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New theory of insular evolution: unifying the loss of dispersability and body-mass change

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ABSTRACT

Loss of dispersability and body-mass change (dwarfism and gigantism) are two common phenomena on islands. Based on Skellam's (1951) theory of dispersal, we suggest a new theory of insular evolution that connects isolation and island size to dispersability and body mass. Using optimal body mass considerations and allometric scaling laws, our new theory predicts: (1) expected direction of body-mass change depends on the relationship between body mass and dispersability; (2) rate of body-mass change (i.e. evolution rate) is inversely proportional to the island's area; (3) the magnitude of the shift in optimal body mass, either towards gigantism or dwarfism, is also inversely proportional to the island's area. Available empirical data support our predictions. Our theory provides new, consistent and testable predictions that connect several known observations on islands.

Keywords: allometry, dispersability, dwarfism, gigantism, insular evolution, island size, optimal body mass.

INTRODUCTION

Insular evolution has attracted the attention of ecologists and evolutionary biologists for many decades (MacArthur and Wilson, 1967; Williamson, 1981). Through unique characteristics, such as increased isolation and decreased size, islands promote extreme evolutionary changes and fast evolutionary selection on organisms (Grant, 1986; Brown and Lomolino, 1998; Whittaker, 1998). These evolutionary changes reflect the selective forces correlated to the unique characteristics of islands (Grant, 1981), and islands are also considered to be 'natural experiments' where different evolutionary processes can be studied (MacArthur and Wilson, 1967; Carlquist, 1974; Williamson, 1981; Whittaker, 1998).

Two well-known observations of insular evolution are loss of dispersability (Darlington, 1943; Brown and Lomolino, 1998; Whittaker, 1998) and the tendency of species to become either smaller (dwarfism) or larger (gigantism) than their mainland populations (Foster, 1964; Case, 1978; Lomolino, 1985; Diamond, 1987; Damuth, 1993). [Note that Foster (1964) has explicitly referred to mammals on islands and termed it 'the island rule'.] Loss of dispersability is usually explained by ecological release (i.e. decreased predation pressure

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and lack of competitors; McNab, 1994a) and by limited resources (McNab, 1994a,b). Body-mass change has many explanations, some of which are universal (Case, 1978) and some of which are clade-specific (Foster, 1964; Diamond, 1987). Throughout this paper we use the term 'body-mass change' to indicate both dwarfism and gigantism. Given that body mass is well correlated with different size dimensions, we expect our predictions to hold for size dimensions equally. Often, the change in body mass is inversely related to the body mass of the organism – small animals become larger while large animals become smaller (Foster, 1964; Lomolino, 1985). Similar to the explanations for the loss of dispersability, and regardless of the specific details of each explanation, body-mass change is also explained by limited resources and by ecological release.

Several biologists have suggested that ecological release and shortage of resources could simultaneously explain the phenomena of loss of dispersability and body-mass change (McNab, 1994a). For example, a lack of predators can promote a flightless bird, after which that bird can evolve increased size due to the unnecessary demand of keeping the aerodynamic dimensions required for flying (Brown and Lomolino, 1998). However, in spite of the apparent relationship between loss of dispersability and body-mass change, they are commonly treated separately. Hence, there is a need for a mutual theory that connects the loss of dispersability and body-mass change together in the context of unique island characteristics. The use of body mass has two advantages for studying evolutionary processes in insular biogeography. First, many ecological processes may be correlated to, as well as directly affected by, body mass (e.g. population density, resource use, extinction probability and dispersability; Peters, 1983; Schmidt-Nielsen, 1984; Calder, 1996). Second, body-mass correlates (or allometric scaling) allow for generalized scaling relationships across a diverse group of organisms (Brown and West, 2000).

In the following section, we develop a new theory to connect body-mass change, island size, dispersability, allometry and evolution rate to provide new predictions of insular evolution: (1) the direction of the body-mass change (either gigantism or dwarfism) depends on the sign of the allometric exponent of dispersability; (2) the rate of body-mass change (or evolution rate) is inversely proportional to the area of the island; (3) the shift in optimal body mass, either towards gigantism or dwarfism, is inversely proportional to the area of the island. Thereafter, we provide examples to demonstrate that natural observations do match our predictions, before stating the implications of our theory for future research.

