

## Regulation of animal size by eNPP, Bergmann's rule, and related phenomena

MICHAEL A. HUSTON<sup>1,3</sup> AND STEVE WOLVERTON<sup>2</sup>

<sup>1</sup>*Department of Biology, Texas State University, San Marcos, Texas 78666 USA*

<sup>2</sup>*University of North Texas, Department of Geography, Denton, Texas 76203-5017 USA*

**Abstract.** Bergmann's rule, which proposes a heat-balance explanation for the observed latitudinal gradient of increasing animal body size with increasing latitude, has dominated the study of geographic patterns in animal size since it was first proposed in 1847. Several critical reviews have determined that as many as half of the species examined do not fit the predictions of Bergmann's rule. We have proposed an alternative hypothesis for geographic variation in body size based on food availability, as regulated by the net primary production (NPP) of plants, specifically NPP during the growing season, or eNPP (ecologically and evolutionarily relevant NPP). Our hypothesis, "the eNPP rule," is independent of latitude and predicts both spatial and temporal variation in body size, as well as in total population biomass, population growth rates, individual health, and life history traits of animals, including humans, wherever eNPP varies across appropriate scales of space or time. In the context of a revised interpretation of the global patterns of NPP and eNPP, we predict contrasting latitudinal correlations with body size in three distinct latitudinal zones. The eNPP rule explains body-size patterns that are consistent with Bergmann's rule, as well as two distinct types of contradictions of Bergmann's rule: the lack of latitudinal patterns within the tropics, and the decline in body size above approximately 60° latitude. Both types of contradictions of Bergmann's rule are consistent with the eNPP rule, as are a wide range of other phenomena.

*Key words:* Bergmann's rule; body size; fish; latitude; mammals; NPP; productivity.

*We are told in our first course in biology that all animals are dependent on plants for food, either directly or indirectly, and that plants in turn obtain their food from the soil and process it in the presence of sunshine, air, and water. This elementary law of nature is so simple and obvious that its import to problems of wildlife conservation has been frequently overlooked. . . . What I am about to say may be interpreted by some as a highly controversial issue . . . .*

—A. H. Denney (1944)

### INTRODUCTION

Variation in body size among animals is of great interest in macroecology, biogeography, and conservation (Margalef 1955, McNab 1971, Peters 1983, Calder 1984, Brown and Nicoletto 1991, Crooks 2002, Meiri and Thomas 2007, Olden et al. 2007, Greve et al. 2008)

and is often linked to other global patterns, such as the latitudinal gradient of species richness (Blackburn and Gaston 1994, 1996, 1998, Johnson 1998a) as well as patterns of extinction (Johnson 1998b, Purvis et al. 2000, Cardillo 2003, Cardillo et al. 2005, Olden et al. 2007) and evolution (Cooper and Purvis 2010). Spatial variation in animal body size has been a major topic since at least 1847, when Bergmann published his iconic paper linking large body size to cold conditions (Bergmann 1847). With the recent development of global data sets, Bergmann's paper has spawned a small industry in body-size analyses, but there are many interpretations of this pattern and there is relatively little consensus (Rosenzweig 1968a, McNab 1983, Geist 1987a, b, Cousins 1989, Ashton et al. 2000, Meiri and Dayan 2003, Meiri et al. 2004, Rodríguez et al. 2006, Meiri and Thomas 2007, Watt et al. 2010, Meiri 2011). Numerous correlates of body-size variation have been investigated, including latitude, latitudinal range, geographical range size, temperature, temperature range, annual precipitation, precipitation range, net primary

Manuscript received 6 August 2010; revised 1 March 2011; accepted 2 March 2011. Corresponding Editor: A. M. Ellison.

<sup>3</sup> E-mail: hustonma@txstate.edu

production (NPP), food supply, and species richness, the last of which potentially involves a sampling effect that may skew data (Meiri and Thomas 2007).

Meiri (2011) points out that Bergmann's rule is actually an empirical generalization that describes a common intraspecific pattern in endotherms. An empirical generalization "is a statement concerning known phenomena that is *treated* as a law that holds in all times and places. The statement is not really *known* to be a law; instead this stature is assigned to empirical generalizations based on repeated, non-contradictory observations" (Wolverton and Lyman 2000:237; emphasis in original). Bergmann (1847) hypothesized that heat conservation was the explanatory mechanism underlying his rule. We note, however, that process and pattern are often conflated in the literature, and that a single type of pattern may have multiple causal processes operating at different times and places. What is needed to overcome this problematic empirical generalization is an explanatory rule that ascribes an ecologically sound mechanism for patterns in animal growth, body size, and biomass that is independent of latitude and geographic scale.

The literature on Bergmann's rule has been described as "chaotic" (McNab 2010). In spite of intense interest in this subject, there is argument about whether size variation should be analyzed at the intra- or interspecific level, or even at higher taxonomic levels (e.g., Lindsey 1966). There is even disagreement over the taxonomic level at which Bergmann intended his rule to apply (cf. James 1970, Blackburn et al. 1999, Meiri and Thomas 2007, Meiri 2011). At the intraspecific level, where much of the recent work has been done, the focus has been on determining which taxa show the expected latitudinal pattern. Most groups of homeotherms show the pattern predicted by Bergmann (Ashton et al. 2000, Meiri and Dayan 2003). However, many groups of poikilotherms, which are not subject to the heat-conservation mechanisms underlying Bergmann's rule, also show the same pattern of increasing body size with latitude (Ray 1960, Lindsey 1966, Atkinson 1994, Ashton 2002, Ashton and Feldman 2003).

At the interspecific, "community," or assemblage level, most studies find the expected positive correlation between mean body size and latitude for birds (Blackburn and Gaston 1996) and mammals (Blackburn and Hawkins 2004, Rodríguez et al. 2006, Cooper and Purvis 2010) consistent with Bergmann's rule. However, Meiri and Thomas (2007) point out that part of the pattern may be an artifact of there being fewer small-bodied species where species richness is low, as at high latitudes. This is a valid concern, and points toward fundamental problems with this approach. One critical flaw has been that there is no scaling by species abundance for determining the community mean. Any species that is present in a region, no matter how rare, is included in "average body size" of the assemblage in that region. Thus, the body size of a rare large animal contributes as

much as that of a common smaller animal. This problem persists regardless of whether a species is analyzed on the basis of the centroid of its range or its presence in each grid cell or region encompassed by its range (e.g., Blackburn et al. 1999, Blackburn and Hawkins 2004). The approach is unsound as currently applied and is unlikely to lead to a functional or mechanistic understanding of factors that influence either average body size in an assemblage or the distribution of body sizes (sensu Cooper and Purvis 2010, McNab 2010).

A more appropriate way to calculate mean community body mass would be to scale body size by the total mass of all individuals of each species present in an area (converted to a proportion of the total mass of all species). Unfortunately, such data are very scarce and logistically challenging to collect, so there are few publications that provide a functionally relevant mean assemblage biomass. Alternatively, because outlier species (usually with large body size) skew community means, a simple compromise is to compare communities using median size, which is less sensitive to problems of skewness (McGrew and Monroe 2000, Weiss 2002, Cooper and Purvis 2010). The issue of functionally relevant proportional representation is most problematic in mammals, which have a huge range in body size. In contrast, the relatively small body-size range of birds should reduce the bias introduced by variation in species richness and seems to produce interpretable results (e.g., Blackburn and Gaston 1996). Natural selection and the vicissitudes of evolutionary history have led to many situations such as the co-occurrence of large elephants and small rodents in the same habitat. Neither the mean of these species summed, nor the range of body mass they represent, are likely to teach us much about the effects of environmental conditions on animal body size.

Given the problems associated with the current emphasis on the "community approach" to evaluating Bergmann's rule, we focus primarily on intraspecific size variation, which eliminates several alternative (and therefore confounding) mechanisms that may operate at the interspecific or community level. The excluded mechanisms are (1) selection for alternative life history strategies and body sizes in the same environment; (2) consequences of random ancestral colonization and diversification of large-bodied or small-bodied species; (3) selective advantage of traits linked to, but functionally unrelated to, body size; and (4) higher migration ability of large-bodied species for recolonizing deglaciated areas (more likely to be important for mammals than for birds). Each of these mechanisms could potentially operate on the large variation in size found between species, but is unlikely to be relevant to the much smaller size range found between populations of the same species (Blackburn and Hawkins 2004). So, what are the potential mechanisms that are relevant at the intraspecific level?

Scientists have long realized that Bergmann's rule is not really about latitude, but rather about something

correlated with latitude. While Bergmann's original focus was clearly on the implications of relative body surface area for the conservation of heat in cold climates, investigators over the past century have realized that there are a number of factors other than temperature that could be the ultimate cause of whatever correlations exist between body size and latitude. Numerous hypotheses have been proposed. We believe that there is some, as yet unrecognized (or, at a minimum, underappreciated) fundamental cause of the latitudinal variation in body size described by Bergmann's rule. This cause should be mechanistically independent of latitude and its direct correlates such as temperature or insolation, though it must obviously be correlated with latitude in situations where the Bergmann pattern is found. This cause could potentially be related to a wide range of other ecological phenomena in addition to Bergmann's rule. For example, animal body size, which for many taxonomic groups is highest in the high temperate latitudes, is obviously and inversely correlated with the general latitudinal gradient of species diversity, which for most taxonomic groups is lowest in the high latitudes. Interesting evidence related to the mechanistic independence of the body-size pattern from latitude was reported by Blackburn and Gaston (1996) who found that body size was more strongly correlated (negatively) with species richness in neotropical birds than it was with latitude (positively) (see also Cooper and Purvis 2010).

Much of the debate on Bergmann's rule centers on mechanisms that have little to do with phenotypic plasticity in body-size variation at the intraspecific level, including heat conservation (Bergmann 1847, Rodríguez et al. 2006), heat dissipation (James 1970), and starvation resistance (Lindsey 1966, Rosenzweig 1966, Calder 1984, Lindstedt and Boyce 1985, Kooijman 1986). In our opinion, the fact that these mechanisms, rather than a simple explanation such as food quantity and quality, have been the focus of efforts to explain body size is the consequence of a fundamental misunderstanding of the latitudinal distribution of terrestrial NPP and thus of the pattern of food availability for virtually all animals (see Huston 1994, Geist 1998, 1999, Huston and Wolverton 2009, Wolverton et al. 2009a). In a recent paper, we reevaluated evidence for the global distribution of net primary production and proposed a new concept, ecologically and evolutionarily relevant NPP (eNPP, Huston and Wolverton 2009); eNPP, defined as net primary production during the growing season, is highest in the temperate regions/latitudes of the world.

The significance of the eNPP concept is that it specifically addresses the NPP that is available to meet the energetic and nutritional demands of animals (and plants) during that time when they are reproducing and growing. This period, generalized as the "growing season," is when ecological processes, such as competition and predation, and evolutionary processes, such as

reproduction and gene flow, occur with their greatest intensity. In the many regions of the world where there is also a non-growing, dormant, or "starvation" season, the survival of organisms depends on the amount of resources that they have acquired during the growing season. eNPP, then, refers to the rate of production of energy-rich plant compounds that also contain chemical elements and complex organic molecules that animals are unable to produce by themselves, specifically during the time when they are critical to growth and reproduction. In contrast to this concept, NPP is conventionally expressed as an annual rate, which sums fluctuations in plant growth rates over the entire year, during which they may vary from very high to zero, particularly in climates that have high seasonality due to fluctuations in either temperature or precipitation.

In the humid tropics, where seasonality is low, the total annual NPP is apparently about the same as that in most temperate forests (Huston 1994, Huston and Wolverton 2009). However, because this tropical NPP is spread over the entire year, it actually represents chronically low productivity during the times of reproduction and growth (i.e., eNPP), which may or may not vary in length or timing, depending on the species and on rainfall seasonality. In contrast, in the temperate zone, and the seasonal tropics, the short-term rate of plant growth (i.e., eNPP) is very high during part of the year and low or zero the rest of the year. In these seasonal environments, the reproduction and growth of plants and animals is concentrated into the time period when the rate of plant growth is highest. During the unfavorable season, most plants and some animals become dormant (e.g., hibernate or aestivate), while some animals migrate to other areas, and others remain and survive on whatever food they can find, generally losing mass until the arrival of the growing season.

The principles of trophic dynamics and energetics extend the consequences of eNPP from the primary producer level to the higher trophic levels of herbivores and carnivores, with the inevitable approximate 90 percent loss of energy with each trophic transfer (consumption event). Thus, it is appropriate to consider secondary productivity (animal growth rate) in the same seasonal framework as eNPP. The short-term animal growth rate (interpreted at either the individual or population level), is designated here as eNSP (ecologically and evolutionarily relevant net secondary production), which varies seasonally from high positive values during the growing season, to negative values for most species during the non-growing (winter or dry) season.

In addition to the temporal fluctuations in short-term productivity (i.e., eNPP and eNSP) due to seasonality, there are also spatial variations in eNPP due to differences in the availability of water and/or nutrients, either in the soil, or dissolved in the waters of oceans, lakes, and rivers. Globally, temperature and water-dependent biogeochemical processes operate to cause soil weathering and leaching processes to operate most

rapidly in the tropics, leading to nutrient loss and infertile soils. In the temperate zone, where these processes occur more slowly, and periodic glaciation refreshes mineral resources, soil fertility tends to be higher. Thus in the temperate latitudes soils are rich and the climate allows rapid plant growth during the growing season.

In contrast, in the tropics, while solar energy input is high and water is abundant, soils are often infertile (Uehara and Gillman 1981, Richter and Babbar 1991), which limits eNPP and thus the quantity as well as the quality of plant material as food (Albrecht 1941, 1955, 1957, Trowell 1949, Meggers 1971, McKey et al. 1978, Gartlan et al. 1980). In the arctic region, although soils may be rich, the growing season is extremely short. Thus the tropics are nutrient limited, the arctic is limited by growing season duration, and the temperate region reflects the beneficial intersection of soils that have been reworked by glaciation and deglaciation and climate that permits seasonally high NPP with high nutrient and protein content. As a result, the bread baskets of the world, contrary to what might be expected from the conventional belief that NPP is highest in the tropics, occur at the temperate latitudes within specific regions of climatically driven soil development (Albrecht 1957, Huston 1993, 1994, 2005). That eNPP is highest in the temperate latitudes is reflected in several relevant data sets that have been overlooked in part because forests in these regions have been highly modified or eradicated over the past few centuries or millennia, while, at least until recently, most tropical rain forests were mature or old growth (Huston and Wolverton 2009). Indeed, it has recently been recognized that ecosystems at temperate latitudes are important (often unrecognized) global carbon sinks (Enting and Mansbridge 1991, Ciais et al. 1995, Enting 2000, Myneni et al. 2001).

Our current understanding of the mean latitudinal distribution of eNPP is summarized in Fig. 1. These data from ground-based measurements of forest above-ground annual NPP, converted to eNPP by dividing by the length of the growing season (Huston and Wolverton 2009: Fig. 10E; based on Olson et al. 2001a, b), represent the best current empirical estimate of the global distribution of forest aboveground NPP (there are insufficient data to generalize for other vegetation types). The average monthly eNPP (thick solid line) is nearly twice as high in the temperate zone as in the tropics, while the maximum values of eNPP (thin solid line) increase to approximately five times higher around 50° north latitude before declining toward the poles.

We believe that the historical misunderstanding of the global distribution of NPP and eNPP as being highest in the tropics has hampered the development of a coherent ecological understanding of spatial variation in animal body size. Specifically, we will demonstrate that the distribution of eNPP explains not only cases in which body size in animals conforms to Bergmann's rule but

also many cases in which body-size patterns contradict Bergmann's rule, as well as numerous body-size clines that are not related to latitude. When the global distribution of eNPP is understood correctly, most of the "evidence" for Bergmann's rule disappears. We conclude that the distribution of temperature has little to do with animal body size (Geist 1987a; see also Ho et al. 2010 for insects), other than temperature's direct and indirect effects on the distribution of plant productivity. Instead, intraspecific body-size variation, as well as maximum body size within clades, is regulated primarily by the geographic distribution of the food for animals provided by plant growth (eNPP). In short, the largest individuals within species and the highest population- and community-level animal biomass should occur in the same regions as the bread baskets of the world, where soils are the most fertile and where plants are abundant, productive, and nutritious.

In a recent paper addressing Bergmann's rule in mammals, McNab (2010) postulates that the availability of resources, i.e., food, drives variability in mammalian body size. He terms this relationship the "resource rule" and discusses how it accounts for most of the mechanisms suggested to explain Bergmann's rule and its exceptions. We presented a very similar hypothesis in our NPP paper (Huston and Wolverton 2009), but there are subtle and important differences between McNab's "resource rule" and the explanations we propose for variability in animal body size. Our argument is that the global distribution of net primary productivity during the growing season (eNPP) is the fundamental pattern of energy and nutrient availability that explains spatial patterns of secondary production, intra-clade body size, and the growth and reproduction of all animals, not only mammals. Because eNPP is the mechanism driving food availability, which in turn influences the growth rates and body sizes of primary consumers (i.e., net secondary production, or eNSP) and thus the production of higher trophic levels as well, the general rule should be termed the "eNPP rule" or "Geist's rule," with recognition of the seminal contributions of Valerius Geist who first introduced this fundamental concept in the context of cervid body size (Geist 1987a, 1998).

The eNPP rule addresses spatial (and also temporal) variation in animal body size and is based on the effect of food availability on growth (see Plate 1). It can be stated as: in species or groups of closely related species with geographic distributions that span a range of environmental conditions, the largest individuals and the highest ontogenetic growth rates, and/or the highest population densities and highest population growth rates, will occur in the portions of their range where food availability (eNPP) is highest.

We emphasize "ontogenetic growth rates" because animal body size is not a simple property, and the mass of a single individual can vary dramatically over time, particularly in animals that accumulate or metabolize various tissue types. By "ontogenetic growth," we mean

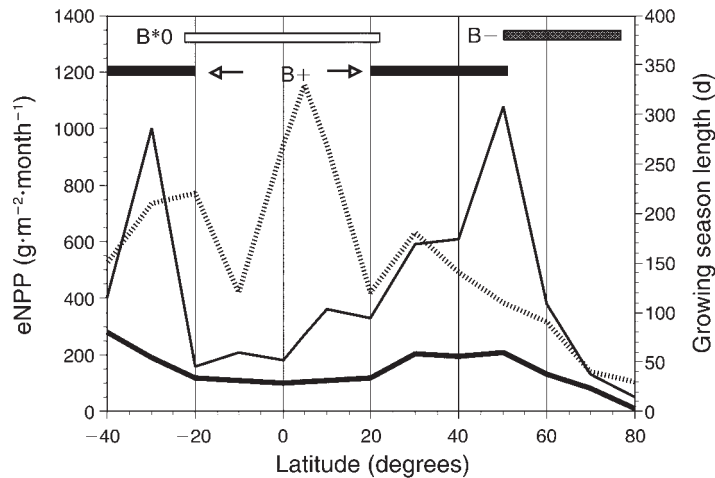


FIG. 1. The global average latitudinal patterns of growing season length (hatched line) and ecologically and evolutionarily relevant NPP (eNPP) that are the basis of latitudinal predictions of the “eNPP rule.” The solid thick line is mean eNPP, and the solid thin line is maximum eNPP, per  $10^\circ$  latitudinal band, based on 362 forest sites from a large, well-documented compilation of measurements of forest aboveground NPP (ecosystem model–data intercomparison [EMDI] Classes A and B) collected over the past 50 years (based on Huston and Wolverton [2009: Fig. 11D, F], using data from Olson et al. [2001a, b]). Animal body size is predicted to be positively correlated with eNPP, particularly the maximum values (thin solid line), which correspond to the locally most productive habitats that are preferred by most animals. B\*0 is the latitudinal range over which we predict no correlation of body size with latitude. B+ is the range over which we predict a positive correlation of body size with latitude, consistent with Bergmann’s rule, and B– is the range over which we predict that body size will be negatively correlated with latitude, contradicting Bergmann’s rule. While these eNPP values are based on the best NPP compilation of actual measurements available, they are from forests only, and the geographical coverage is extremely uneven. High-latitude herbaceous and shrub NPP (above tree line) is probably underestimated, and the actual patterns in different parts of the world will vary from the global averages summarized here. Negative latitudes are south of the equator.

the increase in size of an animal’s structural framework, such as the skeleton of vertebrates or the exoskeleton of many invertebrates. In animals with indeterminate growth, the period of ontogenetic growth may be the entire lifespan of the individual. However, in animals with determinate growth, which includes endothermic vertebrates and most insects, the period of ontogenetic growth may range from weeks or months to decades. Once the individual reaches physiological maturity, its skeletal dimensions are fixed, and any further change in mass can result only from increases or decreases in the amount of various tissues supported by the skeleton. Consequently, measurements of body mass, which may increase or decrease by 50% or more in a single individual due to the gain or loss of fat and muscle, can be highly variable over time and represent responses to current environmental conditions, specifically the short-term abundance of food. In animals with determinate growth the size of the mature skeleton remains fixed, and represents the effect of environmental conditions during the period of ontogenetic growth, which is generally a relatively short period of time during which the increase in size is very rapid. Care must be taken when interpreting and comparing body sizes, particularly in distinguishing skeletal dimensions from live mass. Use of either can be informative, but they respond to environmental conditions at different temporal scales and stages of life.

Just as high food availability produced by high eNPP can lead to high ontogenetic growth rates and large body size for individual organisms, it can also allow high population growth rates (e.g., fecundity and survival) and high population densities. However, because high population densities can reduce the food available to individual animals, there may be some tradeoffs between population size and body size, as suggested by the “energetic-equivalence rule” (Damuth 1981, 1987, 1991, Allen et al. 2002) and documented by numerous studies of population density and growth rates (discussed in *Effects of Latitude and Food Availability on Intraspecific Variation in Body Size*). The energetic basis of the eNPP rule means that population biomass density should be highest where eNPP is highest. Other environmental or behavioral conditions that affect life history strategies may alter the relative contributions of body size vs. population density to total biomass density.

We emphasize that the eNPP rule does not mention latitude because eNPP varies along many different types of environmental gradients and is not mechanistically linked with latitude per se. In large-scale geographic cases in which the rule applies across latitude or other axes, it is because spatial differences in maximum rates of food availability during the growing season drive variations in ontogenetic growth rates, body size, and biomass across space.

Of the reported body-size patterns associated with latitude, some are positively correlated with latitude,

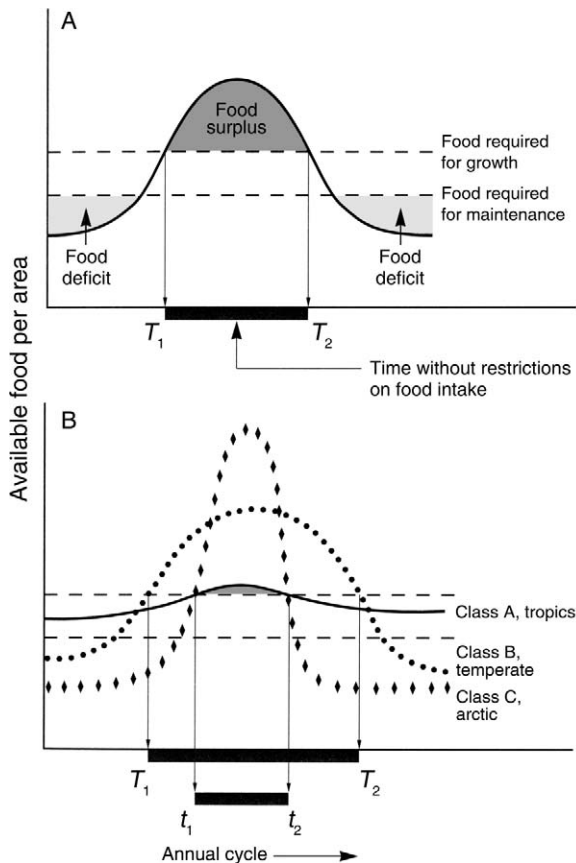


FIG. 2. Geist's model of seasonal and latitudinal variation in food availability. (A) Seasonal cycle of food surplus and food deficit that corresponds to periods of the year when animals gain or lose mass. (B) Latitudinal differences in the duration and magnitude of the seasonal pulse of food availability (analogous to eNPP; from Geist [1998: Fig. 1.8]).  $T_1$  and  $T_2$  are the beginning and end of the seasonal resource pulse in the temperate zone;  $t_1$  and  $t_2$  are the same for the tropics. The figure is reprinted with the permission of Stackpole Books.

consistent with Bergmann's rule (Fig. 1, latitudinal range B+), others are negatively correlated with latitude and thus the opposite of Bergmann's rule (Fig. 1, latitudinal range B-), and others, particularly across the tropics, show little or no relationship to latitude, and are thus also inconsistent with Bergmann's rule (Fig. 1, latitudinal range B\*0). Nearly all of these latitudinal body-size distributions track the latitudinal distribution of eNPP and thus are consistent with the eNPP rule, regardless of whether or not they are consistent with Bergmann's rule. Some of the examples we review in the following sections of this paper are limited in spatial scale and simply discuss difference in food availability as a product of difference in population density or habitat across small areas or short time periods. These smaller-scale cases illustrate the proximate mechanism underlying the eNPP rule: food availability. We believe that the eNPP rule is a relatively simple explanation for many geographic patterns that has been generally overlooked

because of a fundamental misunderstanding of the global distribution of NPP and eNPP (Huston and Wolverton 2009).

#### *Geist's model of animal body size in relation to latitude*

The basic ideas behind our hypothesis were independently explained by Valerius Geist, a wildlife biologist who focused his research on studying the evolutionary biology and ecology of cervids and other ungulates (Geist 1987a, b, 1998, 1999, see also Albrecht 1944, Denney 1944, Crawford 1950). His graphical model (Fig. 2) elegantly demonstrates what we consider to be the latitudinal distribution of eNPP on its y-axis. Geist (1978, 1998) explicitly links phenotypic plasticity in ecomorphology (e.g., body size) to habitat variability, mainly in terms of food availability during the period of reproduction and growth. But Geist (1978) states that such variability may also be epigenomic, such that individuals comprising the same genome can express ecomorphology in very different ways in different habitats (see Bogin and Rios [2003] for an example in *Homo sapiens*). He identifies epigenetic and phenotypic plasticity as particularly important in driving variability in body size and other expressions of phenotypes in cervids between populations (or between closely related subspecies and species). That Geist (1978) highlighted epigenetic responses as critical to understanding variability in ecomorphology has generally been overlooked, and only recently have wildlife biologists, evolutionary biologists, and anthropologists begun to recognize that population genetics is not the explanation for all (or perhaps not even most) intraspecific variability in ungulate body and horn or antler size (Bossdorf et al. 2008, Pfennig et al. 2010) or body size in other animals, including humans.

We believe Geist's model has received so little attention in studies that examine geographic patterns of body size primarily because the distribution of terrestrial NPP has been thought to be the opposite of the seasonal pulses that Geist proposed, since NPP has been considered to be highest in the tropics (Westlake 1963, Leith and Whittaker 1975, Ajtay et al. 1979, Olson et al. 1983, Field et al. 1998, Saugier et al. 2001). Numerous wildlife studies highlight that body-size patterns related to eNPP occur at multiple spatial scales and with a variety of latitudinal, longitudinal, and elevational orientations (e.g., Crawford 1946, 1950, Murphy and Porath 1969, Jacobson 1984, Maehr et al. 2001, Wolverton et al. 2009a).

In the following sections, we review multiple studies of body size in Northern Hemisphere large cervids and carnivores, other mammals (including *Homo sapiens*), birds, insects, and marine fish in order to evaluate the role of phenotypic plasticity in ontogenetic growth rate as the primary mechanism causing the relationship of animal body size to food quantity and quality, eNPP, and latitude. In some cases, the studies are small in geographic scale and are thus relatively "controlled" in terms

of determining the distribution of food resources and body size. In other cases, we review studies that examine latitudinal gradients in body size to determine whether or not patterns in size reflect the average latitudinal distribution of eNPP as we understand it (Fig. 1). We expect that there will be numerous examples of studies that contradict our general predictions about the latitudinal distribution of body size because eNPP is not always positively correlated with latitude (e.g., the African Sahel and other desert margins) and latitudinal productivity gradients differ somewhat between the Earth's major regions (i.e., New World, Europe/Africa, and Asia). We also acknowledge that other factors can cause geographic variability in body size, particularly at the interspecific level, such as phylogenetic history, behavioral ecology, longitudinal variability in climate, soils, and habitat properties, species range size, contingencies of reproduction, and competition, among others. Our purpose here is not to be exhaustive, but to highlight multiple cases in which variation in food availability driven by eNPP relates closely to animal body size, as well as to address apparent exceptions to the eNPP rule.

We begin our review by examining intraspecific body-size patterns in northern palearctic and nearctic mammals for several reasons. First, large mammals have large geographic ranges and thus can be examined under a variety of habitat conditions. Second, terrestrial species have relatively small migration ranges, thus it is easier to study intraspecific body-size effects in specific habitats than in species that migrate long distances (e.g., migratory birds). Third, our primary focus is on whether or not the terrestrial distribution of eNPP explains the spatial distribution of intraspecific body size, so terrestrial mammals with large geographic ranges are ideal species to study. We extend our review to interspecific body-size variation in later sections.

#### EFFECTS OF LATITUDE AND FOOD AVAILABILITY ON INTRASPECIFIC VARIATION IN BODY SIZE

##### *Geographic variation in body size of cervids*

In North America, body size in cervids varies along the latitudinal gradient. Members of this family are smallest in the tropics, largest in the temperate latitudes, and decrease in size north of 60° N latitude (Fig. 3), which matches the currently available information on the mean latitudinal distribution of forest eNPP (Fig. 1; Huston and Wolverton 2009: Fig. 11E). Geist (1987a, b, 1998) attributes this size variability in Cervidae directly to the greater seasonal resource pulse evident in Fig. 2 at temperate latitudes. That is, the largest species of North American cervid, Moose (*Alces alces*), has a geographic range that spans roughly 50–60° N latitude (though this range is expanding southward today in some areas [Franzmann 2000]). Just as revealing, however, are the intraspecific distributions of body size within the two species that cover the greatest latitudinal ranges, caribou (*Rangifer tarandus*) and white-tailed deer (*Odocoileus*

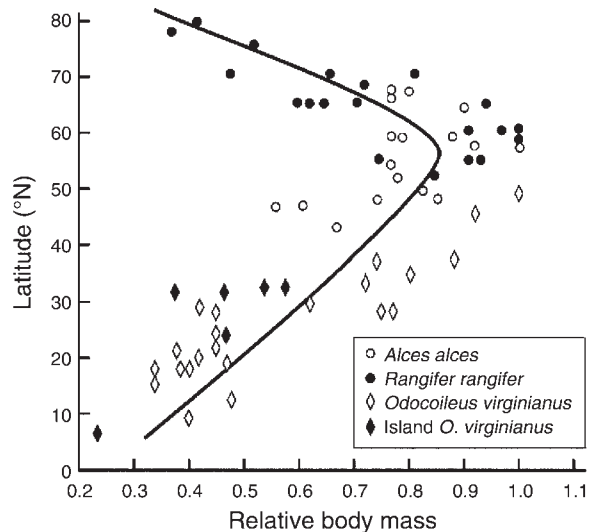


FIG. 3. The distribution of body size in North American Cervidae, which peaks at 50–60° N latitude, conforming to the eNPP rule and Geist's rule (from Geist [1998: Fig. 1.9]). The figure is reprinted with the permission of Stackpole Books.

*virginianus*). There is much to be gained not only from closely inspecting Geist's analysis of cervid size by latitude, which highlights that white-tailed deer and caribou body size are greatest at 50–60° N latitude, where they overlap with moose, but from understanding the mechanisms that produce phenotypically plastic effects on body size at smaller spatial scales. Below we present evidence showing that where food availability per animal during the growing season is high, ontogenetic growth rate and body size (usually measured as body mass) are also high. There are two primary factors that influence food availability per animal: competition for food (e.g., population density) and habitat productivity (eNPP; Wolverton et al. 2009a). Intraspecific variation in body size simply reflects variation in food availability per animal.

##### *Moose*

Moose (*Alces alces*) are generalist browsers that occupy large resource patches for long periods (Geist 1998). Good habitat includes a fire-disturbance regime that provides early successional regrowth of nutritious browse peaking in quality at roughly 30-year intervals (Franzmann 2000). Moose feed on trees and shrubs in the winter and herbaceous plants during the summer (Coady 1982), when aquatic habitats provide browse high in mineral nutrients (Jordan 1987, Shipley et al. 1998). Coady (1982:911) summarizes the seasonal cycle in the following way, "the energy derived from food during winter is less than that required for survival, and stored fat and protein are catabolized, resulting in weight loss. During the summer more energy is produced from food than is required, and the excess energy is stored as body tissue and results in weight

gain." Clearly, the largest moose should occur where summer-food quality and quantity allow the greatest mass gain in relation to the mass loss during the winter.

Sand et al. (1995) published a comprehensive study of latitudinal variability in moose in Sweden. They demonstrate that "moose living at northern latitudes [roughly 66° N] grow to a 15–20% larger adult body mass, and have a growth period on average 2 years longer than moose living at southern latitudes" (roughly 58° N; Sand et al. 1995:439). Their results also indicate that body size is negatively correlated with population density across the study populations (from 56° to 68° N). Although Sand et al. (1995) state that their low-latitude populations occur in relatively high productivity habitats, they suggest that the larger seasonal amplitude of body mass variation associated with high seasonal food quality and quantity in summers at high latitude may explain why moose from northern populations are larger (*sensu* Suttie and Webster 1995 for caribou/reindeer). Interestingly, Sand et al. (1995) demonstrate that moose in northern populations are not larger in terms of skeletal indicators of size but only in terms of body mass (see Simard et al. 2008 for a similar effect in white-tailed deer). This aligns with their separate conclusion that growth after the juvenile stage accounts for much of the variability and difference in body size between populations. They conclude that "nutritional quality may therefore in some latitudinal interval impose a major effect on body growth and adult body size among populations of ungulates, outweighing the effects of land productivity and thus the quantity of forage available" (Sand et al. 1995:440).

Ferguson et al. (2000) more explicitly link ontogenetic growth rate and body size in moose to the effects of population density on food availability. Ferguson et al. (2000, Ferguson 2002) compare North American populations of moose from coastal (Newfoundland) and inland (Ontario) settings. In general, inland populations were lower in density, due to higher rates of predation and harvest, and had more rapid growth rates and larger body size. Ferguson (2002:309) concludes that "moose in coastal environments live at higher densities relative to available forest cover, have later age at maturity, slower [ontogenetic] growth rates, and lower reproduction." Paramount to this explanation is the role of food availability per animal in determining adult body size, the proximate mechanism underlying the eNPP rule.

#### *Caribou/reindeer*

Caribou (*Rangifer tarandus*) dwell in the taiga and tundra biomes of the northern latitudes in large social herds that are migratory in open northern habitats and less migratory in relatively closed habitats to the south. In terms of diet caribou "have catholic tastes . . . are opportunistic [leading] relative availability [to be] a prime factor in [plant] utilization" (Bergerud 2000:663), but they also complement their diet at times with high protein animal matter, such as fish carrion and remains

of small rodents (Geist 1998). Summer and winter ranges differ and caribou follow a common cervid pattern of summer nutrition for growth and winter nutrition for maintenance (Soppela and Neiminen 2001, Parker et al. 2005). Summer nutrition is typically those components of eNPP that have high protein:carbon ratios, while winter nutrition is derived from the durable components of eNPP that can survive freezing temperatures, which generally have a low protein:carbon ratio.

Caribou/reindeer reach their largest size near the southern portion of their range and their size decreases northward. This matches the latitudinal distribution of eNPP in our data analysis (Huston and Wolverton 2009) and body-size model (Fig. 1, zone B–). At the northern end of their range, caribou and other high-latitude cervids experience a very short seasonal pulse of reduced eNPP (see also Suttie and Webster 1995). In comparison, the seasonal pulse at slightly lower latitudes is longer and higher. Klein et al. (1987) attribute a decrease in caribou leg length (and by correlation stature) with latitude to just these energetic constraints. Though longer legs increase efficiency of locomotion, investment in larger body size requires relatively high growth and maintenance costs and possibly also a decrease in foraging efficiency for low-lying browse.

Similar density-dependent body-size effects occur among reindeer/caribou as among moose (Reimers et al. 1983, Skogland 1990, Tveraa et al. 2007). Skogland (1986) demonstrates that reindeer populations in Norway are food limited (*sensu* Sinclair 1977) at high population densities at which their body size decreases (see also Tveraa et al. 2007). In the absence of predation (large predators such as *Canis lupus* have been exterminated in much of Norway), reindeer overbrowse their winter food supply, which consists in large part of lichens (Nellemann 1996, van der Wal et al. 2001). When densities of reindeer increase dramatically, lichens are overbrowsed and body size during ontogeny and at maturity decreases significantly because wintertime food availability is compromised (Skogland 1983, 1990, van der Wal et al. 2001). Late spring through early fall foraging plays a critical role for body size in reindeer from three populations in Norway (Reimers et al. 1983), whereas nutrition during winter affects maintenance and survival, but not size (Skogland 1990, Parker et al. 2005).

In general, the populations with the highest density, and, as a result, overbrowsed range, produced smaller individuals in all sex/age classes (in terms of body mass and skeletal size measurements). Reimers et al. (1983), noted that the area with the earliest gestation and longest summer foraging season had a shortened lactation period, produced the highest post-winter body mass recovery in adult females (see also Skogland 1983, Tveraa et al. 2007), as well as the highest growth rate in calves. Adult males and females from that population were consistently larger (in terms of average body mass and skeletal size measurements) than those from the



TABLE 1. Characteristics of white-tailed deer bucks on the George Reserve, Michigan (McCullough 1984).

Time period	Number of deer	Average mass (kg)	Deer density (no./ha)	Buck biomass (density $\times$ mass)
1941–1942	126	66.4	0.27	18.03
1958–1971	67	71.3	0.14	10.30
1971–1975	10	75.9	0.02	1.64
1980–1981	130	77.6	0.28	21.74

other study areas, confirming the importance of high eNPP for herbivore body size.

