

Directionality theory and the evolution of body size

Lloyd Demetrius

Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, MA 02138, USA (ldemetr@oeb.harvard.edu)

Directionality theory, a dynamic theory of evolution that integrates population genetics with demography, is based on the concept of evolutionary entropy, a measure of the variability in the age of reproducing individuals in a population. The main tenets of the theory are three principles relating the response to the ecological constraints a population experiences, with trends in entropy as the population evolves under mutation and natural selection. (i) Stationary size or fluctuations around a stationary size (bounded growth): a unidirectional increase in entropy; (ii) prolonged episodes of exponential growth (unbounded growth), large population size: a unidirectional decrease in entropy; and (iii) prolonged episodes of exponential growth (unbounded growth), small population size: random, non-directional change in entropy.

We invoke these principles, together with an allometric relationship between entropy, and the morphometric variable body size, to provide evolutionary explanations of three empirical patterns pertaining to trends in body size, namely (i) Cope's rule, the tendency towards size increase within phyletic lineages; (ii) the island rule, which pertains to changes in body size that occur as species migrate from mainland populations to colonize island habitats; and (iii) Bergmann's rule, the tendency towards size increase with increasing latitude. The observation that these ecotypic patterns can be explained in terms of the directionality principles for entropy underscores the significance of evolutionary entropy as a unifying concept in forging a link between micro-evolution, the dynamics of gene frequency change, and macro-evolution, dynamic changes in morphometric variables.

Keywords: Cope's rule; the island rule; Bergmann size clines; evolutionary entropy

1. INTRODUCTION

An organism's size imposes constraints on its physiology and determines its life-history and ecological traits. Size is a relatively easy trait to measure precisely; accordingly, it has been an important index in empirically delineating temporal and spatial ecotypic patterns in evolution. This article invokes a new synthesis of population genetics with ecology, based on the concept, evolutionary entropy—a measure of the variability in the age of reproducing individuals in a population (Demetrius 1974)—to provide adaptive explanations of three ecotypic patterns: changes in body size within phyletic lineages (Cope 1886); changes in body size as species migrate from mainland to islands (Foster 1964; Lomolino 1985); and trends in body size within species across latitudes (Bergmann 1847).

Cope's rule asserts that in certain vertebrate lines there is a general trend towards size increase over geological time. The island rule posits that relative to mainland populations, there is a widespread tendency for small mammals to evolve to large body size on islands and large mammals to evolve to smaller size. Bergmann's rule asserts that within many species of birds, mammals and reptiles, body size tends to increase with increasing distance from the equator. There is now substantial empirical support for the validity of these rules; however, explanations of the patterns are varied and controversial. In the case of Cope's rule, a common rationale is that proposed by Stanley (1973) and Gould (1988). These authors claim that size change within phyletic lineages is a statistical property. According to the model, size increase is a consequence of random evolution away from small size: since the founding species are small, the range of size can only expand in one direction. As regards the

island rule, it has been proposed (see Bonner 1988, ch. 3) that since islands have small populations, a necessary condition for the operation of genetic drift, the size differences between the mainland and island groups may be due to stochastic effects. With respect to Bergmann's size clines, a common model, originally advanced by Bergmann and expanded by Mayr (1956) and Rensch (1960), among others, is based on the notion of size as a physiological adaptation for energy conservation. Heat production in organisms is proportional to volume, whereas heat loss varies with surface area. The larger the organism the greater the volume in proportion to the surface area, hence the easier it is for large organisms to conserve heat in cooler climates.

