulder height, and the middle sized deer measures at 80-100 cm at shoulder height. (Benton 2010)

(rabbits and hares). Conversely, gigantism among insular fauna was also observed and found primarily in rodents and occasionally marsupials (Foster, 1964). The phenomenon drew the attention of biogeographers as it became increasingly evident that the trend for size difference between islands and mainland was not a chance happening. The patterning was so thoroughly observed that it became known as the Island Rule for the ubiquity of the event among islands (Van Valen, 1973). The rule, however, was modified from Foster's original description. Instead of being limited to the taxa Foster initially described, it generally stated that large mainland species decrease in size and small mainland species grow on island habitats. Several explanations are proffered to account for this trend, of which the more credible hypotheses include: 1) Resources act as a limiting factor, 2) Ecological release, 3) Niche expansion, 4) Lack of interspecies competition, and 5) The effect of predators or the absence therein (Lomolino, 2005).

Body size on islands is especially fundamental in that it directly relates to immigration potential, ecological interactions, and resource utilization. The limited size of islands often facilitates dispersed fauna to adjust metabolism and diet according to the specifics of the insular environment (Lomolino, 2005). Islands are well known to vary in a number of aspects, not least withstanding primary productivity, climate, size, and

available resources. Due to the intrinsic uniqueness of individual islands, there remains a great deal of information that must be accounted for in order to understand the variation of insular body size evolution (Lomolino, 2005). From the study of the island rule and its effects, it is possible to better understand the dynamics that govern insular evolution, which in turn may shed light on processes potentially mirrored in mainland animal development.

The Influence of Resources and the Environment

The theory of island size evolution follows two major lines of thinking: 1) Larger animals will be selected for smaller size due to limited available energy, and 2) Small animals will grow in size depending on island area and the presence of predation. The former involves the necessity of island populations to curtail previous energy allocations thus leading to evolutionary dwarfism. The latter case involves the growth of small taxa due to new access to larger amounts of resources on islands too small to support predators. This in turn decreases competition and allows for a higher average of energy consumption per animal (Lomolino, 2005). An animal's body size is likely to determine the amount of energy it requires from an environment. As a result, evolutionary forces will be selected for the optimum body size suited for that particular location (Case, 1978). It is generally agreed upon that highly abundant and energetically available foods tend to lead to an increase in size (Raia & Meiri, 2006).

The trend for increased body size, however, is sometimes tempered by physical caveats. Perching behavior and flight in birds will sometimes prevent avifauna from

progressing past a certain size in order to retain those abilities. Other animals, such as lizards and burrowing rodents, also depend on maintaining relatively small sizes to preserve crucial aspects of their behavior (i.e. vertical movement for lizards and prevention of tunnel collapse for rodents) (Case, 1978). The availability of food does indeed play a factor in determining body size, especially in carnivores, but it appears that prey size also plays a factor in evolutionary body shifts. Schoener, in his 1969 article titled “Models of Optimum size for Solitary Predators”, describes the event in which predators will evolve to best suit the size of their prey: large prey call for large predators, and small prey call for smaller predators (Schoener, 1969).

This occurrence of prey affecting predator size is seen in a study regarding Australian Tiger snakes where adult sizes closely correspond to the local prey available (Keogh *et al.*, 2005). In Keogh *et al.*'s study, the authors analyzed the evolution of Tiger Snakes on multiple islands and found that body size evolution arose independently in several populations according to the size type of the prey animals. Analysis of these separate Tiger Snake populations has shown that their size shifts may also be due in part to a genetic and adaptive plasticity that allowed for rapid size change (Keogh *et al.*, 2005). Keogh *et al.*'s results are confirmed somewhat by Raia and Meiri, whose results regarding large mammals have shown that carnivore size is affected primarily through resource availability. From their study, it appeared that island area, phylogenetic affinities, and ancestral body size had little or no effect on carnivorous animals. However, dwarfism was also observed in carnivores where there was no occurrence of large prey to act as a selective force for larger sizes. An example of this is the case of island foxes (*Urocyon littoralis*) regarding the availability of rabbits. In the presence of rabbits, island foxes

retain relatively large body morphs, but will evolve dwarfed forms if the rabbits are absent from island ecology (Raia & Meiri, 2006).