#### *White-tailed deer*

White-tailed deer (*Odocoileus virginianus*) are *r* selected and paedomorphic compared to other cervids in North America; that is, they reproduce more rapidly and attain a comparatively small adult body size relatively early in life (Geist 1998). Hesselton and Hesselton (1982:883) characterize this species as “one of the most adaptable species in the world... liv[ing] from the near arctic to the tropics... eat[ing] a tremendous variety of foods [through an] uncanny ability to select the most nutritious foods when it has an opportunity to be selective” (see also Swift 1948, Demarais et al. 2000). White-tailed deer, however, are “by no means ‘super ruminants’—they cannot use some woody browse species as well as cattle [or other Old World ungulates] can” (Verme and Ullrey 1984:111). For example, in areas of North America today where free-ranging introduced fallow deer (*Dama dama*) and sika deer (*Cervus nippon*) share habitat with white-tailed deer, the exotic species more efficiently digest native forage than do white-tailed deer (Demarais et al. 2003). Despite poor digestive efficiency, the white-tailed deer thrives by food switching in poor-quality habitat (Tremblay et al. 2005) and through dramatic diminution in body size in unproductive or crowded environments (Kie et al. 1983, Wolverson et al. 2007, 2009a, Simard et al. 2008). Such phenotypic plasticity in body size and the white-tailed deer’s highly generalized diet allow its non-migratory, low-dispersal, highly philopatric, maintenance phenotype (Geist 1998, Purdue et al. 2000, Comer et al. 2005). This strategy is advantageous where environmental conditions fluctuate over time, which has allowed *Odocoileus* to thrive in many parts of the New World today.

Within a single region, white-tailed deer in areas with high population densities have relatively small body size compared to areas with low densities. This has been documented in fenced population studies (e.g., McCullough 1979, Kie et al. 1983, McCullough 1984), for island subpopulations (e.g., Simard et al. 2008), and in unfenced populations (Teer et al. 1965, Teer 1984, Lesage et al. 2001). Numerous studies document the impacts that white-tailed deer at high densities have on habitat quality, food availability, and plant diversity (McShea et al. 1997, Waller and Alverson 1997, Rooney and Waller 2003; see summary in Côté et al. 2004).

At high densities, negative feedbacks develop in which deer populations overbrowse forage (e.g., Leopold 1947, 1950, Rooney 2001, Stewart et al. 2006 for North American elk), switch food to secondary and tertiary browse (Tremblay et al. 2005), shift reproductive strategies (Simard et al. 2008), and decrease body size, while at times remaining at very high population densities despite a reduction in food availability (Kie et al. 1983, Tremblay et al. 2005, Simard et al. 2008; see Ferguson et al. 2000 and Ferguson 2002 for moose). For example, Kie et al. (1983) subdivided a white-tailed deer population into two groups, those within and those outside of a predator-free 391-ha enclosure from 1973 to 1976 at Welder Wildlife Refuge in south Texas, USA. Deer from both groups were compared during the period July 1975 to May 1976 to assess the effects of population density. Without the population-limiting effects of predation, average eviscerated carcass masses were significantly lower within the higher-density enclosure population (28.8 kg at 72.5 deer/km<sup>2</sup>) compared to those outside (34.4 kg at 44.5 deer/km<sup>2</sup>), while there was no difference in age/sex structure for adults and fawns. Significant differences were also found between the two groups in terms of several measures related to health of individuals, with kidney and marrow fat indices and a host of blood parameters being impacted in the more crowded group in the enclosure (Kie et al. 1983: Table 1). Thus, high population density resulted in a substantial decrease in ontogenetic growth rate, body size, and health, apparently as a result of lower food quantity and/or quality per animal. Similar effects in humans are discussed in *Non-latitudinal Variation in Body Size: Intraspecific Patterns*.

A classic study on the effects of harvest on white-tailed deer population ecology was conducted at the University of Michigan’s George Reserve, in Livingston County, Michigan, USA (McCullough 1979, 1982a, b, 1984, 1997). After years of unmanaged population growth on the 464-ha fenced area, overbrowsing occurred and hunting was initiated in 1933. By 1966, biologists at the University of Michigan began to manipulate population density on the reserve. From 1966 to 1980 population size fluctuated between 10 and 212 bucks. McCullough (1982a, 1984) reported that periods with low population densities produced bucks with higher body mass and larger antlers (Table 1). Kie’s and McCullough’s studies are some of the many examples that link body size in white-tailed deer to the proximate mechanism of food availability.

TABLE 2. Estimated biomass of white-tailed deer bucks at high population densities in three areas.

Location	Time period	Average mass (kg)	Density (no. deer/ha)	Total biomass (density × mass)	Source
George Reserve, Michigan	1941–1942	66.4	0.27	18.03	McCullough (1984:234, Table 28)
George Reserve, Michigan	1980–1981	77.6	0.28	21.74	McCullough (1984:234, Table 28)
Llano Basin, Texas	1953–1960	30.9	0.36	11.0	Teer et al. (1965:24–25)
Edwards Plateau, Texas	1953–1960	37.3	0.22	8.28	Teer et al. (1965:24–25)
Edwards Plateau, Texas	1980–1981	34.5†	0.15	5.18	Cook (1984:461–463, Tables 70 and 73)
Midwest low estimate	1977–1982	57‡	0.39	22.23	Torgerson and Porath (1984:416–417, Table 64)
Midwest high estimate	1977–1982	69§	0.78	53.82	Torgerson and Porath (1984:416–417, Table 64)

† Midpoint of 1.5–7.5-year-old averages.

‡ Conservative estimate, mean of 1.5-year-old bucks.

§ Estimate based on mean of bucks older than 2.5 years.

Despite these close relationships between population density, food available per animal, ontogenetic growth rate, and ultimately body size in white-tailed deer at local scales, the relationship between these variables has been rarely studied at larger spatial scales, for example by latitude (but see Geist 1987a, 1998, Crête 1999). It is clear that white-tailed deer body size increases with latitude (Fig. 3), but it is not clear if total deer population biomass increases. If the northward increase in body size is associated with a decrease in local population densities, then the increase in body size is not necessarily explained by increased eNPP. Only if both total deer biomass and deer body size increased, could the pattern be attributed to better habitat (higher eNPP) to the north.

Contrary to our prediction, Crête (1999) estimated that white-tailed deer population biomass increases with decreasing latitude south of gray wolf (*Canis lupus*) range, and he relates the pattern to an increase in productivity toward the south. However, he estimated productivity using actual evapotranspiration (AET), an approach we believe produces inaccurate results (Huston and Wolverton 2009). While deer population density may be high in some portions of southern North America, Crête's estimates of white-tailed deer biomass in areas of Texas differ considerably from what we have encountered in our own work and in the published wildlife literature. Further, the high-biomass areas he identifies in his study, such as Minnesota, Pennsylvania, Michigan, Ohio, New York, eastern Canada, and Indiana are parts of the north temperate forest and Midwestern agricultural region. This is where our analysis indicates high eNPP and where we expect the highest mammal biomass and body sizes (Huston and Wolverton 2009). Consistent with our interpretation, Teer et al. (1965, Teer 1984) suggest that the Edwards Plateau ecoregion in central Texas has one of the highest deer population densities in North America (a situation that has not changed much since their papers were published), and they argue that this contributes to stunting of body size in already low-quality habitat, which leads to low total population biomass.

Comparisons of studies on deer body mass where population densities are high suggest that deer population biomass per area increases with latitude into the agricultural Midwest (Table 2). For example, relatively high-density populations at the George Reserve in Michigan produced estimated buck population biomass of 18.03 kg/ha and 21.74 kg/ha (Table 1). Even these biomass estimates from high-density, and potentially stunted, populations in Michigan are much higher than values from the high density and stunted unmanaged populations of central Texas (Table 2).

While there are potential problems with comparing the small, intensively managed and monitored deer herd of the George Reserve to the much larger region of unmanaged deer of central Texas, regional deer data from the Midwest show patterns consistent with this comparison. Although regional estimates of deer density in the Midwest can be quite high, the average body mass of adult bucks ranges between 57 and 69 kg. Total male deer biomass has been estimated at between 22 and 54 kg/ha even at these very high population densities (Table 2). These biomass values are multiple times larger than those found in central Texas. This comparison of biomass at high population densities across regions indicates that not only ontogenetic growth rate and body size in white-tailed deer increase with latitude but that total population biomass does as well. This mirrors an interspecific pattern documented in African ungulates by Owen-Smith (1988:268–269), in which body size tends to increase as population density decreases, but both maximum population biomass and body size increase with increasing productivity. Analogous effects are observed with plants in relation to density and growth conditions at both the intra- and interspecific levels (Diggle 1976, Harper 1977, Westoby 1981, Lonsdale and Watkinson 1983, Huston 1986, Huston and DeAngelis 1987, 1994, Huston et al. 1988, Morris and Myerscough 1991).

In order to make a direct comparison between white-tailed deer in the agricultural Midwest and in central Texas, we examined the size of the astragalus bone from hind limbs. The astragalus matures by 6 months of age, so these comparisons are age-independent (Purdue 1987,

Wolverton 2008). We analyzed samples from central Missouri and from a population in western Travis County in the Edwards Plateau region of Texas, from both modern and late Holocene populations. Central Missouri white-tailed deer are significantly larger and barely overlap in size distribution with central Texas deer, both currently and during the late Holocene (Wolverton et al. 2009a: Fig. 4B). If Torgerson and Porath's (1984) assessment that deer can reach very high population densities in the Midwest is correct (see also Nixon et al. 1991, Hansen et al. 1997), our data support the conclusion that total deer biomass is substantially higher in the Midwest than in central Texas, and has been so for thousands of years. The same patterns holds for subtropical southeast Texas where body size and astragalus size are small and estimated total biomass is low compared to northern regions (Table 2; Cook 1984, Wolverton et al. 2009a).

#### *Other cervids*

Many of the body-size patterns and relationships for white-tailed deer, caribou, and moose hold for other cervids at similarly large scales (Langvatn and Albon 1986, Mysterud et al. 2001a, b, c, 2002). For example, Mysterud et al. (2001a) demonstrate that body size of elk (*Cervus elaphus*) in southern Norway is largest at relatively low population density, and that altitudinal diversity in habitat also produces large elk. They conclude that altitudinal range affects body size because elk can track the altitudinal progression of the pulse of high eNPP and thus take advantage of emerging (highly nutritious) forage for a longer period of time (see Reimers et al. 1983, Weladji et al. 2002 for similar examples with caribou).

Langvatn and Albon (1986) link plant phenology and forage quality to the latitudinal increase in elk body size in similar fashion. They surmise that, at high latitudes, the nutritive content of digestible plant materials increases because lower light availability, lower water supply, and lower temperature conditions decrease lignification (production of wood tissue). In addition, the soluble carbohydrate and protein fractions of plants have been found to increase in these conditions because the proportion of plant matter that comprises cell walls decreases (Langvatn and Albon 1986:291). Similar body and antler size effects as those documented by Langvatn and Albon (1986) have been observed by Schmidt et al. (2001) in red deer on the Isle of Rum in northern Scotland, as well as in roe deer (Hewison et al. 2002, Kjellander et al. 2006, Toigo et al. 2006), white-tailed deer (McCullough 1984), and sika deer (Yokoyama et al. 2000).

These studies of cervid body size suggest that ontogenetic growth rates track both the local and global distribution of eNPP and available food per individual, just as we propose. In areas with more fertile soils, i.e., many temperate and high-latitude areas, both growing season NPP (eNPP) and forage quality ought to be high

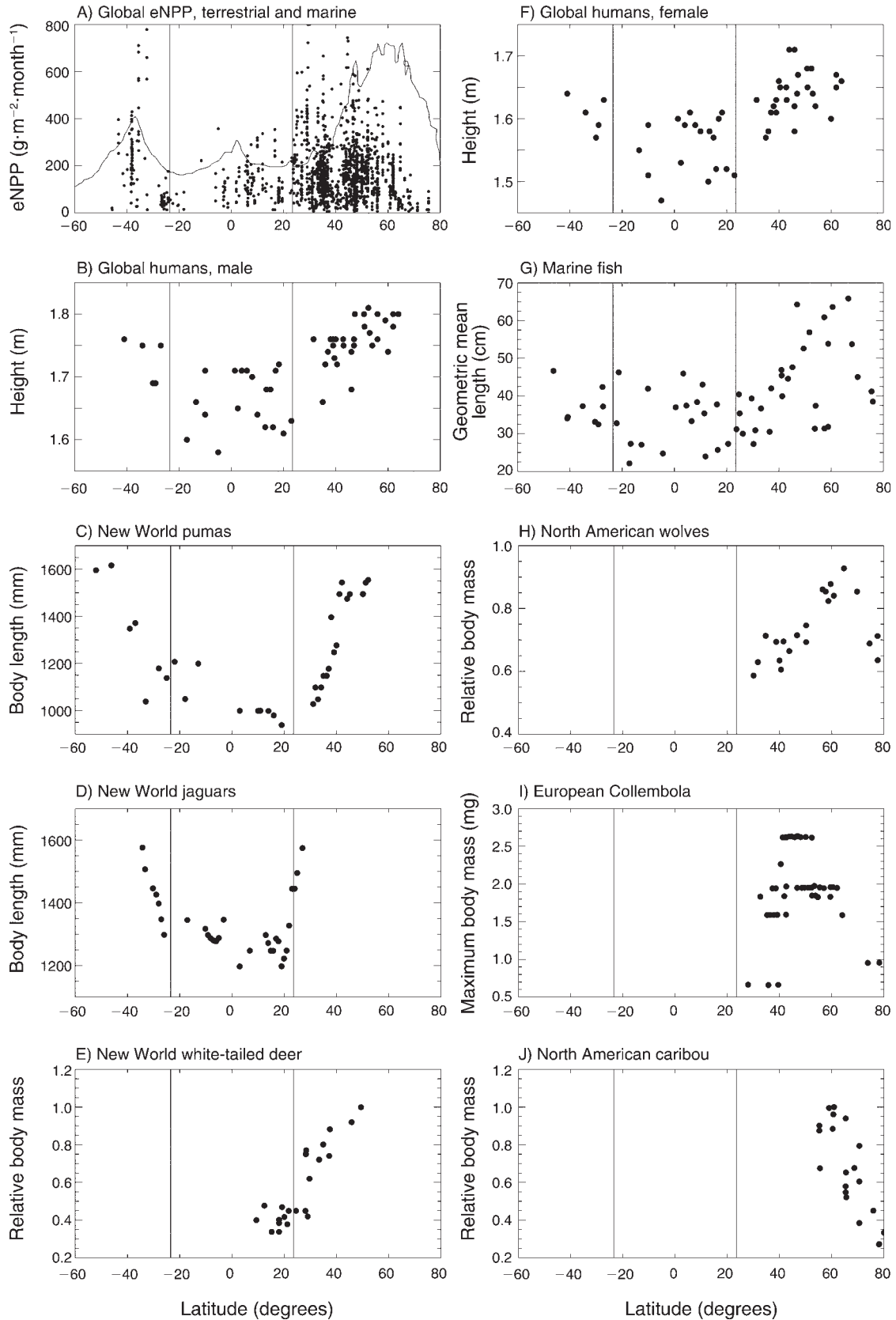
compared to the lower latitudes. At a minimum, this high eNPP should accelerate the ontogenetic growth rate and increase adult body size, as has been observed for deer, caribou, and moose. In general, total population biomass should increase with eNPP due to either an increase in body size at constant density or an increase in density at a constant body size, or an increase in both, as have been observed for white-tailed deer.

#### *Geographic variation in body size of mammalian carnivores and other homeotherms*

The apparent effect of eNPP on cervid body size is paralleled by the distribution of body size in multiple species of carnivores, some of which are predators of cervids. If prey species reach their largest body size and highest biomass at temperate latitudes, it makes sense that large carnivore species with broad latitudinal ranges should exhibit a similar body-size distribution to maintain efficiency of prey capture. The distributions of body size in several large carnivores are also consistent with the expectation that food availability per animal (as eNSP) is highest in the temperate latitudes. In some cases, such as bears, other aspects of behavioral ecology (e.g., hibernation) may also influence the latitudinal distribution of growth rate and body size.

Predator body size generally increases with the body size of their prey (McNab 1971, Gittleman 1985, Owen-Smith and Mills 2008, Troost et al. 2008). In addition, the inverse relationship between carnivore population density and carnivore body size at the intraspecific level is well known (e.g., Cavallini 1995, Carbone and Gittleman 2002, Zedrosser et al. 2006). Several studies have shown that body size in carnivores is influenced by food availability. However, it has rarely been suggested that predators follow Bergmann's rule because the availability of prey increases with latitude.

The latitudinal distribution of body size for the gray wolf (*Canis lupus*) mirrors that of cervids in North America, peaking at 50–60° N latitude where cervids are the largest (Geist 1987a) and eNPP the highest, then declining at higher latitudes (Fig. 4H; McNab 1971). The size of the red fox (*Vulpes vulpes*) also increases with latitude (Meiri et al. 2004). Although Cavallini (1995) suggests that regional variability in size of the red fox in Italy may relate to differences in population density, he states that size differences at larger spatial scales are likely to be associated with genetic differences between populations. However, he does not present any genetic data and thus we cannot reject the hypothesis that latitudinal differences in red fox body size are simply related to differences in eNPP. We agree with Cavallini (1995:426) that "more data need to be collected," specifically genetic data and information on food availability and ontogenetic growth rate in the red fox. Gortázar et al. (2000) provide such data from Spain where they studied male and female red fox body size in contiguous (no barriers between) low- and high-quality habitat. In both areas, male and female foxes were



significantly larger in high-quality habitat, and Gortázar et al. (2000) discuss food availability and prey size along with behavioral ecology and character displacement as possible causes.

Two species of large, widely distributed felids in the New World exhibit latitudinal size distributions outside the tropics that follow Bergmann's rule, the puma (*Puma concolor*; Newman 1953, Kurtén 1973, Iriarte et al. 1990, Gay and Best 1996) and the jaguar (*Panthera onca*; Iriarte et al. 1990:189) (Fig. 4C and D). However, neither species shows any trend in body size across the tropics (23.5° S to 23.5° N, Fig. 4C and D, see Fig. 1, zone B\*0). Gay and Best (1996) found that puma size correlates with temperature (negatively) and latitude (positively), but most strongly with latitude, particularly outside the tropics (e.g., Fig. 1, latitudinal zone B+). Iriarte et al. (1990) observe that the positive relationship between puma body size and latitude corresponds positively to prey body size and negatively to niche breadth. In North America, puma are large vertebrate prey specialists, and they achieve body lengths at the high-latitude ends of their range equivalent to the largest jaguars, which reach their maximum lengths outside the tropics. The puma's body size declines and their food niche broadens to include a higher proportion of medium and small prey at tropical latitudes where eNPP and eNSP are lower, and consequently deer are smaller and large vertebrates are relatively rare.

McNab (1971) noted that the puma is smallest in body size where its range overlaps with the jaguar, and proposed competitive character displacement as the explanation. However, this area of overlap is also where eNPP is lower, the jaguar is smaller (Fig. 4D), and prey such as deer are much smaller than farther north (Fig. 4E), beyond the jaguar's range. This raises an important point concerning the relationship of carnivore body size to food availability. Character displacement in predator body size and food niche occurs in many carnivores when the range of one predator overlaps with that of another, typically larger, competitor (Rosenzweig 1966).

Such niche differentiation occurs in pumas and jaguars (Taber et al. 1997, Scognamiglio et al. 2003), and character release of body size in puma and in ocelots associated with shifting to larger prey has been observed in areas where jaguars have been extirpated (Moreno et al. 2006). However, Iriarte et al. (1990) conclude that puma body-size variability at larger spatial scales simply relates to prey availability and vulnerability, or what we are calling the distribution of eNSP.

A recent analysis of Bergmann's rule in Carnivora was based on a new compilation of skull measurements from museums around the world for 44 species (of which 4 had separate data from Old and New World populations; thus we treat their total as 48 species) and found support for the existence of Bergmann's pattern in only 22 of the species (Meiri et al. 2004). In their analysis, either males, females, or both from 24 carnivore species had no significant increase in cranial length with latitude. They conclude their "finding that less than 50% of carnivore species adhere to Bergmann's rule suggests its validity in the Mammalia might be questioned" (Meiri et al. 2004:585). We agree, but for reasons that were not addressed by Meiri et al. (2004).

Meiri et al. assumed that latitudinal gradients of body size were linear and did not change with latitude, and consequently reported only the sizes of the ranges over which their samples were collected, rather than the actual locations of the ranges. Because the eNPP rule is based on the global distribution of eNPP, which has a complex, nonlinear latitudinal pattern (Figs. 1 and 4A), it is impossible in most cases to determine whether their results that apparently contradict Bergmann's rule are actually consistent with the eNPP rule. In some cases, where a species' known range is limited to a linear portion of the latitudinal eNPP gradient (i.e., between 23.5° S and 23.5° N, or from 23.5° to approximately 50° across either the southern or northern temperate zones, or above about 60°) a linear analysis is informative. Across the tropics, the eNPP rule predicts no change in body size, contradicting Bergmann's rule, while from

←

FIG. 4. Latitudinal distributions of eNPP and animal body size. (A) Distribution of ecologically and evolutionarily relevant aboveground NPP (eANPP) for terrestrial vegetation types (e.g., forest, grassland, desert, tundra) from the Global Primary Production Data Initiative (GPPDI; Olson et al. 2001a, b) showing 1562 of the total 2525 values in the combined Class A and B data sets, excluding managed systems and wetlands. The pattern is similar to our summary based on forests only from a different data set (Fig. 1). The thin line is the global latitudinal average of marine eNPP, calculated as the maximum of the three-month mean for either December–February (austral summer) or June–August (boreal summer). Marine units are  $\text{g C}\cdot\text{m}^{-2}\cdot\text{month}^{-1}$ , multiplied by 15 for visualization. Terrestrial units are in dry biomass. Note that the spatial distribution of the terrestrial data is not uniform and does not represent all regions of the globe, nor does it represent an adequate sample to identify regional or local patterns. (B) Height of human males based on average values by country (data sources in Supplement 2). (C) Body and tail length of pumas (*Puma concolor*) across the New World (based on Iriarte et al. [1990: Fig. 3]). Data are from McNab (1971), Schaller and Vasconcelos (1978), Anderson (1983), Currier (1983), Rabinowitz and Nottingham (1986), and Mondolfi and Hoogsteijn (1986). (D) Body and tail length of jaguars (*Panthera onca*) across the New World tropics and subtropics (data from same sources as for panel C). (E) Relative body size in white-tailed deer (*Odocoileus virginianus*) (based on Geist [1998: Fig. 1.9]). (F) Height of human females based on average values per country (data and sources in Supplement 2). (G) Geometric mean length of marine fish species recorded in coastal regions designated as Large Marine Ecosystems (LMEs; based on Fisher et al. [2010: Table 1]). (H) Relative body mass of gray wolves (*Canis lupus*) in North America (based on Geist [1987a: Fig. 3]). (I) Maximum body sizes of springtail (Hexapoda: Collembola) assemblages comprising 2102 species across 52 European countries and islands (based on Ulrich and Fiera [2010: Fig. 3B]). (J) Relative body sizes of North American caribou (*Rangifer tarandus*) (based on Geist [1998: Fig. 1.9]).

TABLE 3. Characteristics of 44 carnivore species (with four reported on two continents) evaluated by Meiri et al. (2004).

Species	Common name	Sex	Sample size	Sample latitudinal range	Species latitudinal range
<i>Alopex lagopus</i>	Arctic fox	mf	136	20.13	29
<i>Canis aureus</i>	golden jackal	mf	97	33.70	50
<i>Canis latrans</i>	coyote	mf	147	33.02	66
<i>Canis lupus</i> New World	gray wolf	mf	152	22.07	75
<i>Canis lupus</i> Old World	gray wolf	mf	60	31.27	75?
<i>Pseudalopex griseus</i>	Argentine gray fox	m	30	22.80	40
<i>Urocyon cinereoargenteus</i>	gray fox	mf	71	22.95	45
<i>Vulpes vulpes</i> New World	red fox	mf	196	34.93	62
<i>Vulpes vulpes</i> Old World	red fox	mf	240	55.78	62?
<i>Felis benegalensis</i>	leopard cat	f	28	31.52	50
<i>Felis benegalensis</i>	leopard cat	m	33	39.50	50
<i>Felis canadensis</i>	Canada lynx	mf	188	22.73	25
<i>Felis chaus</i>	jungle cat	mf	77	26.03	40
<i>Felis concolor</i>	puma	mf	58	50.91	111
<i>Felis pardalis</i>	ocelot	mf	46	7.84	65
<i>Felis rufus</i>	bobcat	mf	69	22.91	40
<i>Felis silvestris</i>	wild cat	m	40	29.42	90
<i>Panthera tigris</i> †	tiger	m	21	25.00	59
<i>Ursus americanus</i>	American black bear	mf	52	37.85	40
<i>Ursus arctos</i>	brown bear	mf	118	20.38	40
<i>Eira barbara</i>	tayra	mf	51	8.40	50
<i>Gulo gulo</i>	wolverine	f	44	19.51	38
<i>Gulo gulo</i>	wolverine	m	75	22.25	38
<i>Herpestes edwardsii</i>	Indian gray mongoose	mf	100	22.10	25
<i>Herpestes javanicus</i>	small Indian mongoose	mf	110	29.60	40
<i>Lontra canadensis</i>	American river otter	mf	137	39.15	40
<i>Lutra lutra</i>	European otter	f	32	41.87	59
<i>Lutra lutra</i>	European otter	m	34	51.46	59
<i>Martes americana</i>	American marten	mf	276	22.76	33
<i>Martes flavigula</i>	yellow-throated marten	mf	56	45.08	50
<i>Martes foina</i>	beech marten	mf	196	22.79	40
<i>Martes martes</i>	European pine marten	f	63	18.53	30
<i>Martes martes</i>	European pine marten	m	68	18.55	30
<i>Martes pennanti</i>	fisher	f	54	18.15	30
<i>Martes pennanti</i>	fisher	m	47	23.83	30
<i>Meles meles</i>	Japanese badger	mf	248	36.82	48
<i>Melogale personata</i>	Javan ferret badger	m	21	6.95	20
<i>Mephitis mephitis</i>	striped skunk	m	22	14.90	35
<i>Mustela erminea</i> New World	ermine	mf	491	27.53	45
<i>Mustela erminea</i> Old World	ermine	f	102	24.46	45?
<i>Mustela erminea</i> Old World	ermine	m	154	25.53	45?
<i>Mustela frenata</i>	long-tailed weasel	f	36	46.20	73
<i>Mustela frenata</i>	long-tailed weasel	m	86	42.55	73
<i>Mustela nivalis</i> New World	least weasel	m	20	25.18	45
<i>Mustela nivalis</i> Old World	least weasel	mf	497	38.53	45?
<i>Mustela putorius</i>	European polecat	f	113	17.65	30
<i>Mustela putorius</i>	European polecat	m	185	19.40	30
<i>Mustela sibirica</i>	Siberian weasel	m	30	27.75	54
<i>Mustela vison</i>	mink	mf	271	32.75	45
<i>Paguma larvata</i>	masked palm civet	f	21	29.70	40
<i>Paradoxurus hermaphroditus</i>	Asian palm civet	mf	101	25.00	43
<i>Spilogale gracilis</i>	western spotted skunk	mf	91	26.67	30
<i>Viverra zibetha</i>	large Indian civet	mf	48	32.91	36
<i>Viverricula indica</i>	small Indian civet	f	41	27.20	40
<i>Viverricula indica</i>	small Indian civet	m	60	29.80	40
<i>Nasua narica</i>	white-nosed coati	f	23	17.10	23
<i>Procyon lotor</i>	raccoon	mf	103	41.62	52

Notes: Latitudinal breadth and midpoint of species' ranges is from Meiri et al. (2007: supplemental material). Predicted direction of correlation based on the eNPP rule assumes that samples cover the full latitudinal range of the species (which is not the case for many of the species). Male (m) and female (f) results are reported separately for species in which they had significantly different results. For species in which males and females had statistically equivalent results, indicated by "mf" in the Sex column, sample latitudinal range is that for the females, sample size is for both sexes summed, and rho is the mean of the correlation coefficients for both sexes. Slopes are predicted to be positive (+), negative (-), not sloped (0), or to change from positive to negative (+-). "YES" highlights cases where the data fit the eNPP rule but do not fit Bergmann's Rule. Question marks indicate cases in which the data are inadequate to determine whether the patterns does or does not fit the eNPP rule. The full table with all information for males and females is available in Supplement 1.

\* Significant at  $P < 0.05$ , see Supplement 1 for details.

† Does not include Siberian tiger.

TABLE 3. Extended.

Species range midpoint	rho	eNPP predicted slope	Fits Bergmann's rule	Fits eNPP rule
66	-0.02	-	no	no
20	0.39*	+	yes	yes
38	0.58*	+	yes	yes
48	0.08	+ -	no	?
48?	0.91*	+ -	yes	?
-34	0.21	+	no	no
28	0.51*	+	yes	yes
41	0.65*	+	yes	yes
41?	0.61*	+	yes	yes
25	-0.25	+	no	no
25	0.70*	+	yes	yes
58	0.41*	+	yes	yes
30	0.60*	+	yes	yes
5	0.62*	+	yes	yes
3	-0.16	0	no	YES
40	0.17	+	no	no
10	0.37*	+	yes	yes
21	0.26	+	no	no
45	0.01	+	no	no
50	0.09	+	no	no
-5	-0.18	0	no	YES
64	0.28	+ -	no	?
64	0.32*	+ -	yes	?
23	-0.17	0	no	YES
15	-0.58*	0	no	no
45	0.01	+	no	no
36	0.51*	+	yes	yes
36	0.13	+	no	no
52	0.56*	+	yes	yes
25	0.56*	+	yes	yes
48	0.29*	+	yes	yes
55	-0.04	+ -	no	?
55	0.26*	+ -	yes	?
45	0.53*	+	yes	yes
45	0.03	+	no	no
44	0.62*	+	yes	yes
20	-0.33	0	no	YES
43	0.47*	+	yes	yes
58	0.44*	+ -	yes	?
58?	0.14	+ -	no	?
58?	-0.22*	+ -	no	?
19	0.57*	+	yes	yes
19	-0.03	+	no	no
53	-0.70*	+ -	no	?
53?	-0.30*	+ -	no	no
50	-0.19*	+	no	no
50	0.06	+	no	no
33	-0.35	+	no	no
48	0.57*	+	yes	yes
15	-0.63*	+	no	no
12	0.12	0	no	YES
35	0.00	+	no	no
18	0.07	0	no	YES
15	0.42*	+	yes	yes
15	0.16	+	no	no
19	-0.15	0	no	YES
34	0.05	+	no	no

23.5° to approximately 50° or 60° across the temperate zones, both Bergmann's and the eNPP rule make the same prediction of an increase in body size. Above 60°, Bergmann's rule predicts a linear increase in body size, while the eNPP rule predicts a linear decrease. However, ranges that span either 23.5° or 50–60° are predicted to have a nonlinear pattern of body size in relation to

latitude. These nonlinear patterns cannot be resolved using the information published by Meiri et al. (2004), because the actual latitudes from which the samples were collected were not reported and in many cases the latitudinal range of the samples is less than half of the species' latitudinal range. Only in cases where the species' known ranges are limited to the linear sections of the latitudinal eNPP distribution that contradict the Bergmann prediction of a linear increase with latitude, can we evaluate whether the Meiri et al. results conform to the eNPP rule while contradicting Bergmann's rule. These data are summarized in Table 3.

Of the species that Meiri et al. identified as not following Bergmann's rule, the arctic fox (*Alopex lagopus*) occurs only at high latitudes, where the eNPP rule predicts a decline in body size (Fig. 1, zone B-), but the data showed no change with latitude. The range of the gray wolf extends through subtropical montane and temperate latitudes into high latitudes, and in North America this species also exhibits a decrease in size north of 60°N where eNPP and the size of its ungulate prey decline (Fig. 4H and J; Geist 1987a). However, Meiri et al. report no change with latitude in North American wolves but a strong positive response in European wolves. In both cases, the latitudinal range of the samples is less than half the latitudinal range of the species, which spans the breakpoint (approximately 50° N) where we expect the relationship of body size (and eNPP) with latitude to reverse. However, the actual latitudinal position of this reversal may depend on the influence of maritime climate and continentality on temperature and growing season in parts of northern Europe (also an important consideration for large cervids in this region). Without knowing the actual geographic locations of the samples, it is impossible to determine whether they are consistent with the eNPP rule. Nine of the nonconforming species are mustelids, viverrids, procyonids, and felids that occur at low latitudes (tropics and subtropics) only, where eNPP is typically low and changes little with latitude (Fig. 1, zone B\*0). Two non-conforming species are temperate zone ursids that hibernate, and two additional species are partially or fully non-terrestrial (otters). Meiri et al. (2004:585) concede that omission of the Siberian tiger, which is the largest, northernmost of the subspecies (*Panthera tigris altaica*), may have influenced the latitudinal size distribution of tigers in their analysis.

Meiri et al. (2004) conclude that the relationship between latitude and size for the bobcat (*Lynx rufus*) is not significant, but they cite other studies of the bobcat, which have larger sample sizes, that indicate Bergmann's rule holds for this species (Sikes and Kennedy 1992, Wigginton and Dobson 1999). The remaining seven non-conforming species are several temperate latitude mustelids and the raccoon (*Procyon lotor*). However, other studies based on biometry of skull size or body mass suggest that Bergmann's rule does hold for the raccoon (Kennedy and Lindsay 1984 [skull size],

Mugaas and Seidensticker 1993 [body mass]). While we agree with Meiri et al. (2004) regarding problems with Bergmann's rule, we think it important to note that many exceptions to Bergmann's rule in Carnivora tend to have biogeographic ranges that conform to the distribution of body size predicted by the eNPP rule (Fig. 1). Based on an examination of the reported latitudinal ranges of these mammals (Meiri et al. 2004), we conclude that while only 24 of 48 species conform to Bergmann's rule, body-size patterns of at least 31, and potentially as many as 41 of the 48 are consistent with the predictions of the eNPP rule (Table 3). Note that there will be many situations where the actual distribution of eNPP differs from the global average patterns we present in Fig. 1, due to the effects of local soil properties, maritime climate, continentality or other factors. In these cases, use of latitude without actual measurements of eNPP will not be informative. A more detailed analysis of the Meiri et al. (2004) data, as well as collection of body size and eNPP data across the full latitudinal ranges of all the species would be very interesting. Unfortunately, sufficient data on intraspecific variation in animal body size have not yet been collected or compiled to allow a definitive test of either Bergmann's or the eNPP rule.

One of the problems in comparing body size is the various types of measurements that have been collected, including different measurements of mass and a variety of skeletal dimensions. As discussed previously, components of size vary over different temporal scales, which raise problems of interpretation. The data for bears are particularly problematic and have led to opposing conclusions. Body size has been reported to *decrease* with latitude among American black bears (*Ursus americanus*; Kennedy et al. 2002) and European brown bears (*U. arctos*; Kojola and Laitala 2001). However, Kojola and Laitala's (2001) study examined brown bear size from 60° to 68° N latitude, where a negative relationship with latitude is predicted by the eNPP rule (assuming no effects of maritime climate or other local factors that would cause departure from the global average). Other authors (e.g., Rausch 1963, Meiri et al. 2004) report that size of brown bears *increases* with latitude, conforming to Bergmann's rule. Those who observe a decrease in size with latitude (B- pattern), regardless of latitudinal position of the range covered, attribute it to reduction in foraging time and growing season caused by an increase in hibernation periods at higher latitudes. However, determination of whether or not body size in ursids follows Bergmann's rule (or the eNPP rule) requires additional research. One problem is that the distribution of bear body size described by Kennedy et al. (2002), Rausch (1963), and Meiri et al. (2004) relied on biometric analysis of the skull and upper teeth. Head size, and especially tooth size, in ursids display relatively weak, nonsignificant ( $\alpha = 0.05$ ) relationships with body mass compared to other carnivores (Van Valkenburgh 1990:192–194), so intra-

specific variability in body size may not be accurately reflected by head and tooth size. For example, Harlow (1962) found that, despite larger skull size in Florida black bears compared to Virginia black bears, body mass did not differ. In addition, Meiri et al. (2004) argue that Kojola and Laitala's (2001) study of differences in body mass in European brown bears encompassed too small a latitudinal range to determine whether or not Bergmann's rule holds. However, Meiri et al. conclude that brown bear size increases with latitude based on a smaller sample size that covers a larger latitudinal range.

Black bears are omnivorous, as are humans. We postulate that the eNPP rule applies to all higher trophic levels and thus do not consider omnivory a confounding factor. If anything, an omnivorous diet reflects an adaptation tailored to extract calories and nutrients from the environment as efficiently as possible for a particular place and time by taking advantage of both eNPP and eNSP. Body size, growth rate, and biomass of bears, humans, and all other animals are related directly to food availability, and show a variety of patterns that appear to conform to the eNPP rule or other constraints on food availability.

Bears (and a variety of other animals) have the adaptation of hibernating during periods of low food availability or otherwise unfavorable conditions. Hibernation in bears is the ultimate adaptation to the combination of high eNPP and a long season of scarcity. Hibernation, which reaches its longest duration at northern latitudes, is only a successful strategy if individual bears are able to accumulate enough fat reserves during the summer period of high eNPP to make it through the winter with no additional food. Mass loss during hibernation is primarily lipid mass, not lean body mass (Hellgren et al. 1993, Harlow et al. 2002). Accumulation of fat body mass during the growing season determines when bears can enter hibernation (Klenner and Kroeker 1990, Schooley et al. 1994), and whether or not females will reproduce (Elowe and Dodge 1989, Samson and Huot 1995, Harlow et al. 2002), as well as litter size (Samson and Huot 1995). Although among cervids at high temperate latitudes, the resource pulse provides a concentrated period of rapid growth and mass gain, while winter is a period of gradual mass loss despite continued foraging, among bears the eNPP pulse provides the opportunity to accumulate enough fat reserves to survive mass loss during the complete fasting of hibernation. Similarly, seasonal mass loss has also been observed in humans in environments where a period of food scarcity precedes the agricultural harvest (Gamboa and Garcia 2007).