These models view ecotypic patterns in body size as the outcome of either statistical processes or physiological adaptation, rather than the result of natural selection. There is, however, strong evidence (see the discussion in Bonner (1968), as regards Cope's rule and the island rule, and the analysis in Partridge & Coyne (1997), with respect to Bergmann size clines) that the size differences that describe these ecotypic norms have a genetic basis—a condition which points to natural selection on genetic variation as the driving mechanism. Consistent with this selection hypothesis, a body of literature has emerged proposing explanations of the different ecotypic patterns based on various criteria of selective advantage. Thus, Brown & Maurer (1986) proposed as a model for Cope's rule, that size increase within phyletic lineages derives from the advantages of large size in tolerating short-term variation in the physical environment. Damuth's (1993) rationale for the island rule resides on the postulate of an optimum body size and the claim that on islands where the species' usual competitors and predators are absent,

evolution towards the optimum body size will occur. McNab (1971), in his argument in support of Bergmann's rule, claims that the correlation of body size with latitude reflects the size of the available prey and the selective advantage that increased size confers on predators subject to competition for the available prey. These arguments, although they all appeal to selective criteria, are not embedded in any theory of evolutionary dynamics, and hence do not provide any genetic mechanism that would drive changes in body size over evolutionary time.

The neo-Darwinian theory asserts that macro-evolutionary changes, such as trends in body size, are the outcome of the micro-evolutionary processes of population genetics. Accordingly, any evolutionary explanation of ecotypic patterns must be based on models that integrate the dynamics of gene frequency change with dynamic changes in morphometric and morphological variables under different ecological constraints.

The Standard model, the Wright–Fisher model of population genetics, has often been invoked to explain macro-evolutionary patterns in terms of the dynamics of gene frequency change (see for example, the studies of long-term evolution of bacterial populations described in Elena & Lenski (1997)). However, the Standard model is essentially concerned with the dynamics of gene frequency change under viability selection. Fitness in this model refers to the number of offspring that a typical individual of a given genotype is expected to bring up to reproductive age. It is usually represented relative to the corresponding viability of a particular genotype, which is assigned the value 1. The cornerstone of the Standard model is Fisher's fundamental theorem of natural selection, which predicts an increase in mean fitness. As is now generally conceded (see for example, Karlin 1992), Fisher's theorem pertains uniquely to local instantaneous changes in mean fitness: the theorem is an assertion about the relative viabilities of individuals in the population, a condition, which may have little relevance to properties such as absolute survival and reproduction of the population. The Standard model, with its focus on viability selection, essentially ignores the impact of ecological factors on evolutionary change. The model furthermore assumes that individual differences in fecundity and mortality due to differences in age, size or physiological condition—properties which play a crucial role in long-term evolution—can be neglected in describing the dynamics of gene frequency change.

Directionality theory (Demetrius 1992, 1997, 2000) defines a new class of models that integrates Mendelian processes with demography. A cornerstone of this theory is the concept of evolutionary entropy, a demographic parameter that describes the variability in the age of reproducing individuals in a population. Entropy is the rate of increase of an effective population size, a quantity defined by assigning weights to individuals in the different age classes according to the frequency distribution of the genealogies they generate (Demetrius 1983). Directionality theory considers evolution as a two-step process, involving mutation where new types are introduced into the population, and natural selection, which modulates the outcome of competition between the incumbent and the mutant types. The main tenets of the theory are a series of directionality theorems—extensions of Fisher's

fundamental theorem of natural selection—which describe the global changes in entropy that ensue as one population replaces another under the mutation–selection dynamics. Directionality theory thus forges a link between the local dynamics of gene frequency change and the global dynamics of changes in the life-history properties of a population. In this article we will invoke certain scaling relations between life-history parameters and the morphometric variable body size, to establish an allometric relationship between entropy and body size, thus generating a link between population genetics and the dynamics of morphometric change. This article exploits this new synthesis to provide evolutionary genetic explanations of Cope's rule, the island rule and Bergmann size clines.