Concerning dwarfism, a reduction in body size may be attributed to a genetic response in relation to environmental stresses. Insular habitats can greatly differ from mainland ecology, often lending a lower degree of resource availability unable to sustain larger body sizes (Case, 1978; Lomolino, 2005; Lomolino *et al.*, 2006). As a result, the organism's genetic code gradually acts to optimize resource utilization by producing reduced size morphologies best suited to the insular environment (Case, 1978; Meiri *et al.*, 2006; Wasserburg *et al.*, 1979). Other explanations include the theory that smaller animals are better adapted to surviving periods of resource depression, their inherent small size entailing a decreased need for large amounts of food. Subsequently, natural selection acts against larger animals in the population and selects for only the sufficiently small to survive and propagate. This differs from genetic plasticity in that an active selection takes place to isolate individuals already encoded for relatively decreased body size (Lomolino, 2005). As it was stated above, size shifts tending toward pygmy forms also apply to artiodactyls (even toed ungulates). It is theorized that the need for anti-predatory behavior and competition between species is unnecessary on some islands, thereby reducing the need to maintain the larger body sizes seen in mainland environments. The energy is instead directed toward reproduction, which as a result leads to decreased adult body mass (Raia & Meiri, 2006).

The scenarios for explaining island dwarfism are also compounded by the fact that large herbivores, such as deer, elephants, rhinoceroses, etc. often require large tracts of

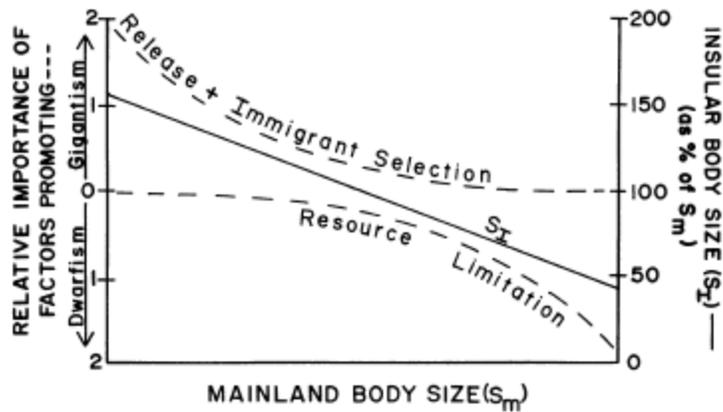


Figure 2. Simple graph showing the relative importance of factors that promote dwarfism (resource limitation) and gigantism (ecological release and immigrant selection) on islands. (Lomolino 1985)

land to accommodate foraging behavior. Obviously, such behavior for island bound fauna would be greatly limited. As a result, dwarfing is the alternative solution for emigrated herbivores in the face of extinction (Benton *et al.*, 2010).

The availability of resources is a broad generalization of how the island rule may operate. As was discussed, insular populations are able to either grow in size or shrink almost exclusively dependent on type and abundance of resources present. As a general theory, resource availability includes a number of aspects that can be further broken down into sub categories.

Ecological Release and Niche Expansion

Of the many possible scenarios that may account for insular size change, ecological release and niche expansion are perhaps two theories that are integral to understanding island species dynamics (Benton *et al.*, 2010). The premise of ecological release is based on the idea that, once species find themselves isolated in an island habitat,

they are freed from the ecological pressures that they were originally subjected to on the mainland. This entails a decrease in the selective pressures attributed to competitors, predators, and parasites (Foster, 1964, Lomolino, 2005, Raia & Meiri, 2006). The absence of large predatory birds or mammals allows for smaller insularly established animals to become larger due to the absence of mainland threats. Typically, large herbivores and higher order predators, which are usually found in low abundance on the mainland, are rarely ever seen in island environments (Benton *et al.*, 2010). The witnessed gigantism of island avifauna is likely explained by ecological release as well. With the threat of predators removed, insular birds have been observed to relegate energy toward a larger morphology that is typically coupled with wing reduction and flightlessness, as was seen in the now extinct example of the dodo bird (Benton *et al.*, 2010).

Related to ecological release is the concept of niche expansion, which details the capacity for species to capitalize on new diets and opportunities that can be found in insular habitats. The sheer dearth of occupants on an island, as well as the potential absence of predators, allow for a virtual re-acclimation of species to new biotic roles. Small sized animals from the mainland are then able to capture niches that once belonged to the middle to large-sized species that dominated the mainland (Benton *et al.*, 2010; Meiri *et al.*, 2006; Millien & Damuth, 2004).