That the duration of hibernation shortens and disappears southward in bears suggests not only that hibernation is not as necessary as it is farther north, but also that it may not be advantageous, or even possible, where accumulation of sufficient fat reserves is prevented by the typically lower eNPP at lower latitudes (Pelton 1982, 2000, Larivière 2001). The fact that undernour-



ished bears, both young and old, delay hibernation and/or cannot hibernate at high latitudes indicates that growing-season fat accumulation is paramount in ursid behavioral and functional ecology. Contrary to the common conception that hibernation in bears is simply an adaptation to long winters, it may be that non-hibernation among individuals of hibernating species represents a more recent (poorly fitted) adaptation to low eNPP at low latitudes.

In the context of intraspecific body-size variation, the most widely distributed vertebrate species is *Homo sapiens*, which occupies all continents except Antarctica. The general conformity of human body size to Bergmann's rule has long been recognized (Fig. 4B and F; Coon et al. 1950, Schreider 1950, Newman 1953, Roberts 1953, 1978, Bindon and Baker 1997, Ruff 1994, 2002). However, there is also substantial geographical variation that is independent of latitude. As in other animals, we are confident that much of the spatial population-level variation in *Homo sapiens* body size can be explained by variation in eNPP caused by differences in soil fertility and water availability. However, a comprehensive evaluation of this hypothesis would require a detailed study that is beyond the scope of this paper (but see Newman 1953).

Intraspecific body-size variation in numerous species of herbivorous, carnivorous, and omnivorous mammals shows latitudinal patterns that are consistent with the predictions of the eNPP rule, as well as with Bergmann's rule over restricted latitudinal ranges. However, the eNPP rule is not restricted to latitudinal patterns, because the factors that regulate NPP and eNPP have significant variation that is independent of latitude.

#### NON-LATITUDINAL VARIATION IN BODY SIZE: INTRASPECIFIC PATTERNS

While the geometry of the Earth's energy balance results in more rapid soil weathering and loss of fertility in the tropics, as well as other areas where precipitation exceeds evapotranspiration, geological processes such as volcanism, orogeny, sediment deposition, and glaciation produce significant variation in soil fertility that is independent of latitude and rainfall. The eNPP rule is not limited to latitudinal variation and predicts that differences in body size and related properties will occur wherever there are significant differences in food produced from eNPP, which is determined primarily by soil fertility, water availability, and temperature.

In the early 1940s, a major wildlife study (Pitman-Robertson Program) in Missouri focused on the effects of soil fertility on game animal body size and harvest number. During 1941 and 1942, the masses of 8180 raccoons (21% of the total harvest) were recorded at the county level. County-level averages for male raccoons ranged from 11.98 to 18.54 pounds (5.39–8.34 kg; a 55% increase in average mass) and for females from 8.58 to 17.64 pounds (3.86–7.94 kg; a 106% increase). Data from 89 counties were grouped into eight soil fertility

classes for ANOVA and linear regressions (Fig. 5A). Both raccoon body size and harvest correlate strongly (positively) with soil fertility and presumably productivity in Missouri (Nagel 1943, Crawford 1950; V. L. Sharpe, *unpublished analysis*). The decline in the harvest of raccoons (Fig. 5B) and other furbearers in the regions with highest soil fertility was probably due to reduced habitat availability in the intensively cultivated areas of the state (Crawford 1950). This type of regional spatial variation in eNPP as affected by soils and climate across the range of raccoons may increase variance and obscure latitudinal patterns, as observed by Meiri et al. (2004), although in Missouri, the best soils (and largest raccoons) are in the northern part of the state, and the poorest soils (and smallest raccoons) in the southern part (B. Crawford, *personal communication*). A similar pattern of body size in relation to soil fertility across Missouri was found for cottontail rabbits in a study of 175 864 live-trapped individuals from 14 locations across the state. Average body size ranged from 2.1 to 2.8 pounds (0.95–1.26 kg; a 33% increase), with mass positively correlated with soil fertility (Crawford 1950). In addition to the pattern in raccoons, harvest numbers, which are presumably correlated with population size, were positively or unimodally related to soil fertility in striped skunks, spotted skunks, muskrats, mink, and red foxes, and inversely related to soil fertility in opossums and gray foxes (Nagel 1943), which may have been affected by competition and predation by the red fox. Dalke et al. (1946) believed that soil fertility affected the distribution and population density of wild turkeys in Missouri. Boyce (1978) reported spatial patterns of body size in muskrats across North America, with small body size associated with low productivity, and large body size found in areas with "high seasonality," which we now recognize to be associated with high eNPP over muskrat range.

Similar spatial patterns of body size in relation to soils have been found in white-tailed deer across Missouri (Murphy and Porath 1969) and elsewhere (Murphy and Coates 1966, Jacobson 1984, Strickland and Demarais 2000, 2006, 2008). Strickland and Demarais (2000, 2006, 2008) studied differences in growth rate, antler size, and body mass in five soil regions in Mississippi. In regions with comparatively high soil fertility, males and females grew for longer periods (up to 4.5 years) and to larger body size (Strickland and Demarais 2000). Males exhibited larger antler size in the fertile regions. In the least fertile regions, body mass in both sexes and antler size were smaller and growth occurred for only 3.5 years. Regional effects on body size were significantly different for all male age classes (Fig. 6) as well as female age classes (not shown).

Jones et al. (2008), building on Strickland and Demarais' (2000, 2006) spatial analysis of white-tailed deer in Mississippi, studied crude protein (CP) content in eight forage species in areas that had not been recently fertilized across the same regions. In general, Jones et al.

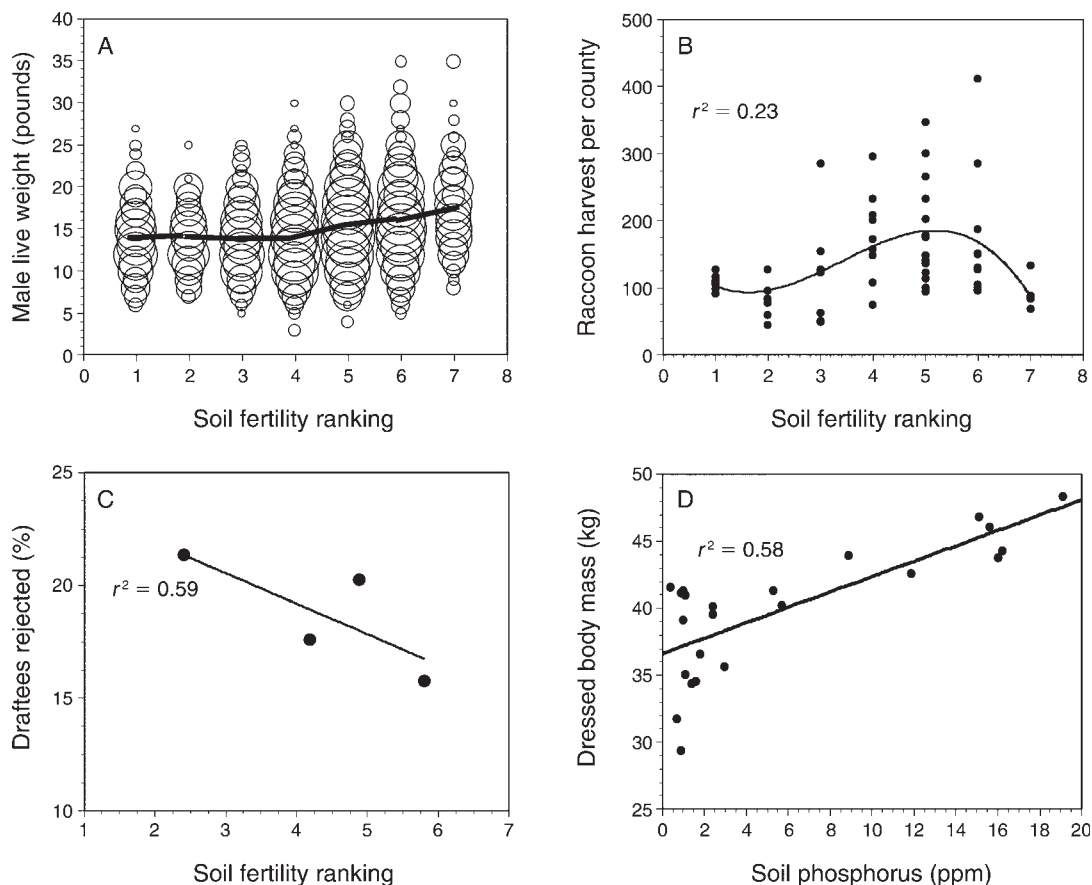


FIG. 5. Animal body size, population density, and health in relation to soil fertility. (A) Raccoon body size (weight in pounds; 1 pound = 0.45 kg) based on 5567 male raccoons harvested in 1941 and 1942 in 95 counties across Missouri (Crawford 1950) stratified by seven soil fertility classes. Circles indicate relative number of individuals in each 1-pound size class (from V. L. Sharpe, unpublished analysis; see Supplement 4). Thick line indicates mean mass. (B) Total number of raccoons harvested in each of 95 Missouri counties ranked by soil fertility, showing only counties with 20 or more raccoons harvested (from Noren 1943). (C) Percentage of World War II Army draft registrants rejected for health reasons in four regions of Missouri, with regional soil averages based on the same soil classification as in panels A and B (from Albrecht 1957). (D) Deer size (dressed body mass) in relation to soil phosphorus for 1.5-year-old male deer harvested from 23 areas in Mississippi (based on Jacobson [1984: Table 4]).

found that areas with larger deer in Strickland and Demarais' study corresponded with areas with high CP forage. In an earlier study, Jacobson (1984) linked deer body mass to a variety of soil-quality parameters in Mississippi, demonstrating significantly larger size in bucks and does from areas with relatively high-phosphorous-content soils (Fig. 5D). Together, the Mississippi white-tailed deer studies indicate that body mass increases with greater soil fertility. These results confirm those of earlier studies that linked body size in white-tailed deer and other species to nutrition, vegetation management for nutritious species, and soil fertility (e.g., Crawford 1950, Gill 1956, Thorsland 1966, Brown and Lee 1969, Murphy and Porath 1969, Jacobson 1984, Soper et al. 1993).

In black bears and brown bears, food availability also appears to drive intraspecific variability in body size at smaller spatial scales unrelated to latitude (Rausch 1963, Hilderbrand et al. 1999a, b, Maehr et al. 2001). Meiri et

al. (2007) clearly establish that grizzly bears (*U. arctos*) are largest in body size in areas near streams with reliable salmon runs and decrease in size with distance from those sources (see Hilderbrand et al. 1999a, b). Along similar lines, Maehr et al. (2001) found that at the same latitude in two populations of black bears, those in the more productive region attained larger body size. Access to suburban and urban garbage leads to an increase in body size and a decrease in foraging radius at relatively high population densities in American black bears (Beckmann and Berger 2003, Weaver 2004). Thus, body size in bears at local spatial scales is directly related to food availability, the proximate mechanism underlying the eNPP rule.

Several studies in Australia have found gradients in the population density of small marsupial species related to soil fertility, with the highest densities on the most fertile soils. In most cases, there was little or no difference in body size within a species across the

relatively short distances of the soil contrasts (Braithwaite et al. 1984, Kavanagh and Lambert 1990, Jones et al. 1994, Johnson et al. 2005), which is consistent with the predictions of the eNPP rule regarding population biomass density in cases where body size remains constant, but higher food availability allows higher population density.

In addition to nutrients, precipitation can also be a major limiting factor for eNPP, and Australia has strong precipitation gradients from the coast to the interior. The cicada *Aleeta curvica* occurs along the eastern coast of Australia and decreases in size from the coast inland, with individuals from areas receiving less than 1000 mm annual precipitation being smaller than those from wetter areas (Moulds 2003; M. S. Moulds, *personal communication*).

It is particularly interesting that the large-scale spatial distribution of human body size during the Pleistocene is similar to that observed today (Ruff and Walker 1993, Ruff 1994, Holliday 1997), which suggests that some critical spatial properties of the environment have remained stable over this time period. Given the well-documented variability of temperature and precipitation over the past several hundred thousand years, this suggests an important role for a more stable environmental property, such as soil mineralogy and rates of pedogenesis.

At the global scale, the shortest humans are currently found on the highly leached, infertile soils of rainforests in the high-rainfall regions of Africa (Hiernaux 1975: Table 6), South America (Stinson 1990), and Australia (Birdsell 1993: Figs. A-8 and E-2). In a study of 25 022 children from 735 villages distributed across 17 provinces of Papua New Guinea, genetic differentiation had little relationship with stature of children under five years of age (Smith et al. 1993). Stature of the children was positively correlated with the ratio of protein to energy intake ( $r = 0.59$ ,  $P < 0.05$ ) and the ratio of fat to energy intake ( $r = 0.72$ ,  $P < 0.01$ ). Child stature was not linearly related to altitude, being greatest at low elevations and very high elevations (Smith et al. 1993: Fig. 2). However, the stature of children decreased linearly from “dry” regions (0–2000 mm annual rainfall) to very wet regions (4000+ mm) (Smith et al. 1993: Fig. 3), which is consistent with the soil weathering and leaching effects of high rainfall. The staple foods in this region are locally grown root crops that contribute up to 83% of the total dietary energy, but are low in protein and fat (cf. Trowell 1949, Albrecht 1957). Based on global standards for developing countries, about half of the children in the study would have been considered malnourished (Smith et al. 1993:17). Food quality and quantity are key determinants of growth in children, and are clearly correlated with environmental conditions that are negatively affected by high rainfall.

Larger human body size (specifically height, or stature) is found in seasonal grassland or savanna environments, including the African Sahel (Hiernaux

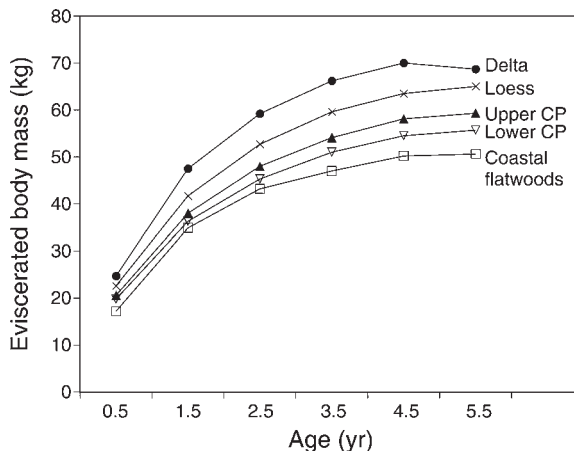


FIG. 6. Average male white-tailed deer body mass by tooth-eruption/wear age class for five soil regions in Mississippi (data from Strickland and Demarais [2006: Table 2]). Rank order of regional soil fertility declines from Delta to CF (Coastal Flatwoods). CP stands for Coastal Plain.

1975) and the North American prairies (Newman 1953, Prince 1995, Steckel and Prince 2001), high latitudes, and coastal environments. Bindon and Baker (1997) note that the primary exceptions to Bergmann’s rule for human body size are the tropical islanders of Polynesia, Melanesia, and Micronesia. However, the ready access of these and other coastal peoples to marine protein (eNSP) confirms that these tropical exceptions to Bergmann’s rule are consistent with the eNPP rule.

In summary, the eNPP rule provides a simple explanation for body-size differences at the intraspecific level across many types and scales of environmental variation. Unfortunately, high-quality body-size data with good coverage of a species range are available only for *Homo sapiens*. Consequently, for most species it is simply not possible to test the predictions of the eNPP rule at the intraspecific level, where the effects of food availability are likely to be much stronger than the effects of phylogenetic history.

#### INTERSPECIFIC PATTERNS OF VARIATION IN BODY SIZE

A paucity of body-size data is not a problem at the interspecific level, where “typical” sizes, as well as size ranges, are available for most described animal species (e.g., Silva and Downing 1995, Dunning 2007). While we have been critical of some applications of the “community” approach to studying latitudinal (or other) variation in body size, we are nonetheless confident that the effects of eNPP on body size will also be detected within higher taxonomic levels, e.g., genera or families, across gradients or contrasts in eNPP.

Patterns of body-size variation at higher taxonomic levels and larger geographic scales clearly involve mechanisms in addition to the direct effect of eNPP on ontogenetic growth rates. We postulate that the

ontogenetic developmental effects of eNPP on female body size lead to epigenetic and/or phenotypically plastic effects on the size of offspring, an effect that can be rapidly amplified toward larger or smaller body size over multiple generations (e.g., Wurm 1982, 1984). These epigenetic effects would very likely lead to genetic changes due to selective pressures toward smaller body size based on mortality caused by insufficient food availability in unproductive environments or toward larger body size based on efficiency of food acquisition and intraspecific or interspecific competition in productive environments. In a recent paper on the role of phenotypic plasticity in speciation, Pfennig et al. (2010) postulate just this kind of evolutionary scenario leading to genetic accommodation and assimilation after long periods of ecomorphological divergence related to habitat differences. An effect of this type has been reported for seed-parasitizing insects (Fox and Savalli 1998).

Wherever there is long-term stability of eNPP at low levels, or periodic reductions of eNPP to low levels, we expect to see reductions in body size due to selection for both individual survival and population survival. Where there is long-term stability of eNPP at high levels, we expect that the relaxation of these constraints will allow the evolution of larger body sizes in response to other selective forces, producing interspecific patterns of body size across geographical gradients of eNPP. There are numerous published reports on interspecific body-size variation within taxonomic groups with a relatively small range of body sizes (e.g., a few orders of magnitude).

#### *Interspecific patterns in Homeotherms*

Birds, like mammals, are endotherms, and conformation to Bergmann's rule has been demonstrated for various types of birds in different regions of the world, primarily at the interspecific level (Hamilton 1961, James 1970, Graves 1991, Blackburn and Gaston 1996, Gaston and Blackburn 1996, Ashton 2002, Greve et al. 2008, Guillaumet et al. 2008, Boyer et al. 2010). Bergmann's rule holds for New World birds at the genus level and higher (Blackburn and Gaston 1996: Fig. 7) mirroring the distribution of eNPP. In addition to bird body size, bird clutch size has long been recognized to increase across similarly sized species from small clutches in birds that breed in the tropics to larger clutches in birds that breed in the temperate and boreal zones (Lack 1947, 1948, 1968, Lack and Moreau 1965), a latitudinal correlation that is much stronger than that for body size (Boyer et al. 2010). Similarly, the litter sizes of squirrels, ground squirrels, cricetid rodents, and other small mammals have also been found to increase with latitude (Lord 1960, Moore 1961, Smith and McGinnis 1968), and small-mammal body size increases with latitude (and eNPP) as well (Smith and McGinnis 1968, Heaney 1984, Quin et al. 1996, Johnson 1998a).

There is also support for the eNPP rule in ursids at the interspecific level. It is well known that the smallest bears occur in the tropics (*Helarctos malayanus*) and the largest bears inhabit temperate latitudes and subarctic and arctic areas with high availability of food from marine sources (Rausch 1963, Nowak and Paradiso 1983, Welch et al. 1997, Meiri et al. 2007). During the Pleistocene multiple species of giant cave bear (e.g., *U. spelaeus* and *U. deningeri*) inhabited temperate Europe (Kurtén 1963, 1976, Kurtén and Anderson 1980, Stiner 1998, Wolverson 2006). In addition, the giant short-face bear (*Arctodus simus*) and other massive Pleistocene carnivores (e.g., *Panthera atrox*, *Smilodon* sp., *Canis dirus*) inhabited the temperate latitudes of North America (Kurtén and Anderson 1980, Graham et al. 1996, Geist 1999).

Since the eNPP rule is independent of latitude and should apply wherever there are differences in eNPP, there are numerous opportunities for continental-scale comparisons, particularly at the interspecific level or higher. Soil fertility differs greatly among the three major tropical rainforest regions, being on average highest in the Malay Archipelago, and by far the lowest in the Amazon Basin of South America (Richter and Babbar 1991, Huston 1994, Huston and Wolverson 2009). Since all three tropical rainforest regions have similarly adequate precipitation and warm temperatures, the primary limiting factor that could cause differences in plant growth (eNPP) and nutritional quality is soil nutrients. Thus, the straightforward prediction of the eNPP rule, as it influences and limits natural selection for body size at higher taxonomic levels, is that animal body size and total animal biomass should increase from the lowest values in South America to higher values in Africa and the Malay Archipelago (considering the potentially diminutizing and/or gigantizing effects of islands for some Indo-Malayan and Madagascan animals).

Anecdotally, one cannot help but note the much greater abundance, size, and, in some cases, diversity of mammals of all types in Africa and Southeast Asia, as compared to South America. The maximum size of the largest predators increases from approximately 150 kg (jaguar) in South America to 250 kg (lion) in Africa to 300 kg (tiger) in Southeast Asia (Nowak and Paradiso 1983), paralleling the differences in soil fertility (Richter and Babbar 1991, Huston and Wolverson 2009). While the population density of these large predators varies greatly within each region, largely due to variation in prey densities (e.g., Karanth et al. 2004, Barlow 2009), population densities of the lion and tiger tend to be higher than those of the jaguar (Creel and Creel 1997, Sunquist and Sunquist 2002, Silver et al. 2004).

The much larger sizes of the Old World monkeys compared to the New World monkeys have long been recognized (Terborgh 1983, Kappeler and Heymann 1996). The median size (based on non-pregnant female mass) of New World primates is only 0.24 of the median

TABLE 4. Comparison of primate body sizes in the New World, Africa, and Asia.

Family	Common names	Earliest fossils	New World		Africa		Asia	
			Median	Range	Median	Range	Median	Range
All primates			0.86	0.12–8.8	3.62	0.069–93	5.9	0.11–37
Soil fertility (Total exchangeable bases [cmol/kg])			3	0–76	6	0–89	9	0–49
Suborder Strepsirhini								
Lorisidae	loris, potto, galago	early Miocene			0.25	0.07–1.24	0.19	0.193
Suborder Haplorhini								
Tarsidae	tarsiers	early Miocene					0.22	0.11–0.195
Cebidae	New World monkeys	late Oligocene	2.3	0.46–8.8				
Callitrichidae	marmosets, tamarins	middle Miocene	0.46	0.12–0.8				
Cercopithecidae	Old World monkeys	early Miocene			5.35	1.12–16.8	6.6	3.0–12.0
Hylobatidae	gibbons, siamang	Oligocene					5.8	5.3–10.6
Pongidae	great apes	Oligocene			32.9	31–93	37	37

*Notes:* Masses (kg) are for non-pregnant females in most cases. New World median body mass is less than African and Asian medians for all primates ( $P < 0.001$ ). (Primate data based on Kappeler and Heymann [1996] and Nowak [1999]). Median soil total exchangeable bases (TEB) were calculated using the Harmonized World Soil Database V1.0 (FAO 2008) over the approximate total range of New World monkeys in the Americas and the separate ranges of Old World monkeys in Africa and Asia.

for African primates, and 0.15 of the median for Asian primates, while the maximum size of South American primates is 0.09 and 0.24, respectively, of the maximum sizes of African and Asian primates (Table 4). This dramatic contrast has been explained as the result of early evolutionary divergence into clades with significantly differently sized lineages, with subsequent conservation of body size between lineages (Cooper and Purvis 2010). If this were true, it would be merely a coincidence that small primates ended up in a region with very poor soils and the large primates in a region with much more fertile soils, including soils good enough to support the even larger great apes.

However, it seems just as plausible to hypothesize that primate lineages with similar evolutionary potential ended up on continents with very different soils and productivity. The fossil record suggests similar ages for both the New World and Old World monkeys, with the New World record being slightly older (Table 4; Martin 1990, Nowak 1999). Thus, these related lineages have been evolving for about the same length of time in different environments. The smaller primates of Africa and Asia (Tarsidae, Lorisidae, and Galagidae, as well as the primates of Madagascar) represent older lineages than the more closely related and similarly sized Old and New World monkeys (Purvis 1995: Fig. 9). In Africa and Asia, with more fertile soils, the primary off-branch from the Cercopithecidae was the much larger great apes and Hominids, while in South America, with less fertile soils, the primary off-branch from the Cebidae was the diminutive Callitrichidae (marmosets and tamarins), which are found in and around the Amazon Basin, where soil nutrient levels are lowest (Purvis 1995: Fig. 9). Focusing on the relatively similar Cebidae (New World monkeys) and Cercopithecidae (Old World monkeys), the median size of the Cebidae is 0.43 and 0.35 of the median size of Cercopithecidae in Africa and Asia,

respectively. These size differences are similar to the 0.5 and 0.33 difference in median soil fertility (as estimated by total exchangeable bases or TEB) across the ranges of these monkeys, comparing South America to Africa, and Asia (Table 4). Virtually none of the world's soils with TEB levels of 3 cmol/kg or lower are used for agriculture, while many of the world's most productive farmlands have TEB levels in the range of 8 to 10 (Huston 2005). These differences apparently allowed some members of the Cercopithecidae (as well as the great apes) on the more fertile soils of Africa and Asia to evolve larger sizes, while the Cebidae on the poorer soils of South America could not evolve large species because the productivity was too low to support them.

Nutritional constraints on primates in America are also suggested by the facts that there are no strictly folivorous primates in America, in contrast to Africa and Asia, while there is a much larger proportion of frugivore-faunivores in America. These are potential indications that a purely plant-based diet does not provide sufficient nutrition in the American tropics (Kappeler and Heymann 1996: Fig. 4). The evolution of the Great Apes, as well as the hominids, in Africa may be in part a consequence of the more fertile soils, particularly in contrast with South America.

Another interesting continental-scale comparison is between Australia and the rest of the world (Flannery 1994). The continent of Australia has ancient, highly weathered landforms with very little recent volcanic or orogenic activity. Consequently, most of the soils of Australia are highly weathered and infertile (Wild 1958), which, combined with the aridity of most of the continent, leads to very low NPP and eNPP except in a few isolated regions (e.g., mountain ash forests in southeastern Australia). This is a potential explanation for the relatively small body sizes of both contemporary and prehistoric Australian mammals (Flannery

1994:108–129) and many other vertebrates (e.g., the “little penguin”), compared to species with similar functional roles on other continents.

The continent of Australia provides many types of productivity gradients. Of particular interest are the longitudinal gradients associated with declining precipitation from the coast toward the interior, most dramatically along the east coast and the southwest coast. Intraspecific variation in body size has not been compiled for most species, but there are a few examples of what is likely to be a very common phenomenon at both the intra- and interspecific levels. At the interspecific level for Australian marsupials, Cooper and Purvis (2010: Fig. 2A) report a gradient of declining median ln-transformed body mass from the coast inland, which is most pronounced along the east and southwest coasts. Along the east coast, the latitudinal gradient is also a productivity gradient, from the wet tropics in the north to the high temperate wet forests of Tasmania in the south, as noted by Yom-Tov and Nix (1986), who found that intraspecific body-size variation within five species (echidna, *Tachyglossus aculeatus*; brush-tailed possum, *Trichosurus vulpecula*; eastern gray kangaroo, *Macropus giganteus*; western gray Kangaroo, *M. fuliginosus*; red kangaroo, *M. rufus*) conformed to Bergmann’s rule. Body size in four of the five species, excepting the red kangaroo, was also correlated with indices of biomass productivity, which the authors note are difficult to separate from the correlated trend in ambient temperature. Yom-Tov and Geffen (2006) reported similar precipitation-related size gradients in 11 species of mammals in Israel that they interpreted as responses to productivity.

Within Africa, there is great variation in soil fertility, the amount and seasonality of precipitation, and thus of eNPP. Owen-Smith (1988) reports that body size of large herbivore species, both ruminants and non-ruminants, is positively correlated with total population biomass (measured as kg/km<sup>2</sup>; Fig. 7B). Total herbivore biomass is, in turn, positively correlated with mean annual rainfall (Fig. 7A) and presumably eNPP across a set of national parks. Total herbivore biomass reaches its maximum around 900 mm of rainfall and apparently declines at higher levels of precipitation, where increased leaching causes loss of cations (e.g., K<sup>+</sup>, Ca<sup>+</sup>, NH<sub>4</sub><sup>+</sup>) and reduces soil fertility (Albrecht 1957, Meggers 1971, Huston 1980, 1994, Uehara and Gillman 1981). The parks with the highest biomass of large herbivores are located on volcanic soils in or near the Rift Valley (Virunga, Zaire; Manyara, Tanzania; Rwenzori, Uganda; Murchison Falls South, Uganda).

#### *Interspecific patterns in poikilotherms*

Bergmann (1847) may have intended his rule to apply only to homeotherms (Margalef 1955, Meiri 2011), but there have nevertheless been numerous publications addressing latitudinal body-size variation in poikilotherms, at both the intraspecific and interspecific levels

(see Ashton and Feldman 2003). Similar to the proportion of mammals that conform to Bergmann’s rule, about 75% of terrestrial vertebrate and invertebrate poikilotherms match the predictions of Bergmann’s rule, based on both experimental work within species (Ray 1960) and literature reviews at the interspecific level (Ray 1960, Lindsey 1966).

However, Bergmann’s heat-balance mechanism obviously does not apply to poikilotherms, which raises the critical question of why so many seem to follow Bergmann’s rule. A number of alternative mechanisms have been proposed to explain geographical body-size variation in poikilotherms (reviewed in Entling et al. 2010), including some based on the relationship between body size, metabolic rate, and temperature that predict larger body size in terrestrial poikilotherms under warmer temperatures (Makarieva et al. 2005). Supporting evidence for this mechanism includes the observation that in 24 of 25 families of insects, spiders, and other invertebrates plus frogs, snakes, and lizards found from the temperate zones through the tropics, the largest species were found in the tropics (Makarieva et al. 2005). Similarly, a survey of the average size of spiders in local assemblages across Europe found that body size declined with latitude between 35° and 65° N, with the largest average size in warm, dry conditions (Entling et al. 2010).

The size–temperature–metabolic-rate mechanism (Makarieva et al. 2005) is postulated to act as a size constraint on natural selection that varies with temperature, but does not preclude the operation of the eNPP rule at the intraspecific level as well. Most reported data on body-size gradients in poikilotherms are at the interspecific or community level, rather than the intraspecific level where we have focused on the short-term effects of food availability and eNPP on body size. While we argue that food availability as regulated by eNPP can lead to natural selection for larger or smaller body size and specific life history strategies, this is clearly not the only influence on the evolution of body size or life history attributes. Interestingly, the predictions of the size–temperature–metabolic-rate model proposed by Makarieva et al. are the opposite of Bergmann’s rule and the eNPP rule for terrestrial poikilotherms, but the same as those of Bergmann’s rule and the eNPP rule for aquatic or marine poikilotherms, based on the lower oxygen concentration of water as compared to air, as well as the sensitivity of oxygen concentration to water temperature. The implications for marine fish are discussed in *Abundance, biomass, size, and diversity in the oceans*.

The sensitivity of insect body size to food availability, the fundamental mechanism underlying the eNPP rule, is illustrated by several groups of parasitic wasps that lay their eggs in the larvae or pupae of their hosts. Female parasites prefer to lay their eggs in larger larvae or pupae, and preferentially lay female eggs in the largest hosts, which produce larger female offspring that can in

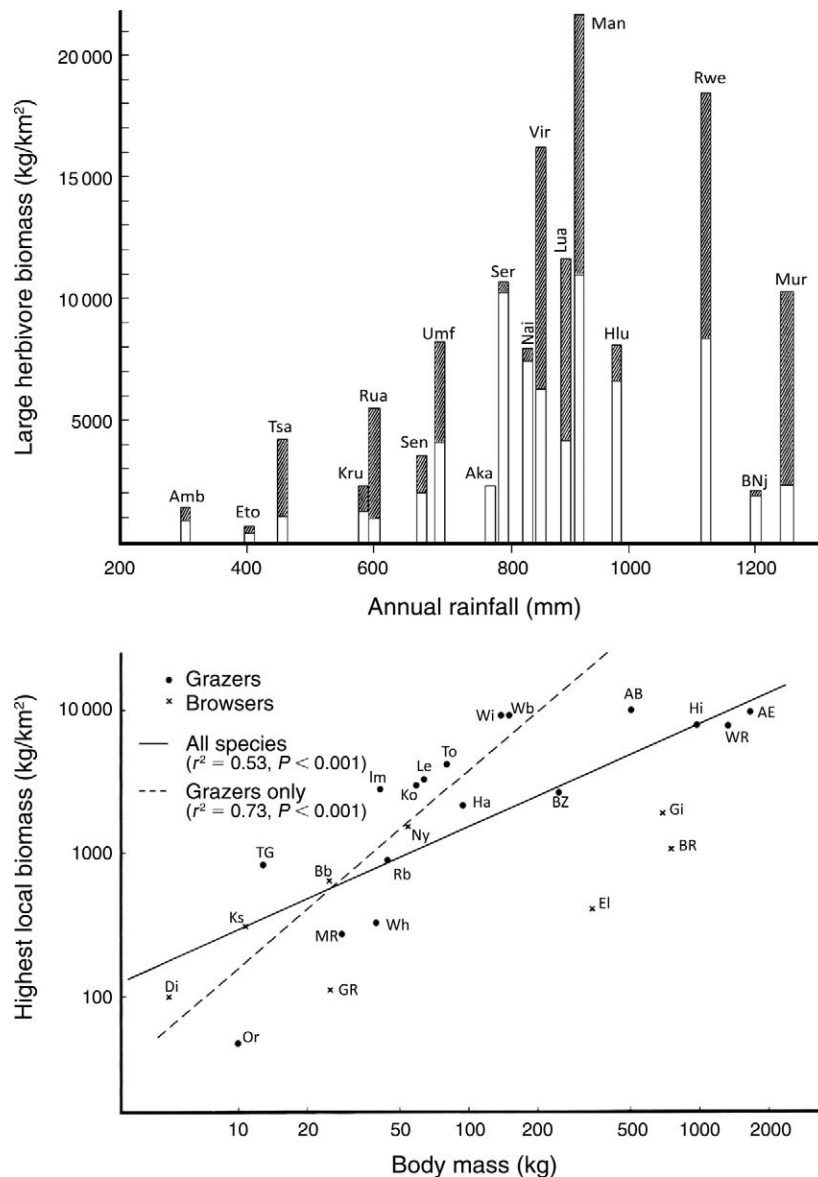


FIG. 7. (A) Effect of precipitation on herbivore biomass in national parks in Africa. The shaded portion of each bar represents the contribution of megaherbivores (elephants, rhinoceros, giraffes) to the total large herbivore biomass in a specific park. (B) Relationship of body size to maximum population biomass for a range of herbivore species in Africa (from Owen-Smith [1988: Figs. 14.2, 14.3]; reprinted with the permission of Cambridge University Press). Abbreviations are for large mammals from African parks; a full description of the species represented can be found in Appendix I of Owen-Smith (1988: Table I.1).

turn lay more eggs and handle larger hosts for their own oviposition (Chewyreu 1913, Brunson 1937, Clausen 1939, Charnov et al. 1981) illustrating an epigenetic positive feedback that we believe is quite common. Blanckenhorn (1998) reported a strong effect of larval food supply on adult size in dung flies that was largely independent of development time. Stockhoff (1993) reported reduced pupal mass and extended development time for gypsy moth larvae fed a diet that was either very high (4.75%) or very low (1.25%) in nitrogen content, compared to a diet of 3.0% nitrogen content. However, Twombly and Tisch (2000) found strong growth

compensation and little size variation in copepods fed diets that varied in quantity and quality (see however Berg 1936). Overall, we expect strong effects of food quantity and quality (e.g., protein or nitrogen content) on the ontogenetic growth rates of larvae, duration of instars, and adult body sizes of insects and other invertebrates.

Understanding of multiple factors, and region-specific data on eNPP, temperature, and precipitation, will be necessary to explain contrasting interspecific patterns such as the latitudinal increase in mean butterfly size (male wing length) in North America (25–75° N), the

decline in Australia (12–38° S), and the lack of any pattern in Europe (32–68° N; Hawkins and Lawton 1995). Ulrich and Fiera (2010) report a unimodal latitudinal pattern of the maximum body size across 52 country-level assemblages based on 2102 out of the total of 2500 described European collembola species. The decline with latitude above 50° N (Fig. 6I) is consistent with the predictions of the eNPP rule. Blanckenhorn and Demont (2004) describe and synthesize additional evidence for clear Bergmann and inverse Bergmann patterns in arthropods. They conclude, however, that their “study does not elucidate at all the underlying cause of Bergmann’s rule, the mystery of which must therefore continue” (Blanckenhorn and Demont 2004:422). Some of this mystery is explained by the eNPP rule, but other mechanisms must also be involved, particularly at higher taxonomic levels.

One particularly comprehensive invertebrate data set is for ants across a latitudinal gradient of 49 sites in the New World (involving species in 31 genera), where Kaspari (2005) found that the body mass of individual ants, as well as the number of workers per colony each varied by two orders of magnitude over a variety of temperate and tropical habitats. The extremes in both body mass and worker numbers were found at ~35° N, across a range of habitats from deserts (0.06 mg body mass, 9057 workers per colony) to evergreen and deciduous forests (2.34 mg, 63 workers), corresponding to a strong longitudinal gradient in NPP and eNPP. Worker mass and worker number were uncorrelated across the 49 sites. However, the mean mass of individual worker ants at a site was approximately 10 times greater at high latitudes and colder temperatures than in the warm tropics (Kaspari 2005: Fig. 1A), while the number of workers per colony was also about 10 times higher in the temperate zone where the ants were largest (Kaspari 2005: Fig. 2A, Kaspari and Vargo 1995). This pattern might be consistent with the energetic-equivalence hypothesis (Allen et al. 2002) if the density of ant colonies were much higher in the tropics and thus total ant biomass were constant across the gradient. However, it would be consistent with the eNPP rule if total ant biomass were lower in the tropics.

Across the same 49 sites, Kaspari (2001) also measured the density of colonies (ant nests) in 30 1-m<sup>2</sup> plots along 330-m transects at each site, which revealed that the density of colonies was approximately three to four times higher in tropical forests than in temperate forests (Kaspari 2001: Fig. 2). However, this increase in colony density does not compensate for the approximate order of magnitude difference in both colony size and individual mass, suggesting that total ant biomass might be substantially higher in productive temperate environments than in tropical rain forests. Kaspari’s work focused on ground ants, and there is potentially a large biomass of forest canopy ants in tropical forests, and possibly in temperate forests as well.