2. DIRECTIONALITY THEORY

Darwin's theory of evolution by natural selection postulates that adaptation, that marvellous fit of organisms to the environment, is the outcome of a gradual dynamic process that operates on two time-scales. The first process, which acts on a short time-scale, is the introduction of new variation by mutation. This event is random in the sense that it is not related to the current needs of the organism nor to the exigencies of the environment. The second process, which occurs over a much longer time-scale, is the selective event. It discriminates between types according to their capacity to survive and reproduce in the existing environment. This selective process is deterministic in the sense that the ultimate fixation of the new type within the population will be induced by the response of the organism to the environmental condition. According to the mutation–selection dynamic, the less fit organisms, that is, the individuals less well adapted to the environmental condition, will be replaced by the more fit, with the process ultimately driving the population to a state of optimal fitness and adaptation to the environment.

Fitness in Darwin's theory has a variety of connotations depending on the behavioural features and ecological situation being considered. It includes, according to context, physiological and behavioural features such as visual acuity, muscular strength and foraging ability. These attributes confer a capacity to survive and reproduce in a given environment, and are expected to improve over generations under the force of selection.

An operational measure of fitness, the Malthusian parameter, was proposed by Fisher (1930), to provide a mathematical representation of Darwin's theory. The Malthusian parameter, a function of the age-specific fecundity and mortality of the individuals in a population, describes the rate of increase of total population numbers. In populations of effectively infinite size, the Malthusian parameter determines the condition for invasibility of a new allele (see for example, Charlesworth & Williamson 1975; Pollack 1976). As shown, however, in Demetrius & Gundlach (1999), this condition no longer obtains in populations of finite size—invasibility in finite size populations is a stochastic process that depends on the Malthusian parameter and the demographic variance, the variance in the ages at which reproduction occurs. These invasibility conditions can be expressed in terms of

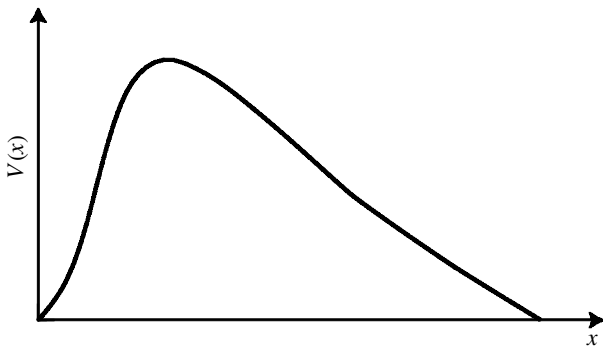


Figure 1. Graph of net reproductive function $V(x)$.

a unique demographic parameter, evolutionary entropy, a measure of the rate of increase of an effective population size. Directionality theory invokes entropy as a new operational measure of Darwinian fitness, and exploits this parameter to provide a quantitative model of the Darwinian process.

(a) Evolutionary entropy

The fitness measure entropy can be analytically expressed in terms of the life-history characteristics of a population, as defined by the net reproductive function $V(x)$ (see figure 1), a product of $l(x)$, the probability that an individual born at age zero survives to age x , and $m(x)$, the mean number of offspring produced at age x .

The growth rate of a population, with life-history properties described by the net reproductive function $V(x)$, is the unique real root, r , of the Lotka equation:

$$1 = \int_0^{\infty} \exp(-rx) V(x) dx. \quad (1)$$

The function $p(x) = \exp(-rx)V(x)$ is a probability density function that describes the age of the mother of a randomly chosen newborn. Evolutionary entropy, denoted H , is given by $H = S/T$, where

$$S = - \int_0^{\infty} p(x) \log p(x) dx; \quad T = \int_0^{\infty} xp(x) dx.$$

The function S is a measure of the degree of iteroparity of the population, that is, the variability in the age of reproducing individuals in the population. The quantity T describes the generation time, the mean age of individuals at the birth of their offspring.

We shall assume that the probability density function $p(x)$ is bounded, and that the random variable X which defines $p(x)$ has a finite variance. We also restrict the model to distributions $p(x)$ which ensure that S is positive. In this case, S can be interpreted as a measure of the dispersion of the net reproductive function.