The concepts of ecological release and niche expansion complement one another, specifically in that the former begets the latter. With the removal of selective pressures that were present during mainland species dynamics, insular fauna are allowed to adapt and evolve in a different trajectory than their mainland counterparts. Furthermore, insular

adaptation and radiation attributed to ecological release and niche expansion may be similar to processes that govern species' evolution following large scale extinction (e.g. mammalian replacement of former dinosaur-filled niches).

Life History Traits

Among the theories more strongly evidenced for explaining the island rule, there is also the belief that optimization of life history traits act as factors for size differentiation (Benton *et al.*, 2010). Metabolic rate, gestation time, time until maturity, birth and death rates, trophic level, and population data are some of the aspects of a species that generally determine an organism's size potential. Consequently, open island habitats may allow for body size shifts among animals largely as a result of those life traits. For example, r-selected organisms, those that are generally small in size with high numbering progeny, short lifetimes, and relatively low survivability rates, may be especially well suited to adapting to isolated island environments (Lomolino *et al.*, 2006, Raia & Meiri, 2006). Their capacity to rapidly fill empty niches and evolve accordingly with speed may allow them to gain differentiated size when compared to mainland counterparts. Specifically, this theory of optimization is important to recognize due to the implication that trends observed for the island rule may not follow traditionally prescribed routes (Benton *et al.*, 2010).

Rather than the simplistic statement that small species will grow large and large species will grow small on islands, body size evolution may be a result of circumstantial events or factors that were pre-determined prior to colonization for some populations.

The capacity for change may only proceed to certain extents dependent on limiting factors of the organism observed. A gross simplification of this process can be equated to the growth potential of arthropods: an insect can only grow as large as their body structure allows (i.e. there will most likely never be hordes of giant ants large enough to carry away adults) (Palmer 2002).

Other models for the Island Rule

There remain several other explanations that have been proposed to account for size change in insular vertebrates. However, they can be argued to lack in evidence and strength compared to the theories discussed above. An early hypothesis attributed to trends observed in island fauna was presented by M.C.T. Hinton (1926) and I. Cowan (1935) in which the possibility of relict populations could account for the Island Rule. The relict population hypothesis centered on the belief that mainland competition, as well as other external factors led to the selection against larger body morphs. Conversely, the same selective forces that acted on the mainland did not apply to insular habitats. As a result, fauna isolated on islands were capable of maintaining their initial large size. Hinton and Cowan apply this theory expressly to rodent populations as an example, possibly due to the success that rodents have in dispersal and population abundance (Benton *et al.*, 2010). However, this hypothesis operates on several tenuous premises. The relict population viewpoint implies that ancestral populations were widespread enough to have reached island environments, suggesting that modern large rodents seen on islands today were once incredibly profuse. Foster later rejected this theory on the

basis that differences in giant insular rodents debunk that hypothesis. Foster argued that rodents originating from a widespread ancestral population would evince similar body plan details characteristic of a common ancestor (Keogh *et al.*, 2005). Additionally, there is little evidence that smaller body morphs of rodents actually displaced larger mainland forms. There is also no clear indication that large body plans in rodents are the default forms from an evolutionary perspective (Benton *et al.*, 2010; Lomolino, 2005).

Another theory that was suggested to explain differential body morphs was detailed by Lomolino (2005), where he uses the shipwreck metaphor to describe how some large forms may persist on islands. The shipwreck

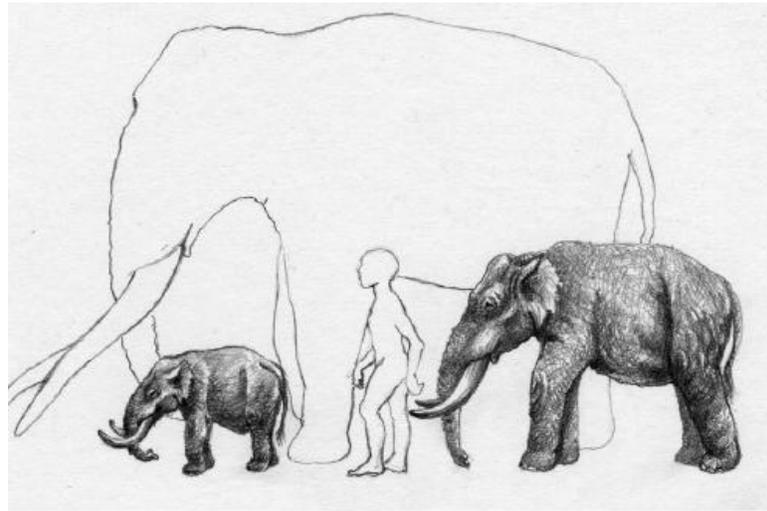


Figure 3. Artist's reconstruction using the outline of a human for scale. The outline of the elephant in the back is the supposed ancestor of the two smaller body morphs. The elephant on the left measures 1.6-1.8 m height at the shoulder, and the elephant on the right measures 3.0-3.5 m at the shoulder (Pulled from Benton 2010, drawn by Cristina Andreani).