THE THEORY

Here we propose a new theory that connects and unifies the loss of dispersability with the tendency of species to become either smaller or larger on isolated islands. We build our theory on Skellam's (1951) diffusion-reaction equation, which describes the spread of organisms in a landscape through a random-walk dispersal, assuming that the spatial distribution of dispersed offspring is normal with zero mean and a standard deviation, a. Because a is also the average dispersal distance of an offspring from its source, it reflects dispersal distance. Given that Ψ is the function of individual density at each point in space, G is generation time, c is the intrinsic exponential growth rate of the population and ∇^2 is the Laplacian differential operator, Skellam's equation takes the following form:

$$\frac{\partial \Psi}{\partial t} = \frac{a^2}{G}\nabla^2 \Psi + c\Psi = D\nabla^2 \Psi + c\Psi \tag{1}$$

where D ($D = a^2/G$) is the diffusion coefficient. For simplicity, equation (1) is based on Skellam's exponential growth equations. However, the Appendix shows that when population size and growth are limited (i.e. density-dependent), our predictions of the exponential growth model should still hold. Biologically, D can be viewed as dispersability, representing the rate at which an organism spreads in space, being affected by dispersal distance and generation time.

Solving equation (1) for the circular island case (i.e. where $c > 0$ and $\Psi > 0$ in a circular area of radius r_b, while $\Psi = 0$ outside the circle), Skellam showed that the dominant solution grows exponentially with a growth rate:

$$c_{\text{island}} = c - j_1^{\,2}\,\frac{a^2}{r_b^{\,2}} \tag{2}$$

where j_1 is a constant equal to 2.405 (Arfken and Weber, 1995). (G does not appear in the solution, since Skellam chose a time-scale for which $G = 1$.)

Generalizing Skellam's result to account for arbitrary time-scale and island shape, we introduce a new formulation for the population growth rate on the island:

$$c_{\text{island}} = c - k\,\frac{D}{A} \tag{3}$$

where A is the island's area and k is some positive numerical constant, which is determined by island shape. Biologically, using equation (3) we describe how population growth rate is affected by island shape, island size and dispersability of the organisms, variables known to affect population persistence on islands (MacArthur and Wilson, 1967; Williamson, 1981; Brown and Lomolino, 1998; Whittaker, 1998). Because c_{island} is negatively correlated with D, it suggests that, for the same values of c, individuals (or phenotypes) with lower dispersability (i.e. lower D values) have an advantage on islands by having a higher growth rate. Additionally, the decrease in c_{island} is proportional to $1/A$, which suggests that the change in population growth is stronger on smaller islands than on larger ones. We assume throughout our development that c does not change in the transition from mainland to island, and therefore we ignore factors such as change in physical conditions and interspecific interactions, which may affect the intrinsic growth rate itself.

We define D_{mainland} as the mainland's optimal dispersability (i.e. $\mathrm{d}c/\mathrm{d}D = 0$ at $D = D_{\text{mainland}}$). An individual arriving on an island possesses the mainland dispersability D_{mainland}. Taking the derivative of equation (3) at D_{mainland} reveals that the insular selection pressure on dispersability is:

$$\left.\frac{\mathrm{d}c_{\text{island}}}{\mathrm{d}D}\right|_{D = D_{\text{mainland}}} = -\frac{k}{A} \tag{4}$$

Because the right-hand side of equation (4) is always negative, the selection pressure always favours a reduction in dispersability. Additionally, the change in dispersability is strongly affected by both the size of the island and its shape; the smaller the island and the higher the k values (greater dissimilarity of the island's dimensions) are, the faster the change in dispersability. Therefore, the smaller the island's area, the higher the evolutionary rates of the loss of dispersability.

Demographic parameters, including population growth rate, have already been shown to depend on body mass (Peters, 1983; Schmidt-Nielsen, 1984; Calder, 1996), hence we assume that $c = c(M)$. Similarily, we assume that locomotion, and therefore dispersability, also depend on body mass (Calder, 1996), hence $D = D(M)$. As in the above case of the relationship between growth rate and dispersability, a mainland population can maximize its growth rate with respect to body mass and converges to a certain mainland optimal body mass (for previous use of 'optimal body size', see Case, 1978; Brown *et al.*, 1993), M_{mainland} (when $\mathrm{d}c/\mathrm{d}M = 0$ at $M = M_{\text{mainland}}$). Because the island optimal body mass maximizes c_{island}, it differs from M_{mainland}. This results in a selection pressure on body mass, given by:

$$\left.\frac{\mathrm{d}c_{\text{island}}}{\mathrm{d}M}\right|_{M = M_{\text{mainland}}} = -\frac{k}{A}\left.\frac{\mathrm{d}D}{\mathrm{d}M}\right|_{M = M_{\text{mainland}}} \tag{5}$$

Equation (5) shows that the change of body mass on an island, relative to that on the mainland, does not have a single direction, but rather may be positive (becoming 'giant') or negative (becoming 'dwarf'), depending on the sign of the derivative of $D(M)$ at M_{mainland}: if the derivative is negative the organism shows gigantism, while if it is positive then dwarfism occurs. As in the above case of reduced dispersability, the selection pressure for gigantism or dwarfism is stronger on smaller islands due to the reciprocal relationship between c_{island} and A.