The population growth rate, or the Malthusian parameter, as defined by equation (1), can be expressed as the sum of two functions, evolutionary entropy H , and the reproductive potential Φ :

$$r = H + \Phi, \quad (2)$$

where

$$\Phi = \frac{\int_0^{\infty} p(x) \log V(x) dx}{\int_0^{\infty} xp(x) dx}.$$

The numerator in the function Φ , is the total net offspring averaged over the different age classes.

We infer from equation (2) the following implications:

$$\Phi < 0 \Rightarrow r < H; \quad \Phi > 0 \Rightarrow r > H.$$

Accordingly, the function Φ can be used to classify populations in terms of their growth rate: $\Phi < 0$ (bounded growth) describes a population whose growth rate is bounded by entropy; $\Phi > 0$ (unbounded growth) represents a population whose growth rate always exceeds entropy.

Evolutionary entropy parameterizes the changes in genetic and phenotypic composition that occur when new types are introduced into the population by mutation, and the ancestral and mutant types compete due to selection. We distinguish between the different events that determine the global change in entropy.

(i) Mutation

The mutation model considers a population at demographic equilibrium described in terms of a stable age distribution and an entropy H . Random mutations occur in a small subset of the population. These mutations will transform the net fecundity distribution $V(x)$ into a function $V^*(x)$, which we assume can be represented by the change $V^*(x) = V^{1+\delta(x)}(x)$, where $\delta(x)$ is monotonic in x (Demetrius 1992).

Let Δr and ΔH denote the changes in the demographic variables r and H which result from the mutation event. For mutations with small effects, we have

$$\Delta r = \Phi \delta_1, \quad \Delta H = -\sigma^2 \delta_2, \quad (3)$$

where $\delta_1, \delta_2 > 0$, with the parameter σ^2 , the demographic variance, given by

$$\sigma^2 = \frac{\int_0^{\infty} p(x) W(x)^2 dx}{\int_0^{\infty} xp(x) dx}, \quad (4)$$

here, $W(x) = -x\Phi + \log V(x)$.

We also have that the change in the demographic variance σ^2 due to mutational changes in $V(x)$ is given by $\Delta\sigma^2 = \gamma\delta_3$, where $\delta_2, \delta_3 > 0$ and γ , the correlation index is given by

$$\gamma = 2\sigma^2 - \frac{3\sigma^2}{T} \int_0^{\infty} xp(x) W(x) dx + \frac{1}{T} \int_0^{\infty} p(x) W(x)^3 dx.$$

The equation (3) implies, since $\sigma^2 > 0$, the following set of mutation relationships: $\Phi < 0 \Rightarrow \Delta r \Delta H > 0$; $\Phi > 0 \Rightarrow \Delta r \Delta H < 0$.

The correlation index γ may in general assume positive and negative values. However, numerical studies of typical life-tables, that is, life-tables defined by a net reproductive function $V(x)$ with the unimodal form given in figure 1, show that $\gamma > 0$. Accordingly, we obtain that the relation, $\Delta H \Delta\sigma^2 < 0$ holds.

Table 1. *Invasion criteria*

ecological constraints	demographic condition	selective outcome
bounded growth ($\Phi < 0$)	$\Delta H > 0$	mutant invades almost surely (a.s.)
	$\Delta H < 0$	mutant becomes extinct a.s.
unbounded growth ($\Phi > 0$) unbounded population size ($N > \gamma/\Phi$)	$\Delta H < 0$	mutant invades a.s.
	$\Delta H > 0$	mutant becomes extinct a.s.
unbounded growth ($\Phi > 0$) bounded population size ($N < \gamma/\Phi$)	$\Delta H < 0$	mutant invades with a probability that increases with population size
	$\Delta H > 0$	mutant becomes extinct with a probability that increases with population size