hypothesis describes the decision of good swimmers to brave waters to potentially reach safety on new island lands following catastrophe. Conversely, weaker swimmers would more likely opt for known safety and remain where they are already situated. Comparing the shipwreck metaphor to animal dynamics, it is intuitive to gather that larger and subsequently stronger animals would be better able to endure long, arduous journeys to reach distant and ecologically open habitats (Lomolino, 2005; Meiri *et al.*, 2008). This theory seems possible in some cases, though it is unlikely to apply to many others where gigantism is observed. However, there remains the need to explain how the large animals

would be able to survive on an island where the resources may be too limited to maintain its large size following initial population. It is possible that, once established, the newly immigrated animal will instead undergo dwarfing processes rather than one geared toward gigantism. This could potentially explain the existence of pygmy elephants and hippos (Case, 1978; Foster, 1964; Raia & Meiri, 2006).

Sexual selection is also described as being a possible selective pressure for gigantism in island habitats. It is feasible that insular populations will be sexually selected to take on larger body characteristics to better attract mates. A prime example of sexual selection acting on insular body size may be seen in certain primates that have high levels of intraspecific competition (Lindenfors 2002). As a result, sexually dimorphic species may be capable of evolving large body sizes on a relatively short time scale due to already present genetic plasticity (Bromham and Cardillo 2007). This theory, however, is dependent on mainland factors suppressing sexual selection for large body morphs that can only be sustained on island environments (Benton *et al.*, 2010).

Though each of these theories has merit in potentially accounting for island body shifts, they are also weakened by inherent pitfalls in their theories. Despite the pitfalls, it is likely that individual cases of island body size shift can be explained by one or several of these theories.

Predation vs. Competition

Two major premises that are believed to affect insular body morphs are the concepts of predation and competition (Michaux *et al.*, 2002). It is posited that

emigration to distant islands devoid of or exhibiting low levels of either would allow for new selective forces to be applied. This in turn would account for evolutionary effects on size to take place. The question that follows ecological release is one of whether predation or competition applies a heavier selective force.

Lomolino (2005) observed that a trend for gigantism was common on island habitats across many taxa where interspecies competition was relatively low compared to continent faunas. As a result of this “empty niche space”, it became easier for gigantism to develop as a means of filling those ecological roles. It was also hypothesized that islands with high rates of competition would lead to dwarfism following the idea that resources would be more limited (Pregill, 1986). Lomolino also observed that smaller body morphs were especially prevalent in large bodied mammals dealing with high densities of competition. This pattern may be attributed to the fact that large bodied mammals are more likely to require large amounts of energy compared to organisms such as poikilothermic reptiles.

Contrastingly, Michaux et al. (2002) assert that the number of predators is more likely to influence the effects of the island rule when compared to competition. In their study of the woodmouse species *Apodemus sylvaticus*, Michaux et al. found that a decrease in competitive species seems to have little to no effect in determining body size. The conclusion was based on the idea that especially large islands in island biogeography act as equivalents to mainland systems. Large islands are capable of sustaining larger numbers of animals because of their ability to sustain higher degrees of resources. It was found that the number of competitors inhabiting a large island within this study was on the same order of the number of competitors found on a smaller island. This observation

was significant because of the quality that larger islands also tend to have higher rates of competition, which in turn mutes the occurrence of insular gigantism. As expected, large-bodied morphs of *Apodemus* were absent on the larger island, but the event did not seem to be due to competition (Michaux *et al.*, 2002). However, in the case of the woodmouse, island size appeared to have little effect in determining competitor numbers.

Instead, large bodied woodmice were found exclusively on smaller islands where predators were found to be non-existent. The lack of gigantism among *Apodemus* on large islands imply that the presence of predators act as the limiting factor for large body morphs. This is reinforced by the observation that giant woodmice were found on islands where the predacious weasel, *Mustela nivalis*, was absent (Michaux *et al.*, 2002).

