On dwarf elephants and giant rabbits

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Welcome to the biggiesmalls project! Biggiesmalls is a model of body size evolution on islands.

1 Background

The island rule is a common pattern in animals, especially in mammals (Lomolino 1985, 2005). It refers to the tendency of large species to become smaller (i.e. dwarfism), and of small species to become larger (i.e. gigantism) upon colonization of an island. Two extreme (extinct) cases of this phenomenon are the lagomorph *Nuralagus rex* from Minorca and the dwarf elephant *Palaeoloxodon fosteri* from Sicily. Even though these examples are now extinct, the pattern holds for many extant species (Lomolino 2005, Lomolino et al. 2012).

Several explanations have been proposed to explain this phenomenon, among which e.g. the ecological release hypothesis, the immigration selection hypothesis or the resource limitation hypothesis.

The ecological release hypothesis states that because of competitive interactions between the numerous species present on the mainland, species have been driven away from each other in body size through character displacement. In this context, islands represent oases free of competition because they carry less species. This hypothesis provides an explanation for both dwarfism of large mammals and gigantism of small mammals. The prediction of this theory is that dwarfism and gigantism should be more pronounced on islands with less competing species.

The immigration selection hypothesis suggests that, in small animals, larger individuals are positively selected during the colonization process because they can survive better long journeys at sea (e.g. because they have larger fat reserves). This hypothesis offers an explanation to gigantism of small mammals, but not to dwarfism of large mammals. It predicts that more isolated islands should show more pronounced gigantism.

The resource limitation hypothesis states that large mammals dwarf on islands because resources are more scarce than on the mainland, therefore large bodied animal populations cannot be sustained. This offers an explanation for dwarfism of large mammals, but not to gigantism of small mammals. It predicts that dwarfism should be more pronounced on smaller islands (assuming resources are rarer on smaller islands).

In 2012, Lomolino et al. investigated potential biotic and abiotic factors that explain best the patterns of gigantism and dwarfism on islands worldwide. They found strong support for several factors, including the ecological release hypothesis (body size changes are more pronounced on islands with less competitors) and the immigration selection hypothesis (small species grow bigger on more isolated islands). However, they found no support for the resource limitation hypothesis, i.e. they did not see more pronounced dwarfism on smaller islands (independently of the presence of competitors). What is more, they actually found more pronounced gigantism in small species on smaller islands, a result that is at odds with what the resource limitation hypothesis predicts. Indeed, resource limitation should not affect small species and therefore dwarfism should not be affected by resource quantity.

Here, we propose a model to explain this pattern. There may be several reasons why, independently of other factors such as the number of competitors on the island, dwarfism is not affected by island area but gigantism is more pronounced on smaller islands.

2 Hypotheses

We propose that increased gigantism in small species on smaller islands is driven by asymmetric competition. It is easily conceivable that within a species, larger individuals are favored when acquiring food because they usually win competitive interactions with smaller individuals. On smaller islands, resource is more scarce and this advantage of being bigger may become critical and induce a strong selection for larger body sizes.

However, this should also apply to large species i.e. large species should also increase in body size on smaller islands, which is contrary to the observed pattern. One possible explanation is genetic drift. If larger animals have lower carrying capacities (i.e. the island can support less individuals), then population size of large animals may become too small on small islands for selection to really have an effect. Instead, genetic drift is expected to have a strong effect on the evolution of body size on smaller islands, which may explain the absence of response to selection and the absence of relationship with island area.

One important point is that we assume that resource limitation has two antagonistic effects. First, resource limitation induces selection for larger body sizes because of asymmetric competition, which is an aspect that has been overlooked in the literature. Second, larger body sizes have lower carrying capacities, which reflects the classically expected consequence of scarce resource i.e. that populations of too large individuals cannot be sustained if the resource is too scarce.

Another possible explanation for the absence of relationship between dwarfism of large mammals and island area is generation time. Larger mammals typically have longer generation times, therefore mutations accumulate more slowly and evolution (response to selection) is expected to take more time than in small species. We also know that islands are usually short-lived and therefore the islands we see nowadays are relatively young. It may be that resource limitation induces selection for increased dwarfism in large mammals, but that the response to selection takes too long to be visible yet, and that islands disappear before animals have responded to selection.