(ii) *Invasion–extinction*

The conditions for invasability of a mutant gene can be analysed in terms of a synthesis of diffusion processes and the ergodic theory of dynamic systems (Demetrius & Gundlach 1999). Diffusion processes have been exploited by Kimura (1962) and Gillespie (1974) to study the invasion dynamics of populations with non-overlapping generations. The analysis in Demetrius & Gundlach (1999) appeals to ideas from the ergodic theory of dynamical systems to extend the classical invasion analysis to populations described by overlapping generations. These new studies show that the outcome of competition between the incumbent allele and the mutant type is a stochastic event determined by the parameter s , where

$$s = \Delta r - \frac{1}{N} \Delta \sigma^2,$$

with N denoting the population size.

The above expression for s indicates that the conditions for invasion will be determined by the parameters Δr and $\Delta \sigma^2$. In view of the correlations between the changes Δr and ΔH , and the changes ΔH and $\Delta \sigma^2$, we can express the invasion conditions uniquely in terms of the demographic parameter ΔH , and a set of ecological constraints on growth rate and population size defined in terms of the parameters Φ and γ . We recall that the population growth is said to be bounded, if $\Phi < 0$, and unbounded if $\Phi > 0$. We now characterize a population size as bounded, if $N < \gamma/\Phi$, and unbounded, if $N > \gamma/\Phi$.

The invasive criteria, expressed in terms of the measure of selective advantage given by $s = \Delta H$, and the constraints on growth rate and population size, are represented in table 1.

(iii) *Selection dynamics: long-term*

The invasion–extinction dynamic process describes the dynamics of new alleles on a short time-scale. In the event that the new alleles become established in the population, the new types will mate with the ancestral types according to the Mendelian laws, thus generating new genotypes. The selective process now unfolds on a time-scale that is much longer than the invasion event. During this process, ecological factors will regulate the evolutionary dynamics and the number of genotypes will vary with respect to density-dependent and frequency-dependent effects. This process can be described in terms of the dynamic systems generated by the different

genotypes. As shown in Demetrius (1992), this coupled dynamic system will converge to a new steady state described by a new entropy. Moreover, if ΔH denotes the change in entropy as the population evolves from one demographic equilibrium to the next, and $\Delta \tilde{H}$ denotes the change in entropy that characterizes the invading mutant, we have

$$\Delta H \Delta \tilde{H} > 0. \quad (5)$$

The directionality principles for evolutionary entropy are theorems describing global changes in entropy. These theorems are a consequence of the local changes in entropy resulting from the invasion of new mutants, and the correlation between local and global changes described by equation (5). The directionality theorems can be expressed in terms of the relationships between (i) ecological constraints, as defined by bounds on the population growth rate, and bounds on the population size, and (ii) global changes in entropy as one population replaces another under the combined action of mutation and selection. We have H(i) populations with bounded growth: a unidirectional increase in entropy; H(ii) populations with unbounded growth and large population size: a unidirectional decrease in entropy; H(iii) populations with unbounded growth and small population size: random, non-directional changes in entropy.

We will now derive an allometric relationship between the entropy function S and body size, and use this property, together with the directionality principles for entropy given by H(i), H(ii) and H(iii) to provide explanations of Cope's rule, the island rule and Bergmann size clines in terms of population genetics.

3. ENTROPY AND BODY SIZE

Body size, more than any other descriptive property, is the fundamental factor that defines the physiological and morphological requirements, as well as the ecological constraints of the organism. Individuals of different sizes perform similar functions—a condition that is expressed in terms of a nonlinear scaling of life-history and physiological variables, \mathcal{Y} , with body size, W . This scaling relation can be expressed as a power function (Kleiber 1961): $\mathcal{Y} = aW^b$.