To achieve workable predictions from our development, we use power-law allometric relationships (Peters, 1983; Schmidt-Nielsen, 1984; Calder, 1996; Brown and West, 2000) to describe more realistically how dispersability changes with body mass ($D = D_0 M^{\delta}$, where D_0 is a coefficient of proportion, representing effects on dispersability other than body mass, and δ is the power coefficient). Replacing D in equation (5) by the allometric relationship, we obtain:

$$\left.\frac{\mathrm{d}c_{\text{island}}}{\mathrm{d}M}\right|_{M = M_{\text{mainland}}} = -\frac{k}{A} D_0 \delta (M_{\text{mainland}})^{\delta - 1} \tag{6}$$

Equation (6) also allows us to predict the tendency of an organism to become either giant or dwarf using the sign of the exponent: $\delta < 0$ results in gigantism, while $\delta > 0$ results in dwarfism. Given that $D = a^2/G$, the allometric relationship for dispersability can be further separated into two allometric equations: $a = a_0 M^{\alpha}$ and $G = G_0 M^{\gamma}$. As a result, we can define the relationship between the different allometric exponents such that: $\delta = 2\alpha - \gamma$. Therefore, given equation (6) we can now predict that if $\alpha < \gamma/2$ gigantism is expected, while if $\alpha > \gamma/2$ dwarfism is expected. The latter condition and the conditions given by equations (5) and (6) provide equivalent forms of the same prediction regarding gigantism and dwarfism.

Considering the selection pressure operating towards reducing dispersability as given in equation (4) and the separation of dispersability (D) into effects of body mass (represented by M^{δ}) and effects other than that of body mass (represented by D_0), we can rewrite equation (4) as two equations:

$$\left.\frac{\partial c_{\text{island}}}{\partial M}\right|_{M = M_{\text{mainland}}} = -\frac{k}{A} D_0 \delta M^{\delta - 1} \tag{7a}$$

$$\left.\frac{\partial C_{\text{island}}}{\partial D_0}\right|_{D_0 = D_{0\text{mainland}}} = -\frac{k}{A} M^{\delta} \tag{7b}$$

Equation (7b) suggests that regardless of the tendency of the organism to have a lower or larger body mass, organisms on islands will tend towards lower values of D_0, which consequently implies reduced dispersal organs and appendages.

Similar to the tendency of individuals on the mainland to show an optimal body mass, individuals of populations occurring on an island should move towards an optimal body mass, such that population growth rate, with respect to body mass, is maximized. We approximate $c(M)$ and $D(M)$ as Taylor polynomials of the first significant order (first-order for $D(M)$ and second-order for $c(M)$) around $M = M_{\text{mainland}}$. The difference between island optimal mass and mainland optimal mass is

$$\Delta M = \frac{k}{A} \cdot \left[\frac{\left.\dfrac{\mathrm{d}D}{\mathrm{d}M}\right|_{M = M_{\text{mainland}}}}{\left.\dfrac{\mathrm{d}^2 c}{\mathrm{d}M^2}\right|_{M = M_{\text{mainland}}}} \right] \tag{8}$$

Equation (8) adds a new prediction regarding body-mass evolution. Not only is the rate of body-mass evolution expected to be proportional to $1/A$ (equation 5), but the magnitude of the change in optimal body mass is proportional to the area of the island (i.e. $\propto 1/A$). Noting that $\mathrm{d}^2c/\mathrm{d}M^2$ is negative because $c(M)$ reaches its maximum at M_{mainland}, we predict also here that, as in equation (5), if the derivative of $D(M)$ is positive we get dwarfism ($\Delta M < 0$), whereas if it is negative we get gigantism ($\Delta M > 0$).