Kaspari’s work apparently shows the effect of productivity, operating through selection at the interspecific level, on individual ant size, colony size, and colony density, although total ant biomass across all of the sites could not be evaluated from the published data. Unfortunately, Kaspari’s NPP estimates were based on actual evapotranspiration, which is likely to lead to substantial overestimates of tropical productivity (see Huston and Wolverson 2009). The diversity of ground ants is clearly highest in the tropical rainforest sites where body size is small (Kaspari et al. 2000), similar to the inverse body-size–diversity correlation in New World birds (Blackburn and Gaston 1996). Substantial additional research, as well as further analysis of available data, will be necessary for a quantitative assessment of latitudinal and other patterns of total ant biomass, individual size, and species diversity.

#### TEMPORAL VARIATION IN BODY SIZE

All of the previously discussed patterns of body size are based on spatial variation in eNPP, assuming averaging of interannual temporal variation. However, it is well-documented that both weather and climate vary temporally over a range of scales relevant to physiological, developmental, ecological, and evolutionary processes. Consequently, just as there is a clear signal of body size in relation to spatial differences in eNPP, we expect that there will be clear responses of body size in relation to temporal differences in eNPP and other factors that affect food availability. The range of time spans over which eNPP can vary extends the potential effects on body size from intraspecific variation in ontogenetic growth to evolutionary changes leading to speciation.

Since animals vary in the rate at which they mature to adult size, we can expect to see intraspecific body-size variation due to temporal variation in conditions that affect physiological processes and ontogenetic growth at temporal scales ranging from minutes (bacteria, e.g., Kuuppo 1994) to weeks (zooplankton, e.g., Berg 1936, Bayliss and Laybourn-Parry 1995), months, years, and even decades for some large vertebrates. At evolutionary timescales of centuries to thousands or millions of years we can expect to see signals at the interspecific level and higher taxonomic levels caused by the interaction of epigenetic processes (e.g., maternal size) with selection for individual and population survival in low-productivity environments, and for resource capture and competition in high-productivity environments.

For large vertebrate species, gradual changes in size over time may result from gradual changes in climate (e.g., Purdue 1989, Guthrie 2003, Lyman 2004a), or from gradual changes in density due to management or other factors (e.g., Hill et al. 2008, Wolverson 2008). However, abrupt changes in the body size of entire cohorts within a population may be caused by extreme events, such as droughts, that significantly reduce eNPP during a time period critical to the growth of certain



TABLE 5. Temporal and spatial differences in human stature during the Upper Paleolithic.

Sex	Height (cm)				
	Early Upper Paleolithic		Late Upper Paleolithic		
	Europe†	Europe†	Southeast Asia	Nile Valley	Mediterranean
Male	174.1 ± 1.5 (10)	165.3 ± 3.7 (15)	153.1 ± 5.6 (3)	170.2 ± 1.2 (15)	168.4 ± 1.3 (12)
Female	161.8 ± 3.2 (5)	154.5 ± 3.4 (7)	147.8 ± 2.17 (7)	162.4 ± 0.7 (16)	161.7 ± 2.4 (4)

Notes: Values are means with standard errors. Sample sizes are shown in parentheses. Based on Holt and Formicola 2008. Data are from Shackelford (2007) and Holt and Formicola (2008) unless otherwise noted.

† Data from Holt (2003).

(generally the youngest) members of the population. Longer droughts, or other events that reduce eNPP, may cause a reduction in the body size of an entire generation, which can have potential longer-term consequences through the effect on maternal size. Larger-scale climate cycles can cause substantial changes in eNPP and food available at millennial scales or longer (Purdue 1989, Lyman 2004a).

While we expect that intrapopulation size variation driven by short- and intermediate-term temporal variability in eNPP and food availability occurs in all relatively long-lived animals, the most detailed documentation of such effects is for *Homo sapiens*. The Dutch Famine of 1944–1945 was caused by World War II and lasted eight months with a reduction of caloric intake of 60% (van Noord and Arias-Careaga 1995). Data from a breast cancer study involving 18 000 women born between 1911 and 1945 showed that the cohort with the highest famine exposure ( $N = 1901$ ) had a significant ( $P < 0.0001$ ) reduction in height as well as in arm span and leg length compared to the non-exposed population. Critical ages for height reduction due to the famine were 0–9 and 12–16 years, with no effect detected in girls who were 16 or older, or who were around 10–11, when the growth spurt typically occurs (van Noord and Arias-Careaga 1995). China's Great Famine of 1959–1961 was due to administrative rather than environmental factors and is estimated to have killed between 16 and 31 million people (Meng and Qian 2009). Based on county-level data from the 1990 population census and the 1989 China Health and Nutritional Survey, the famine is estimated to have reduced the number in the 1959–1961 cohort by 36% in relation to the number in the 1952–1954 cohort. For the individuals in the 90th height percentile, most of whom are assumed to have survived the famine, in utero exposure is estimated to have reduced adult height by 2.8 cm and mass by 1.42 kg, while early childhood exposure reduced adult height by 2.7 cm and mass by 3.03 kg (Meng and Qian 2009). Dietary and health differences are the apparent explanation for the average 10.21 cm height difference and different body proportions (legs average 7.02 cm longer) between Mayan children 6–12 years of age growing up in the United States and those of the same age growing up in Guatemala (Bogin and Rios 2003).

At a somewhat longer timescale, analysis of height measurements made in 1906–1907 of 223 male Oglala (Teton) Sioux on the Pine Ridge Reservation revealed significant differences of as much as 4 cm in average height between decadal birth cohorts from 1830 to 1880 with an overall trend of increasing height over the time period (Prince 1995). While the actual cause of these differences in height cannot be unequivocally determined, they may be related to a combination of western droughts during the 1800s (Piechota et al. 2004) and stresses associated with Indian wars and persecution by the U.S. government.

Over the past millennium, average height in northern Europe declined from nearly modern levels during the Middle Ages (800–1300 AD), which included the 500 year “Medieval Warm Period,” to a low in the 1600s and the “Little Ice Age” (Parker and Smith 1997) before recovering during the 1800s. In addition to the climatic deterioration during the 17th century, political and religious turmoil, as well as new diseases associated with global colonization, may have contributed to a reduction in the food supply and overall health (Steckel 2001). Beginning in the 19th century, body size began to increase and continued to do so through most of the 20th century, presumably because of better nutrition and health care (Wurm 1982, 1984, Gustaffson et al. 2007). From 1880 to 1980 mean height in Europe increased about 1 cm/decade (Eveleth and Tanner 1990).

Over the Paleolithic period (40–10 kya [kya stands for thousands of years ago]), human body size in Europe declined from the early Upper Paleolithic (EUP, 40–20 kya) to the late Upper Paleolithic (LUP, 19–10 kya), associated with the warming following the Last Glacial Maximum (Holt and Formicola 2008; Table 5). Although the Paleolithic was affected by extreme and rapid climatic fluctuations (van Andel et al. 2003), it is not obvious why body size should decline with an apparent improvement in mean climate. Increased population densities and overexploitation of natural resources have been identified as one potential explanation for the observed decline in prey body size (Stiner et al. 1999), although variation in eNPP remains an alternative hypothesis. The reduced stature of Europeans in the late Upper Paleolithic contrasts with the substantially taller LUP people of the fertile Nile Valley, and the much shorter people of Southeast Asia (Table

5). There is as yet no definitive explanation for the small size of Southeast Asians of this period (Shackelford 2007), although the same pattern (at least for the Japanese) persisted through the mid-19th century (Steckel and Floud 1997: Table 11.2), perhaps due in part to high population densities that could have reduced per individual food availability.

Over evolutionary time scales, there should be numerous examples of body-size responses to changes in productivity found in the fossil record for all types of organisms. One well-documented example is the diminution of a number of mammal species in what is now northwestern Wyoming, about 55 million years ago during a brief warm dry period. This event, known as the Paleocene-Eocene temperature maximum (PETM), lasted about 86 000 years, during which species in several genera, including *Hyracotherium*, *Copecion*, and *Ectocion* were rapidly replaced by species (or diminutized ecotypes) that were about 50% of the mass of those in the preceding and/or following time periods (Gingerich 2003, 2008). Whether the diminutized individuals should be considered separate species (as they usually are) or whether they simply represent phenotypic plasticity within a single species remains to be determined. Interestingly, there was a sharp jump in the number of mammal species in this fauna over the brief period of the PETM (Vrba 1985, Webb and Opdike 1995). While there are no data on NPP during this time period, it seems likely that the warmer, drier conditions were associated with a water-limited decline in NPP and eNPP.

Over the past 15 000 years, there has been a significant diminution in size of numerous species of mammals in North America (Hooijer 1950, Guthrie 1984, Lyman 2004a, b, Lyman and O'Brien 2005), as well as the extinction of many of the largest species (Grayson 2007, Wolverson et al. 2009b). In many of these cases, declines in both size and abundance are associated with a shift to warmer, drier conditions during the Altithermal (Purdue 1989, Grayson 1998, 2000, Lyman 2004a, Lyman and Wolverson 2002), which is consistent with changes expected with decreasing eNPP.

An example of rapid response to very recent climate change provides a temporal analogy of the spatial increase in body size as latitude declines from 80° to 60° N. Ogzul et al. (2010) conducted a long-term (1976–2008) study of a marmot (*Marmota flaviventris*) population in a subalpine valley (2950 m above sea level) in the Colorado Rockies. Over the duration of the study, the growing season increased in length, with marmots emerging from their six to seven month hibernation earlier each year, with corresponding decreases in birthing and weaning dates. With the increased time for feeding, the mean 1 August mass of 2-year-old or older females increased by 11% (to 3433 g) between the first and second halves of the study. Beginning in 2000, there was a sudden increase in population growth rate from 0.56 marmots per year to 14.2 marmots per year

(Ogzul et al. 2010). This increase in both body size and population density of marmots with increased length of the eNPP pulse matches the predictions of the eNPP rule, and shows the same effect on body size as observed with caribou, wolves, and marine fish as growing-season length increases with decreasing latitude from 80° N to approximately 60° N (Fig. 1, zone B–). Interestingly, a size increase has also been reported for the arboreal mustelid predator, the Marten (*Martes americana*) in Alaska, as climate has warmed over the past fifty years (Yom-Tov et al. 2008).

Temporal variation in animal body size is evident over a broad range of time scales, and it seems likely that a substantial amount of the variability in body size (age and sex corrected) within populations of long-lived species may be due to variation in food availability caused by climatic fluctuations or other factors that affect eNPP during critical periods of ontogenetic growth and maturation. We also hypothesize that differences in the maximum body size observed within higher taxonomic levels (e.g., genera, families, and orders of fish, reptiles, birds, and mammals) across geological time scales in different regions of the Earth are at least partially due to variation in eNPP as a result of varying rates of geological processes such as volcanism, orogeny, erosion, deposition, and sea level fluctuations, interacting with regional scale climate. The generally warm, wet climate (e.g., McElwain et al. 1999) and high tectonic activity of the Mesozoic Era contributed to high productivity that may help explain the large body sizes of some dinosaurs and other reptiles during much of that period. Over the geological history of life on Earth, as plate tectonics have opened and closed seaways and oceans, with varying nutrient inputs from terrestrial sediments (e.g., Blakey and Ranney 2009), we hypothesize that the ratio of terrestrial nutrient input to ocean volume has produced huge spatial and temporal variation in marine NPP and thus in the body size and abundance of marine organisms, analogous to the spatial and temporal variation of NPP on land.

#### BEYOND BODY SIZE

If food quantity and quality, as proposed in the eNPP Rule, are the primary explanation for geographical patterns of animal size, it should have implications for other organismal and ecological properties that are not addressed by Bergmann's rule or by most of the body-size literature (see however, Kaspari 2001, as well as the vast anthropological and human health literature). The two most significant ecological properties that are dependent on food and energy availability are the abundance of a species (regardless of body size) and the total biomass per unit area of a species, which is obviously the product of population density and individual biomass. Additional individual and population-level properties that are dependent on food and energy availability include health, strength, reproductive rates, and other traits associated with evolutionary

fitness. The eNPP rule makes the simple prediction that body size and/or abundance, as well as total species biomass, individual health, and fecundity should all be positively correlated with eNPP because they are all derived from eNPP. Since all of these traits are directly related to the growth rates and survival of populations, we can expect that eNPP will also have an effect on species diversity through both speciation and extinction rates (e.g., Huston 1994; M. A. Huston, *unpublished manuscript*).

#### *Abundance, biomass, size, and diversity on land*

The idea that organismal abundance is a direct function of available energy is not new (Lindeman 1942, Damuth 1981, 1987, 1991) and is a central idea behind energy–diversity theory and “more individuals” explanations for species diversity (Wright 1983, Currie 1991, Currie and Fritz 1993, Wright et al. 1993), as well as the metabolic theory of ecology (MTE; Brown et al. 2004). These theories propose that the key driver of species diversity is animal density or population size, which at high levels reduces the probability of stochastic extinction and should lead to the highest diversity where average population densities are highest (Wright 1983, Currie 1991, Allen et al. 2002). According to the “energetic-equivalence rule,” the total energy flux of a population within a specific area is invariant with regard to body size (Damuth 1987, Enquist and Niklas 2001, Allen et al. 2002). Because individual metabolic demand increases (logarithmically) with body size (Benedict 1938), the energetic-equivalence rule predicts that body size should be inversely correlated with population density, assuming that the amount of energy available, that is, eNPP, is constant across the areas being compared.

Proponents of metabolic theory and the energetic-equivalence rule predict that species population densities and, consequently, species diversity should be highest in the tropics because of the high temperatures (assumed to correspond to high available energy) combined with (incorrectly) presumed high productivity (Allen et al. 2002, Brown et al. 2004). However, this prediction is the opposite of the eNPP rule, which predicts that animal body sizes and/or population densities should be low in the tropics because of low eNPP (Huston and Wolverton 2009), and that likewise, total population biomass should also be lower in the tropics, or anywhere eNPP is low. These low-eNPP and low-population density conditions are where other ecological (Huston 1979, 1994) and evolutionary (Huston 1994:304–318; M. A. Huston, *unpublished manuscript*) hypotheses predict that species diversity should be highest.

The challenge in testing these alternative hypotheses is the lack of adequate data on spatial variation in animal population densities, and thus on total population biomass. This deficiency is paralleled by the lack of spatial information on intraspecific variation in body size across virtually all taxa (except for humans and a

few other mammals). The most extensive data on body-size variation are at the interspecific level, with spatial variation in species composition being the driver of differences in mean community body size (an approach we criticized in the introduction). While these are relatively weak data for evaluating the mechanisms underlying the predictions of the MTE and the eNPP rule, they do offer the possibility of evaluating some of the correlations among body size, total population biomass, population density, and species richness.

Johnson (1998a) found that population densities of Australian mammals (comparing 69 species) were lower in the tropics, where both geographical range sizes and body sizes were also smaller. For 13 species with ranges that included the tropical and temperate zones, he found that population densities tended to be greater in the temperate portion of their range, and that for some of the species body size also increased in the temperate portion. On average, based on body size and population density, he estimated that the “tropical populations used about one order of magnitude less energy than did temperate populations of the same species” (Johnson 1998a:692). Similar patterns of increasing population density, as well as increasing body size, with increasing latitude have been found across multiple species of Australian honeyeaters (Aves: Meliphagidae; Symonds et al. 2006, Symonds and Johnson 2006) as well as among other species of birds and mammals (Currie and Fritz 1993, Gaston and Blackburn 1996).

Across multiple species of African ungulates in a variety of major national parks, the maximum local population biomass per unit area increases as the mean body size of the species increases (Fig. 7B; Owen-Smith 1988). This is not consistent with the “energetic-equivalence” hypothesis, which predicts an adjustment between body size and density to maintain an equilibrium energy flow, and by association, biomass. However, this is consistent with the prediction of the eNPP rule. At the spatial scale over which ungulate size varies by more than two orders of magnitude there is no significant variation in either temperature or latitude, but there is variation in savanna productivity (Owen-Smith 1988, 2002).

Consistent with the well-known body-size differences between New and Old World primates discussed previously, there is evidence that total primate biomass is higher (by a factor of 4 or more) in Old World primate communities than in New World communities on poorer soils (Terborgh 1983, cited in Huston 1994). At smaller spatial scales, it is apparent that total herbivore biomass in Africa is positively correlated with annual precipitation, which is an indicator of eNPP (Fig. 7A). At the intraspecific level, raccoon body size in Missouri is correlated with soil fertility, as is raccoon population density (where there is sufficient habitat unimpacted by agriculture; Fig. 5A and B).

In addition to the previously discussed information on latitudinal patterns of ant body size, colony size, and

colony density from Kaspari's work (Kaspari and Vargo 1995, Kaspari 2005), Hails (1982) documented that the biomass of flying insects is an order of magnitude higher in the temperate zone (Scotland) than in the tropics (Malaysia) (Huston and Wolverton 2009: Fig. 14). This latitudinal difference in insect biomass helps explain marked differences in foraging efficiency and insect capture rates in insectivorous passerine birds between the temperate zone (France) and the tropics (French Guiana; Thiollay 1988). Supplemental food for breeding temperate zone warblers increased the number of second broods, decreased the time females spent foraging, and increased the time they spent near the nest (Nagy and Holmes 2005), illustrating the critical importance of food availability even in areas with high eNPP. Such differences in food availability for insectivores mirror the latitudinal patterns in avian body and clutch size.

Nearly all of the data on body size, reproductive rates, population density, and total population biomass are consistent with our conclusion that eNPP in tropical rain forests is much lower than in the temperate zone. The apparently lower population densities of tropical organisms imply that the "more individuals" explanation for high tropical diversity, as proposed in the context of the metabolic theory of ecology (Brown et al. 2004) and the "energetics-equivalence rule" is invalid. High tropical diversity is apparently maintained in spite of the lower population densities and lower population growth rates in the tropics. This suggests that a new set of theories are needed to explain evolution, speciation, and high diversity in the tropics (see Huston 1979, 1980, 1985, 1994:304–318).

#### *Abundance, biomass, size, and diversity in the oceans*

While the available measurements of terrestrial NPP are extremely limited in spatial coverage and eNPP must be "back-calculated" by dividing annual measurements of NPP by the estimated length of the growing season at each location (Huston and Wolverton 2009), the marine NPP data are incomparably better. Annual marine NPP is calculated by summing multiple short-term estimates of eNPP based on complete global satellite coverage every two days by the SeaWiFs or MODIS sensors (e.g., Behrenfeld and Falkowski 1997, Behrenfeld et al. 2001). Estimates of marine eNPP are based on colorimetric determination of the amount of algal chlorophyll in the upper portion of the water column, converted to eNPP using algorithms such as the vertically generalized production model (VGPM; Behrenfeld and Falkowski 1997, Behrenfeld et al. 2001) or subsequent modifications (e.g., Behrenfeld et al. 2005, 2006). Daily estimates of eNPP ( $\text{g C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ ) can be averaged to provide monthly estimates of eNPP comparable to those calculated for terrestrial ecosystems (Figs. 4A, 8A, 10A; Huston and Wolverton 2009: Fig. 11E, F).

At the global scale, one of the largest and longest-term data sets on animal biomass is the harvest data from marine fisheries. These data, compiled by the United

Nations Environment Program (Sherman and Hempel 2009), extend back to 1950 for many regions of the world, and are used extensively for fisheries management and conservation planning. The catch data, plus a large amount of ancillary data, such as NPP estimates and sea surface temperatures, have recently been compiled for a set of 64 regions called large marine ecosystems (LMEs), which account for 80–90% of the world's fisheries harvest (Fig. 9; Sherman et al. 2009a, b). The LMEs are primarily continental shelf areas, and large bays such as the Gulf of Mexico and the Bay of Bengal, and do not include the open ocean. Major nongovernmental projects, such as FishBase and the Sea Around Us Project (see projects *online*),<sup>4,5</sup> have compiled species lists, size records, and other catch parameters for all of the LMEs, which have been used to generate community-level estimates of average fish size, based on the maximum reported size for each species (Fisher et al. 2010; also see Supplement 3).

Mean fish body size (at the interspecific level, based on maximum sizes of the species found in each LME) is nonlinearly related to latitude (Fisher et al. 2010; Fig. 8B), as predicted in part by Bergmann's rule and completely by the eNPP rule, including an apparent decline in mean body size and marine eNPP above 60° N, similar to the pattern found in terrestrial ungulates at the inter- and intraspecific levels (Fig. 3), as well as in numerous other species (Fig. 4). Sea surface temperatures (SSTs) obviously decrease with latitude (Fisher et al. 2010: Fig. 11), while fisheries catches increase with latitude, particularly in the Northern Hemisphere, following the pattern of average marine eNPP (Fig. 8A). Although there is strong seasonality in sunlight, water temperature, and eNPP in the higher latitudes (Behrenfeld et al. 2001, Huston and Wolverton 2009), the lower temperatures of sea water at these latitudes do not seem to have any negative effect on eNPP during the growing season (Figs. 8A and 10A), nor on total annual marine NPP, both of which are highest at high latitudes.

Low temperatures may actually have a positive effect on eNPP and eNSP through lowering respiration rates in plants and ectothermic animals. The high fisheries catches and large body sizes at these latitudes are consistent with this interpretation, assuming that fisheries catch is representative of secondary productivity and correlated with primary productivity. It is significant that the high eNPP and high fisheries catches are primarily near the continental margins, where terrestrial nutrient inputs are high, but solar radiation and water temperatures are basically the same as in the open ocean. Sea surface temperature seems to have relatively little direct effect on eNPP when solar radiation and nutrients are adequate (Trujillo and Thurman 2005:385–401).

<sup>4</sup> [www.fishbase.org](http://www.fishbase.org)

<sup>5</sup> [www.seaaroundus.org](http://www.seaaroundus.org)

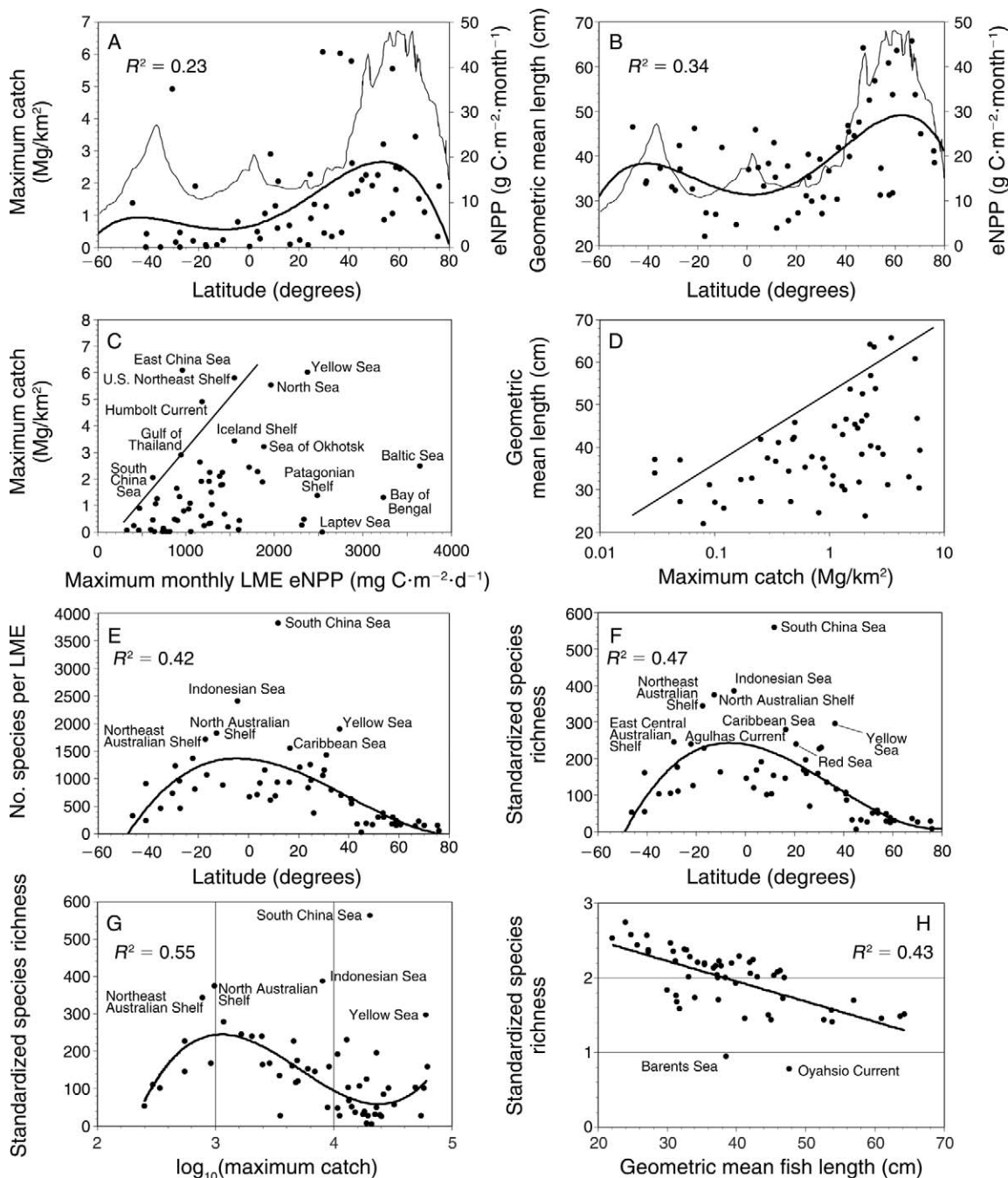


FIG. 8. Latitudinal and other patterns of data on fisheries catch, fish length, and fish species richness for 56 large marine ecosystems (LMEs). Eight Arctic and Antarctic LMEs are excluded because of insufficient catch records. The thin line in panels A and B is the global average ocean eNPP based on Behrenfeld et al. (2001: Fig. 3), as also shown in Fig. 4A. LME data are from FishBase and The Sea Around Us Project (see footnotes 4 and 5). See Fig. 9 and Supplement 3 for locations, names, and data for individual LMEs. Maximum catch is for the period 1950–2006. See discussion in *Abundance, biomass, size, and diversity in the oceans*.

Just as most of the world’s forests have been severely impacted by human activities that complicate the interpretation of global patterns of forest productivity and structure (Huston and Wolverton 2009), the long history of marine exploitation has altered the structure

of marine ecosystems. While the eNPP rule predicts that fisheries catches and fish body size (at both the intra- and interspecific levels) should be positively correlated with primary and secondary productivity, fisheries harvests can alter this relationship. It is now

well known that most fisheries rapidly eliminate the largest individuals, regardless of species, and also tend to greatly reduce the populations at the highest trophic levels, which are typically large species. This phenomenon, called “fishing down the food web” (Pauly et al. 1998, 2002) is consistent with the expected greater sensitivity of higher trophic levels to mortality because of the trophic inefficiency of energy transfer (Huston 1994: Fig. 5.13). As a consequence of these processes, the currently observed body sizes and catch levels in any region may not reflect the potential body sizes and population biomasses that could be supported by local eNPP in the absence of current or historical overfishing. This will produce more scatter and lower values in the data than would otherwise be expected.

The smaller catches in most tropical LMEs (Fig. 8A), combined with the smaller sizes (based on species' maximum lengths) in the tropical assemblages (Fig. 8B) lead to the inescapable conclusion that fish body size is positively correlated with total fish biomass and marine eNPP, consistent with the eNPP rule, but contradicting the energetic equivalence hypothesis and the MTE. The causal connection between eNPP and body size is traced in Fig. 8C and D. The pattern of maximum catch (standardized for area as Mg/km<sup>2</sup> of the variably sized LMEs) in relation to eNPP in Fig. 8C is a classical “triangular distribution” that is often observed when factors in addition to the independent variable (i.e., eNPP) affect the dependent variable (i.e., fisheries catch; Cade et al. 1999, Cade and Guo 2000, Huston 2002, Cade and Noon 2003). This suggests a strong positive and probably linear effect of eNPP on fish biomass, which is reduced below the “pure” eNPP effect (indicated by the diagonal line, which represents the upper limit, e.g., 95th quantile of the distribution) as a result of other, unquantified variables such as overfishing. A similar pattern appears in the relationship between mean catch and mean fish body length (Fig. 8D), with reduced lengths below the diagonal of the linear relationship caused, at least in part, by overfishing.

While eNPP is predicted to have direct positive effects on body size and/or population density, and total population and community biomass, as seen in both direct analyses (Fig. 8C, D) and the indirect relationships with latitude (Fig. 8A, B), eNPP is also hypothesized to have effects on species richness. The metabolic theory of ecology and the “more individuals” hypothesis, as well as most other prominent diversity hypotheses (e.g., Dobzhansky 1950, Fischer 1960, Federov 1966, Connell and Orias 1964, Pianka 1966, Palmer 1994, Moritz et al. 2000, Willig et al. 2003, Currie et al. 2004, Evans and Gaston 2005, Evans et al. 2005, Mittelbach et al. 2007) predict that diversity will be highest where productivity is highest, as a result of both ecological and evolutionary processes. In contrast, the dynamic equilibrium hypothesis (Huston 1979, 1994) predicts that diversity will be highest where productivity

is low, as a result of reduced individual and population sizes and reduced intensity of competition. In addition to these hypothesized effects of eNPP on ecological processes such as competition (Huston 1979, 1980, 1985, 1994, 1999b, Huston and DeAngelis 1994) that decrease diversity under high-productivity conditions, the “productivity regulation of gene flow” (PRGF) hypothesis predicts that reduced gene flow and increased genetic isolation will lead to the highest rates of speciation where productivity is low (Huston 1994:309–312; M. A. Huston, *unpublished manuscript*).

The pattern of marine fish species richness among the LMEs clearly shows that species richness is highest in the tropics, where eNPP, fisheries catch, and fish size are lowest (Fig. 8E, F), contradicting the metabolic theory of ecology, and most other theories of species diversity. Fig. 8E is based on species lists for the LMEs, which differ in area by more than an order of magnitude. Because sample size, or the total number of individuals, is often correlated with species richness in samples, LME species richness has been “standardized” by dividing total richness by the log<sub>10</sub> of the mass of fish harvested from each LME (as the maximum catch from 1950–2006; Fig. 8F). The patterns of both standardized and unstandardized species richness with latitude are similar, but not identical (Fig. 8E, F). Independent of latitude, there are strong negative correlations between these measures of species richness and two independent indicators of secondary productivity, maximum fisheries catch per km<sup>2</sup> (Fig. 8G) and mean fish length (Fig. 8H). Examination of the negative correlation between fish species richness and log<sub>10</sub> maximum catch demonstrates that the actual pattern is unimodal, with a rapid increase in species richness with increasing catch to a maximum at very low catch levels, followed by a linear decline with increasing catch. This is similar to the pattern observed in many plant communities, as well as theoretical models, in which there is a steep increase to maximum diversity at very low levels of productivity, or indicators of productivity such as soil nutrients (Huston 1979, 1980, Huston and DeAngelis 1994).

While there is some scatter in the data, it is clear that these negative correlations of species richness with indicators of population size and productivity contradict the predictions of “energy–diversity” hypotheses such as the metabolic theory of ecology (MTE) and the “more individuals” hypothesis, as well as virtually all other diversity hypotheses (see review in Palmer 1994), but are consistent with hypotheses that predict highest species richness at low productivity, caused by the effects of nutrient limitation and other factors on both ecological and evolutionary processes (Huston 1979, 1994; M. A. Huston, *unpublished manuscript*). The negative correlation between fish length and fish species richness is analogous to the negative correlation of bird body mass with bird species richness in the neotropics (Blackburn and Gaston 1996), as well as the negative correlation between ant body size and ant species diversity across

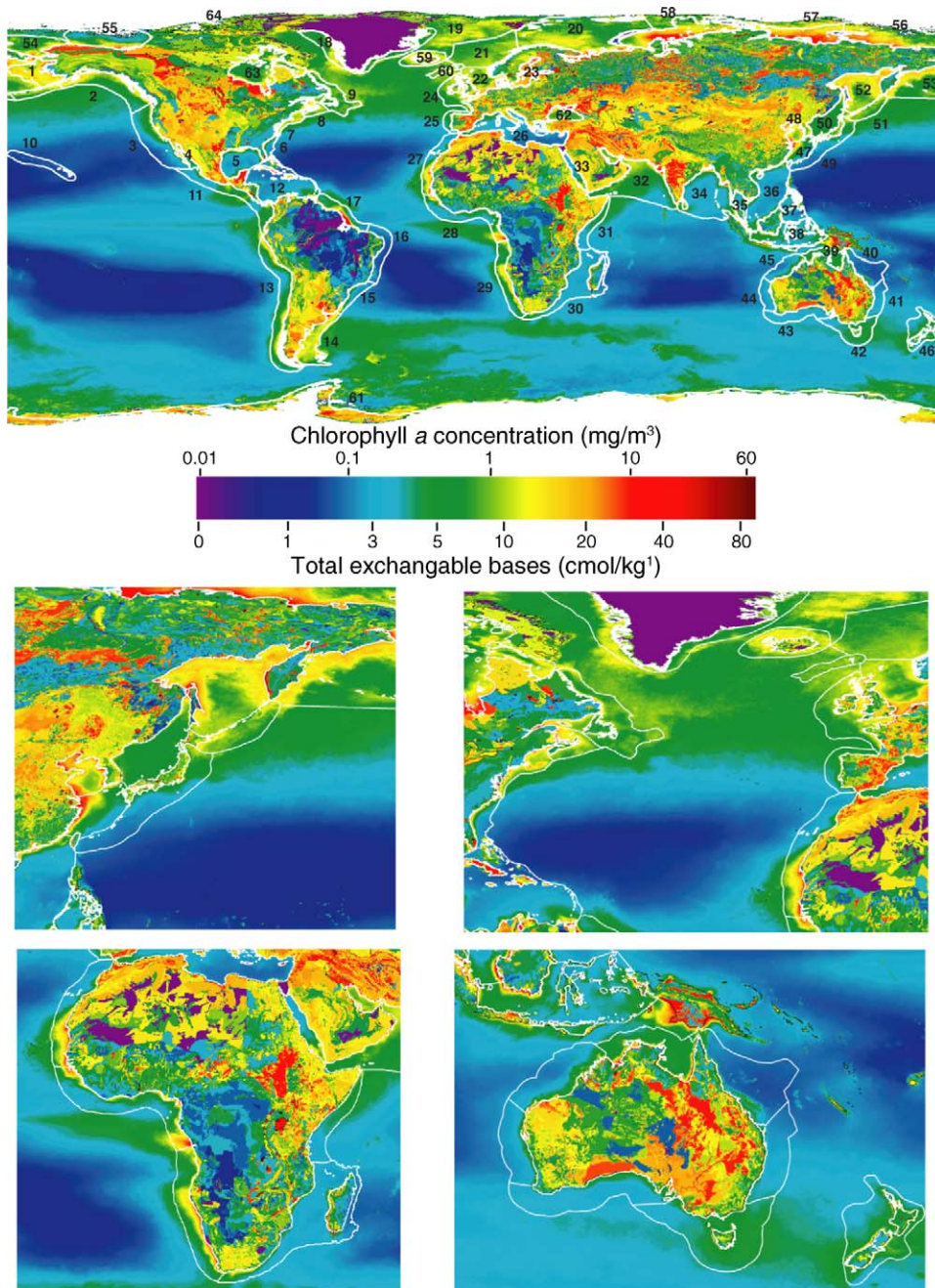


FIG. 9. Map of SeaWiFS 1997–2007 mean annual chlorophyll values for ocean waters, with FAO (2008) harmonized soil map of the world data for total exchangeable bases (TEB, meq/g) in soils, showing outlines of the 64 LMEs, which include 80–90% of the global fisheries catch and are primarily coastal (LME names and data listed in Supplement 3).

latitude in the New World (Kaspari et al. 2000, Kaspari 2005). Species diversity is highest where body sizes are small, and body sizes are small where eNPP is low.

The latitudinal asymmetry of marine eNPP, fish catch, fish length, and fish species richness (Fig. 8A, B, E, F) provides potentially useful information about the underlying causes of these patterns. There are no significant differences in sea surface temperatures

between the northern and southern hemispheres (Belkin 2009, Fisher et al. 2010: Fig. 11), so temperature cannot explain the asymmetry in eNPP, fish size, fisheries catch, and species richness. However, there is great asymmetry in the amount of land. The northern hemisphere has twice as much land area as the southern hemisphere, with land to water ratios of 0.65 and 0.24, respectively. Because most of the nutrients in the oceans are derived

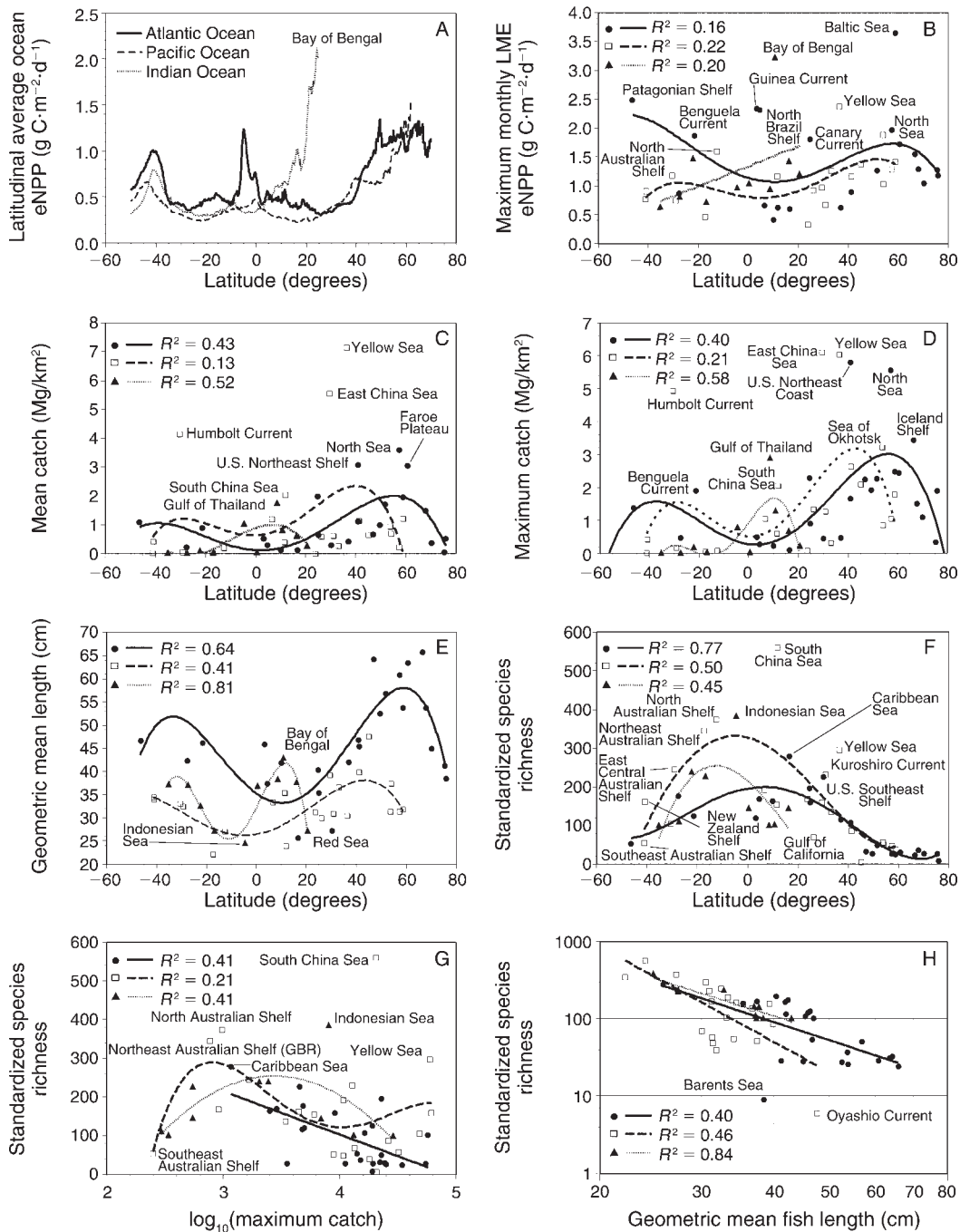


FIG. 10. Latitudinal and other patterns of marine eNPP, fisheries catch, fish length, and fish species richness for 56 LMEs separated into three groups: the Atlantic Ocean (solid circles, solid lines), Pacific Ocean (open squares, dashed lines), and the Indian Ocean (solid triangles, dotted lines). Data in panel A are latitudinally averaged eNPP based on seasonal (austral and boreal summer) three-month daily average values from eight years (July 2002–June 2010) of MODIS images converted to NPP using the VGPM algorithm, provided by the Ocean Productivity Project, Oregon State University (R. O'Malley, *personal communication*). LME data from FishBase and The Sea Around Us Project (see footnotes 4 and 5). See Fig. 9 and Supplement 3 for locations, names, and data for individual LMEs. Maximum catch is for the period 1950–2006; mean catch is for the period 2000–2004. See discussion in *Abundance, biomass, size, and diversity in the oceans*.