Here, a denotes a proportionality constant that varies with the nature of \mathcal{Y} and the kind of organism. The

exponent b is known to fall into certain patterns determined by the dimension of the variable \mathcal{V} : volume rate, such as metabolic rate ($b \cong 3/4$); and cycle time, such as generation time ($b \cong 1/4$) (Calder 1984; Peters 1983). We will exploit these empirical relations to show that (up to additive constants) the entropy function S is isometric to body size:

$$S = kW. \quad (6)$$

In deriving equation (6), we consider a population of organisms with net reproductive function $V(x)$ and we assume that reproduction occurs only over part of the life span, between ages α and ω , say. The quantity $-\{1/V(x)\}\{dV(x)/dx\}$ represents the rate of net offspring production, denoted $g(x)$, of individuals at age x .

Now the metabolic rate, denoted P , is the rate at which chemical energy is being transformed from nutrients into the biochemical energy within the organism. This rate can be measured by the total heat production of the organism, or by the amount of oxygen used in oxidation processes.

The quantity P will typically be a function of age. Studies based on multicellular organisms and cells (cf. Trincher 1965) show that P increases during the growth phase of the organism, then decreases to some value that is maintained constant during the stationary phase of the adult organism. We will assume that, during this stationary phase, the energy generated by the metabolic processes is allocated uniquely to survivorship and reproduction. When this condition holds, the rate of net offspring production, $g(x)$, which can be assumed constant in the adult organism, will be proportional to the metabolic rate P , and we have

$$-\frac{1}{V(x)} \frac{dV(x)}{dx} = kP \quad (7)$$

where $k > 0$. Write $E = \int_{\alpha}^{\omega} p(x) \log V(x) dx$. By integrating (7) we obtain

$$E = - \int_{\alpha}^{\omega} kPx p(x) dx = -kP \int_{\alpha}^{\omega} xp(x) dx = -kPT, \quad (8)$$

where T denotes the generation time.

In view of the allometric relationships $P \sim W^{3/4}$ and $T \sim W^{1/4}$, we obtain from equation (8) the isometric relationship $E = -kW$, where k denotes a proportionality constant.

Now, we observe from equation (2) that $rT = E + S$.

We now distinguish between two constraints on population growth rate: the stationary phase ($r = 0$), and the exponential phase ($r > 0$). Under stationary growth constraints ($r = 0$), we have $E + S = 0$, hence $S = kW$ and the isometric relationship equation (6) holds.

Under exponential growth conditions ($r > 0$), we have $S = kW + rT$. Now, in view of the allometric relations $r \sim W^{-1/4}$, $T \sim W^{1/4}$ (see Calder 1984; Peters 1983) the product rT is independent of body size, hence $S = kW + c$, where c denotes a positive constant.

We should point out at this juncture that there exist several efforts to give a theoretical basis for the empirical relationships between body size, and the parameters generation time and metabolic rate—the scaling laws we have invoked to derive equation (6). Models based on

mechanical considerations are described in McMahon (1973); network models involving structural and hydrodynamic constraints are treated in West *et al.* (1997). The class of assumptions considered by each of these authors imposes certain limits on the range of applicability of these models. However, as noted in Hemmingsen (1960), the scaling relationships are universal—they apply to cellular systems, plants and animals—groups of organisms that differ significantly in terms of the mechanical, structural and hydrodynamic constraints they experience. The restricted domain of application of the different theories indicates that the problem of understanding the empirical relationships between body size and metabolic rate valid across all taxa remains unresolved.

4. TRENDS IN BODY SIZE: COPE'S RULE, THE ISLAND RULE AND BERGMANN'S RULE

We will now invoke the principles expressed by H(i), H(ii) and H(iii) to derive a set of directionality principles for the entropy function S , and then use equation (6) to predict evolutionary trends in body size.

(a) Directional changes in the entropy function S

The entropy function S is given by the relationship $S = HT$. The perturbation analysis (Demetrius 1992) shows that the change ΔS due to small perturbations of the net fecundity function $V(x)$ is given by

$$\Delta S = \rho \delta, \quad (9)$$

where $\rho = \int_0^{\infty} p(x)W(x) \log p(x) dx$, with $W(x)$ given by equation (4) and $\delta_3 > 0$.