3 The model

Biggiesmalls is an individual-based simulation model, meaning it simulates each individual animal in a population. More precisely, it is a birth-death process, meaning that individuals can either give birth or die. Birth and death rates are calculated from the Lotka-Volterra model for growth under competition, where the growth rate of a category i of individuals (e.g. a given body size) is:

$$\frac{dn_i}{dt} = R_i\left(1 - \frac{N_i}{K_i}\right)n_i$$

Where n_i is the number of individuals of type i in the population, R_i is the net per capita growth rate (without accounting for competition) and $\frac{N_i}{K_i}$ quantifies density-dependence, with N_i being the effective population density that affects class i, and K_i being the carrying capacity of class i.

The effective population density N_i competing with and individual of body size x_i depends on the body sizes of the other individuals in the population:

$$N_i = 1 + \sum_{j=1, j\neq i} C(x_i - x_j)$$

where $C(x_i - x_j)$ reprensents the intensity of competition perceived by an individual with body size x_i from an individual with body size x_j. $C(x_i - x_j)$ ranges from zero (not affected at all) to one (fully affected) and is a logistic function, reflecting the asymmetry in the outcome of competition based on the difference in body size:

$$C(x_i - x_j) = \frac{1}{1 + e^{-\alpha(x_i - x_j)}}$$

where α is the intensity of asymmetric competition. When i is much larger than j, it is not affected by competing with j (since it does not get its food stolen), while if i is much smaller than j, it experiences a high cost of competition.

The carrying capacity $K(x_i)$ depends on body size, with the idea that an island of given size can support less large animals than small animals:

$$K(x_i) = K_0 x^{\kappa}$$

where κ controls the strength of the decrease in carrying capacity with increasing body size. K_0 is the basal carrying capacity (for hypothetical animals of body size zero), which represents island size (i.e. resource availability).

The net per capita growth rate without competition, R_i, is the difference between the intrinsic birth rate $b(x_i)$ and the intrinsic death rate $d(x_i)$:

$$R(x_i) = b(x_i) - d(x_i)$$

where $b(x_i)$ is an allometric function of body size given by (Blueweiss et al. 1978):

$$b(x_i) = 0.025 x^{-0.25}$$

and $d(x_i)$ is the inverse of longevity, which is also an allometric function of body size, given by (Blueweiss et al. 1978):

$$d(x_i) = \frac{1}{630 x^{0.17}}$$

The growth rate of an individual i can therefore be written from the Lotka-Volterra equation:

$$R(x_i) - R(x_i)\frac{1 + \sum_{j \neq i} C(x_i - x_j)}{K(x_i)}$$

which can be decomposed into a birth rate,

$$B_i = R(x_i)$$

and a death rate,

$$D_i = R(x_i)\frac{1 + \sum_{j \neq i} C(x_i - x_j)}{K(x_i)}$$

which are the two rates used to simulate the birth-death process. The simulation code is based on the Doob-Gillespie algorithm, a practical algorithm that allows to simulate continuous-time models. In brief, this algorithm simulates the process by (1) drawing the time to the next event (here, from an exponential distribution), then (2) sampling what event happens (either birth or death, with probabilities derived from the rates above), and (3) re-iterate that process many times until the time limit is reached.

4 On to the simulation

You will find the R script for the simulation on my GitHub repository. Go to GitHub, and look for RapSch. You will find a folder there with the code, in a file called biggiesmalls.R. Don't confuse it with biggiesmalls.txt, which is the C++ version of the program!

The code is organized in the following parts: (1) the parameters, which you can change, (2) some accessory functions that are used to calculate the birth and death rates, (3) the main function, which contains all the information to run the simulation and (4) a command to actually launch the simulation. Have a look at the code and try to understand what every line is doing. If you have questions, don't hesitate to ask on Whatsapp. To run the code on your computer, just open the script in RStudio, set the parameters as you wish, then Ctrl+A to select all the text and Ctrl+Enter to run it all. At each birth or death, the simulation time and population size will be printed to the command prompt.

Your exercise for Monday: determining what are the parameters you could play with to test the hypotheses we propose for the observed pattern of no relationship of dwarfism with island size and increased gigantism on smaller islands. Then, we'll discuss your propositions and set a plan for what simulations to do. You will then play a bit with the simulation on your laptops, but in a few days you'll be able to launch them on the cluster (Rampal has requested access for you). I will show you next week how to launch stuff on the cluster. Good luck!