TABLE 6. Properties of the three major oceans related to input of nutrients from terrestrial runoff.

Ocean	Surface area (km <sup>2</sup> )	Watershed area (km <sup>2</sup> )	Percentage of global land	OA:WA	Ocean volume (km <sup>3</sup> )	Runoff volume (km <sup>3</sup> )	Percentage of global runoff	OV:RV
Atlantic	106 400 000	70 001 800	47	1.52	354 700 000	19 270	47	18 407
Pacific	155 557 000	19 362 200	13	8.03	671 077 274	5330	13	125 906
Indian	73 556 000	19 362 200	13	3.80	292 131 000	5330	13	54 809

Note: Values are based on information in Gotthold and Gotthold (1988), Gleick (2000), and Pidwirny (2006).

from sediments and dissolved solids that have been eroded from the land and transported to the ocean by rivers, this suggests that southern hemisphere oceans should have an average nutrient concentration roughly 37% that of the northern hemisphere oceans. Such a nutrient differential could be a major driver of the observed differences in ocean eNPP, fisheries catches, and fish length, as well as of fish species richness, between the northern and southern hemispheres.

In the context of the patterns of primary and secondary marine productivity discussed above, marine fish diversity in the LMEs is highest in the tropics and the southern hemisphere where productivity is lower, and declines toward higher latitudes, particularly in the northern hemisphere, where marine (as well as terrestrial) eNPP is highest (Figs. 4A, 8E, F).

Fisher et al. (2010: Fig. 3A) also noted a strong longitudinal gradient of fish length, in addition to the latitudinal pattern, and observed that there was a strong negative correlation between fish length and species richness in the northeast Atlantic, but no relationship in the northwest Pacific (Fisher et al. 2010: Fig. 7). Latitude and longitude are crude and indirect correlates of many different environmental properties, and a more detailed examination of the geographical patterns of fish biomass, size, and diversity provides further insights into the regulation of marine primary and secondary productivity, as well as of fish diversity.

Inspection of the spatial patterns of marine chlorophyll and eNPP suggests a simple, but fundamental, explanation for both the latitudinal and longitudinal variation in eNPP, fish body size, and fisheries catch, as well as fish diversity across the Earth's oceans. It is evident that the largest areas of high chlorophyll concentrations and high eNPP are found in the north Atlantic, and to a lesser extent in the south Atlantic, with smaller areas in the Pacific and Indian oceans (Figs. 9, 10A, B). Fish body sizes (interspecific mean of maximum lengths, Fig. 10E), as well as mean and maximum catch (Mg/km<sup>2</sup>) also tend to be higher in the Atlantic than in the Indian and Pacific Oceans (Fig. 10C, D). Maximum species richness is shifted toward the southern hemisphere in both the Pacific and Indian Oceans, but not the Atlantic (Fig. 10F).

One conspicuous physical difference between the Atlantic and the Indo-Pacific oceans is that the relatively young Atlantic has less than half the surface area of the Indian and Pacific Oceans combined (Table 6). More significant than the difference in surface area are the

differences in the land areas contributing runoff to these oceans. The smaller Atlantic receives runoff from 47% of the Earth's total land area, while the drainage areas for the Pacific and Indian Oceans are each only 13% of the total land area. The differences based on ocean volume in relation to runoff volume are even greater (Table 6). The average nutrient concentrations in the Atlantic Ocean, based on the ratio of runoff volume to ocean volume, are potentially 6.8 times higher than in the Pacific and 3 times higher than in the Indian Ocean.

The physical geography of the Earth's oceans, both in terms of latitudinal gradients and differences between the major oceans, apparently creates a pattern of nutrient loading that is consistent with the observed patterns of ocean eNPP (Figs. 9, 10A, B), fisheries catches (Fig. 10C, D), and average fish length (Fig. 10E). Some of the scatter in the data for ocean eNPP within the large marine ecosystems (Fig. 10B) is likely due to the fact that many of the LMEs are centered on the outflows of the Earth's largest rivers, which create local nutrient enrichment on the continental shelves near their mouths (see Fig. 9), creating variability that is independent of latitude and differs from the average eNPP across the entire ocean (Fig. 10A). Multiple major rivers empty into all three of the large oceans. The Atlantic receives the outflow of four out of the world's six largest rivers (based on flow volume), the Amazon, Congo, Orinoco, and Parana/La Plata, all of which flow into the open ocean and create small hotspots of high eNPP (Fig. 9). Of the other two rivers in the top six, the Ganges carries nutrients eroded from the Himalayas and flows into the Indian Ocean, creating extremely high eNPP in the Bay of Bengal (Fig. 10A, B), while the Yangtze drains the eastern side of the Tibetan and Yunnan Plateaus and flows into the Pacific, supporting the high eNPP and extremely high fisheries catches in the large continental shelf embayments of the East China Sea, and, supplemented by the Yellow River, the Yellow Sea (Fig. 10B, C, D). The nutrient-poor central gyres of the northern and southern Pacific are much larger than the central gyres of the Atlantic (Fig. 9).

The primary driver of ocean NPP and eNPP is the concentration of nutrients derived from terrestrial runoff. However, as on land, the temporal variation in production that defines eNPP is driven by the seasonality of solar radiation and, to a lesser degree than on land, temperature. The apparent shift of the peak of maximum marine eNPP to higher latitudes than the maximum terrestrial eNPP (Fig. 4A) may be due to the

much higher heat capacity of water, but nonetheless demonstrates the need for a major new research program on terrestrial eNPP to confirm or reject the difference between these two fundamental global patterns.

The response of productivity across multiple trophic levels, from algal eNPP to the production of the secondary, tertiary, and higher trophic levels of the fish assemblage, forms a consistent set of patterns (Fig. 10A–D) that are all related to fish body size (Fig. 10E), most strongly at the higher trophic levels reflected by fisheries catch and mean body size (compare Fig. 10C and D to Fig. 10E). These connections closely match the predictions of the eNPP rule for both body size and total biomass, and demonstrate that the gradients of primary and secondary productivity, animal body size, total animal biomass, and species richness are essentially the same in the oceans as on land. This is contrary to the widely accepted belief that the productivity gradient on land is the opposite of the marine gradient, which would imply that the effects of productivity on both body size and species diversity are completely reversed between the two major environments on Earth (see discussion in Huston and Wolverton 2009).

Nonetheless, the fact that the latitudinal pattern of productivity in the LMEs is relatively weak for eNPP (Figs. 8A and 10B) and does not match the global mean patterns of marine eNPP (Figs. 8A and 10A), while the match to the global mean eNPP is much greater for fish size and catch (compare Fig. 8A to 8B and C) raises some questions. There are many potential anomalies and technical problems in both the marine eNPP estimates and the marine catch data from the LMEs, which are affected in unquantified ways by both fisheries effort and the effects of past harvest and overharvests. Also, the values of eNPP within the LMEs may not represent the actual eNPP that influences the fish captured in the LMEs, since the LMEs cover only 25% of the total ocean area, are primarily coastal, and have higher nutrient inputs and higher eNPP than most of the ocean area. While the globally averaged latitudinal gradients of growing season marine eNPP are quite strong, particularly in the northern hemisphere (Figs. 8A, 10A; Behrenfeld et al. 2001), it seems likely that there may be other physical and biological factors in addition to NPP involved in determining the strong patterns of secondary production and fish body size.

Fish are poikilotherms, and their body temperatures closely match the temperature of the water in which they live. The MTE (Allen et al. 2002, Brown et al. 2004) predicts that higher temperatures and smaller body sizes lead to higher metabolic rates, shorter generation times, and that “the natural logarithm of mass-corrected population density should be a linear function of  $1000/T_{\text{env}}$  [where  $T_{\text{env}}$  is the temperature of the environment in degrees Kelvin]” (Allen et al. 2002:1546; Gillooly et al. 2001, Charnov and Gillooly 2004). This is consistent with the long-recognized negative relationship between

body size and metabolic rate (Hemmingsen 1960), but not necessarily with the generalization from physiological research that the enzyme systems of species acclimate to temperature, resulting in little difference in base metabolic rates between species found across a broad range of temperatures (Prosser 1973: Fig. 5-14). Consistent with the MTE, experimental results show that fish acquire food more rapidly, digest it more efficiently, and grow faster at higher temperatures than at lower temperatures (e.g., Windell et al. 1978, Brett 1979, Boehlert and Yoklavich 1983, Cuenco et al. 1985, Buckel et al. 1995).

However, the observed patterns of fish growth, size, and total biomass in the oceans are the opposite of these theories and experiments. The marine data suggest that fish size and total biomass are highest where the water is cold, but not the coldest, since fish catch (Figs. 8A and 10C, D) and fish body size (Figs. 8B and 10E) decline between 60° and 80° N, just as terrestrial eNPP (Figs. 1 and 4A) and caribou and wolf body size (Fig. 4J, H) decline above 60° N. Among the LMEs, the negative correlation of sea surface temperature with both fish length and fisheries catch is stronger than the positive correlations of length and catch with eNPP (maximum monthly NPP, Table 7). Inclusion of maximum monthly eNPP only slightly improved the  $R^2$  for regression on body size from 0.30 for SST alone to 0.34 with both variables. The explanatory power of eNPP and SST for fisheries catch was substantially lower than for body size (Table 7). The differences between the regressions for the 2000–2004 mean catch vs. the 1950–2008 maximum catch may in part be due to the effects of overfishing, which substantially reduced the catch in some LMEs toward the end of the record (Sherman et al. 2009a, b), when the 2000–2004 means were calculated.

The surprising result that fish size and biomass are highest at low rather than high temperatures (and more strongly correlated with temperature than with estimated NPP) may in part be explained by an ontogenetic shift in optimum temperature as fish increase in size. Numerous studies report a strong shift in the temperature for optimal growth as fish increase in size, with the optimal temperature declining as fish become larger (Boehlert and Yoklavich 1983, Fonds et al. 1992, Imsland et al. 1996, 2005). Most of these studies looked at fish over a relatively small size range, but if the optimal temperature continues to decrease with increasing size, this may help explain the dramatic positive latitudinal and negative temperature correlations with fish body size. Boehlert and Yoklavich (1983) observed that “Under starvation conditions, mass loss increased with increasing temperature.” This is consistent with data analysis indicating that natural fish mortality increases with temperature and decreases with increasing body size (Pauly 1980, Charnov and Gillooly 2004), and provides a potentially important explanation for why fish in unproductive tropical waters remain relatively small and fish of all sizes, particularly large fish, can

TABLE 7. Analysis of relationship of NPP and sea surface temperature (SST) to fish size in 56 large marine ecosystems (LMEs) with fish size (estimated as the mean of the recorded maximum lengths of all species harvested) and with the spatially averaged fish catch (expressed as the annual mean catch from 2000–2004 or the maximum annual catch recorded between 1950 and 2006).

Dependent and independent variables	Slope	<i>t</i> or <i>F</i> ratio†	Prob > $ t $ or <i>F</i>	Adjusted $r^2$
Mean maximum fish length (cm)				
MaxNPP per month	0.006104	9.48 (df = 1,54)	0.0033	0.134
SST 2002 (°C)	-0.653045	24.26 (df = 1,54)	<0.0001	0.297
MaxNPP + SST		14.99 (df = 2,53)	<0.0001	0.337
MaxNPP	0.003761	2.06	0.0439	
SST	-0.567436	-4.19	0.0001	
2000–2004 mean catch (Mg/km <sup>2</sup> )				
MaxNPP per month	0.0007022	6.74 (df = 1,54)	0.0121	0.095
SST 2002 (°C)	-0.03934	3.64 (df = 1,54)	0.0616	0.046
Maximum annual catch (Mg/km <sup>2</sup> )				
MaxNPP per month	0.000779	6.25 (df = 1,54)	0.0155	0.087
SST 2002 (°C)	-0.070348	9.79 (df = 1,54)	0.0028	0.138
MaxNPP + SST		6.56 (df = 2,53)	0.0028	0.168
MaxNPP	0.0005389	1.73	0.0903	
SSST	-0.058082	-2.50	0.0154	

Notes: No significant interactions were found. See Supplement 3 for data and sources.

† *F* ratios are followed by degrees of freedom values.

survive the seasonal fluctuations of NPP at high latitudes. This is analogous to the winter mass loss of cervids on low nutrient winter forage, as well as mass loss by bears and other hibernating mammals, all of which gain mass and store fat during the high eNPP of temperate, boreal, and arctic summers.

Consistent with this interpretation, Andersen and Pauly (2006) analyzed 190 sets of growth parameters for fish along the east and west coasts of Australia, and found that fish in the warmer waters north of 28° S had higher values for von Bertalanffy's *K* parameter (i.e., slower growth rates) than fish from the cooler waters to the south. They attribute this to the higher respiration rates in the warmer waters leading to increased energy expenditures for moving water across the gills to obtain oxygen, which occurs at lower concentrations in warm than cold water (Pauly 1981). Thus, higher overall fish growth rates under cold conditions than under warm conditions could potentially be caused by higher respiration rates and energetic losses under warm conditions, even with the same level of energy and resource inputs, as also suggested by Makarieva et al.'s (2005) model of poikilotherm energetics. A similar mechanism has been proposed as one of the reasons for the slower growth rate and smaller size of tropical trees as compared to temperate trees (Huston 1994: Fig. 14.23). Temperature-dependent respiration rates and oxygen concentrations provide two positive energetic mechanisms for the latitudinal increase in fish body size, secondary productivity, and population biomass, in addition to the positive effects of eNPP.

The clear latitudinal and inter-ocean patterns of marine secondary productivity (based on fisheries catch data) and fish body size, both of which have highest values at high latitudes, contrast dramatically with the pattern of fish species richness, which is highest in the tropics where productivity and body size are lowest, and

declines toward the higher latitudes where both productivity and body size are high. A predominantly negative unimodal or negative log-log correlation of fish species richness appears with the two productivity correlates, fisheries catch (Figs. 8G and 10G) and mean fish size (Figs. 8H and 10H). These results, which are consistent across the world's oceans, directly contradict the predictions of the MTE and most other ecological and evolutionary hypotheses for explaining global diversity patterns, nearly all of which explain why diversity is highest where productivity is supposedly highest (Dobzhansky 1950, Fischer 1960, Connell and Orias 1964, Federov 1966, Pianka 1966, Palmer 1994, Moritz et al. 2000, Willig et al. 2003, Currie et al. 2004, Evans and Gaston 2005, Evans et al. 2005, Mittelbach et al. 2007).

Thus, bigger primates, larger herbivores, and heavier raccoons occur on the more fertile and productive areas of Africa, the Malay Archipelago, and Missouri for the same reason that bigger fish occur in the most productive parts of the world's oceans. Globally, similar latitudinal patterns of body size and species diversity are found on land as in the oceans, in herbivores, carnivores, omnivores, and even detritivores (Fig. 4I).

#### *Fecundity, life history, health, wealth, and happiness*

The apparently ubiquitous effects of the carbon, protein, and energy provided by eNPP on the body size, abundance, and population biomass of animals throughout the Earth's terrestrial and marine ecosystems suggest that many additional individual, population, community, and ecosystem properties are likely to be affected by eNPP. We briefly review a small subset of the properties that can be affected by eNPP, with the recognition that virtually all elements of physiology, growth, and development, demography, population dynamics, life history, and ecological and evolutionary processes, including human culture and economics, are

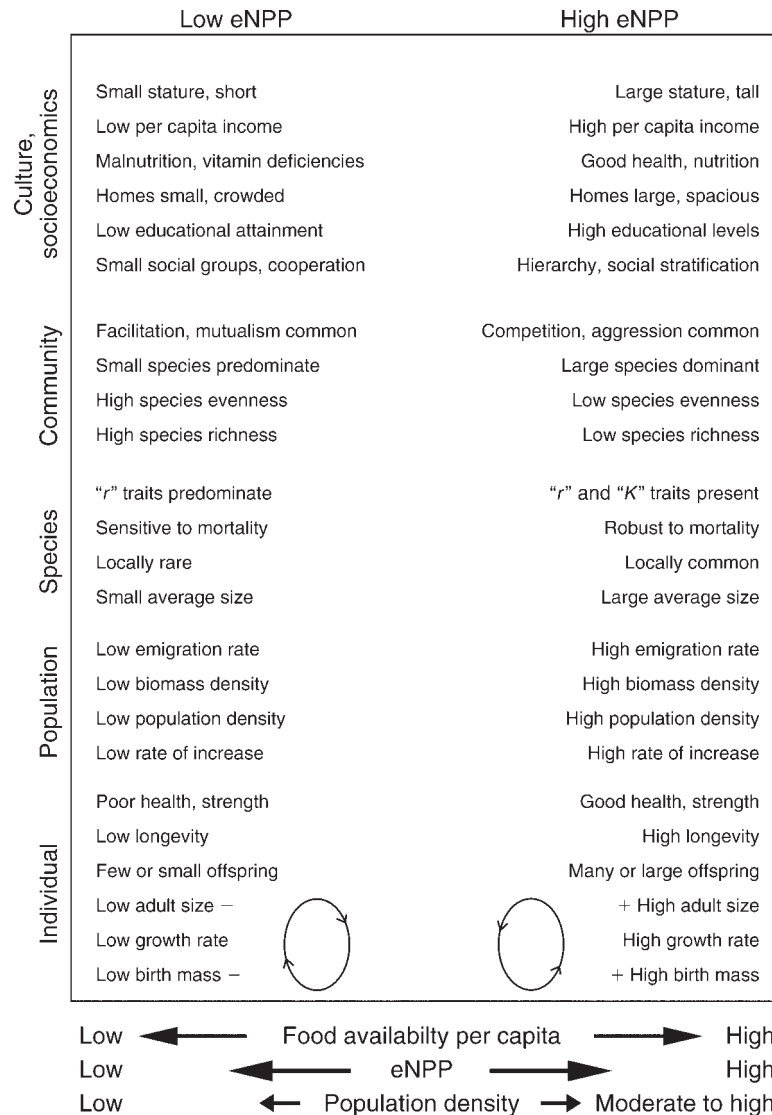


FIG. 11. Examples of predictions of the eNPP rule across a range of organizational levels in animal and human ecology. The two ovals with arrows indicate the positive feedback between female size and offspring size that can produce rapid epigenetic changes leading to body size and reproductive differences that can persist across generations. Similar predictions apply to plants, which are not addressed in this review.

influenced by the availability of energy and resources when organisms are reproducing and growing, as summarized in Fig. 11. We intentionally follow the implications of these relationships to what some might consider extreme conclusions in order to stimulate discussion about the full implications of the ideas we have proposed.

It is obvious that, in live-bearing organisms, larger females can produce either larger single offspring, or a greater number of offspring of a given size than can females that are smaller. This inevitable allometry has important implications for ecology and evolution. In most situations, larger offspring have a higher probability of surviving to reproductive size than do smaller offspring. However, in some situations with extremely

high mortality and/or extreme scarcity of suitable habitats, producing larger numbers of smaller offspring is the best strategy for assuring continuation of the species or genotype.

This simple dichotomy underlies what is perhaps the most powerful and robust generalization in ecology and evolution, the "inverse  $r$ - $K$  continuum." Named for the two fundamental parameters of the logistic growth equation, as well as the Lotka-Volterra competition equations, the inverse  $r$ - $K$  concept summarizes a wide range of unavoidable energetic and physiological constraints that limit the adaptations and performance of all organisms, plants and animals, and cause these two properties (size vs. number of offspring), among many others, to be inversely related across most

organisms. The parameter  $r$  is the per capita maximum rate of population increase (or intrinsic growth rate), which in its simplest formulation represents the sum of the maximum potential birth rates minus that component of death rates that is independent of population density, but it can be generalized to include all traits that contribute to a higher growth rate, such as high fecundity, small offspring size, rapid sexual maturation, etc. The parameter  $K$  represents the maximum number of individuals (or total biomass of individuals) that can be supported in a specific environment, but can be generalized to include all traits related to large size in individuals or populations, such as fewer, larger offspring, greater longevity, strength, and disease resistance, the ability to take up or capture resources efficiently, greater competitive ability, etc.

These constraints are summarized by the simple observation that with a given amount of tissue, a female organism can either produce a few large offspring or many smaller offspring, but it is physically impossible to produce many large offspring, which would generally be the ideal reproductive strategy. Thus, all organisms are faced by constraints that force compromises or tradeoffs over the course of evolution that limit them to developing adaptations that are well suited for a specific set of environmental conditions, but that are completely unsuited to many other sets of environmental conditions (Southwood 1977, 1988).

Instantaneous resource availability, or eNPP, interacts directly with natural selection as it operates within the constraints of the  $r$ - $K$  continuum. With higher eNPP, organisms can potentially produce larger offspring or more, smaller offspring, while with low eNPP, offspring are inevitably smaller and/or fewer. Biologists have noted the incidental adaptation that results from this situation when low productivity represents a chronic condition. If food availability is chronically low, then small individuals will have an advantage over larger individuals because they require less food, and thus are more likely to avoid starvation and survive (Blanckenhorn 1998, Bateson 2001, Bateson et al. 2004, Kuzawa 2007, Wells 2010). Over multiple generations, the effect of maternal size on offspring size produces a positive feedback cycle (e.g., DeAngelis et al. 1986) in which epigenetic mechanisms (including ontogenetic growth and female-offspring allometry) produce an adaptive change in body size in response to environmental conditions (eNPP). Over time, natural selection may reinforce these epigenetic changes and create genetic constraints on body size. Nonetheless, the effects of eNPP on body size through epigenetic effects seems to be extremely powerful and to represent one of the most important examples of adaptive morphological plasticity that operates, at least initially, outside the realm of genetics and natural selection. This effect could significantly alter our understanding of many aspects of life history theory, such as allocation of maternal effort to male vs. female offspring (Trivers and Willard 1973,

Charnov 1982). The epigenetic effects of body-size allometry may go far beyond the female “quality” argument developed by Leimar (1996).

In addition to the smaller size and potentially smaller number of offspring produced by small females and/or females under conditions of low eNPP (e.g., Williams and Caskey 1965, Jacobson et al. 1977), there are many physiological and health-related responses associated with reduced food availability and small size. These are extensively documented in the large literature on human health, as well as in experimental animal studies (e.g., Wurm 1982). Reproductive function in both males (Albrecht 1943, 1944, Cicognani et al. 2002) and females (Smith and Albrecht 1941, Cheatum and Severinghaus 1950, Albrecht 1952, Ibanez et al. 2000, 2002, 2003) is reduced in individuals that are “small for gestational age,” which may be caused by the small size of the mother or inadequate nutrition during pregnancy (Kuzawa 2007). A study of 307 223 children born to 194 835 women in 42 developing countries found a negative correlation between maternal height and child mortality (Monden and Smits 2009). In general, reproductive success in humans is correlated with body size, particularly in underdeveloped rural settings (Lasker and Thomas 1976, Mueller 1979, Kirchengast 2000, Prasad and Al-Taher 2002, Pollet and Nettle 2008).

The size of living humans, as well as the skeletons of deceased humans, have long been recognized as indicators of the health and history of an individual (Wells 1964, Tanner 1986, Frisancho 2007) and leg length seems to be the most sensitive and diagnostic element of growth response (Wadsworth et al. 2002, Bogin and Rios 2003). While small size caused by food shortage during some phase of development is often seen as a negative or detrimental response, small size may actually increase survival if the food shortage is chronic or worsens (Lasker 1969, Kuzawa 2007, Schell and Magnus 2007). However, both acute and chronic food shortage during development may have health effects beyond mortality and growth retardation. Exposure to famine during early gestation can have a number of long-term negative consequences, including glucose intolerance, obesity, and coronary heart disease (CHD; Barker 1990, Barker 1998, Godfrey and Barker 2000, Roseboom et al. 2006). Reduced height, due to various combinations of food shortage and other stresses during post-natal development, is associated with a variety of negative health consequences, particularly CHD, although there is also a suite of diseases that are more common in taller people (Batty et al. 2009).

Physiological stress, due to inadequate nutrition or other problems during childhood, reduces the deposition of enamel on teeth, producing a characteristic thinning called linear enamel hypoplasia (LEH). This dental record of severe stress reveals both temporal patterns and spatial variation in the nutrition and health of Ancestral Puebloan populations during an 800-year

TABLE 8. Relationship of soil fertility to physical properties of femur bones of 450 cottontails (*Silvilagus floridanus*) collected from 38 soil regions in Missouri (based on Crawford [1950]).

Soil fertility	Estimated body mass (kg)	Average femur mass (gm)	Average femur length (cm)	Average femur bone wall thickness (mm)	Average femur breaking strength (pounds)
High	1.13 (1.00)	4.17 (1.00)	8.03 (1.00)	0.82 (1.00)	44.50 (1.00)
Medium	1.09 (0.96)	3.84 (0.92)	7.87 (0.98)	0.74 (0.90)	36.70 (0.82)
Low	1.03 (0.91)	3.40 (0.82)	7.32 (0.91)	0.68 (0.83)	27.30 (0.61)

Notes: Values in parentheses are proportions of maximum value. One pound = 0.45 kg. Soil fertility was determined by calcium, nitrogen, phosphorus, and potassium contents and crop yields. Body mass was estimated from Crawford (1950: Table 3).

period on the Colorado Plateau (Malville 1997) and intergenerational differences in body size and LEH in current populations (Floyd 2007).

Small body size and nutrition-related health deficiencies also exhibit strong spatial patterns due to chronic low quantity and/or quality of available food, which are often related to soil fertility and eNPP (Smith and Albrecht 1941, Albrecht 1942, 1943, 1947a, b, 1955). This can be seen in the distribution of body size and bone strength of cottontail rabbits in relation to variation in soil fertility across the state of Missouri (Table 8), and perhaps also in the negative relationship between soil fertility and the percentage of draftees rejected by the Army across Missouri (Albrecht 1957; Fig. 5C). Nutrient deficiencies, and increased rates of disease and mortality are found on nutrient-poor soils in the Amazon basin (Gurven et al. 2007, Castro et al. 2009), as well as across much of New Guinea (Smith et al. 1993) and presumably other regions with nutrient deficient soils that affect eNPP and thus the quantity and quality of food (Sheets 1946, Trowell 1949, Albrecht 1957, Meggers 1971). A rapidly developing literature on the epigenetic effects of parental nutrition and health on the growth, health, and reproductive potential of children and even grandchildren (Pembrey et al. 2006, Heijmans et al. 2008, Whitelaw and Whitelaw 2008, Carone et al. 2010), emphasizes how quickly food quality and quantity, as well as other environmental conditions, can alter the body size and physiology of human populations, a mechanism that presumably operates in other animals as well.

Soil nutrients and water availability vary across a huge range of spatial scales, from a few meters or less to the entire globe. Consequently, eNPP and the food available to animals and people also varies across this range of scales, with the ability of organisms to integrate over spatial variation in eNPP depending primarily on their size, and for humans, on the availability of transportation and storage technology and the energy to use it. The global patterns of agricultural productivity and also of average per capita income ([gross domestic product, GDP]/population) have a strong positive correlation with soil nutrient content, following the general latitudinal gradient of soil fertility and eNPP increasing from lowest values in the tropics to the highest values in the north temperate and boreal regions

(Huston 1993, 1994, Huston and Wolverton 2009). This implies that the global distribution of poverty is negatively correlated with soil fertility and eNPP.

It is probably not a coincidence that per capita income remains uniformly low within the tropics (23.5° S to 23.5° N, Huston 1993, 1994), the same range over which the eNPP rule predicts no change in eNPP and body size, and over which there is little change in the body size of jaguars, pumas, and humans (Fig. 4B, C, D, F), and little change in average body size of marine fish (Figs. 4G, 8B, 10E) and marine fisheries catch (Figs. 8A, 10C, D). These strong geographical patterns of soil fertility, terrestrial and marine eNPP, and wealth are almost certainly the mechanistic explanation for the correlated patterns of body size (of humans and other animals), as well as health, longevity, educational attainment, and other physical and social attributes associated with access to food and the resources to buy food and other essentials for health. Currently, over much of the world, particularly the developed countries and large urban areas in all counties, survival depends not on direct agricultural activity, but on having sufficient money to buy food and other necessities.

Consequently, even in regions with fertile soils and productive agriculture, the ability of individuals to access the food and other resources they require is often based on their social and economic status (Anderson 2010). Innumerable studies have documented that height, mass, infant mortality, longevity, and many other aspects of health and well-being are directly correlated with socioeconomic status, with the poor and lower-class populations suffering disproportionately from all of the health and social problems associated with inadequate nutrition (Himes and Mueller 1977, Malina et al. 1983, Hamilton et al. 1984, Jones et al. 1985, Dufour et al. 1994, Gaur and Singh 1994, Steckel 1995, Cavelaars et al. 2000, Floud 2003, Khan and Ahmed 2005, Crooks et al. 2007, Moffat and Galloway 2007, Batty et al. 2009, Rao and Apte 2009). Chronic stresses associated with low socioeconomic status, only some of which may be directly related to food availability, can lead to both physical responses, such as reduced body size (Widdowson 1951) and psychological problems (Brunner 1997).

There is a long history of studies that have linked mental development and the heritability of IQ to

environmental conditions related to socioeconomic status (Wiseman 1966, Scarr-Salapatek 1971, Scarr 1981, Bronfenbrenner and Ceci 1994, Turkheimer et al. 2003, Tucker-Drob et al. 2011). While most of this research focuses on the components of the environment related to mental stimulation, it is likely that other aspects, such as nutrition and infectious diseases, also influence differences between socioeconomic levels. A key result of this work has been the demonstration of an environment  $\times$  phenotype interaction in which genetic differences in IQ are expressed strongly in favorable environments and weakly in unfavorable environments (Bronfenbrenner and Ceci 1994, Turkheimer et al. 2003). This type of interaction, assuming it applies to a broad range of genetic traits in addition to intelligence, has major implications for ecological and evolutionary processes. If phenotypic expression of certain genetic differences is weak under unfavorable conditions (e.g., stressed, nutrient deficient, etc.), then there is likely to be reduced effectiveness of genotypes with superior performance in a wide range of processes, such as competition or survival. Consequently there would be weakened selection for these genotypes under unfavorable conditions, but strong selection for them under favorable conditions. The implications of such environmental effects on the strength of natural selection and the dynamics of speciation have yet to be fully explored.

This brings us to the ill-defined emotion called happiness, which does not play a role in either ecological or evolutionary theory (although it does figure in economics, and perhaps history and culture), but is likely to be strongly related to short-term energy and resource availability as quantified by eNPP. Individuals suffering from malnutrition or chronic nutrition-related disease are probably less likely to be “happy” and more likely to be depressed, angry or irritable than healthy individuals (e.g., Subramanian et al. 2005). On a shorter term, hungry individuals are less likely to be relaxed and more likely to be aggressive than well-fed individuals. To the extent that various types of animals express these emotions and behaviors, these generalizations should apply to animals as well as people.

On the longer term, where population dynamics and ecology transition into anthropology and economics, human populations with abundant food (provided by fertile soils and high eNPP and/or high wealth) may spend less time procuring and processing food, and thus have more time available for other activities (e.g., Hyams 1952, Meggers 1971, Sebastian 1991; but see Lee 2003 for an interesting opposing argument about hunter-gatherer dietary quality and leisure time). This additional time may provide the opportunity for specialization and perhaps artistic expression, eventually leading to art that is not directly related to survival or fitness, such as music, literature, visual arts, and theater, which is a hallmark of civilization (Wenke 1980, Scarre 2009). It is not coincidental that all of the world’s early civilizations developed in areas with fertile soils and

abundant water (Hyams 1952). We do not mean to imply that “civilization” is a more advanced evolutionary adaptation, or even a more desirable human condition than horticulture, pastoralism, or hunting and gathering. However, in a global society that increasingly relies on agriculture for its food, the distribution of agricultural potential based on climate and soil fertility likely explains many aspects of the human condition, including the distribution of poverty, which is certainly not a happy condition (Anderson 2010).

Human nutrition, height, health, longevity, and fecundity are linked with a broad suite of socioeconomic properties, including food and wages, that together comprise the broad concepts “quality of life” and “standard of living” (Floud et al. 1990, Steckel 1995, Komlos 1996, Steckel and Floud 1997, Leon and Walt 2000). All of these properties can be measured in contemporary human societies, and many of them can be tracked over the past 20 000 years or more of human history through archaeology, based on skeletal size and condition, the size, number, and quality of tools such as pottery or glassware, as well as the sizes and number of rooms and stories in houses. For example, the increase in per capita resources leading up to the golden age of Greece, is reflected in an increase in the median size of houses from 51 m<sup>2</sup> in 800–700 BC to 240 m<sup>2</sup> in 400–300 BC (Morris 2005). Today, and presumably throughout human history, it is in those regions, or groups of people, where a consistent food supply, and adequate energy and resources are available (including clean water and the ability to sanitize sewage) that human health is greatest, and people consider themselves most “happy” (Subramanian et al. 2005), although happiness is certainly subjective and culturally relative (see definitions in Brown 2008).

Not all of these contrasts will appear when comparing hunter-gatherers to agriculturalists across the broad continuum of human economics (Bates 2001); however, modern societies must face the fact that the world is now “one big farm” (Anderson 2010:170). Given that agriculture, and increasingly industrial agribusiness, has become the norm in terms of human subsistence, understanding the influence of the eNPP on agricultural productivity and sustainability and its relationship to poverty, health, and human happiness is increasingly important. This will require the fusion of ecology, public health medicine, anthropology, and economics.

The extension of the eNPP rule to the fields of health, medicine, anthropology, and socioeconomics leads to the prediction that across local, regional, and global spatial scales, as well as temporal and socioeconomic scales, attributes such as fecundity, health, cultural development, educational attainment, wealth, and happiness should be positively correlated with eNPP, either directly, or indirectly through the various mechanisms and media by which eNPP is redistributed.

Our linkage of eNPP with human biology and culture might be characterized by some as environmental determinism. Even if our hypothesized mechanisms prove to be incorrect, the existence of these strong correlations between eNPP and humanity must be recognized and understood. In addition to implications for economics and human health, we believe this exercise will be philosophically valuable in the context of ecological, anthropological, and environmental ethics. Rozzi (1999) states that humans cannot hope to change environmental ethics at the global scale without more direct linkages to the environment. Regardless of how one goes about valuing the environment (Rolston 1988), the patterns we describe clearly tie human biological and social well-being to eNPP, whether or not those patterns are deterministically linked.

#### DISCUSSION

Variation in animal body size has long been a focus of anthropologists and biologists (e.g., Bergmann 1847, Newman 1953, Roberts 1953, Peters 1983, Brown et al. 1993), yet discussion of the causes of body-size variation has involved virtually no mention of spatial variation in the source of energy and matter from which animal bodies are made, the net primary production of plants (see however, Rosenzweig 1968a, Geist 1978). Likewise, although the factors that regulate plant growth have been known by both subsistence and industrial agriculturalists for a long time, variation in factors such as soil fertility have never been part of the ecological discussion about animal body size. Never, that is, except for a brief period in Missouri during the 1940s, when wildlife biologists working together with soil scientists during the first years of federally funded wildlife research (under the Pitman-Robertson Act; Sousa 1982) used patterns of soil fertility to interpret a state-wide wildlife population structure and distribution survey involving multiple wildlife species. The peer-reviewed papers from this project were apparently so far ahead of their time or so distant from the shining towers of academia that they have been almost completely ignored. *Wildlife relationships to soil types* (Denney 1944) has been cited three times in 66 years, and *Soil fertility and wildlife: cause and effect* (Albrecht 1944) has been cited four times in the same 66 years. *Some specific relationships between soils and wildlife* (Crawford 1950) has been cited eight times in 60 years. *Soil fertility and biotic geography* (Albrecht 1957) has been cited twice in 53 years. So the idea that soil fertility through plant productivity has a strong influence on animal body size, and many other aspects of plant, animal, and human ecology, may come as a surprise to many ecologists today (cf. Jacobson 1984, Strickland and Demarais 2000, Jones et al. 2008), but it was common knowledge among the biologists and soil scientists working with the Missouri Conservation Commission 70 years ago.