Typical net reproductive functions $V(x)$, see figure 1, are positive and concave. Computing the second derivative of $W(x)$ shows that $W(x)$ is also concave. Moreover, by the mean value theorem, we have, $\rho = W(\xi) \int_0^{\infty} p(x) \log p(x) dx$, where $0 < \xi < \infty$. Hence $\rho = -SW(\xi)$.

Numerical studies of typical net reproductive functions show that $W(\xi) > 0$, hence $\rho < 0$. We conclude from equations (3) and (9) that $\Delta H \Delta S > 0$. We can therefore appeal to the directionality principles H(i), H(ii) and H(iii) to infer similar dependencies between ecological constraints and directional trends in the entropy function S . We have S(i) bounded growth conditions: a unidirectional increase in S ; S(ii) unbounded growth conditions, large population size: a unidirectional decrease in S ; S(iii) unbounded growth conditions, small population size: random, non-directional changes in S .

(b) Directional trends in body size

Now bounded growth pertains to populations with stationary size or populations the total numbers of which vary around some constant value, whereas unbounded growth refers to populations that spend the greater part of their evolutionary history in the exponential growth phase. Hence, in view of the isometric relation between S and body size, we can now infer the following series of relations between the response to ecological constraints, and trends in body size, namely W(i) populations that spend the greater part of their evolutionary history with total population numbers constant or varying around

some constant value: a unidirectional increase in body size; W(ii) large populations that spend the greater part of their evolutionary history in the exponential growth phase: a unidirectional decrease in body size; W(iii) small populations that spend the greater part of their evolutionary history in the exponential growth phase: random, non-directional changes in body size.

(i) *Cope's rule*

The predictions expressed in W(i), W(ii) and W(iii) provide a new perspective on Cope's rule. Our analysis points to the context-dependency of evolutionary trends in body size: a unidirectional increase in size will only prevail when ecological factors induce bounded growth conditions; a unidirectional decrease in size or a random non-directional trend will emerge when the ecological constraints induce a state of unbounded population growth. The context dependency of trends in body size is illustrated by the horse clade, an example discussed in Jablonski (1996). This clade has often been considered to be a canonical example of Cope's rule. However, a more detailed study (MacFadden 1986), has shown that the pattern of size changes in North America and Europe are quite distinct. The clade in North America can be characterized by two phases: a static condition, during the early part of the group's history, and a unidirectional increase in body size from the late Miocene to the Pleistocene. The Plio–Pleistocene lineage in Europe, however, is described by a unidirectional decrease in body size. These differences in the North American and European patterns are correlated with the different ecological constraints that define the two regions. These correlations underscore our prediction that evolutionary trends in body size are modulated by the ecological constraints that the species endure. The predictions also elucidate the empirical observation that trends over long-term and trends over short-term scales have different signatures. The demographic condition defined by small population size and rapid exponential growth evidently can only prevail over short periods of time; consequently, we predict that random non-directional changes in body size will only be observed over short periods of a species' evolutionary history. Most mammals spend the greater part of their evolutionary history with a total population size that is constant or varying around some constant value. Hence, in accordance with W(i), most mammalian lineages over the long term will be characterized by an increase in body size.