Though the Island Rule may be governed by multiple factors, results from Michaux *et al.* provide evidence that the rate and presence of carnivores may be more important than interspecies competition.

Island Area and Distance to the Mainland

The degree of isolation is regarded as one of the major factors that influence the study of island biogeography. It is no surprise then that the Island Rule is also affected by aspects such as distance from the source population, or mainland, and the overall size of the island itself (Meiri *et al.*, 2006). The effect island size has on its overall resource capacity has already been discussed, but island size is also important in that total area may affect the process of genetic drift (White & Searle, 2007).

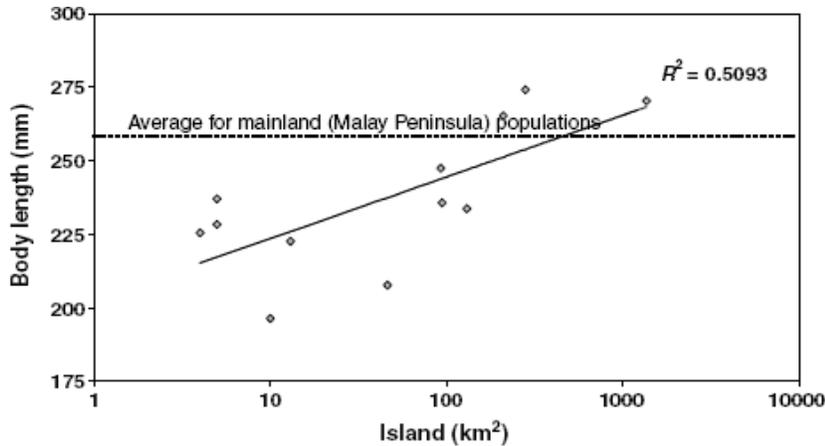


Figure 4. Graph shows the body size of the tri-colored squirrel “*Callosciurus prevosti*” and how its size correlates with increasing island area. This may be due to higher levels of resource availability that allows for evolutionary growth. (Pulled from Lomolino 2005).

Defined as the frequency by which a specific allele appears in a population, genetic drift operates on the random sampling and passive chance of genes to be incorporated and dispersed within a population. Islands with small areas are more susceptible to genetic drift due to increased chance of encounters within a relatively small population. Because of that quality, natural selective pressures found on some islands suffer the possibility of being negated by the effects of genetic drift. Smaller islands are less able to respond

selection pressures compared to larger islands where populations may be larger and have a larger genetic pool to draw upon (White & Searle, 2007).

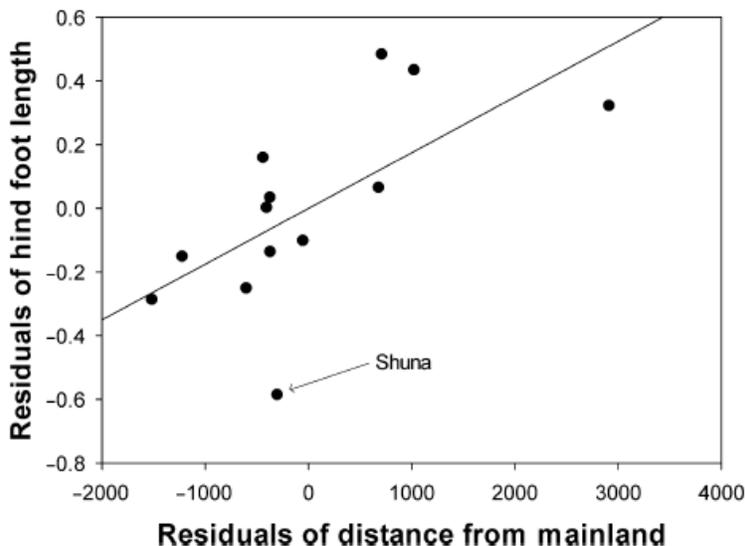


Figure 5. Relationship between hind foot length in the shrews studied by White and Searle and distance from mainland. Body size seems to increase with distance from the island, supporting Lomolino’s shipwreck hypothesis. (Pulled from White and Searle 2007)