It seems obvious that large body size has an energetic cost, and energy is supplied by food. The effect of food

quality and quantity on animal growth, body size, and health has been verified time and again experimentally and at small spatial scales, particularly in animal husbandry (Henry 1898, Smith 1905, Woll 1915, Henry and Morrison 1923, Smith and Albrecht 1941, Albrecht 1943, May and Loosli 1962, National Research Council 1976, Ensminger and Olentine 1978). Why has this mechanism been virtually ignored as a potential cause of large-scale ecological patterns in animal body size in spite of the fact that food is well known to affect ontogenetic growth rates in mammals as demonstrated both in feeding studies and at small spatial scales under natural and experimental conditions? There are probably several reasons for this omission. First, the distribution of body size in animals across geographic space is usually discussed specifically in relation to Bergmann's rule (e.g., Peters 1983). Wherever Bergmann's rule holds, there has been little incentive to suggest that any other mechanism, such as the geographic distribution of food, affects body size, particularly given the traditional belief that terrestrial net primary production is highest in the tropics, where body sizes are small.

Second, studies of Bergmann's rule have encompassed a broad range of taxonomic scales from intraspecific to higher taxonomic levels and multi-taxon community aggregates. There has been little or no consideration of what taxonomic or geographical scales are most appropriate for examining the effects of specific *mechanisms* to explain variations in body size (sensu McNab 2010), such as those often found in wildlife biology studies (Kie et al. 1983, Reimers et al. 1983, Toigo et al. 2006, Simard et al. 2008). We believe that the effect of the spatial distribution of food on the geographic distribution of body size has been ignored precisely because, under the conventional interpretation of the latitudinal pattern of NPP, food appears to have nothing to do with any latitudinal patterns of body size.

Third, arguments tend to focus on whether or not Bergmann's rule applies to a species or a group of species, and cause is inferred post hoc as an empirical generalization (Meiri 2011). That is, there have been fewer attempts to develop ecological theory that independently explains the geographic distribution of body size than there have been attempts to evaluate whether Bergmann's rule applies in a specific situation by analyzing the correlations among variables related to body size and variables related to latitude (see summary by McNab 2010).

Fourth, the idea that variability in body size can result from phenotypic plasticity within a species has received much less attention than the evolution of genotypic differences in body size (Wright and Lundelius 1963, Brown et al. 1993, Cavallini 1995, see Bossdorf et al. 2008, Cooper and Purvis 2010). The possibility that variability in body size within a species and/or between related species may be due to epigenomic causes is only



beginning to receive attention in ecological and evolutionary studies of animal body size (but see Geist 1978).

For example, Cooper and Purvis (2010) used a global database of mammal body size in conjunction with a recent “supertree” for mammalian phylogeny to evaluate both body size and the rate of body-size evolution in mammals in relation to environmental and ecological variables across global ecoregions. Their ecoregion-scale assessment of median body size reveals clear geographical patterns, including strong latitudinal gradients in the New World, and clear longitudinal gradients in Australia (Cooper and Purvis 2010: Fig. 2B), both of which match the predictions of the eNPP rule. Their estimates of the “relative rate of evolution” show latitudinal patterns and eNPP-related patterns, particularly in the New World (Cooper and Purvis 2010: Fig. 2A), and have their strongest correlations (negative) with factors that are negatively correlated with latitude (temperature and number of species), thus following the general predictions of both Bergmann’s rule and the eNPP rule.

However, their conclusions about the evolution of body size in primates (discussed previously) illustrate the potential pitfalls of ignoring the role of eNPP in such studies. Cooper and Purvis’s analysis suggests “that relatively early in their evolution the clades split into significantly differently sized lineages (i.e., the large Old World monkeys, the small New World species, and the even smaller strepsirrhines, e.g., lemurs and galagos), but that body size was conserved in these lineages” (Cooper and Purvis 2010:735). A purely phylogenetic interpretation of these continental-scale differences in the size of primates is challenged by the fact that soil fertility, and consequently eNPP, is much lower within the range of New World monkeys than in the ranges of the much larger Old World monkeys and apes in Africa and the Malay Archipelago, large parts of which have active volcanoes and/or soils that are periodically replenished by volcanic ash (e.g., Wallace 1869). Geographical variation in eNPP potentially explains a significant proportion of body-size variation in numerous clades that has been previously attributed solely to phylogenetic history.

An understanding of the global distribution of eNPP helps explain the selective forces underlying two of the most remarkable adaptations in animal behavior, long-distance migration and hibernation. Both of these behaviors can be seen as adaptations for maximizing growth and reproduction by selecting regions with the highest food availability during the period of reproduction and growth (i.e., eNPP), while avoiding the negative consequences of the fact that most regions with very high eNPP have a long period of the year in which short-term NPP is very low or zero. The longest-distance migrants are the seabirds and cetaceans that move between the high eNPP of the north temperate summer and the high eNPP of the south temperate summer, avoiding the low productivity of both winters and tropical waters.

There are clearly cost–benefit issues for both migration and hibernation. The costs in energy loss and potential mortality during either long-distance migration or hibernation must be less than the benefit gained by utilizing the highest eNPP available during the growing season. Clearly, the benefits must be very high to outweigh the great distances that many birds migrate, or the long period of hibernation of some mammals. For tropical-temperate migrants, the benefits of reproducing in the temperate or boreal zone must substantially outweigh the sum of the cost of migration plus the benefit of reproducing in the tropics. While it is difficult to attribute body size in migratory animals to a specific environment, small body size in many tropical-temperate migrants may actually be an adaptation for surviving low eNPP on their winter range in the rainforest.

Based on our evaluation of global patterns of soil fertility and forest productivity, the greatest productivity contrast for long-distance migrants is that between the neotropics and temperate North America, the contrast between the African tropics and temperate Europe are less, and the productivity contrast between the SE Asian tropics and eastern Asia is the smallest of all. This would lead to the prediction that fewer species would gain significant benefit from tropical-temperate migration in southeast Asia than in the New World, while Africa would be intermediate. These predictions should be easy to test.

#### IMPLICATIONS FOR FUTURE RESEARCH

The strong effect of mineral nutrients and eNPP on the spatial and temporal variability in a wide range of individual and population-level processes and properties, community and ecosystem dynamics, as well as on the higher level phenomena of human culture and socioeconomics, suggests that a new paradigm (sensu Kuhn 1962), or “templet” (sensu Southwood 1977, 1988) is needed for virtually all of ecological and evolutionary research and theory, extending into the fields of economics, environmental justice, and anthropology. This framework should be based on the resources and processes that provide the energy and nutrients upon which all life depends. Such a framework could potentially form the underpinnings for much of ecological and evolutionary theory, if it is able to summarize the physical template over which all life, both terrestrial and marine, is distributed, and thus where all theory must be testable and tested.

This framework might also help reduce the over-emphasis on equilibrium explanations for ecological and evolutionary phenomena, as well as the over-emphasis on phylogenetic history as the primary explanation for all variation in organismal traits and adaptations (e.g., Gould and Lewontin 1979). Ecological and evolutionary processes operate in a world with high temporal and spatial variability. In general, we would expect temporal variability to increase variance in the highly deterministic and often convergent adaptations of organisms to

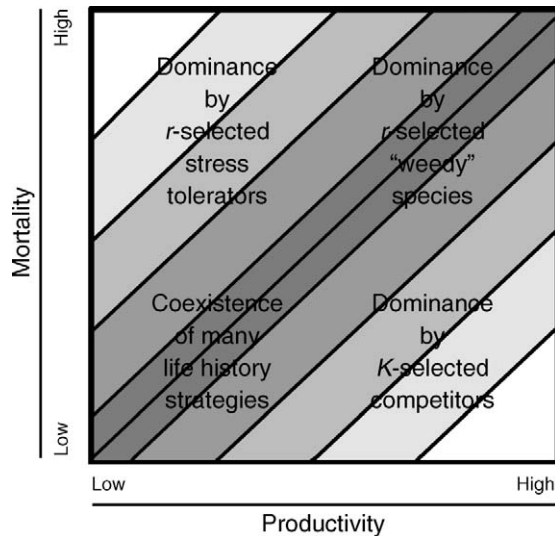


FIG. 12. Predicted distribution of life history strategies in productivity–mortality space, where productivity refers to the maximum potential population growth rates supported by local levels of eNPP, and mortality refers to the frequency and or intensity of mortality-causing events such as natural disturbance, harvest, herbivory, or predation. Shading indicates predicted levels of species diversity produced by nonequilibrium competitive dynamics under various combinations of productivity and mortality (based on Huston 1994: Fig. 5.11). Reprinted with the permission of Cambridge University Press.

their environments. In particular, our understanding of the evolution of life history strategies, as well as all types of adaptations, must reflect the strong effect of environmental conditions, particularly the nutrients and energy provided by eNPP, on all biological processes at the individual, population, community, ecosystem, and landscape levels (e.g., Fig. 11).

A simple conceptual framework would include productivity as one axis. The other axis should also be a major driver of ecological processes and life history strategies, for which mortality, specifically the frequency and intensity of mortality, is a strong candidate. Such a framework, expressed as productivity–mortality space, has proven useful for understanding the complex patterns and dynamics of species diversity, succession, and spatial patterns (Huston 1979, 1985, 1994, 1999a, b, 2004, Smith and Huston 1989, Huston et al. 1999) as well as the spatial distribution of different life history strategies (Fig. 12; Huston 1994). This framework helps clarify the role of epigenetic effects, such as variation in ontogenetic growth rates and the positive feedback cycles that can occur with maternal and offspring size, on spatial and temporal variation in organismal and ecological properties, as well as on the context in which natural selection operates (Fig. 11).

Of course, before new paradigms can be developed and accepted, the old paradigms must be convincingly rejected. Specifically, there is no need for a new framework or paradigm *if* the traditional belief that

terrestrial productivity is highest in the tropics and declines toward the poles is found to be true. In this case, most of our conclusions about the explanations of latitudinal patterns discussed in this paper must be wrong. Thus, it is essential to test our hypothesis (Huston and Wolverton 2009) that the latitudinal patterns of eNPP are the same in both the oceans and on land, with low eNPP near the equator and eNPP increasing with latitude to a maximum somewhere around 50–60°. However, it is necessary to recognize that latitude per se has little to do with any of these patterns, and that it is spatial variation in resources, specifically soil nutrients and water, plus temperature, that regulate eNPP and create the complex spatial (and temporal) patterns in body size, abundance, biomass, diversity, and all the other ecological, evolutionary, and socioeconomic properties we have discussed.

If our analysis of the global patterns of NPP and eNPP (Huston and Wolverton 2009) is proven to be incorrect, we are left with an expanded set of paradoxes similar to those we addressed in our 2009 paper. If the traditional belief that terrestrial NPP is highest in the tropics and declines monotonically toward the poles is upheld, we are faced with the paradox that the regulation of species diversity differs fundamentally between terrestrial and marine environments, because the diversity of both systems is highest in the tropics. Specifically, marine diversity is highest in tropical seas, where marine NPP is known to be very low, while terrestrial diversity is highest in tropical rainforests, where NPP has been assumed to be very high. Likewise, the observed latitudinal and other spatial patterns of animal body size, population biomass, health, and so on, which we hypothesize are very simply explained by the spatial distribution of eNPP, present a similar set of paradoxes. Fish body size and community biomass (based on catch records) are highest at high latitudes, where marine chlorophyll and eNPP are known to be high, while the body sizes and population biomass of most terrestrial animals (particularly at the intraspecific level) are also highest at high latitudes, where NPP has been assumed to be very low. This seems to be an irresolvable paradox, unless we are willing to make the perverse assumption that the physiology and energetics of animal growth differ sufficiently between terrestrial and marine environments that low productivity produces large size in terrestrial vertebrates, while high productivity produces large size in marine vertebrates (as well as invertebrates). Our solution is much simpler.

In the face of modern global environmental crises, it is critical that ecologists and anthropologists, as well as economists, be able to provide valid recommendations for maintaining productivity, conserving biodiversity, encouraging sustainability, and promoting human health and welfare. Many of the conservation and development recommendations that are made in the context of the current assumptions about patterns of global NPP and the relationship between productivity



PLATE 1. American Bison (*Bison bison*) in forb-rich prairie at the Nature Conservancy's Tallgrass Prairie Preserve in northern Oklahoma, USA. Bison, which declined in size over the course of the Quaternary (Lyman 2004a), are a good example of a formerly abundant, large mammal living in a highly productive environment, most of which has now been converted to agriculture. Photo credit: M. A. Huston.

and species diversity are the opposite of those that would be made on the basis of our analysis of NPP and its ramifications for all animal life. Many issues related to environmental justice cannot be addressed effectively without a correct understanding of the distribution of the most critical resource provided by the environment, namely food, as well as the wealth that depends on food. We assert that it is most parsimonious to conclude that soil fertility, through its effect on the distribution of eNPP, is an important contributor to the global distribution of poverty (e.g., Huston 1993, 1994), particularly in a world that has now (nearly universally) undergone the demographic transition from hunting and gathering to agriculture (Anderson 2010).

Philosophical arguments that call for changes in environmental ethics emphasize the need for change in the ways that modern humans relate to their environment (Rolston 1988, Callicott 1989, Rozzi 1999, Frode-man 2000, Anderson 2010). However, the called-for ethical changes will be ineffective if they are not based on an accurate model of the environmental potential for agricultural change and sustainable development. Rational change in environmental ethics and policy cannot take place without a clear understanding of the environment.

Little progress can be made on any of these scientific, social, economic, and political issues without a much more accurate and spatially complete understanding of the distribution of eNPP over the Earth's surface,

particularly on land, where the sampling is grossly inadequate in comparison to the marine data. Measuring terrestrial NPP is not a simple or easy task, and precise measurement of every component of NPP may be impossible (Clark et al. 2001a, b). However, virtually all of the remote-sensing methods and computer models that have been used to estimate terrestrial NPP have failed, and show a pattern that is essentially the opposite of the pattern shown by field measurements (Huston and Wolverton 2009). An interpretation of global patterns of terrestrial NPP based on actual measurements, and expressed as eNPP, eliminates the need for the complex and contorted explanations that have been developed to explain why ecological patterns that should logically be related to productivity are not related to productivity, or at least not related to the patterns of productivity that were assumed to exist in accordance with traditional beliefs and conventional models.

For example, Rosenzweig (1968a) reasonably hypothesized that wolf body size should be positively correlated with NPP, but found instead a unimodal relationship, with wolf size declining above intermediate levels of NPP, which he estimated on the basis of AET (actual evapotranspiration) using a regression model he had just published (Rosenzweig 1968b). What Rosenzweig did not realize, and what is not realized today by most of the scientists still using AET as an estimator of NPP, is that AET is strongly correlated with precipitation, and that high levels of precipitation (specifically, levels of

precipitation that exceed the rate of potential evapotranspiration [Albrecht 1957]), lead to loss of soil nutrients due to accelerated weathering and leaching (see also Huston 1980, 1994, Uehara and Gillman 1981). Thus, Rosenzweig's complex explanation of why wolf body size declined at high levels of productivity was unnecessary because wolf body size actually does increase with productivity (Fig. 6H) when it is measured appropriately. Similarly tortuous arguments would be necessary to explain why the humans who live in tropical rain forests, supposedly the most productive terrestrial environments on the planet, are among the smallest people on Earth, regardless of which continent they occupy. Likewise, complex arguments involving finely tuned mortality rates have been developed to explain why bird clutch sizes decrease from high latitudes to lowest numbers in the tropical rain forests, which have been assumed to be much more productive than high-latitude forests (Ricklefs 1970). Such arguments are probably unnecessary, since bird clutch size is positively correlated with eNPP. This is a perfect opportunity to reformulate our ideas about the evolution of body size, reproductive characteristics, and life histories (e.g., Case 1978).

The geographic distribution of animal growth rates, body size, and other components of secondary productivity—at all scales and based on previously collected or new data—should receive as much attention and support from funding agencies as do studies of primary productivity. Geographic studies of animal biomass should not take a back seat to studies of the global distribution of NPP for several reasons. First, animal body size and population densities are relatively simple to measure, and secondary productivity and animal biomass directly reflect primary productivity, which is more complex and difficult to measure over large spatial scales. The implications of such research extend from animal biology and wildlife management to human health, social justice, and economic development (Steckel 1983, 2000, Huston 1993, 1994, 2005, Leon and Walt 2000).

Too little research on the mechanisms underlying body-size variability and Bergmann's rule has been published in the ecological literature, where the focus has tended to be on macrogeographic studies of correlates to body size (see however, Geist 1987a, b, Simard et al. 2008). One must turn to the wildlife management literature to encounter mechanistic studies of mammal body size (e.g., Kie et al. 1983, Strickland and Demarais 2006) and to the experimental nutrition literature across the full range of taxa (Smith 1905, Church 1991, Widdowson and Mathers 1992, Pond et al. 1995). There is a need for ecological studies of body size at multiple spatial scales, in fact, at any spatial scale over which food availability varies (*sensu* Meiri et al. 2007). The null hypothesis in studies that focus on the mechanisms underlying variability in animal body size should be that availability of food per individual is the

primary cause of differences in individual and population growth rates, adult body size, and animal biomass *because that hypothesis is parsimonious*. It will obviously be found that other mechanisms influence growth rates and size distributions, such as character displacement and release, behavioral ecology, evolutionary biology, and so on. However, these should be accepted as alternative hypotheses only if their effect remains after the response due to variation in food availability has been statistically removed.

Our eNPP rule should be treated as an ecological hypothesis, with innumerable opportunities for independent tests. Detailed harvest records exist for numerous game species at a variety of spatial scales that can be used to test the eNPP rule (some of which we discussed earlier in this paper, e.g., Crawford 1950, Gill 1956, Strickland and Demarais 2000, Jones et al. 2008). In order to use such records, however, ecologists and wildlife biologists must overcome the biased notion that many such data sets are hopelessly flawed because animals have passed through the selective filter of managed (or unmanaged) sport harvest. There are no perfect data sets (Hutchins 1995:1326), and harvest data sets can be used selectively. For example, the 1.5-year-old buck age-sex cohort is often the most common cohort in white-tailed deer harvest data. Using this categorization removes age and sex hunting biases from assessment of variability in size across space. Upon considering white-tailed deer age, one immediately confronts the criticism that age determination on the basis of tooth wear is flawed (Ryel et al. 1961, Van Deelan 2000, Gee et al. 2002), particularly for older animals. However this can be overcome by assessing younger age cohorts (Gee et al. 2002), the aging of which relies on tooth eruption and wear (or lack thereof). Hunters certainly select bucks to harvest based on size, but we doubt that hunters are able to age deer through the rifle scope. Considering the cost of replacing harvest data with new data collected in a more controlled manner; there is no excuse for "paralysis of analysis" unless researchers are willing to call for cessation of tax-funded harvest data collection across the board. For the most part these massive data sets remain unused; it is time to dust them off (e.g., Crawford 1950), and the study of the spatial distribution of animal body size and biomass is a perfect motivation to do so.

While more work needs to be done to test the eNPP rule, it is important to recognize that, if validated, it potentially provides a new approach to estimating relative variation in eNPP (and thus annual NPP), which could potentially be calibrated to absolute values. Plant biologists have long recognized the value of using plants as indicators of environmental conditions that affect plant growth, a concept known as the "phytometer," or among foresters as the "site index." Chemical extraction and measurement of soil nutrients is an attempt to approximate the amounts of nutrients available to plants, but the growth of actual plants is

the ultimate indicator of soil nutrient availability. Genetically identical plants can be used as phytometers to evaluate the capability of different soil types to support the growth of particular species. Likewise, plants of potentially different genotypes can be planted together in “common gardens” in different environments to separate genetic and environmental effects on plant growth, as well as gene–environment interactions.

Just as soil chemical analysis provides an approximate, but imperfect, indicator of the nutrients available to support plant growth, physical measurements of NPP provide a spatially and temporally limited estimate of actual NPP that is often difficult to extrapolate to the spatial and temporal scales relevant to many ecological, evolutionary, and ecosystem processes. Measurement of nutrition-based animal properties, including intraspecific body-size variation, population density, and population biomass, can allow animals to be used as “zoometers” to estimate spatial and temporal variation in eNPP, which is the ultimate source of animal nutrition. If animal properties and eNPP are as strongly correlated as the eNPP rule proposes, we may be able to use measurements of animal properties and of eNPP in a complementary manner to greatly improve our understanding of the spatial and temporal variation in both.

#### CONCLUSION

We believe that the mechanism of heat conservation proposed by Bergmann has little or nothing to do with observed latitudinal variation in body size. We expect that intraspecific body-size variation (as well as intraspecific differences in total biomass) of most species will conform to the eNPP rule, and any consistency with the predictions of Bergmann’s rule is coincidental. Over latitudinal ranges that extend from the edge of the tropics through the temperate zone, the eNPP rule predicts an increase in body size that coincidentally matches the prediction of Bergmann’s rule. However, for species that inhabit either low or high latitudes without geographic range extension into the temperate latitudes, we expect conformation to the eNPP rule that will either be the opposite of the Bergmann predictions (60°–90° latitude) or show no apparent pattern (23.5° N–23.5° S latitude).

We have proposed a very simple explanation for spatial and temporal variation in animal body size and a wide range of related phenomena in ecology, evolutionary biology, human health, and socioeconomics that should apply across all environmental gradients where eNPP varies significantly, whether they are related to latitude or not (Fig. 11). Our hypothesis is based on fundamental principles of ecological energetics and nutrition, which affect a wide range of ecological processes from the individual to the ecosystem level, as well as evolutionary processes (Huston 1994:309–312; M. A. Huston, *unpublished manuscript*). Our focus here has been primarily at the individual and population levels, but the same variation in eNPP across any

environmental scales or dimensions is expected to have a strong influence on community-level properties such as species diversity (Huston 1979, 1994), as well as ecosystem dynamics (Huston and Smith 1987, Huston et al. 1988, Garten et al. 1994, Huston 1994). Better measurements of spatial variation in animal body size, in conjunction with better measurement of NPP and eNPP, animal biomass, and secondary production (eNSP) in the areas where body-size data are collected, are required to provide a definitive test of the eNPP rule and related hypotheses.

The eNPP rule opens a new universe of opportunities for theoretical, experimental, and observational advances in our understanding of the energetic and structural patterns of life on our planet. We are optimistic that a relatively small number of ecological and evolutionary processes, combined with a new understanding of the spatial distribution of fundamental resources related to net primary productivity, will provide a simple, cohesive explanation for the major patterns of life on Earth. Assuming that we are correct about the global distribution of NPP and eNPP, there is still much to be learned about ecological, evolutionary, social, and economic phenomena ranging from mechanisms driving animal biomass to global planning for the alleviation of poverty and disease.

#### ACKNOWLEDGMENTS

We thank three anonymous reviewers and Ian Abbott for their helpful comments and questions that allowed us to substantially clarify our presentation. We also thank Bill Crawford and Valerius Geist for their pioneering work and insights into animal body size, and for their encouragement and support of our efforts. We are especially grateful to the researchers at Oregon State’s Ocean Productivity Project for their support of our use of ocean NPP data. Mike Behrenfeld generously allowed us to use data from his 2001 paper, and Robert O’Malley provided support well beyond the call of duty in creating and summarizing latitudinally averaged seasonal NPP values for the world’s three major oceans. M. A. Huston was supported by NSF OPUS Grant 0918927 and a Developmental Leave Grant from Texas State University.

#### LITERATURE CITED

- Ajtay, G. L., P. Ketner, and P. Duvingneaud. 1979. Terrestrial primary productivity and phytomass. Pages 129–182 in B. Bolin, E. T. Deggen, S. Kempe, and P. Ketner, editors. The global carbon cycle, SCOPE 13. John Wiley and Sons, New York, New York, USA.
- Albrecht, W. A. 1941. Biological assays of soil fertility. *Proceedings of the Soil Science Society of America* 6:252–258.
- Albrecht, W. A. 1942. Sound horses are bred on fertile soils. *Percheron News* July 1942:15–22.
- Albrecht, W. A. 1943. Soil and livestock. *Land* 2:298–305.
- Albrecht, W. A. 1944. Soil fertility and wildlife: cause and effect. *Transactions of the North American Wildlife Conference* 9:19–28.
- Albrecht, W. A. 1947a. Climate, soil, and health. II. Managing health via the soil. *Oral Surgery, Oral Medicine, and Oral Pathology* 1:206–214.
- Albrecht, W. A. 1947b. Our teeth and our soils. *Annals of Dentistry* 6:316–323.
- Albrecht, W. A. 1952. The cow ahead of the plow. *Guernsey Breeders’ Journal* 84:1173–1177.

- Albrecht, W. A. 1955. Why your cattle break through the fence. *Western Livestock Journal* 33:35–38.
- Albrecht, W. A. 1957. Soil fertility and biotic geography. *Geographical Review* 47:86–105.
- Allen, A. P., J. H. Brown, and J. F. Gillooly. 2002. Global biodiversity, biochemical kinetics, and the energetic-equivalence rule. *Science* 297:1545–1548.
- Andersen, C., and D. Pauly. 2006. A comparison of growth parameters of Australian marine fishes north and south of 28° South. Pages 65–68 in M. L. D. Palomares, K. I. Stergiou, and D. Pauly, editors. *Fishes in databases and ecosystems*. Fisheries Centre Research Reports 14(4). Fisheries Centre, University of British Columbia, Vancouver, British Columbia, Canada.
- Anderson, E. N. 2010. The pursuit of ecotopia: lessons from indigenous and traditional Societies for the human ecology of our modern world. Praeger, Santa Barbara, California, USA.
- Ashton, K. G. 2002. Patterns of within-species body size variation of birds: strong evidence for Bergmann's rule. *Global Ecology and Biogeography* 11:505–523.
- Ashton, K. G., and C. R. Feldman. 2003. Bergmann's rule in nonavian reptiles: turtles follow it, lizards and snakes reverse it. *Evolution* 57:1151–1163.
- Ashton, K. G., M. C. Tracy, and A. de Queiroz. 2000. Is Bergmann's rule valid for mammals? *American Naturalist* 156:390–415.
- Atkinson, D. 1994. Temperature and organism size: a biological law for ectotherms? *Advances in Ecological Research* 25:1–58.
- Barker, D. J. P. 1990. The fetal and infant origins of adult disease: the womb may be more important than the home. *British Medical Journal* 301:1111.
- Barker, D. J. P. 1998. *Mothers, babies and health in later life*. Harcourt Brace and Company, Edinburgh, Scotland, UK.
- Barlow, A. C. D. 2009. *Sundarbans tigers: adaptation, population status and conflict management*. Dissertation. University of Minnesota, Minneapolis, Minnesota, USA.
- Bates, D. G. 2001. *Human adaptive strategies: ecology, culture, and politics*. Second Edition. Allyn and Bacon, Boston, Massachusetts, USA.
- Bateson, P. 2001. Fetal experience and good adult design. *International Journal of Epidemiology* 30:928–934.
- Bateson, P., et al. 2004. Developmental plasticity and human health. *Nature* 430:419–421.
- Batty, G. D., M. J. Shipoley, D. Gunnell, R. Huxley, M. Kivimaki, M. Woodward, C. M. Ying Lee, and G. D. Smith. 2009. Height, wealth, and health: an overview with new data from three longitudinal studies. *Economics and Human Biology* 7:137–152.
- Bayliss, P. R., and J. Laybourn-Parry. 1995. Seasonal abundance and size variation in Antarctic populations of the cladoceran *Daphniopsis studeri*. *Antarctic Science* 7:393–394.
- Beckmann, J. P., and J. Berger. 2003. Rapid ecological and behavioral changes in carnivores: the responses of black bears (*Ursus americanus*) to altered food. *Journal of Zoology* 261:207–212.
- Behrenfeld, M. J., E. Boss, D. A. Siegel, and D. M. Shea. 2005. Carbon-based ocean productivity and phytoplankton physiology from space. *Global Biogeochemical Cycles* 19:GB1006.
- Behrenfeld, M. J., and P. G. Falkowski. 1997. Photosynthetic rates derived from satellite-based chlorophyll concentration. *Limnology and Oceanography* 42:1–20.
- Behrenfeld, M. J., J. T. Randerson, C. R. McClain, G. C. Feldman, S. O. Los, C. J. Tucker, P. G. Falkowski, C. B. Field, R. Frouin, W. E. Esaias, D. D. Kobler, and N. H. Pollack. 2001. Biospheric primary production during an ENSO transition. *Science* 291:2594–2597.
- Behrenfeld, M. J., K. Worthington, R. M. Sherrell, F. P. Chavez, P. Strutton, M. McPhaden, and D. M. Shea. 2006. Controls on tropical Pacific Ocean productivity revealed through nutrient stress diagnostics. *Nature* 442:1025–1028.
- Belkin, I. M. 2009. Rapid warming of large marine ecosystems. *Progress in Oceanography* 81:207–213.
- Benedict, F. G. 1938. *Vital energetics*. Carnegie Institute of Washington Publication 503:1–215.
- Berg, K. 1936. Reproduction and depression in the Cladocera, illustrated by the weight of the animals. *Archiv für Hydrobiologie* 30:438–462.
- Bergerud, A. T. 2000. Caribou. Pages 658–693 in S. Demarais, and P. R. Krausman, editors. *Ecology and management of large mammals in North America*. Prentice Hall, Upper Saddle River, New Jersey, USA.
- Bergmann, C. 1847. Über die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse. *Göttinger Studien* 3:595–708.
- Bindon, J. R., and P. T. Baker. 1997. Bergmann's rule and the thrifty genotype. *American Journal of Physical Anthropology* 104:201–210.
- Birdsell, J. B. 1993. *Microevolutionary patterns in aboriginal Australia*. Oxford University Press, Oxford, UK.
- Blackburn, T. M., and K. J. Gaston. 1994. The distribution of body sizes of the world's bird species. *Oikos* 70:127–130.
- Blackburn, T. M., and K. J. Gaston. 1996. Spatial patterns in the body sizes of bird species in the New World. *Oikos* 77:436–446.
- Blackburn, T. M., and K. J. Gaston. 1998. Some methodological issues in macroecology. *American Naturalist* 151:68–83.
- Blackburn, T. M., K. J. Gaston, and N. Loder. 1999. Geographic gradients in body size: a clarification of Bergmann's rule. *Diversity and Distributions* 5:165–174.
- Blackburn, T. M., and B. A. Hawkins. 2004. Bergmann's rule and the mammal fauna of northern North America. *Ecography* 27:715–724.
- Blakey, R., and W. Ranney. 2009. *Ancient landscapes of the Colorado Plateau*. Grand Canyon Association, Grand Canyon, Arizona, USA.
- Blanckenhorn, W. U. 1998. Adaptive phenotypic plasticity in growth, development, and body size in the yellow dung fly. *Evolution* 52:1394–1407.
- Blanckenhorn, W. U., and M. Demont. 2004. Bergmann and converse Bergmann latitudinal clines in arthropods: two ends of a continuum? *Integrative and Comparative Biology* 44:413–424.
- Boehlert, G. W., and M. M. Yoklavich. 1983. Effects of temperature, ration, and fish size on growth of juvenile black rockfish, *Sebastes melanops*. *Environmental Biology of Fishes* 8:17–28.
- Bogin, B., and L. Rios. 2003. Rapid morphological change in living humans: implications for modern human origins. *Comparative Biochemistry and Physiology Part A: Molecular and Integrative Physiology* 136:71–84.
- Boschdorf, O., C. L. Richards, and M. Pigliucci. 2008. Epigenetics for ecologists. *Ecology Letters* 11:106–115.
- Boyce, M. S. 1978. Climatic variability and body size variation in the muskrats (*Ondatra zibethicus*) of North America. *Oecologia* 36:1–19.
- Boyer, A. G., J.-L. E. Cartron, and J. H. Brown. 2010. Interspecific pairwise relationships among body size, clutch size and latitude: deconstructing a macroecological triangle in birds. *Journal of Biogeography* 37:47–56.
- Braithwaite, L. W., J. Turner, and J. Kelly. 1984. Studies on the arboreal marsupial fauna of eucalypt forests being harvested for wood-pulp at Eden, N. S. W. III. Relationships between faunal densities, eucalypt occurrence and foliage nutrients, and soil parent materials. *Australian Wildlife Research* 11:41–48.
- Brett, J. R. 1979. Environmental factors and fish growth. Pages 599–675 in W. S. Hoar, D. J. Randall, and J. R. Brett, editors. *Fish physiology*. Volume VIII. Bioenergetics and growth. Academic Press, New York, New York, USA.

- Bronfenbrenner, U., and S. J. Ceci. 1994. Nature–nurture reconceptualized in developmental perspective: a bioecological model. *Psychological Review* 101:568–586.
- Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, and G. B. West. 2004. Toward a metabolic theory of ecology. *Ecology* 85:1771–1789.
- Brown, J. H., and A. K. Lee. 1969. Bergmann's rule and climatic adaptation in woodrats (*Neotoma*). *Evolution* 23:329–338.
- Brown, J. H., P. A. Marquet, and M. L. Taber. 1993. Evolution of body size: consequences of an energetics definition of fitness. *American Naturalist* 142:573–584.
- Brown, J. H., and P. F. Nicoletto. 1991. Spatial scaling of species composition: body masses of North American land mammals. *American Naturalist* 138:1478–1512.
- Brown, M. F. 2008. Cultural relativism 2.0. *Current Anthropology* 49:363–383.
- Brunner, E. 1997. Stress and the biology of inequality. *British Medical Journal* 314:1472–1476.
- Brunson, M. H. 1937. The influence of the instars of host larvae on the sex of the progeny of *Tiphia popillivora* Roh. *Science* 86:197.
- Buckel, J. A., N. D. Steinberg, and D. O. Conover. 1995. Effects of temperature, salinity, and fish size on growth and consumption of juvenile bluefish. *Journal of Fish Biology* 47:696–706.
- Cade, B. S., and Q. Guo. 2000. Estimating effects of constraints on plant performance with regression quantiles. *Oikos* 91:245–54.
- Cade, B. S., and B. R. Noon. 2003. A gentle introduction to quantile regression for ecologists. *Frontiers in Ecology and the Environment* 1:412–420.
- Cade, B. S., J. W. Terrel, and R. L. Schroeder. 1999. Estimating effects of limiting factors with regression quantiles. *Ecology* 80:311–23.
- Calder, W. A., III. 1984. Size, function, and life history. Harvard University Press, Cambridge, Massachusetts, USA.
- Callicott, J. B. 1989. In defense of the land ethic: essays in environmental philosophy. State University of New York Press, Albany, New York, USA.
- Carbone, C., and J. L. Gittleman. 2002. A common rule for the scaling of carnivore density. *Science* 295:2273–2276.
- Cardillo, M. 2003. Biological determinants of extinction risk: why are smaller species less vulnerable? *Animal Conservation* 6:63–69.
- Cardillo, M., G. M. Mace, K. E. Jones, J. Bielby, O. R. P. Bininda-Emonds, W. Sechrest, C. D. L. Orme, and A. Purvis. 2005. Multiple causes of high extinction risk in large mammal species. *Science* 309:1239–1241.
- Carone, B. R., et al. 2010. Paternally induced transgenerational environmental reprogramming of metabolic gene expression in mammals. *Cell* 143:1084–1096.
- Case, T. J. 1978. On the evolution and adaptive significance of postnatal growth rates in the terrestrial vertebrates. *Quarterly Review of Biology* 53:243–282.
- Castro, T. G., L. G. Baraldi, P. T. Muniz, and M. A. Cardoso. 2009. Dietary practices and nutritional status of 0–24-month-old children from Brazilian Amazonia. *Public Health Nutrition* 12:2335–2342.
- Cavallini, P. 1995. Variation in the body size of the red fox. *Annales Zoologici Fennici* 32:421–427.
- Cavelaars, A. E., et al. 2000. Persistent variations in average height between countries and between socio-economic groups: an overview of 10 European countries. *Annals of Human Biology* 27:407–421.
- Charnov, E. L. 1982. The theory of sex allocation. Princeton University Press, Princeton, New Jersey, USA.
- Charnov, E. L., and J. F. Gillooly. 2004. Size and temperature in the evolution of fish life histories. *Integrative and Comparative Biology* 44:494–497.
- Charnov, E. L., R. L. Los-den Hartogh, W. T. Jones, and J. van den Assem. 1981. Sex ratio evolution in a variable environment. *Nature* 289:27–33.
- Cheatum, E. L., and C. W. Severinghaus. 1950. Variations in fertility of white-tailed deer related to range conditions. *North American Wildlife Conference* 15:170–190.
- Chevreux, I. 1913. Le rôle des femelles dans la détermination du sexe et leur descendance dans le groupe des Ichneumonides. *Comptes Rendus des Séances et Mémoires de la Société de Biologie* 74:695–699.
- Church, D. C. 1991. *Livestock feeds and feeding*. Prentice Hall, Englewood Cliffs, New Jersey, USA.
- Ciais, P., P. P. Tans, J. W. C. White, M. Trolier, R. J. Francey, J. A. Berry, D. R. Randall, P. J. Sellers, J. G. Collatz, and D. S. Schimel. 1995. Partitioning of ocean and land uptake of CO<sub>2</sub> as inferred by δ<sup>13</sup>C measurements from the NOAA Climate Monitoring and Diagnostics Laboratory global air sampling network. *Journal of Geophysical Research* 100:5051–5070.
- Cicognani, A., R. Alessandrini, A. Pasini, P. Pirazzoli, A. Cassio, E. Barbieri, and E. Cacciari. 2002. Low birth weight for gestational age and subsequent male gonadal function. *Journal of Pediatrics* 141:376–379.
- Clark, D. A., S. Brown, D. W. Kicklighter, J. Q. Chambers, J. R. Tomlinson, and J. Ni. 2001a. Measuring net primary production in forests: concepts and field methods. *Ecological Applications* 11:356–370.
- Clark, D. A., S. Brown, D. W. Kicklighter, J. Q. Chambers, J. R. Tomlinson, J. Ni, and E. A. Holland. 2001b. NPP in tropical forests: an evaluation and synthesis of existing field data. *Ecological Applications* 11:371–384.
- Clausen, C. P. 1939. The effect of host size upon the sex ratio of hymenopterous parasites and its relation to methods of rearing and colonization. *Journal of the New York Entomological Society* 47:1–9.
- Coady, J. W. 1982. Moose (*Alces alces*). Pages 902–922 in J. A. Chapman, and G. A. Feldhamer, editors. *Wild animals of North America: biology, management, economics*. Johns Hopkins University Press, Baltimore, Maryland, USA.
- Comer, C. E., J. C. Kilgo, G. J. D'Angelo, T. C. Glenn, and K. V. Miller. 2005. Fine-scale genetic structure and social organization in female white-tailed deer. *Journal of Wildlife Management* 69:332–344.
- Connell, J. H., and E. Orias. 1964. The ecological regulation of species diversity. *American Naturalist* 98:399–414.
- Cook, R. L. 1984. Texas. Pages 457–474 in L. K. Halls, editor. *White-tailed deer ecology and management*. Stackpole Books, Harrisburg, Pennsylvania, USA.
- Coon, C. S., S. M. Garn, and J. B. Birdsell. 1950. *Races: a study of the problems of race formation in man*. Springfield, Illinois, USA.
- Cooper, N., and A. Purvis. 2010. Body size evolution in mammals: complexity in tempo and mode. *American Naturalist* 175:727–738.
- Côté, S., T. P. Rooney, C. Tremblay, C. Dussault, and D. M. Waller. 2004. Ecological impacts of deer overabundance. *Annual Review of Ecology, Evolution, and Systematics* 35:113–147.
- Cousins, S. H. 1989. Species richness and energy theory. *Nature* 340:350–351.
- Crawford, B. T. 1946. Wildlife sampling by soil types. *North American Wildlife Conference* 11:357–364.
- Crawford, B. T. 1950. Some specific relationships between soils and wildlife. *Journal of Wildlife Management* 14:115–123.
- Creel, S., and N. M. Creel. 1997. Lion density and population structure in the Selous Game Reserve: evaluation of hunting quotas and offtake. *African Journal of Ecology* 35:83–93.
- Crête, M. 1999. The distribution of deer biomass in North America supports the hypothesis of exploitation ecosystems. *Ecology Letters* 2:223–227.