VALIDATION OF PREDICTIONS

Our new theory of insular evolution provides several important predictions regarding body-mass change. In particular it suggests that:

1. The direction of the body-mass change (either gigantism or dwarfism) depends on the sign of the allometric exponent of dispersability (i.e. $\alpha > \gamma/2$ results in dwarfism, while $\alpha < \gamma/2$ results in gigantism).
2. The rate of body-mass change (or, evolution) is proportional to $1/A$ (i.e. organisms on smaller islands are expected to experience a faster change in body mass than those on larger islands).
3. The change in optimal body mass, either towards gigantism or dwarfism, is proportional to $1/A$ (i.e. organisms are either larger or smaller on smaller islands than on larger islands).

In the following paragraphs we briefly review several examples from the literature that support and validate our predictions.

Validation of prediction 1

With respect to our first prediction – directionality of body-mass change – using allometric relationships (Peters, 1983; Schmidt-Nielsen, 1984; Calder, 1996) we find that generation time scales with body mass to the power of approximately 1/4 (e.g. reproductive maturity in mammals scales as $M^{0.29}$ and age at first breeding in birds scales as $M^{0.23}$; Calder, 1996, pp. 270–272), hence $\gamma = 0.25$. Given our previously developed condition – if $\alpha < \gamma/2$ gigantism is expected, while if $\alpha > \gamma/2$ dwarfism is expected – we can predict species to evolve towards gigantism when $\alpha < 0.125$ and towards dwarfism when $\alpha > 0.125$. For mammals, all the exponents of natal dispersal distances are significantly larger than 0.125 (Sutherland *et al.*, 2000), suggesting that mammals should evolve towards dwarfism. Indeed, most mammals show dwarfism on islands (Case, 1978; Lomolino, 1985; Brown and Lomolino, 1998; Whittaker, 1998). However, Brown and Zeng (1989) have shown that for 11 species of desert rodents, dispersal distance decreases with increasing body mass. Therefore, for rodents, counterintuitively, $\alpha < 0$ (i.e. $\alpha < 0.125$), and consequently gigantism is predicted, as is indeed supported by the many observations of giant insular rodents (Lomolino, 1985; Adler and Levins, 1994). Median natal dispersal distances of herbivorous and omnivorous birds scale as $M^{0.18 \pm 0.18}$ (Sutherland *et al.*, 2000); hence, according to our predicted value, 0.125, both gigantism and dwarfism may evolve in herbivorous and omnivorous birds, as indeed is observed (McNab, 1994a,b; Feduccia, 1996). Carnivorous birds show a scaling exponent of 0.62 ± 0.18 (Sutherland *et al.*, 2000); therefore, they are predicted to evolve towards dwarfism. However, Feduccia (1996) provides several examples of extinct giant owls and hawks in Cuba, Hispaniola and Puerto Rico, as well as of large barn owls on some Mediterranean islands during the Pleistocene. Although these observations represent the few examples that disagree with our prediction, it can be partly attributed to a response of those species to the larger body mass of their prey (i.e. rodents; Rosenzweig, 1966).

Using the observation that dispersal distance of North American mammals is proportional to the square root of home range (Bowman *et al.*, 2002), we can use it as a first approximation for the dispersal–distance relationship, when the latter is not given explicitly. Note that because the relationship between home range and dispersal distance is geometric (i.e. a linear measure scales like the root of an area measure), the results for mammals should be taxon-independent. Based on Calder's (1996) allometric equation of lizards' home range, we obtain $\alpha = 0.475$, predicting that lizards should evolve towards dwarfism. Case (1978) lists different groups of lizards with respect to their body mass trends. Indeed, Teiid, Lacertid and Varanid lizards tend to evolve towards dwarfism (cf. the Komodo monitor, *Varanus komodonesis*).

In plants, dispersability of seeds and fruits (the dispersal units) strongly depends on their mass. Since larger seeds are less likely to be dispersed by winds or animals, we assume $\alpha < 0$ for plants dispersed by those agents, resulting in gigantism according to our prediction. Indeed, many insular plants show gigantism of their seeds and fruits, up to grotesque proportions in some instances (Carlquist, 1974).

Validation of prediction 2

Our second prediction suggests a negative relationship between area and evolution rate. Unfortunately, the literature has few examples that may help test this prediction. We can, however, present a couple of them. Pergams and Ashley (2001) show that island rodents have a significant negative correlation between island size and evolution rates of skeletal variants, such that the evolutionary rate is inversely proportional to island area. Cody and Overton (1996) suggest a similar effect for dispersability in populations of weedy plants on near-shore islands in British Columbia.