(ii) *The island rule*

The relationships between the response to ecological forces and trends in body size, as described by W(i) and W(ii), also provide an explanation of the island rule (Foster 1964; Van Valen 1973). This empirical generalization pertains to changes in body size that occur as species migrate from mainland populations to colonize island habitats. These patterns can be classified in terms of the body size (large, medium, small) of the mainland population as follows: (i) large size: evolution toward smaller sizes; (ii) medium size: no particular trend in size change; (iii) small size: evolution toward larger sizes. The explanation of the island rule we advance derives from (a) the relationship between ecological constraints and

trends in body size, as described by W(i) and W(ii) and (b) the observation that populations in mainland and island populations will be subject to different ecological forces. As noted in Sondaar (1977), among others, carnivores, the main predators of large mammals, are typically widespread on the mainland but largely absent in island populations. However, birds of prey, the main predators of medium-sized organisms, such as insectivores and lagomorphs, will be equally present on the mainland and islands. In the case of large mammals, the absence of predators on islands entails that in island habitats these populations will spend the greater portion of their evolutionary history in the exponential growth phase, a condition that will result in a unidirectional decrease in size. In the case of medium-sized mammals, the presence of predators on both the mainland and the island implies that medium-sized species will be subject to similar ecological constraints in both environments. Since the mainland population would be characterized by a size optimal for these ecological conditions, we infer that the island colonists, subject to the same ecological constraints as their mainland ancestors, will undergo very little change in size. Small organisms, as in the case for medium-sized species, will be subject to the same group of predators, namely birds of prey, on the mainland as on islands. Founder populations of small organisms on islands will initially increase rapidly in numbers and soon exhaust the island resources. These resource limitations will result in constraints on population numbers, consequently, small-sized populations will spend the greater part of their evolutionary history in the stationary phase, or fluctuating around some constant population size, conditions that entail a unidirectional increase in size. This model thus predicts that as species migrate from mainland to island habitats, there will be a decrease in body size (in large organisms), no particular change in size (in medium-sized organisms), and an increase in body size (small organisms). The factors of competitive release and resource limitation that drive our analysis have also been invoked in Lomolino (1985) to explain the island rule. Lomolino's argument, however, was based uniquely on ecological considerations. The model we have described derives from an evolutionary genetic argument—a consequence of the directionality principles for evolutionary entropy, expressed by H(i), H(ii) and H(iii).

(iii) *Bergmann's rule*

The allometric relationship between entropy and body size and the directionality principle for entropy also provides an adaptive explanation for Bergmann's rule, the observation that species exhibit latitudinal clines—larger size in colder regions, smaller size in warmer regions. In order to explain the Bergmann cline, we first observe that different geographical regions will differ in terms of resource productivity. In colder regions, the duration of abundance of forage is short—a condition that will impose limits on the population growth rate, corresponding to stationary or near-stationary states. In the tropics, the wet season will allow a greater abundance of forage, and consequently, organisms will experience a respite from severe competition. This situation will induce frequent and prolonged episodes of rapid exponential growth. Hence populations in the colder climates will

evolve under constraints that induce prolonged episodes of stationary growth, whereas in warmer climates, their evolutionary history will be characterized by extended episodes of exponential growth. We can therefore invoke the directionality principle for entropy to predict Bergmann size clines: large body size in races that occupy colder climates, smaller body size in races that dwell in warmer climates. We conclude that the Bergmann size clines are the consequence of the evolutionary response of different groups to ecological forces: larger size is an evolutionary adaptation to the bounded growth conditions that result from the resource limitations which define races evolving in colder climates.

5. CONCLUSION

The explanations of Cope's rule, the island rule and the Bergmann size cline advanced in this article point to the directionality principle for evolutionary entropy as a unifying tenet in understanding patterns of macro-evolutionary change in terms of the dynamics of gene frequency change. Entropy, a demographic variable, represents an operational measure of Darwinian fitness. This claim derives from two main properties that the entropy parameter characterizes: (i) invasion criteria: the conditions for establishment of a mutant allele; (ii) directionality: the parameterization of the evolutionary process as one population replaces another under mutation and selection. Entropy is also allometrically related to body size. The directionality principles for entropy thus provide a basis for understanding ecotypic patterns involving body size in terms of micro-evolutionary processes.

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As this paper exceeds the maximum length normally permitted, the author has agreed to contribute to production costs.