- Crooks, D. L., L. Cliggett, and S. M. Cole. 2007. Child growth as a measure or livelihood security: the case of the Gwembe Tonga. *American Journal of Human Biology* 19:669–675.
- Crooks, K. R. 2002. Relative sensitivities of mammalian carnivores to habitat fragmentation. *Conservation Biology* 16:488–502.
- Cuenco, M. L., R. R. Stickney, and W. E. Grant. 1985. Fish bioenergetics and growth in aquaculture ponds: II. Effects of interactions among size, temperature, dissolved oxygen, unionized ammonia and food on growth of individual fish. *Ecological Modeling* 27:191–206.
- Currie, D. J. 1991. Energy and large-scale patterns of animal and plant species richness. *American Naturalist* 137:27–49.
- Currie, D. J., and J. Fritz. 1993. Global patterns of animal abundance and species energy use. *Oikos* 67:56–68.
- Currie, D. J., G. G. Mittelbach, H. V. Cornell, R. Field, J.-F. Guegan, B. A. Hawkins, D. M. Kaufman, J. T. Kerr, T. Oberdorff, E. O'Brien, and J. R. G. Turner. 2004. Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecology Letters* 7:1121–1134.
- Currier, M. J. P. 1983. *Felis concolor*. *Mammal Species* 200:1–7.
- Dalke, P. D., A. S. Leopold, and D. L. Spencer. 1946. The ecology and management of the wild turkey in Missouri. Missouri Conservation Commission Technical Bulletin No. 1. Jefferson City, Missouri, USA.
- Damuth, J. 1981. Population density and body size in mammals. *Nature* 290:699–700.
- Damuth, J. 1987. Interspecific allometry of population density in mammals and other animals: the independence of body mass and population energy use. *Biological Journal of the Linnean Society* 31:193–246.
- Damuth, J. 1991. Of size and abundance. *Nature* 351:268–269.
- DeAngelis, D. L., W. M. Post, and C. Travis. 1986. Positive feedback in natural systems. Springer-Verlag, Heidelberg, Germany.
- Demarais, S., J. J. Jackley, B. K. Strickland, and L. W. Varner. 2003. In vitro digestibility of forages by coexisting deer species in Texas. *Texas Journal of Science* 55:175–182.
- Demarais, S., K. V. Miller, and H. A. Jacobson. 2000. White-tailed deer. Pages 601–628 in S. Demarais, and P. R. Krausman, editors. *Ecology and management of large mammals in North America*. Prentice Hall, Upper Saddle River, New Jersey, USA.
- Denney, A. H. 1944. Wildlife relationships to soil types. *Transactions of the North American Wildlife Conference* 9:316–323.
- Diggle, P. J. 1976. A spatial-stochastic model of inter-plant competition. *Journal of Applied Probability* 13:662–671.
- Dobzhansky, T. 1950. Evolution in the tropics. *American Scientist* 38:209–221.
- Dufour, D. L., L. K. Staten, J. C. Reina, and G. B. Spurr. 1994. Anthropometry and secular changes in stature of urban Columbian women of differing socioeconomic status. *American Journal of Human Biology* 6:749–760.
- Dunning, J. B. 2007. *CRC handbook of avian body masses*, Second Edition. CRC Press, Boca Raton, Florida, USA.
- Elowe, K. D., and W. E. Dodge. 1989. Factors affecting black bear reproductive success and cub survival. *Journal of Wildlife Management* 53:962–968.
- Enquist, B. J., and K. J. Niklas. 2001. Invariant scaling relations across tree-dominated communities. *Nature* 410:655–660.
- Ensminger, M. E., and C. G. Olentine. 1978. *Feeds and nutrition complete*. Ensminger Publishing Company, Clovis, California, USA.
- Enting, I. G. 2000. Constraints on the atmospheric carbon budget from spatial distributions of CO<sub>2</sub>. Pages 115–124 in T. M. L. Wigley, and D. S. Schimel, editors. *The carbon cycle*. Cambridge University Press, Cambridge, UK.
- Enting, I. G., and J. V. Mansbridge. 1991. Latitudinal distribution of sources and sinks of CO<sub>2</sub>: results of an inversion study. *Tellus* 43B:156–170.
- Entling, W., M. H. Schmidt-Entling, S. Bacher, R. Brandl, and W. Nentwig. 2010. Body size–climate relationships of European spiders. *Journal of Biogeography* 37:477–485.
- Evans, K. L., and K. J. Gaston. 2005. Can the evolutionary-rates hypothesis explain species–energy relationships? *Functional Ecology* 19:899–915.
- Evans, K. L., P. H. Warren, and K. J. Gaston. 2005. Species–energy relationships at the macroecological scale: a review of mechanisms. *Biological Reviews* 80:1–25.
- Eveleth, P. B., and J. M. Tanner. 1990. *Worldwide variation in human growth*. Cambridge University Press, Cambridge, UK.
- FAO [Food and Agriculture Organization of the United Nations]. 2008. *Harmonized world soil database v1.0*. FAO/IIASA/ISRIC/JRC-EU/Academia Sinica. FAO Land and Water Digital Media Series #34. FAO, Rome, Italy. (<http://www.iiasa.ac.at/Research/LUC/External-World-soil-database/HTML/index.html>)
- Federov, A. A. 1966. The structure of the tropical rain forest and speciation in the humid tropics. *Journal of Ecology* 54:1–11.
- Ferguson, S. H. 2002. The effects of productivity and seasonality on life history: comparing age at maturity among moose (*Alces alces*) populations. *Global Ecology and Biogeography* 11:303–312.
- Ferguson, S. H., A. R. Bisset, and F. Messier. 2000. The influences of density on growth and reproduction in moose *Alces alces*. *Wildlife Biology* 6:31–39.
- Field, C. B., M. J. Behrenfeld, J. T. Randerson, and P. Falkowski. 1998. Primary production of the biosphere: integrating terrestrial and oceanic components. *Science* 281:237–240.
- Fischer, A. G. 1960. Latitudinal variations in organic diversity. *Evolution* 14:64–81.
- Fisher, J. A. D., K. T. Frank, and W. C. Leggett. 2010. Global variation in marine fish body size and its role in biodiversity–ecosystem functioning. *Marine Ecology Progress Series* 405:1–13.
- Flannery, T. 1994. *The future eaters*. Reed Press, Port Melbourne, Australia.
- Floud, R., K. Wachter, and A. Gregory. 1990. *Height, health, and history: nutritional status in the United Kingdom, 1750–1980*. Cambridge University Press, Cambridge, UK.
- Floud, R. 2003. The dimensions of inequality: height and weight variation in Britain 1700–2000. Pages 13–26 in V. Berridge, and S. Blume, editors. *Poor health and social inequality before and after the Black Report*. Frank Cass Publishers, London, UK.
- Floyd, B. 2007. Focused life history data and linear enamel hypoplasia to help explain intergenerational variation in relative leg length within Taiwanese families. *American Journal of Human Biology* 19:358–375.
- Fonds, M., R. Cronie, A. D. Vethaak, and P. Ven Der Puyl. 1992. Metabolism, food consumption, and growth of plaice (*Pleuronectes platessa*) and flounder (*Platichthys flesus*) in relation to fish size and temperature. *Netherlands Journal of Sea Research* 29:127–143.
- Fox, C. W., and U. M. Savalli. 1998. Inheritance of environmental variation in body size: superparasitism of seeds affects progeny and grandprogeny body size via a non-genetic maternal effect. *Evolution* 52:172–182.
- Franzmann, A. W. 2000. Moose. Pages 578–600 in S. Demarais, and P. R. Krausman, editors. *Ecology and management of large mammals in North America*. Prentice Hall, Upper Saddle River, New Jersey, USA.
- Frisancho, A. R. 2007. Relative leg length as a biological marker to trace the developmental history of individuals and populations: growth delay and increased body fat. *American Journal of Human Biology* 19:703–710.
- Frodeman, R., editor. 2000. *Earth matters: the earth sciences, philosophy, and the claims of community*. Prentice Hall, Upper Saddle River, New Jersey, USA.



- Gamboa, J. A. A., and F. D. Gurri García. 2007. Impact of seasonal scarcity on energy balance and body composition in peasant adolescents from Calakmul, Campeche, Mexico. *American Journal of Human Biology* 19:751–762.
- Garten, C. T., M. A. Huston, and C. Thoms. 1994. Topographic variation of soil nitrogen dynamics at Walker Branch Watershed, Tennessee. *Forest Science* 40:497–513.
- Garlan, J. S., D. B. McKey, P. G. Waterman, C. N. Mbi, and T. T. Struhsaker. 1980. A comparative study of the phytochemistry of two African rainforests. *Biochemical Systematics and Ecology* 8:401–422.
- Gaston, K. J., and T. M. Blackburn. 1996. Global scale macroecology: interactions between population size, geographic range size and body size in Anseriformes. *Journal of Animal Ecology* 65:701–714.
- Gaur, R., and N. Y. Singh. 1994. Nutritional status among rural meitei children of Manipur, India. *American Journal of Human Biology* 6:731–740.
- Gay, S. W., and T. L. Best. 1996. Relationships between abiotic variables and geographic variation in skulls of pumas (*Puma concolor*: Mammalia, Felidae) in North and South America. *Zoological Journal of the Linnaean Society* 117:259–282.
- Gee, K. L., J. H. Holman, M. K. Causey, A. N. Rossi, and J. B. Armstrong. 2002. Aging white-tailed deer by tooth replacement and wear: a critical evaluation of a time-honored technique. *Wildlife Society Bulletin* 30:387–393.
- Geist, V. 1978. Life strategies, human evolution, environmental design. Springer-Verlag, New York, New York, USA.
- Geist, V. 1987a. Bergmann's rule is invalid. *Canadian Journal of Zoology* 65:1035–1038.
- Geist, V. 1987b. On speciation in Ice Age mammals, with special reference to cervids and caprids. *Canadian Journal of Zoology* 65:1067–1084.
- Geist, V. 1998. Deer of the world: their evolution, behavior, and ecology. Stackpole Books, Mechanicsburg, Pennsylvania, USA.
- Geist, V. 1999. Periglacial ecology, large mammals, and their significance to human biology. Pages 78–94 in R. Bonnichen, and K. L. Turnmire, editors. Ice age peoples of North America: environments, origins, and adaptations of the first Americans. Oregon State University Press, Corvallis, Oregon, USA.
- Gill, J. 1956. Regional differences in size and productivity of deer in West Virginia. *Journal of Wildlife Management* 20:286–292.
- Gillooly, J. F., J. H. Brown, G. B. West, V. M. Savage, and E. L. Charnov. 2001. Effects of size and temperature on metabolic rate. *Science* 293:2248–2251.
- Gingerich, P. D. 2003. Mammalian responses to climate change at the Paleocene–Eocene boundary: Polecats Bench record in the northern Bighorn Basin, Wyoming. Geological Society of America Special Paper 369. Geological Society of America, Boulder, Colorado, USA.
- Gingerich, P. D. 2008. Environment and evolution through the Paleocene–Eocene thermal maximum. *Trends in Ecology and Evolution* 21:246–253.
- Gittleman, J. L. 1985. Carnivore body size: ecological and taxonomic correlates. *Oecologia* 67:540–554.
- Gleick, P. 2000. The world's water. Island Press, Washington, D.C., USA.
- Godfrey, K. M., and D. J. P. Barker. 2000. Fetal nutrition and adult disease. *American Journal of Clinical Nutrition* 71:1344S–1352S.
- Gortázar, C., A. Travaini, and M. Delibes. 2000. Habitat-related microgeographic body size variation in two Mediterranean populations of red fox (*Vulpes vulpes*). *Journal of Zoology*, London 250:335–338.
- Gotthold, D. W., and J. J. Gotthold. 1988. Indian Ocean: bibliography. Clio Press, Oxford, UK.
- Gould, S. J., and R. C. Lewontin. 1979. The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist paradigm. *Proceedings of the Royal Society B* 205:581–598.
- Graham, R. W., et al. 1996. Spatial responses of mammals to late Quaternary environmental fluctuations. *Science* 272:1601–1606.
- Graves, G. R. 1991. Bergmann's rule near the equator: latitudinal clines in body size of an Andean passerine bird. *Proceedings of the National Academy of Sciences USA* 88:2322–2325.
- Grayson, D. K. 1998. Moisture history and small mammal community richness during the latest Pleistocene and Holocene, northern Bonneville Basin, Utah. *Quaternary Research* 49:330–334.
- Grayson, D. K. 2000. Mammalian responses to Middle Holocene climatic change in the Great Basin of the western United States. *Journal of Biogeography* 27:181–192.
- Grayson, D. K. 2007. Deciphering North American Pleistocene extinctions. *Journal of Anthropological Research* 63:185–212.
- Greve, M., K. J. Gaston, B. J. van Rensburg, and S. L. Chown. 2008. Environmental factors, regional body size distributions and spatial variation in body size of local avian assemblages. *Global Ecology and Biogeography* 17:514–523.
- Guillaumet, A., J.-B. Ferdy, E. Desmarais, B. Godelle, and P.-A. Crochet. 2008. Testing Bergmann's rule in the presence of confounding factors: a case study with three species of Galerida Larks in Morocco. *Journal of Biogeography* 35:579–591.
- Gurven, M., H. Kaplan, and A. Z. Supa. 2007. Mortality experience of Tsimane Amerindians of Bolivia: regional variation and temporal trends. *American Journal of Human Biology* 19:376–398.
- Gustaffson, A., L. Werdelin, B. S. Tullberg, and P. Lindenfors. 2007. Stature and sexual dimorphism in Sweden, from the 10th to the end of the 20th century. *American Journal of Human Biology* 19:861–870.
- Guthrie, R. D. 1984. Alaskan megabucks, megabulls, and megagrams: the issue of Pleistocene gigantism. Pages 482–510 in H. H. Genoways, and M. R. Dawson, editors. Contributions in Quaternary vertebrate paleontology: a volume in memorial to John E. Guilday. Special Publication No. 8. Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA.
- Guthrie, R. D. 2003. Rapid body size decline in Alaskan Pleistocene horses before extinction. *Nature* 426:169–171.
- Hails, C. J. 1982. A comparison of tropical and temperate aerial insect abundance. *Biotropica* 14:310–313.
- Hamilton, S., B. Popkin, and D. Spicer. 1984. Women and nutrition in third world countries. Praeger, New York, New York, USA.
- Hamilton, T. H. 1961. The adaptive significances of intraspecific trends in wing length and body size among bird species. *Evolution* 15:180–195.
- Hansen, L. P., C. M. Nixon, and J. Berringer. 1997. Role of refuges in the dynamics of outlying deer populations: two examples from the agricultural Midwest. Pages 327–345 in W. J. McShea, H. B. Underwood, and J. H. Rappole, editors. The science of overabundance: deer ecology and population management. Smithsonian Books, Washington, D.C., USA.
- Harlow, H. J., T. Lohuis, R. G. Grogan, and T. D. I. Beck. 2002. Body mass and lipid changes by hibernating reproductive and nonreproductive black bears (*Ursus americanus*). *Journal of Mammalogy* 83:1020–1025.
- Harlow, R. F. 1962. Osteometric data for the Florida black bear. *Quarterly Journal of the Florida Academy of Sciences* 24:258–274.
- Harper, J. L. 1977. Population biology of plants. Academic Press, New York, New York, USA.
- Hawkins, B. A., and J. H. Lawton. 1995. Latitudinal gradients in butterfly body sizes: is there a general pattern? *Oecologia* 102:31–36.

- Heaney, L. R. 1984. Climatic influences on life-history tactics and behavior of North American tree squirrels. Pages 43–78 in J. O. Murie, and J. R. Michener, editors. *The biology of ground-dwelling squirrels*. University of Nebraska Press, Lincoln, Nebraska, USA.
- Heijmans, B. T., E. W. Tobi, A. D. Stein, H. Putter, G. J. Blauw, E. S. Susser, P. E. Slagboom, and L. H. Lumey. 2008. Persistent epigenetic differences associated with prenatal exposure to famine in humans. *Proceedings of the National Academy of Sciences USA* 105:17046–17049.
- Hellgren, E. C., L. L. Rogers, and U. S. Seal. 1993. Serum chemistry and hematology of black bears: physiological indices of habitat quality or seasonal patterns? *Journal of Mammalogy* 74:304–315.
- Hemmingsen, A. M. 1960. Metabolism in relation to body size. Report of the Steno Memorial Hospital Nordisk Insulin Lab 9:1–110.
- Henry, W. A. 1898. *Feeds and feeding: a handbook for the student and stockman*. First edition published by the author, Madison, Wisconsin, USA.
- Henry, W. A., and F. B. Morrison. 1923. *Feeds and feeding: a handbook for the student and stockman*. 23rd edition. Henry-Morrison Company, Madison, Wisconsin, USA.
- Hesselton, W. T., and R. A. M. Hesselton. 1982. White-tailed deer (*Odocoileus virginianus*). Pages 878–901 in J. A. Chapman, and G. A. Feldhamer, editors. *Wild animals of North America: biology, management, economics*. Johns Hopkins University Press, Baltimore, Maryland, USA.
- Hewison, A. J. M., J. M. Gaillard, J. M. Angibault, G. Van Laere, and J. P. Vincent. 2002. The influence of density on post-weaning growth in roe deer *Capreolus capreolus* fawns. *Journal of Zoology* 257:303–309.
- Hiernaux, J. 1975. *The people of Africa*. Charles Scribner's Sons, New York, New York, USA.
- Hilderbrand, G. V., S. G. Jenkins, C. C. Schwartz, T. A. Hanley, and C. T. Robbins. 1999a. Effect of seasonal differences in dietary meat intake on changes in body mass and composition in wild and captive brown bears. *Canadian Journal of Zoology* 77:1623–1630.
- Hilderbrand, G. V., C. C. Schwartz, C. T. Robbins, M. E. Jacoby, T. A. Hanley, S. M. Arthur, and C. Servheen. 1999b. The importance of meat, particularly salmon, to body size, population productivity, and conservation of North American brown bears. *Canadian Journal of Zoology* 77:132–138.
- Hill, M. E., M. G. Hill, and C. C. Widga. 2008. Late Quaternary bison diminution on the Great Plains of North America: evaluating the role of human hunting versus climate change. *Quaternary Science Reviews* 27:1752–1771.
- Himes, J. H., and W. H. Mueller. 1977. Age associated statural loss and socioeconomic status. *Journal of the American Geriatric Society* 25:171–174.
- Ho, C.-K., S. C. Pennings, and T. H. Carefoot. 2010. Is diet quality an overlooked mechanism for Bergmann's rule? *American Naturalist* 175:269–276.
- Holliday, T. W. 1997. Body proportions in Late Pleistocene Europe and modern human origins. *Journal of Human Evolution* 32:423–447.
- Holt, B. M. 2003. Mobility in Upper Paleolithic and Mesolithic Europe: evidence from the lower limb. *American Journal of Physical Anthropology* 122:200–215.
- Holt, B. M., and V. Formicola. 2008. Hunters of the Ice Age: the biology of Upper Paleolithic people. *Yearbook of Physical Anthropology* 51:70–99.
- Hooijer, D. A. 1950. The study of subspecific advance in the quaternary. *Evolution* 4:360–361.
- Huston, M. A. 1979. A general hypothesis of species diversity. *American Naturalist* 113:81–101.
- Huston, M. A. 1980. Soil nutrients and tree species richness in Costa Rican forests. *Journal of Biogeography* 7:147–157.
- Huston, M. A. 1985. Patterns of species diversity on coral reefs. *Annual Review of Ecology and Systematics* 16:149–177.
- Huston, M. A. 1986. Size bimodality in plant populations: an alternative hypothesis. *Ecology* 67:265–269.
- Huston, M. A. 1993. Biological diversity, soils, and economics. *Science* 262:1676–1680.
- Huston, M. A. 1994. *Biological diversity: the coexistence of species on changing landscapes*. Cambridge University Press, Cambridge, UK.
- Huston, M. A. 1999a. Local processes and regional patterns: appropriate scales for understanding variation in the diversity of plants and animals. *Oikos* 86:393–401.
- Huston, M. A. 1999b. Forest productivity and diversity: using ecological theory and landscape models to guide sustainable forest management. Pages 329–341 in C. Aguirre-Bravo, and C. R. Franco, editors. *North American science symposium: toward a unified framework for inventorying and monitoring forest ecosystem resources*. USDA Forest Service Proceedings RMRS-P-12. USDA Forest Service, Washington, D.C., USA.
- Huston, M. A. 2002. Introductory essay: critical issues for improving predictions. Pages 7–21 in J. M. Scott, et al., editors. *Predicting species occurrences: issues of scale and accuracy*. Island Press, Washington, D.C., USA.
- Huston, M. A. 2004. Management strategies for plant invasions: manipulating productivity, disturbance, and competition. *Diversity and Distributions* 10:167–178.
- Huston, M. A. 2005. The three phases of land-use change: implications for biodiversity. *Ecological Applications* 15:1864–1878.
- Huston, M. A., and D. L. DeAngelis. 1987. Size bimodality in monospecific populations: a review of potential mechanisms. *American Naturalist* 129:678–707.
- Huston, M. A., and D. L. DeAngelis. 1994. Competition and coexistence: the effects of resource transport and supply rates. *American Naturalist* 144:954–977.
- Huston, M. A., D. L. DeAngelis, and W. M. Post. 1988. New computer models unify ecological theory. *BioScience* 38:682–692.
- Huston, M. A., G. McVicker, and J. Nielsen. 1999. A functional approach to ecosystem management: implications for species diversity. Pages 45–85 in R. C. Szaro, N. C. Johnson, W. T. Sexton, and A. J. Malk, editors. *Ecological stewardship: a common reference for ecosystem management*. Volume II. Elsevier Science, Oxford, UK.
- Huston, M. A., and T. M. Smith. 1987. Plant succession: life history and competition. *American Naturalist* 130:168–198.
- Huston, M. A., and S. Wolverton. 2009. The global distribution of net primary production: resolving the paradox. *Ecological Monographs* 79:343–377.
- Hutchins, M. 1995. Olympic mountain goat controversy continues. *Conservation Biology* 9:1324–1326.
- Hyams, E. S. 1952. *Soil and civilization*. Thames and Hudson, London, UK.
- Ibanez, L., N. Potau, and F. de Zegher. 2000. Ovarian hyporesponsiveness to follicle stimulating hormone in adolescent girls born small for gestational age. *Journal of Clinical Endocrinology and Metabolism* 85:2624–2626.
- Ibanez, L., N. Potau, G. Enriquez, M. V. Marcos, and F. de Zegher. 2003. Hypergonado-trophinaemia with reduced uterine and ovarian size in women born small for gestational age. *Human Reproduction* 18:1565–1569.
- Ibanez, L., N. Potau, A. Ferrer, F. Rodriguez-Hierro, M. V. Marcos, and F. de Zegher. 2002. Reduced ovulation rate in adolescent girls born small for gestational age. *Journal of Clinical Endocrinology and Metabolism* 87:3391–3393.
- Imsland, A. K., A. Foss, A. Folkvord, S. O. Stefansson, and T. M. Jonassen. 2005. The interrelation between temperature regimes and fish size in juvenile Atlantic cod (*Gadus morhua*): effects on growth and feed conversion efficiency. *Fish Physiology and Biochemistry* 31:347–361.
- Imsland, A. K., L. M. Sunde, A. Folkvord, and S. O. Stefansson. 1996. The interaction of temperature and fish

- size on growth of juvenile turbot. *Journal of Fish Biology* 49:926–940.
- Iriarte, J. A., W. L. Franklin, W. E. Johnson, and K. H. Redford. 1990. Biogeographic variation of food habits and body size of the American puma. *Oecologia* 85:185–190.
- Jacobson, H. A. 1984. Relationships between deer and soil nutrients in Mississippi. *Proceedings of the Annual of the Southeastern Association of Fish and Wildlife Agencies* 38:1–12.
- Jacobson, H. A., D. C. Guynn, L. F. Castle, and E. J. Hackett. 1977. Relationships between soil characteristics and body weights, antler measurements, and reproduction of white-tailed deer in Mississippi. Pages 47–55 in *Proceedings of the Joint Northeast-Southeast Deer Study Group*. Virginia Commonwealth Game and Inland Fish Commission, Richmond, Virginia, USA.
- James, F. C. 1970. Geographic size variation in birds and its relationship to climate. *Ecology* 51:365–390.
- Johnson, C. N. 1998a. Rarity in the tropics: latitudinal gradients in distribution and abundance in Australian mammals. *Journal of Animal Ecology* 67:689–698.
- Johnson, C. N. 1998b. Species extinction and the relationship between distribution and abundance. *Nature* 394:272–274.
- Johnson, C. N., K. Vernes, and A. Payne. 2005. Demography in relation to population density in two herbivorous marsupials: testing for source-sink dynamics versus independent regulation of population size. *Oecologia* 143:70–76.
- Jones, B. A., R. A. How, and D. J. Kitchener. 1994. A field study of *Pseudocheirus occidentalis* (Marsupialia: Petauridae). I. Distribution and habitat. *Wildlife Research* 21:175–187.
- Jones, D. Y., M. C. Nesheim, and J.-P. Habicht. 1985. Influences in child growth associated with poverty in the 1970s: an examination of the HANES I and HANES II, cross-sectional U.S. surveys. *American Journal of Clinical Nutrition* 42:714–724.
- Jones, P. D., S. Demarais, B. K. Strickland, and S. L. Edwards. 2008. Soil region effects on white-tailed deer forage protein content. *Southeastern Naturalist* 7:595–606.
- Jordan, P. A. 1987. Aquatic foraging and the sodium ecology of moose: a review. *Swedish Wildlife Research Supplement* 1:119–137.
- Kappeler, P. M., and E. W. Heymann. 1996. Nonconvergence in the evolution of primate life history and socio-ecology. *Biological Journal of the Linnean Society* 59:297–326.
- Karanth, K. U., J. D. Nichols, N. S. Kumar, W. A. Link, and J. E. Hines. 2004. Tigers and their prey: predicting carnivore densities from prey abundance. *Proceedings of the National Academy of Sciences USA* 101:4854–4757.
- Kaspari, M. 2001. Taxonomic level, trophic biology and the regulation of local abundance. *Global Ecology and Biogeography* 10:229–244.
- Kaspari, M. 2005. Global energy gradients and size in colonial organisms: worker mass and worker number in ant colonies. *Proceedings of the National Academy of Sciences USA* 102:5079–5083.
- Kaspari, M., S. O'Donnell, and J. R. Kercher. 2000. Energy, density, and constraints to species richness: ant assemblages along a productivity gradient. *American Naturalist* 155:280–293.
- Kaspari, M., and E. Vargo. 1995. Colony size as a buffer against seasonality: Bergmann's rule in social insects. *American Naturalist* 145:610–623.
- Kavanagh, R. P., and M. J. Lambert. 1990. Food selection by the greater glider, *Petauroides volans*: is foliar nitrogen a determinant of habitat quality? *Australian Wildlife Research* 17:285–300.
- Kennedy, M. L., P. K. Kennedy, M. A. Bogan, and J. L. Waits. 2002. Geographic variation in the black bear (*Ursus americanus*) in the eastern United States and Canada. *Southwestern Naturalist* 47:257–266.
- Kennedy, M. L., and S. L. Lindsay. 1984. Morphologic variation in the raccoon, *Procyon lotor*, and its relationship to genic and environmental variation. *Journal of Mammalogy* 65:195–205.
- Khan, M. R., and F. Ahmed. 2005. Physical status, nutrient intake and dietary pattern of adolescent female factory workers in urban Bangladesh. *Asia Pacific Journal of Clinical Nutrition* 14:19–26.
- Kie, J. G., M. White, and D. L. Drawe. 1983. Condition parameters of white-tailed deer in Texas. *Journal of Wildlife Management* 47:583–594.
- Kirchengast, S. 2000. Differential reproductive success and body size in !Kung San people from northern Namibia. *Collegium Anthropologicum* 24:121–132.
- Kjellander, P., J. M. Gaillard, and A. J. M. Hewison. 2006. Density-dependent responses of fawn cohort body mass in two contrasting roe deer populations. *Oecologia* 146:521–530.
- Klein, D. R., M. Meldgaard, and S. G. Fancy. 1987. Factors determining leg length in *Rangifer tarandus*. *Journal of Mammalogy* 68:642–655.
- Klenner, W., and D. W. Kroeker. 1990. Denning behavior of black bears, *Ursus americanus*, in western Manitoba. *Canadian Field Naturalist* 104:540–544.
- Kojola, I., and H. Laitala. 2001. Body size variation of brown bear in Finland. *Annales Zoologici Fennici* 38:173–178.
- Komlos, J. 1996. The biological standard of living in Europe and America, 1700–1900. University of Chicago Press, Chicago, Illinois, USA.
- Kooijman, S. A. L. M. 1986. Energy budgets can explain body size relations. *Journal of Theoretical Biology* 121:269–282.
- Kuhn, T. S. 1962. The structure of scientific revolutions. University of Chicago Press, Chicago, Illinois, USA.
- Kurtén, B. 1963. Fossil bears from Texas. The Pearce-Sellards Series, Texas Memorial Museum 1:1–15.
- Kurtén, B. 1973. Geographic variation in size in the puma (*Felis concolor*). *Commentationes Biologicae* 63:3–8.
- Kurtén, B. 1976. The cave bear story. Columbia University Press, New York, New York, USA.
- Kurtén, B., and E. Anderson. 1980. Pleistocene mammals of North America. Columbia University Press, New York, New York, USA.
- Kuoppo, P. 1994. Annual variation in the abundance and size of heterotrophic nanoflagellates on the SW coast of Finland, the Baltic Sea. *Journal of Plankton Research* 16:1525–1542.
- Kuzawa, C. W. 2007. Developmental origins of life history: growth, productivity, and reproduction. *American Journal of Human Biology* 19:654–661.
- Lack, D. 1947. The significance of clutch size, Part I. *Ibis* 89:302–352.
- Lack, D. 1948. The significance of clutch size, Part II. *Ibis* 90:24–45.
- Lack, D. 1968. Ecological adaptations for breeding in birds. Methuen, London, UK.
- Lack, D., and R. E. Moreau. 1965. Clutch size in tropical birds of forest and savanna. *Oiseau* 35:76–89.
- Langvatn, R., and S. D. Albon. 1986. Geographic clines in body weight of Norwegian red deer: a novel explanation of Bergmann's Rule. *Holarctic Ecology* 9:285–293.
- Larivière, S. 2001. *Ursus americanus*. *Mammalian Species* 647:1–11.
- Lasker, G. W. 1969. Human biological adaptability. *Science* 166:1480–1486.
- Lasker, G. W., and R. Thomas. 1976. Relationship between reproductive fitness and anthropometric dimensions in a Mexican population. *Human Biology* 48:775–791.
- Lee, R. B. 2003. The Dobe Ju/'hoansi. Third edition. Wadsworth/Thomson Learning, Toronto, Ontario, Canada.
- Leimar, O. 1996. Life-history analysis of the Trivers and Willard sex-ratio problem. *Behavioral Ecology* 7:316–325.
- Leith, H., and R. H. Whittaker. 1975. Primary productivity of the biosphere. Springer-Verlag, New York, New York, USA.

- Leon, D., and G. Walt, editors. 2000. Poverty, inequality, and health. Oxford University Press, Oxford, UK.
- Leopold, A. S. 1947. A survey of over-populated deer ranges in the United States. *Journal of Wildlife Management* 11:162–177.
- Leopold, A. S. 1950. Deer in relation to succession. North American Wildlife Conference 15:571–580.
- Lesage, L., M. Crête, J. Huot, and J. P. Ouellet. 2001. Evidence for a trade-off between growth and body reserves in northern white-tailed deer. *Oecologia* 126:30–41.
- Lindeman, R. L. 1942. The trophic-dynamic aspects of ecology. *Ecology* 23:399–417.
- Lindsey, C. C. 1966. Body sizes of poikilotherm vertebrates at different latitudes. *Evolution* 20:456–465.
- Lindstedt, S. L., and M. S. Boyce. 1985. Seasonality, fasting endurance, and body size in mammals. *American Naturalist* 125:873–878.
- Lonsdale, W. M., and A. R. Watkinson. 1983. Plant geometry and self-thinning. *Journal of Ecology* 71:285–297.
- Lord, R. D. 1960. Litter size and latitude in North American mammals. *American Midland Naturalist* 64:488–499.
- Lyman, R. L. 2004a. Late-Quaternary diminution and abundance of prehistoric bison (*Bison* sp.) in eastern Washington state, U.S.A. *Quaternary Research* 62:76–85.
- Lyman, R. L. 2004b. Prehistoric biogeography, abundance, and phenotypic plasticity of elk (*Cervus elaphus*) in Washington state. Pages 136–163 in R. L. Lyman, and K. P. Cannon, editors. *Zooarchaeology and conservation biology*. University of Utah Press, Salt Lake City, Utah, USA.
- Lyman, R. L., and M. J. O'Brien. 2005. Within-taxon morphological diversity in late-Quaternary Neotoma as a paleoenvironmental indicator, Bonneville Basin, Northwestern, Utah, USA. *Quaternary Research* 63:274–282.
- Lyman, R. L., and S. Wolverton. 2002. The late prehistoric-early historic game sink in the northwestern United States. *Conservation Biology* 16:73–85.
- Maehr, D. S., E. C. Hellgren, R. L. Bingham, and D. L. Doan-Crider. 2001. Body mass of American black bears from Florida and Mexico. *Southwestern Naturalist* 46:129–133.
- Makarievva, A. M., V. G. Gorshkov, and B.-L. Li. 2005. Temperature-associated upper limits to body size in terrestrial poikilotherms. *Oikos* 111:425–436.
- Malina, R. M., B. B. Little, M. P. Stern, S. P. Gaskill, and H. P. Hazuda. 1983. Ethnic and social class differences in selected anthropometric characteristics of Mexican American and Anglo adults: the San Antonio Heart Study. *Human Biology* 55:867–883.
- Malville, N. J. 1997. Enamel hypoplasia in Ancestral Puebloan populations from Southwestern Colorado: I. Permanent dentition. *American Journal of Physical Anthropology* 102:351–367.
- Margalef, R. 1955. Temperatura, dimensiones, y evolución. *Publicaciones del Instituto de Biología Aplicada* 19:13–94.
- Martin, R. D. 1990. Primate origins and evolution. Chapman and Hall, London, UK.
- May, L. A., and J. K. Loosli. 1962. Animal nutrition. McGraw-Hill, New York, New York, USA.
- McCullough, D. R. 1979. The George Deer Reserve deer herd: population ecology of a *K*-selected species. University of Michigan Press, Ann Arbor, Michigan, USA.
- McCullough, D. R. 1982a. Antler characteristics of the George Reserve white-tailed deer. *Journal of Wildlife Management* 46:821–826.
- McCullough, D. R. 1982b. Population growth rate of the George Reserve deer herd. *Journal of Wildlife Management* 46:1079–1083.
- McCullough, D. R. 1984. Lessons from the George Reserve, Michigan. Pages 211–242 in L. K. Halls, editor. *White-tailed deer ecology and management*. Stackpole Books, Harrisburg, Pennsylvania, USA.
- McCullough, D. R. 1997. Irruptive behavior in ungulates. Pages 69–98 in W. J. McShea, H. B. Underwood, and J. H. Rappole, editors. *The science of overabundance: deer ecology and population management*. Smithsonian Books, Washington, D.C., USA.
- McElwain, J. C., D. J. Beerling, and F. I. Woodward. 1999. Fossil plants and global warming at the Triassic-Jurassic boundary. *Science* 285:1386–1390.
- McGrew, J. C., Jr., and C. B. Monroe. 2000. An introduction to statistical problem solving in geography. Second edition. McGraw Hill, Boston, Massachusetts, USA.
- McKey, D. B., P. G. Waterman, C. N. Mbi, J. S. Gartlan, and T. T. Struhsaker. 1978. Phenolic content of vegetation in two African rain-forests: ecological implications. *Science* 202:61–64.
- McNab, B. K. 1971. On the ecological significance of Bergmann's rule. *Ecology* 52:845–854.
- McNab, B. K. 1983. Energetics, body size, and the limits to endothermy. *Journal of Zoology London* 199:1–29.
- McNab, B. K. 2010. Geographic and temporal correlations of mammalian size reconsidered: a resource rule. *Oecologia* 164:13–23.
- McShea, W. J., H. B. Underwood, and J. H. Rappole, editors. 1997. *The science of overabundance: deer ecology and population management*. Smithsonian Books, Washington, D.C., USA.
- Meggens, B. J. 1971. Amazonia: man and culture in a counterfeit paradise. Aldine-Atherton, Chicago, Illinois, USA.
- Meiri, S. 2011. Bergmann's rule—what's in a name? *Global Ecology and Biogeography* 20:203–207.
- Meiri, S., and T. Dayan. 2003. On the validity of Bergmann's rule. *Journal of Biogeography* 30:331–351.
- Meiri, S., T. Dayan, and D. Simberloff. 2004. Carnivores, biases and Bergmann's rule. *Biological Journal of the Linnean Society* 81:579–588.
- Meiri, S., and G. H. Thomas. 2007. The geography of body size—challenges of the interspecific approach. *Global Ecology and Biogeography* 16:689–693.
- Meiri, S., Y. Yom-Tov, and E. Geffen. 2007. What determines conformity to Bergmann's rule? *Global Ecology and Biogeography* 16:788–794.
- Meng, X., and N. Qian. 2009. The long term consequences of famine on survivors: evidence from a unique natural experiment using China's Great Famine. Working Paper 14917. Natural Bureau of Economic Research, Cambridge, Massachusetts, USA.
- Mittelbach, G., et al. 2007. Evolution and the latitudinal diversity gradient: speciation, extinction, and biogeography. *Ecology Letters* 10:315–331.
- Moffat, T., and T. Galloway. 2007. Adverse environments: investigating local variation in child growth. *American Journal of Human Biology* 19:676–683.
- Monden, C. W. S., and J. Smits. 2009. Maternal height and child mortality in 42 developing countries. *American Journal of Human Biology* 21:305–311.
- Mondolfi, E., and R. Hoogesteijn. 1986. Notes on the biology and status of the jaguar in Venezuela. Pages 125–146 in S. D. Miller, and D. D. Everett, editors. *Cats of the world: biology, conservation, and management*. National Wildlife Federation, Washington, D.C., USA.
- Moore, J. C. 1961. Geographic variation in some reproductive characteristics of diurnal squirrels. *Bulletin of the American Museum of Natural History* 122:1–32.
- Moreno, R. S., R. W. Kays, and R. Samudio, Jr. 2006. Competitive release in diets of ocelot (*Leopardus pardalis*) and puma (*Puma concolor*) after jaguar (*Panthera onca*) decline. *Journal of Mammalogy* 87:808–816.
- Moritz, C., J. L. Patton, C. J. Schneider, and T. B. Smith. 2000. Diversification of rainforest faunas: an integrated molecular approach. *Annual Review of Ecology and Systematics* 31:533–563.