Validation of prediction 3

The availability of direct and indirect information on the relationship between the degree of body-mass change and island area allows us to gain much support for our third prediction, which is that the degree of body-mass change is inversely proportional to island area. Tri-coloured squirrels, fruit bats and rails tend to be, within the range of dwarfism, larger on larger islands, demonstrating that the shift in body mass is larger as the island area decreases (Brown and Lomolino, 1998). The flightless Auckland Island's (606 km^2) teal (*Anas aucklandica aucklandica*) and the flightless Campbell Island's (114 km^2) teal (*A. a. nesiotis*) are 84% and 56%, respectively, of the mass of the brown teal (*A. a. chlorotis*), which exists on New Zealand, demonstrating that the smaller the island, the smaller the teals (McNab, 1994a). Similarly, the Hawaiian duck (*Anas p. wyvilliana*) and the Laysan duck (*A. p. laysanensis*) have a body mass that is 63% and 49%, respectively, relative to the mass of the continental mallard (Carlquist, 1965; McNab, 1994a). A similar pattern has been found among island rails, which also tend to dwarf. McNab (1994a) also found a significant correlation between the head–body length of flightless rails and island area on a logarithmic scale. Separating the analysis based on genus – *Gallinula* and *Porphyrio* – reveals similar significant results. The body masses of island populations of the house mouse, *Mus musculus*, which follow the general tendency towards gigantism (Foster, 1964) as predicted for rodents, are significantly larger on Gough Island (65 km^2) than on Tristan da Cuncha Island (111 km^2) (Berry, 1964). Insects, including Coleopterans, tend to exhibit both gigantism and flightlessness on islands (Carlquist, 1974). Individuals of the flightless carabid, *Eurygnathus latreillei*, on the large island of Porto Santo are significantly smaller than those on the smaller Deserta Grande Island, and individuals of *Olisthopus maderensis* are much larger on Deserta Grande Island than on the much larger island of Madeira (Carlquist, 1974). Hence, the mouse, teal and insect examples show that body mass changes with island area regardless of whether organisms evolve towards gigantism or dwarfism.

Carlquist's (1974) examples from the genus *Fitchia* show that, for plants also, the degree of gigantism is inversely proportional to island area. The seeds of the Tahitian (1041 km^2) *F. nutans* are smaller than those of *F. rapensis* from Rapa (171 km^2), which are smaller than the truly gigantic seeds of *F. speciosa* from Rarotonga (67 km^2). Another example is the *Dendroseris* species of the Juan Fernandez Islands: the species on Masafuera and Masatierra (44.64 and 47.11 km^2, respectively) have large-sized seeds, but which are much smaller than the gigantic seeds of *D. litoralis* on Santa Clara (2.23 km^2) (Carlquist, 1974).

Finally, Table 1 summarizes our regression analyses of several data sets of island species. Our analyses demonstrate a significant decrease in body mass (or its correlates) with a decrease in island area.

IMPLICATIONS

The examples used in the previous section demonstrate that natural observations match well with our predictions. We did not intend here to review all the known cases of gigantism and dwarfism; such reviews have already been published (e.g. Carlquist, 1965, 1974; Lomolino, 1985; Adler and Levins, 1994; Brown and Lomolino, 1998; Whittaker, 1998). Furthermore, among the many existing studies of gigantism and dwarfism, only a few quantified all the necessary parameters to allow us to test the specific predictions of our theory; we have used all those that were available to us. This is not surprising, as previous studies were not performed to test our particular theory. One aim of this paper, therefore, is to inspire future work on the specific parameters needed for such tests.

Our theory provides several predictions. We have focused on the three major predictions that connect body-mass change, island size, dispersability, allometry and evolution rate.

Table 1. Explained variance and significance of correlation analysis of body mass with $1/A$ of particular islands

Species	Island(s)	Body size measure	Reference	R^2	P	n
1. *Callosciurus prevosti*	Indonesia (Sunda shelf)	Body length	Heaney (1978)	0.48	< 0.001	21
2. *Asida planipennis*	Balearic Archipelago	Centroid size	Palmer (2002)	0.83	0.0041	7
3. *Lacerta galloti*	Canary Islands	Length	Carlquist (1965)			
Males				0.95	0.0223	4
Females				0.89	0.054	4
4. *Bradypus* species	Islands of Bocas del Toro (Panama)	Skull length	Anderson and Handley (2002)	0.98	0.0086	4
5. *Anolis* species	Greater Antilles	Snout–vent length	http://www.homestead.com/anolis/Index.html			
Males				0.59	0.054	9
Females				0.78	< 0.001	10
6. *Ameiva* species	Lesser Antilles	Snout–vent length	Case (1978)	0.27	0.0778	12

Note: Conservatively, we applied a two-tailed distribution to all our analyses, although our directional prediction justifies the use of a one-tailed distribution. In the case of the latter, even our marginally significant case 6 becomes significant.