Distance from the source population also seems to affect the island rule. According to White and Searle (2007), there appears

to be a positive correlation between distance from the mainland and the increased size of insular fauna (White & Searle, 2007). This phenomenon is thought to be attributed to selection for better immigrants as was described by Lomolino (Lomolino, 2005). This mode of immigration can be applied to terrestrial travel as well, and not limited purely to swimming as the shipwreck hypothesis implies. White and Searle in their study of insular size shift in shrews discuss the selective pressures applied to individuals that were particularly hardy. In their example, it is believed that shrew migration occurred during the last glaciation event to result in the colonization of modern day islands. Though some posit that this migration was made via land bridges, it is much more likely that the shrews dispersed to those areas via ice bridges. Those who were able to undertake the journey were those who were capable enduring long periods of cold exposure and possible food shortages. Naturally, those individuals were most likely larger in order to accommodate larger fat stores that aided them in their survival of the journey (White & Searle, 2007). Though this particular case concerns only the shrews, the concept remains applicable to other fauna as well.

Physical island characteristics also influence whether or not body morphs differ upon islands in relation to the mainland. In order to maintain a genetically stable population, established colonies of island immigrants require a large island to retard or dispel the threat of genetic drift. Additionally, the distance an island has from a mainland may also determine the initial body morphs of the ancestral colonizers. Intuitively, more highly isolated islands force would-be dispersers through a filter that selects for those individuals able to colonize the island. Therefore more distal and isolated islands will

show a founder's effect that has trends leaning toward large size, as was described by Lomolino's shipwreck hypothesis (Lomolino, 2002; White and Searle, 2007).

Climate and Bergmann's Rule

It is possible that observed evolution of body size on islands may also be attributed to an overall shift in climate. Bergmann's rule states that the body size of individuals will be greater at higher latitudes, thus decreasing surface area and reducing the amount of energy that can be lost through exposure (Millien & Damuth, 2004). Bergmann's rule can be found to apply to the Island Rule if island chains span large areas. As a result, latitudinal trends may exist across insular populations to exhibit different body morphs. Size shift associated with Bergmann's rule is often considered to be a direct response to temperature; therefore it remains possible that patterning of size differences between mainland and island habitats may be a result of differences in

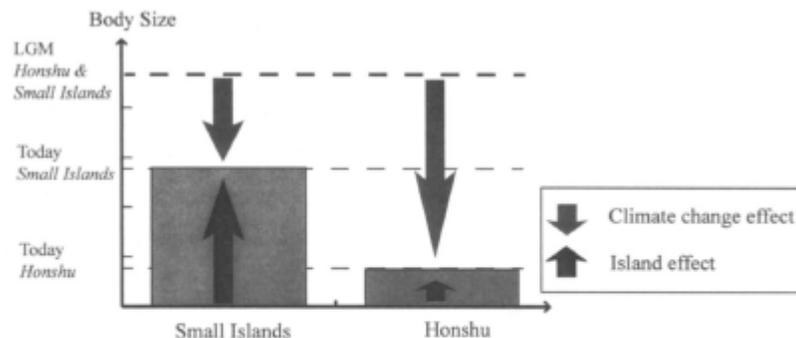


Figure 5. Model showing the net evolutionary size change in "A. speciosus" since the last glacial maximum (LGM). The island of Honshu is considerably large and can be seen to differ greatly from small island ecology. In both situational types, temperature can be seen to select for smaller size. Small islands display a larger morphology, however, due to the island effect allows for larger body morphs to be sustained. (Pulled from White and Searle, 2007)

climate.

(Millien & Damuth 2004)

Millien and Damuth's study of the Japanese rodent, *Apodemus speciosus*, has shown an 8% growth in incisor size as latitude increases from the south to the north of Japan (Millien & Damuth, 2004). Fossil remains of the same species have shown that the rodent reached its maximum size during the last glacial maximum (LGM), and has since then steadily decreased in size, likely due to gradually warming climate. Like other fauna during the LGM, body sizes were relatively large compared to modern standards in order to capitalize on the body type best suited for enduring cold climates, i.e. having the capacity to hold large fat stores (Millien & Damuth, 2004).

White and Searle (2007) also found a negative correlation concerning body size and average climate in their study. Despite this initial finding, it was observed that populations in Eurasia and Alaska showed trends that seemed to contradict Bergmann's rule, showing body size to decrease as latitude increased. This trend may be explained, however, by the influence of resources limiting the capacity for the shrews to adhere to Bergmann's rule (White & Searle, 2007).