Although one would expect all these variables to be hypothetically related in an evolutionary context, previous theories have treated some variable interactions separately to explain specific observations. Our theory provides, for the first time, a framework that allows evolutionary biologists to consider the relationships between these variables as the interplay between evolutionary and ecological processes operating on a mainland and an island. If indeed these variables are connected as suggested by our theory, then additional relations can be predicted. For example, our equation (3) and the following equations suggest that the shape of the island may also affect the magnitude and the rate of body-mass change. Other ecological factors may also affect body-mass evolution if one considers the processes affecting each of the above variables. As a result, we believe that in addition to providing a focus on the specific parameters needed to test our predictions, our new theory provides new lines of investigation as to how insular evolution is affected by various interrelated variables that separately are known to be significant.

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APPENDIX: DENSITY-DEPENDENT POPULATION-GROWTH FUNCTION

Although our theory is based on Skellam's (1951) exponential growth equations, we can also show that when population size and growth are limited (i.e. density-dependent), our predictions of the exponential growth model still hold. For this, we use a version of Chesson's lottery model (Chesson and Warner, 1981), applied for a continuous quantitative trait, body mass. We assume an equilibrium constant population size, K (carrying capacity). Since birth and death processes still occur at equilibrium, evolution can take place through changes in gene frequencies (i.e. the differential success of certain individuals). We denote μ as the relative rate at which individuals die, hence the absolute rate of death is μK. For small time, $\mathrm{d}t$, the number of dying individuals is $\mu K \mathrm{d}t$ and the contribution of each individual is $c\mathrm{d}t$. Assuming that c depends on body mass ($c = c(M)$) and denoting the distribution of body masses in the population as $f(M)$, the distribution of the number of individuals of each body mass is: $n(M) = Kf(M)$. The probability-density function, P, of the event that the individual selected to replace a specific dead individual is of a certain body mass can be written as:

$$P(M) = \frac{c(M)n(M)\mathrm{d}t}{\int c(M)n(M)\mathrm{d}t\mathrm{d}M} = \frac{\mathrm{d}t \cdot c(M)Kf(M)}{\mathrm{d}t\int c(M)Kf(M)\mathrm{d}M} = \frac{K \cdot c(M)f(M)}{K\int c(M)f(M)\mathrm{d}M} = \frac{c(M)}{\langle c(M)\rangle}f(M)$$

The change in the number of individuals of a certain body mass is:

$$\mathrm{d}n(M) = P(M) \cdot \mu K\mathrm{d}t - \mu K\mathrm{d}tf(M) = (P(M) - f(M)) \cdot \mu K\mathrm{d}t$$

If $P < f$, the change is negative; if $P > f$, it is positive. The population dynamics equation becomes:

$$\frac{\mathrm{d}n(M)}{\mathrm{d}t} = (P(M) - f(M)) \cdot \mu K$$

Finally, we can express the change in body-mass frequencies, or the evolutionary dynamics equation, using the latter equation and the expression for P:

$$\frac{\mathrm{d}f(M)}{\mathrm{d}t} = \mu f(M)\left(\frac{c(M) - \langle c(M)\rangle}{\langle c(M)\rangle}\right) = \mu f(M)\left(\frac{\Delta c(M)}{\langle c(M)\rangle}\right)$$

Because no specifics regarding c are assumed and the body-mass variable, M, can be replaced by any other variable, the evolutionary dynamics equation is general. The equilibrium distribution is $f = \delta((M - M_{\mathrm{opt}}))$ – that is, a homogenous population with a body mass of M_{opt}, where $c(M)$ reaches its maximum at $M = M_{\mathrm{opt}}$. Therefore, like the exponential growth case, on the mainland $M_{\mathrm{opt}} = M_{\mathrm{mainland}}$, which satisfies $\partial c/\partial M = 0$. On the island, M_{opt} maximizes c_{island} (equation 2). Overall, our development shows that the same mathematical expressions and predictions developed under the assumption of an exponential population growth are also valid for the case of limited population size.