In summary, recent size shifts since the last glacial maximum may be attributed to a number of factors. What could be called remnant effect of the Island Rule may in fact be evidence of morphologies that were selected for due to adaptation for cold resistance.

Island Rule in a Marine Environment

In a twist on the conventional study of the Island Rule, McClain et al. (2006) attempted to draw parallels from terrestrial size shift to size shift found in marine species, specifically focusing on gastropods. Historically, a large percentage of deep sea fauna

became extinct during the middle of the Cenozoic. As a result, the deep sea virtually became an open niche as organisms from more shallow waters immigrated to replace the vacated ecological roles. It is because of this behavioral aspect of the gastropods, which colonized the deep sea relatively recently (~30 MYA), that McClain et al. were able to equate the deep sea to islands and the near shore as equal to mainlands (McClain *et al.*, 2006).

It was found in their observation that the Island Rule did in fact apply to the study. McClane et al.'s tests showed that originally large gastropods underwent dwarfism, and originally small gastropods experienced gigantism. The end result was that the average shell length in gastropods adopted a much narrower bell curve than that displayed in the range of shell length in gastropod from shallow waters (McClain *et al.*, 2006).

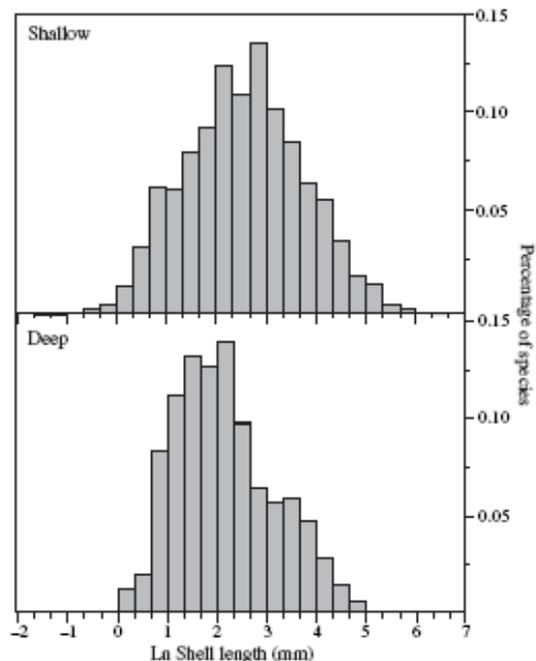


Figure 6. Frequency distributions of gastropods in both shallow and deep sea waters. (Pulled from McClane et. al 2006)

The main selective force that drove this body morphotype shift was most likely attributed to resource availability. Other explanations generally associated with the Island Rule may not fully apply to the marine study, such as the limitations due to island area or predation.(McClain *et al.*, 2006).

McClain *et al.*'s study is a strong example of how island biogeography can be applied to non-literal islands based on the same premises. Specifically, McClain *et al.*'s

study illustrates the importance of resource availability in affecting long term effects for colonizing fauna.

Homo floresiensis

Perhaps one of the most interesting developments in island biogeography is the recent discovery *Homo floresiensis* on the Indonesian island of Flores. Also known colloquially as “hobbits” after the J.R.R.



Figure 7. Skull of a "hobbit" (on left) and a recreation of the brain (on right).

Tolkien fantasy characters, specimens of *Homo floresiensis* have appeared in the fossil record displaying an unusually small stature compared to other hominins (Bromham and Cardillo 2007). Radioisotopic dating of the fossil remains of at least 8 separate individuals place the time frame of these hominins to be as recent as approximately 18,000 to 34, 000 years ago. If true, this would imply that *Homo sapiens* co-existed with hominin contemporaries for far longer than once thought (Martin *et al.* 2006).

Initially regarded as a case for insular dwarfism, *H. floresiensis* was claimed to be the island counterpart of *Homo erectus*. However, comparison of tools associated with *H. floresiensis* did not correspond with known *H. erectus* technology. As a result, there exists some controversy regarding the origin of *H. floresiensis*, as well as determining the veracity of the claim that “hobbits” were truly a separate species from *H. sapiens* (Bromham and Cardillo 2007). Reconstruction of *H. floresiensis* bodies has shown that

“hobbits” were roughly 52% of the mass of modern humans, weighing on average 23 kg (~50 lbs) (Martin et al., 2007). “Hobbit” brains were also very small, presenting a capacity of ~400 cubic centimeters compared to the average 1350 cubic centimeters of *Homo sapiens*. The extreme measurements of *H. floresiensis* have been argued to be evidence against Island Rule effects, the claim being that that degree of dwarfism is not within normal ranges of insular evolution. Instead, it has been posited that the *H. floresiensis* specimens are more likely cases of individuals with microcephaly, a genetic disorder where the head is more than two standard deviations smaller than average (Martin et al. 2007). Evidence for this was found mostly in that fossil remains exhibited a deformation of structure commonly found in modern individuals also afflicted with microcephaly.

In order to assess the validity of the microcephaly argument, Bromham and Cardillo performed a comparative analysis of 39 island endemic primate species to better define ranges of insular dwarfism in primates. Their results yielded that primates do in fact conform to the island rule, and that body size reduction associated with *H. floresiensis* compared to *H. erectus* and *H. sapien* fall within the observed range of insular primate dwarfism (Bromham and Cardillo 2007). In light of that conclusion, Bromham and Cardillo stress that the categorization of “hobbits” as not being products of the Island Rule cannot be solely based on size reduction alone. Though it remains possible that *H. floresiensis* may be representatives of “pygmoid” *H. sapiens* such as those people seen in South America’s Amazon, the authors assert that that degree of dwarfism is within the range of normal Island Rule effects.

Though the controversy still persists, studies of the Island Rule have provided obvious implications that may support the hypothesis that hobbits, *H. floresiensis*, existed as a species separate from humans at one point in time.

Conclusion

Though there are a number of potential explanations and case studies where the Island Rule is analyzed, the phenomenon of evolutionary size shift has many caveats that may illegitimize its status as being a rule in the study of biogeography. Meiri et al. (2007) revisit the concept of the Island Rule and question its validity in an article titled “*The Island Rule: Made*

to be Broken?”

(Meiri *et al.*, 2007).

The authors assert

that, when a

phylogenetic

comparative method

is applied to a large,

high quality data set,

there is no evidence

of a statistically

significant relationship. Rather, the shift in size in insular species seems to be limited to

only a few specific taxa, such as carnivores, artiodactyls, and certain rodents. It is

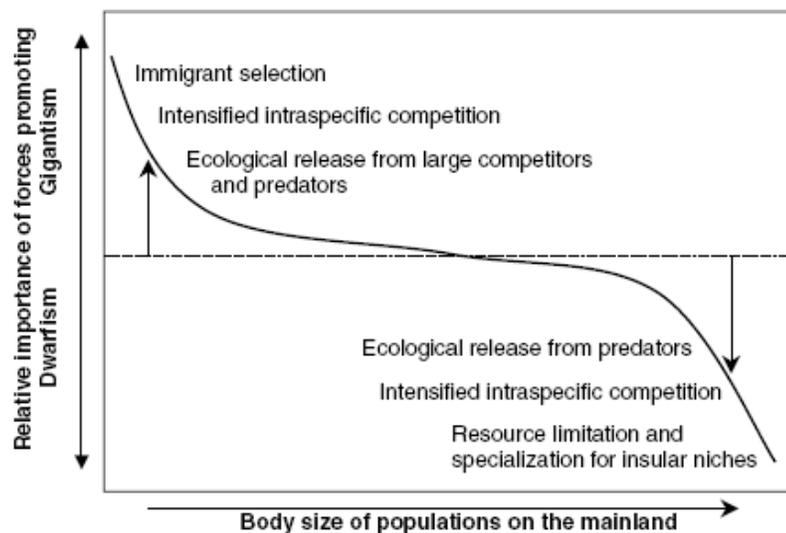


Figure 8. Comprehensive graph of the main factors affecting insular body size. (Pulled from Lomolino 2005)

because of this quality that Meiri et al. hope to dispel the tenet that the Island Rule is an intrinsic quality of insular evolution. Instead, the authors hope to reduce it to being a phenomenon that is sometimes governed by varying effects of biotic and abiotic factors (Meiri *et al.*, 2007). Despite this recent development, the factors surrounding insular body shift remain valid. Large animals immigrate, predation and competition affect population dynamics, and ecological release and niche realization can afford new opportunities for growth and evolution. Summarily, general resource availability and limitation persist as being large factors in determining island population dynamics and remain relevant on the whole to the study of island biogeography. As was stated before, a thorough understanding of the processes affecting islands may very well in turn aid in the understanding of larger scale processes found upon the mainland.

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