- Morris, E. C., and P. J. Myerscough. 1991. Self-thinning and competition intensity over a gradient of nutrient availability. *Journal of Ecology* 79:903–923.
- Morris, I. 2005. Archaeology, standards of living, and Greek economic history. Pages 91–126 in J. G. Manning, and I. Morris, editors. *The ancient economy: evidence and models*. Stanford University Press, Stanford, California, USA.
- Moulds, M. S. 2003. An appraisal of the Cicadas of the genus *Abrieta* Stål and allied genera (Hemiptera: Auchenorrhyncha: Cicadidae). *Records of the Australian Museum* 55:245–304.
- Mueller, W. H. 1979. Fertility and physique in a malnourished population. *Human Biology* 51:153–166.
- Mugaas, J. N., and J. Seidensticker. 1993. Geographic variation of lean body mass and a model of its effects on the capacity of the raccoon to fatten and fast. *Bulletin of the Florida Museum of Natural History Biological Sciences* 36:85–107.
- Murphy, D. A., and J. A. Coates. 1966. Effects of dietary protein on deer. *North American Wildlife and Natural Resources Conference* 31:129–139.
- Murphy, D. A., and W. R. Porath. 1969. Forest soils and game nutrition. *Proceedings of the Southeastern Association of Game and Fish Commissioners* 23:18–25.
- Myneni, R. B., J. Dong, C. J. Tucker, R. K. Kaufmann, P. E. Kauppi, J. Liski, L. Zhou, V. Alexeyev, and M. K. Hughes. 2001. A large carbon sink in the woody biomass of northern forests. *Proceedings of the National Academy of Science USA* 98:147840–14789.
- Mysterud, A., R. Langvatn, N. G. Yoccoz, and N. C. Stenseth. 2001a. Plant phenology, migration and geographical variation in body weight of a large herbivore: the effect of a variable topography. *Journal of Animal Ecology* 70:915–923.
- Mysterud, A., R. Langvatn, N. G. Yoccoz, and N. C. Stenseth. 2002. Large-scale habitat variability, delayed density effects and red deer populations in Norway. *Journal of Animal Ecology* 71:569–580.
- Mysterud, A., F. J. Perez-Barberia, and I. J. Gordon. 2001b. The effect of season, sex and feeding style on home range area versus body mass scaling in temperate ruminants. *Oecologia* 127:30–39.
- Mysterud, A., N. G. Yoccoz, N. C. Stenseth, and R. Langvatn. 2001c. Effects of age, sex and density on body weight of Norwegian red deer: evidence of density-dependent senescence. *Proceedings of the Royal Society B* 268:911–919.
- Nagel, W. O. 1943. A study of the economic value, distribution, trends, and soil relationships of Missouri furbearers. Report of the Missouri Federal Aid to Wildlife Research Project–Pitman-Robertson Program, Mo. 1-5R. Volume VIII. Missouri State Archives, Jefferson City, Missouri, USA.
- Nagy, L. R., and R. T. Holmes. 2005. Food limits annual fecundity of a migratory songbird: an experimental study. *Ecology* 86:675–681.
- National Research Council. 1976. Nutrient requirements of beef cattle. National Research Council. National Academy of Sciences, Washington, D.C., USA.
- Nellemann, C. 1996. Terrain selection by reindeer in late winter in central Norway. *Arctic* 49:339–347.
- Newman, M. T. 1953. The application of ecological rules to the racial anthropology of the aboriginal New World. *American Anthropologist* 55:311–327.
- Nixon, C. M., L. P. Hansen, P. A. Brewer, and J. E. Chelvig. 1991. Ecology of white-tailed deer in an intensively farmed region of Illinois. *Wildlife Monographs* 118.
- Noren, C. R. 1943. Progress report of investigation of raccoon. Missouri Federal Aid to Wildlife Research Project No. 1-5R. Volume VIII. Missouri State Archives, Jefferson City, Missouri, USA.
- Nowak, R. M. 1999. *Walker's primates of the world*. Johns Hopkins University Press, Baltimore, Maryland, USA.
- Nowak, R. M., and J. L. Paradiso. 1983. *Walker's mammals of the world*. Johns Hopkins University Press, Baltimore, Maryland, USA.
- Oguzl, A., D. Z. Childs, M. K. Oli, K. B. Armitage, D. T. Blumstein, L. E. Olson, S. Tuljapurkar, and T. Coulson. 2010. Coupled dynamics of body mass and population growth in response to environmental change. *Nature* 466:482.
- Olden, J. D., Z. S. Hogan, and M. J. Vander Zanden. 2007. Small fish, big fish, red fish, blue fish: size biased extinction risk of the world's freshwater and marine fishes. *Global Ecology and Biogeography* 16:694–701.
- Olson, R. J., K. R. Johnson, D. L. Zheng, and J. M. O. Scurlock. 2001a. Global and regional ecosystem modeling: databases of model drivers and validation measurements. ORNL/TM-2001/196. Oak Ridge National Laboratory. Oak Ridge, Tennessee, USA.
- Olson, R. J., J. M. O. Scurlock, S. D. Prince, D. L. Zhang, and K. R. Johnson, editors. 2001b. NPP multi-biome: global primary production data initiative products. Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, Tennessee, USA. (<http://www.daac.ornl.gov/>)
- Olson, J. S., J. S. Watts, and L. J. Allison. 1983. Carbon in live vegetation of major world ecosystems. Publication ORNL-5882. Oak Ridge National Laboratory, Oak Ridge, Tennessee, USA. (<http://cdiac.esd.ornl.gov/ftp/ndp017/>)
- Owen-Smith, N. 1988. *Megaherbivores: the influence of very large body size on ecology*. Cambridge University Press, New York, New York, USA.
- Owen-Smith, N. 2002. Adaptive herbivore ecology: from resources to populations in variable environments. Cambridge University Press, Cambridge, UK.
- Owen-Smith, N., and M. G. L. Mills. 2008. Predator–prey size relationships in an African large-mammal food web. *Journal of Animal Ecology* 77:173–183.
- Palmer, M. W. 1994. Variation in species richness: towards a unification of hypotheses. *Folia Geobotica Phytotaxa, Praha* 29:511–530.
- Parker, G., and L. M. Smith, editors. 1997. *The general crisis of the seventeenth century*. Routledge, New York, New York, USA.
- Parker, K. L., P. S. Barboza, and T. R. Stephenson. 2005. Protein conservation in female caribou (*Rangifer tarandus*): effects of decreasing diet quality during winter. *Journal of Mammalogy* 86:610–622.
- Pauly, D. 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. *Journal du Conseil International Pour l'Exploration de la Mer* 39:175–192.
- Pauly, D. 1981. The relationships between gill surface area and growth performance in fish: a generalization of von Bertalanffy's theory of growth. *Berichte Deutschen Wissenschaftlichen Kommission für Meeresforschung* 28:251–282.
- Pauly, D., V. Christensen, J. Dalsgaard, R. Froese, and F. C. Torres, Jr. 1998. Fishing down marine food webs. *Science* 279:860–863.
- Pauly, D., V. Christensen, S. Guénette, T. J. Pitcher, U. R. Sumaila, C. J. Walters, R. Watson, and D. Zeller. 2002. Towards sustainability in world fisheries. *Nature* 418:689–695.
- Pelton, M. R. 1982. Black bear (*Ursus americanus*). Pages 504–514 in J. A. Chapman, and G. A. Feldhamer, editors. *Wild animals of North America: biology, management, economics*. Johns Hopkins University Press, Baltimore, Maryland, USA.
- Pelton, M. R. 2000. Black bear. Pages 389–408 in S. Demarais, and P. R. Krausman, editors. *Ecology and management of large mammals in North America*. Prentice Hall, Upper Saddle River, New Jersey, USA.
- Pembrey, M. E., et al. 2006. Sex-specific, male-line transgenerational responses in humans. *European Journal of Human Genetics* 14:159–166.
- Peters, R. H. 1983. *The ecological implications of body size*. Cambridge University Press, Cambridge, UK.
- Pfennig, D. W., M. A. Wund, E. C. Snell-Rood, T. Cruickshank, C. D. Schlichting, and A. P. Moczek. 2010.

- Phenotypic plasticity's impacts on diversification and speciation. *Trends in Ecology and Evolution* 25:459–467.
- Pianka, E. R. 1966. Latitudinal gradients of species diversity: a review of concepts. *American Naturalist* 100:33–46.
- Pidwirny, M. 2006. Introduction to the oceans. Chapter 8 in *Fundamentals of physical geography*. Second edition. (<http://www.physicalgeography.net/fundamentals/8o.html>)
- Piechota, T., J. Timilsena, G. Tootle, and H. Hidalgo. 2004. The western U.S. drought: How bad is it? *Eos* 85:301–308.
- Pollet, T. V., and D. Nettle. 2008. Taller women do better in a stressed environment: height and reproductive success in rural Guatemalan women. *American Journal of Human Biology* 20:264–269.
- Pond, W. G., D. C. Church, and K. R. Pond. 1995. *Basic animal nutrition and feeding*. Fourth edition. Wiley, New York, New York, USA.
- Prasad, M., and H. Al-Taher. 2002. Maternal height and labor outcome. *Journal of Obstetrics and Gynecology* 22:513–515.
- Prince, J. M. 1995. Intersection of economics, history, and human biology: secular trends in stature in nineteenth century Sioux Indians. *Human Biology* 67:387–406.
- Prosser, C. L. 1973. Oxygen: respiration and metabolism. Pages 165–211 in C. L. Prosser, editor. *Comparative animal physiology*. W.B. Saunders Company, Philadelphia, Pennsylvania, USA.
- Purdue, J. R. 1987. Estimation of body weight of white-tailed deer (*Odocoileus virginianus*) from central Illinois. *Journal of Ethnobiology* 7:1–12.
- Purdue, J. R. 1989. Changes during the Holocene in the size of white-tailed deer (*Odocoileus virginianus*) from central Illinois. *Quaternary Research* 32:307–316.
- Purdue, J. R., M. H. Smith, and J. C. Patton. 2000. Female philopatry and extreme spatial genetic heterogeneity in white-tailed deer. *Journal of Mammalogy* 81:179–185.
- Purvis, A. 1995. A composite estimate of primate phylogeny. *Philosophical Transactions of the Royal Society B* 348:405–421.
- Purvis, A., J. L. Gittleman, G. Cowlishaw, and G. M. Mace. 2000. Predicting extinction risk in declining species. *Proceedings of the Royal Society B* 267:1947–1952.
- Quin, D. G., A. P. Smith, and T. W. Norton. 1996. Ecogeographic variation in size and sexual dimorphism in Sugar Gliders and Squirrel Gliders (Marsupialia: Petauridae). *Australian Journal of Zoology* 44:19–45.
- Rabinowitz, A. R., and B. G. Nottingham. 1986. Ecology and behaviour of the jaguar (*Panthera onca*) in Belize, Central America. *Journal of Zoology (London)* 210:149–159.
- Rao, S., and P. Apte. 2009. Social class-related gradient in the association of skeletal growth with blood pressure among adolescent boys in India. *Public Health Nutrition* 12:2256–2262.
- Rausch, R. L. 1963. Geographic variation in size in North American Brown Bears, *Ursus arctos* L., as indicated by condylobasal length. *Canadian Journal of Zoology* 41:33–45.
- Ray, C. 1960. The application of Bergmann's and Allen's rules to the poikilotherms. *Journal of Morphology* 106:85–108.
- Reimers, E., D. R. Klein, and R. Sørungård. 1983. Calving time, growth rate, and body size of Norwegian reindeer on different ranges. *Arctic and Alpine Research* 15:107–118.
- Richter, D. D., and L. I. Babbar. 1991. Soil diversity in the tropics. *Advances in Ecological Research* 21:316–389.
- Ricklefs, R. E. 1970. Clutch size in birds: outcome of opposing predator and prey adaptations. *Science* 168:599–600.
- Roberts, D. F. 1953. Body weight, race and climate. *American Journal of Physical Anthropology* 11:533–558.
- Roberts, D. F. 1978. *Climate and human variability*. Second edition. Cummings, Menlo Park, California, USA.
- Rodríguez, M. Á., I. L. López-Sañudo, and B. A. Hawkins. 2006. The geographic distribution of mammal body size in Europe. *Global Ecology and Biogeography* 15:173–181.
- Rolston, H., III. 1988. *Environmental ethics: duties and values in the natural world*. Temple University Press, Philadelphia, Pennsylvania, USA.
- Rooney, T. P. 2001. Deer impacts on forest ecosystems: a North American perspective. *Forestry* 74:201–208.
- Rooney, T. P., and D. M. Waller. 2003. Direct and indirect effects of deer in forest ecosystems. *Forest Ecology and Management* 181:165–176.
- Roseboom, T., S. de Rooij, and R. Painter. 2006. The Dutch famine and its long-term consequences for adult health. *Early Human Development* 82:485–491.
- Rosenzweig, M. L. 1966. Community structure in sympatric Carnivora. *Journal of Mammalogy* 47:602–612.
- Rosenzweig, M. L. 1968a. The strategy of body size in mammalian carnivores. *American Midland Naturalist* 80:299–315.
- Rosenzweig, M. L. 1968b. Net primary productivity of terrestrial communities: prediction from climatological data. *American Naturalist* 102:67–74.
- Rozzi, R. 1999. The reciprocal links between evolutionary-ecological sciences and environmental ethics. *BioScience* 49:911–921.
- Ruff, C. 2002. Variation in human body size and shape. *Annual Review of Anthropology* 31:211–232.
- Ruff, C. B. 1994. Morphological adaptation to climate in modern and fossil hominids. *Yearbook of Physical Anthropology* 37:65–107.
- Ruff, C. B., and A. Walker. 1993. Body size and body shape. Pages 234–265 in A. Walker, and R. Leakey, editors. *The Nariokotome Homo erectus skeleton*. Harvard University Press, Cambridge, Massachusetts, USA.
- Ryel, L. A., L. D. Fay, and R. C. Van Eiten. 1961. Validity of age determination in Michigan deer. *Michigan Academy of Science, Arts and Letters* 46:289–316.
- Samson, C., and J. Huot. 1995. Reproductive biology of female black bears in relation to body mass in early winter. *Journal of Mammalogy* 76:68–77.
- Sand, H., G. Cederlund, and K. Danell. 1995. Geographical and latitudinal variation in growth patterns and adult body size in Swedish moose (*Alces alces*). *Oecologia* 102:433–442.
- Saugier, B., J. Roy, and H. A. Mooney. 2001. Estimations of global terrestrial productivity: converging toward a single number? Pages 543–557 in J. Roy, B. Saugier, and H. A. Mooney, editors. *Terrestrial global productivity*. Academic Press, San Diego, California, USA.
- Scarr, S. 1981. Race, social class, and individual differences in I.Q.: new studies of old issues. Erlbaum, Hillsdale, New Jersey, USA.
- Scarr-Salapatek, S. 1971. Race, social class, and IQ. *Science* 174:1285–1295.
- Scarre, C., editor. 2009. *The human past: world prehistory and the development of human societies*. Second edition. Thames and Hudson, London, UK.
- Schaller, G. B., and J. M. C. Vasconcelos. 1978. Jaguar predation on capybara. *Zeitschrift für Säugetierk* 43:296–301.
- Schell, L. M., and P. D. Magnus. 2007. Is there an elephant in the room? Addressing rival approaches to the interpretation of growth perturbation and small size. *American Journal of Human Biology* 19:606–614.
- Schmidt, K. T., A. Stein, S. D. Albon, and F. E. Guinness. 2001. Antler length of yearling red deer is determined by population density, weather and early life-history. *Oecologia* 127:191–197.
- Schooley, R. L., C. R. McLaughlin, G. J. Matula, and W. B. Krohn. 1994. Denning chronology of female black bears: effects of food, weather, and reproduction. *Journal of Mammalogy* 75:466–477.
- Schreider, E. 1950. Geographical distribution of the body-weight/body-surface ratio. *Nature* 165:286.
- Scognamillo, D., E. Maxit, M. Sunquist, and J. Polisar. 2003. Coexistence of jaguar (*Panthera onca*) and puma (*Puma*

- concolor*) in a mosaic landscape in the Venezuelan llanos. *Journal of Zoology* 259:269–279.
- Sebastian, L. 1991. Sociopolitical complexity and the Chaco system. Pages 109–143 in P. L. Crown, and W. J. Judge, editors. *Chaco and Hohokam: prehistoric regional systems in the American Southwest*. School of American Research Press, Santa Fe, New Mexico, USA.
- Shackelford, L. L. 2007. Regional variation in the postcranial robusticity of Late Upper Paleolithic humans. *American Journal of Physical Anthropology* 133:655–668.
- Sheets, O. 1946. The relation of soil fertility to human nutrition. Mississippi State College, Agricultural Experiment Station Bulletin No. 437. Mississippi State, Mississippi, USA.
- Sherman, K., I. Belkin, K. D. Friedland, J. O'Reilly, and K. Hyde. 2009a. Accelerated warming and emergent trends in fisheries biomass yields of the world's large marine ecosystems. Pages 41–66 in K. Sherman, and G. Hempel, editors. *The UNEP large marine ecosystem report: a perspective on changing conditions in LMEs of the world's regional seas*. UNEP Regional Seas Report and Studies No. 182. United Nations Environment Programme, Nairobi, Kenya.
- Sherman, K., I. Belkin, K. D. Friedland, J. O'Reilly, and K. Hyde. 2009b. Accelerated warming and emergent trends in fisheries biomass yields of the world's large marine ecosystems. *Ambio* 38:215–224.
- Sherman, K., and G. Hempel, editors. 2009. *The UNEP large marine ecosystem report: a perspective on changing conditions in LMEs of the world's regional seas*. UNEP Regional Seas Report and Studies No. 182. UNEP, Nairobi, Kenya.
- Shipley, L. A., S. Blomquist, and K. Danell. 1998. Diet choices by free-ranging moose in relation to plant distribution, chemistry and morphology in northern Sweden. *Canadian Journal of Zoology* 76:1–12.
- Sikes, R. S., and M. L. Kennedy. 1992. Morphologic variation of the bobcat (*Felis rufus*) in the eastern United States and its association with selected environmental variables. *American Midland Naturalist* 128:313–324.
- Silva, M., and J. A. Downing. 1995. *CRC handbook of mammalian body masses*. CRC Press, Boca Raton, Florida, USA.
- Silver, S. C., L. E. T. Ostro, L. K. Marsh, L. Maffei, A. J. Noss, M. J. Kelly, R. B. Wallace, H. Gomez, and G. Ayala. 2004. The use of camera traps for estimating jaguar *Panthera onca* abundance and density using capture/recapture analysis. *Oryx* 38:148–154.
- Simard, M. A., S. Côté, R. B. Weladji, and J. Huot. 2008. Feedback effects of chronic browsing on life-history traits of a large herbivore. *Journal of Animal Ecology* 77:678–686.
- Sinclair, A. R. E. 1977. *The African buffalo: a study of resource limitation of populations*. University of Chicago Press, Chicago, Illinois, USA.
- Skogland, T. 1983. The effects of density dependent resource limitation on size of wild reindeer. *Oecologia* 60:156–168.
- Skogland, T. 1986. Density dependent food limitation and maximal production in wild reindeer herds. *Journal of Wildlife Management* 50:314–319.
- Skogland, T. 1990. Density dependence in a fluctuating wild reindeer herd; maternal vs. offspring effects. *Oecologia* 84:442–450.
- Smith, G. E., and W. A. Albrecht. 1941. Biological assays of soil fertility. *Proceedings of the Soil Science Society of America* 6:252–258.
- Smith, H. R. 1905. *Profitable stock feeding; a book for the farmer*. Published by the author, Lincoln, Nebraska, USA.
- Smith, M. H., and J. T. McGinnis. 1968. Relationships of latitude, altitude, and body size to litter size and mean annual production of offspring in *Peromyscus*. *Research in Population Ecology* 10:115–126.
- Smith, T., J. Earland, K. Bhatia, P. Heywood, and M. Singleton. 1993. Linear growth of children in Papua New Guinea in relation to dietary, environmental, and genetic factors. *Ecology of Food and Nutrition* 31:1–25.
- Smith, T. M., and M. A. Huston. 1989. A theory of the spatial and temporal dynamics of plant communities. *Vegetatio* 83:49–69.
- Soper, R. B., R. L. Lochmiller, D. M. Leslie, and D. M. Engle. 1993. Condition and diet quality of white-tailed deer in response to vegetation management in central Oklahoma. *Proceedings of the Oklahoma Academy of Science* 73:53–61.
- Soppela, P., and M. Neiminen. 2001. The effect of wintertime undernutrition on the fatty acid composition of leg bone marrow fats in reindeer (*Rangifer tarandus tarandus* L.). *Comparative Biochemistry and Physiology Part B* 128:63–72.
- Sousa, R. J. 1982. A national overview of wildlife management investigations funded by the Pitman-Robertson (P-R) Program. *Wildlife Society Bulletin* 10:254–258.
- Southwood, T. R. E. 1977. Habitat, the templet for ecological strategies. *Journal of Animal Ecology* 46:337–365.
- Southwood, T. R. E. 1988. Tactics, strategies and templets. *Oikos* 52:3–18.
- Steckel, R. H. 1983. Height and per capita income. *Historical Methods* 6:1–7.
- Steckel, R. H. 1995. Stature and the standard of living. *Journal of Economic Literature* 33:1903–1940.
- Steckel, R. H. 2000. Industrialization and health in perspective. Pages 37–57 in D. Leon, and G. Walt, editors. *Poverty, inequality, and health*. Oxford University Press, Oxford, UK.
- Steckel, R. H. 2001. Health and nutrition in the pre-industrial era: insights from a millennium of average heights in Northern Europe. Working Paper 8542, National Bureau of Economic Research, Cambridge, Massachusetts, USA. ([www.nber.org/papers/w8542](http://www.nber.org/papers/w8542))
- Steckel, R. H., and R. Floud, editors. 1997. *Health and welfare during industrialization*. University of Chicago Press, Chicago, Illinois, USA.
- Steckel, R. H., and J. M. Prince. 2001. Tallest in the world: Native Americans of the Great Plains in the nineteenth century. *American Economic Review* 91:287–294.
- Stewart, K. M., R. T. Bowyer, R. W. Ruess, B. L. Dick, and J. G. Kie. 2006. Herbivore optimization by North American elk: consequences for theory and management. *Wildlife Monographs* 167.
- Stiner, M. C. 1998. Mortality analysis of Pleistocene bears and its paleoanthropological relevance. *Journal of Human Evolution* 34:303–326.
- Stiner, M. C., N. D. Munro, T. A. Surovell, E. Tchernov, and O. Bar-Yosef. 1999. Paleolithic population growth pulses evidenced by small animal exploitation. *Science* 283:190–194.
- Stinson, S. 1990. Variation in body size and shape among South American Indians. *American Journal of Human Biology* 2:37–51.
- Stockhoff, B. A. 1993. Diet heterogeneity: implications for growth of a generalist herbivore, the Gypsy Moth. *Ecology* 74:1939–1949.
- Strickland, B. K., and S. Demarais. 2000. Age and regional differences in antlers and mass of white-tailed deer. *Journal of Wildlife Management* 64:903–911.
- Strickland, B. K., and S. Demarais. 2006. Effectiveness of the State Soil Geographic Database (STATSGO) to predict white-tailed deer morphometrics in Mississippi. *Wildlife Society Bulletin* 34:1264–1272.
- Strickland, B. K., and S. Demarais. 2008. Influence of landscape composition and structure on antler size of white-tailed deer. *Journal of Wildlife Management* 72:1101–1108.
- Subramanian, S. V., J. Kim, and I. Kawachi. 2005. Covariation in the socioeconomic determinants of self-rated health and happiness: a multivariate multilevel analysis of individuals and communities in the USA. *Journal of Epidemiology and Community Health* 59:664–669.
- Sunquist, M. E., and F. C. Sunquist. 2002. *Wild cats of the world*. University of Chicago Press, Chicago, Illinois, USA.

- Suttie, J. M., and J. R. Webster. 1995. Extreme seasonal growth in arctic deer: comparisons and control mechanisms. *American Zoologist* 35:215–221.
- Swift, R. W. 1948. Deer select most nutritive forage. *Journal of Wildlife Management* 12:109–110.
- Symonds, M. R. E., L. Christidis, and C. N. Johnson. 2006. Latitudinal gradients in abundance, and the causes of rarity in the tropics: a test using Australian honeyeaters (Aves: Meliphagidae). *Oecologia* 149:406–417.
- Symonds, M. R. E., and C. N. Johnson. 2006. Determinants of local abundance in a major radiation of Australian passerines. *Journal of Biogeography* 33:794–802.
- Taber, A. B., A. J. Novaro, N. Neris, and F. H. Colman. 1997. The food habits of sympatric jaguar and puma in the Paraguayan Chaco. *Biotropica* 29:204–213.
- Tanner, J. M. 1986. Growth as a mirror of the condition of society? Secular trends and class distinctions. Pages 3–34 in M. B. Dubue, and A. Demirjian, editors. *Human growth: a multidisciplinary review*. Taylor and Francis, London, UK.
- Teer, J. G. 1984. Lessons from the Llano Basin, Texas. Pages 261–290 in L. K. Halls, editor. *White-tailed deer ecology and management*. Stackpole Books, Harrisburg, Pennsylvania, USA.
- Teer, J. G., J. W. Thomas, and E. A. Walker. 1965. Ecology and management of white-tailed deer in the Llano Basin of Texas. *Wildlife Monographs* 15.
- Terborgh, J. 1983. *Five New World primates: a study in comparative ecology*. Princeton University Press, Princeton, New Jersey, USA.
- Thiollay, J.-M. 1988. Comparative foraging success of insectivorous birds in tropical and temperate forests: ecological implications. *Oikos* 53:17–30.
- Thorsland, O. A. 1966. Nutritional analyses of selected deer foods in South Carolina. *Proceedings of the Southeastern Association of Game and Fish Commissioners* 20:84–104.
- Toigo, C., J. M. Gaillard, G. Van Laere, A. J. M. Hewison, and N. Morellet. 2006. How does environmental variation influence body mass, body size, and body condition? Roe deer as a case study. *Ecography* 29:301–308.
- Torgerson, O., and W. R. Porath. 1984. Midwest oak/hickory forest. Pages 427–440 in L. K. Halls, editor. *White-tailed deer ecology and management*. Stackpole Books, Harrisburg, Pennsylvania, USA.
- Tremblay, J., I. Thibault, C. Dussault, J. Huot, and S. Côté. 2005. Long-term decline in white-tailed deer browse supply: can lichens and litterfall act as alternative food sources that preclude density-dependent feedbacks. *Canadian Journal of Zoology* 83:1087–1096.
- Trivers, R. L., and D. E. Willard. 1973. Natural selection of parental ability to vary the sex ratio of offspring. *Science* 179:90–92.
- Troost, T. A., B. W. Kooi, and U. Dieckmann. 2008. Joint evolution of predator body size and prey-size preference. *Evolutionary Ecology* 22:771–799.
- Trowell, H. C. 1949. Malignant nutrition (Kwashiorkor). *Transactions of the Royal Society of Tropical Medicine and Hygiene* 42:417–442.
- Trujillo, A. P., and H. V. Thurman. 2005. *Essentials of oceanography*. Eighth edition. Pearson/Prentice Hall, Englewood Cliffs, New Jersey, USA.
- Tucker-Drob, E. M., M. Rhemtulla, K. P. Harden, E. Turkheimer, and D. Fask. editors. 2011. Emergence of a gene  $\times$  socioeconomic status interaction on infant mental ability between 10 months and 2 years. *Psychological Science* 22:125–133.
- Turkheimer, E., A. Haley, M. Waldron, B. D'Onofrio, and I. I. Gottesman. 2003. Socioeconomic status modifies heritability of IQ in young children. *Psychological Science* 14:623–628.
- Tveraa, T., P. Fauchald, N. G. Yoccoz, R. A. Ims, R. Aanes, and K. A. Høgda. 2007. What regulates and limits reindeer populations in Norway? *Oikos* 116:706–715.
- Twombly, S., and N. Tisch. 2000. Body size regulation in copepods. *Oecologia* 122:318–336.
- Uehara, G., and G. Gillman. 1981. *The mineralogy, chemistry, and physics of tropical soils with variable charge clays*. Westview Press, Boulder, Colorado, USA.
- Ulrich, W., and C. Fiera. 2010. Environmental correlates of body size distributions of European springtails (Hexapoda: Collembola). *Global Ecology and Biogeography* 19:905–915.
- van Andel, T. H., W. Davies, and B. Weniger. 2003. The human presence in Europe during the Last Glacial Period I: migrations and the changing climate. Pages 31–56 in T. H. van Andel, and W. Davies, editors. *Neanderthals and modern humans in the European landscape during the last glaciation*. McDonald Institute for Archaeological Research, Cambridge University Press, Cambridge, UK.
- Van Deelan, T. R., K. M. Hollis, C. Anchor, and D. R. Etter. 2000. Sex affects age determination and wear of molariform teeth in white-tailed deer. *Journal of Wildlife Management* 64:1076–1083.
- van der Wal, R., R. Brooker, E. Cooper, and R. Langvatn. 2001. Differential effects of reindeer on high arctic lichens. *Journal of Vegetation Science* 12:705–710.
- van Noord, P. A. H., and S. Arias-Careaga. 1995. The Dutch Famine 1944–45: lasting effects on adult height. *American Journal of Epidemiology* 141:S11–S44.
- Van Valkenburgh, B. 1990. Skeletal and dental predictors of body mass in carnivores. Pages 181–205 in J. Damuth, and B. J. McFadden, editors. *Body size in mammalian paleobiology: estimation and biological implications*. Cambridge University Press, New York, New York, USA.
- Verme, L. J., and D. E. Ullrey. 1984. Physiology and nutrition. Pages 91–118 in L. K. Halls, editor. *White-tailed deer ecology and management*. Stackpole Books, Harrisburg, Pennsylvania, USA.
- Vrba, E. S. 1985. Environment and evolution: alternative causes of the temporal distribution of evolutionary events. *South African Journal of Science* 81:229–236.
- Wadsworth, M. E. J., R. J. Hardy, A. A. Paul, S. F. Marshall, and T. J. Cole. 2002. Leg and trunk length at 43 years in relation to childhood health, diet and family circumstances; evidence from the 1946 national birth cohort. *International Journal of Epidemiology* 31:383–390.
- Wallace, A. R. 1869. *The Malay Archipelago: the land of the Orang-Utan and the Bird of Paradise. A narrative of travel, with studies of man and nature*. Harper and Brothers Publishers, New York, New York, USA.
- Waller, D. M., and W. S. Alverson. 1997. The white-tailed deer: a keystone herbivore. *Wildlife Society Bulletin* 25:217–226.
- Watt, C., S. Mitchell, and V. Salewski. 2010. Bergmann's rule: a concept cluster? *Oikos* 119:89–100.
- Weaver, H. W. 2004. *Biometric analysis and aversive conditioning of black bears in southern West Virginia*. Thesis. West Virginia University, Morgantown, West Virginia, USA.
- Webb, S. D., and N. D. Opdike. 1995. Global climate influences on Cenozoic land mammal faunas. Pages 184–208 in S. M. Stanley, et al., editors. *Effects of past global change on life*. National Academies Press, Washington, D.C., USA.
- Weiss, N. A. 2002. *Introductory statistics*. Addison Wesley, Boston, Massachusetts, USA.
- Weladji, R. B., D. R. Klein, Ø. Holand, and A. Mysterud. 2002. Comparative response of *Rangifer tarandus* and other northern ungulates to climatic variability. *Rangifer* 22:29–46.
- Welch, C. A., J. Keay, K. C. Kendall, and C. T. Robbins. 1997. Constraints on frugivory by bears. *Ecology* 78:1105–1119.
- Wells, C. 1964. *Bone, bodies, and disease*. Thames and Hudson, London, UK.
- Wells, J. C. K. 2010. Maternal capital and the metabolic ghetto: an evolutionary perspective on the transgenerational basis of health inequalities. *American Journal of Human Biology* 22:1–17.
- Wenke, R. J. 1980. *Patterns in prehistory: humankind's first three million years*. Oxford University Press, Oxford, UK.



- Westlake, D. F. 1963. Comparisons of plant productivity. *Biological Review* 38:385–425.
- Westoby, M. 1981. The place of the self-thinning rule in population dynamics. *American Naturalist* 118:581–587.
- Whitelaw, N. C., and E. Whitelaw. 2008. Transgenerational epigenetic inheritance in health and disease. *Current Opinion in Genetics and Development* 18:273–279.
- Widdowson, E. M. 1951. Mental contentment and physical growth. *Lancet* June 16 1(6668):1316–1318.
- Widdowson, E. M., and J. C. Mathers, editors. 1992. The contribution of nutrition to human and animal health. Cambridge University Press, New York, New York, USA.
- Wigginton, J. D., and F. S. Dobson. 1999. Environmental influences on geographic variation in body size of western bobcats. *Canadian Journal of Zoology* 77:802–813.
- Wild, A. 1958. The phosphate content of Australian soils. *Australian Journal of Agricultural Research* 9:193–204.
- Williams, C. E., and A. L. Caskey. 1965. Soil fertility and cottontail fecundity in southeastern Missouri. *American Midland Naturalist* 74:211–224.
- Willig, M. R., D. M. Kaufman, and R. D. Stevens. 2003. Latitudinal gradients of biodiversity: pattern, process, scale and synthesis. *Annual Review of Ecology, Evolution, and Systematics* 34:273–309.
- Windell, J. T., J. W. Foltz, and J. A. Sarokan. 1978. Effect of fish size, temperature, and amount fed on nutrient digestibility of a pelleted diet by Rainbow Trout, *Salmo gairdneri*. *Transactions of the American Fisheries Society* 107:613–616.
- Wiseman, S. 1966. Environmental and innate factors and educational attainment. Pages 64–80 in J. Meade, and A. Parkers, editors. Genetic and environmental factors in human ability. Oliver and Boyd, London, UK.
- Wolverton, S. 2006. Natural-trap ursid mortality and the Kurten Response. *Journal of Human Evolution* 50:540–551.
- Wolverton, S. 2008. Harvest pressure and environmental carrying capacity: an ordinal scale model of effects on ungulate prey. *American Antiquity* 73:179–199.
- Wolverton, S., M. A. Huston, J. H. Kennedy, K. Cagle, and J. D. Cornelius. 2009a. Conformation to Bergmann's rule in white-tailed deer can be explained by food availability. *American Midland Naturalist* 162:403–417.
- Wolverton, S., J. H. Kennedy, and J. D. Cornelius. 2007. A paleozoological perspective on white-tailed deer (*Odocoileus virginianus texana*) population density and body size in central Texas. *Environmental Management* 39:545–552.
- Wolverton, S., and R. L. Lyman. 2000. Immanence and configuration in analogical reasoning. *North American Archaeologist* 21:233–247.
- Wolverton, S., R. L. Lyman, J. H. Kennedy, and T. W. La Point. 2009b. The terminal Pleistocene extinction in North America, hypermorphic evolution, and the dynamic equilibrium model. *Journal of Ethnobiology* 29:28–63.
- Wright, D. H. 1983. Species–energy theory: an extension of species–area theory. *Oikos* 41:496–506.
- Wright, D. H., D. J. Currie, and B. A. Maurer. 1993. Energy supply and patterns of species richness on local and regional scales. Pages 66–74 in R. E. Ricklefs, and D. Schluter, editors. Species diversity in ecological communities: historical and geographical perspectives. University of Chicago Press, Chicago, Illinois, USA.
- Wright, T., and E. Lundelius. 1963. Post-Pleistocene raccoons from central Texas and their zoogeographic significance. *Pearce-Sellards Series: Texas Memorial Museum* 2:1–21.
- Wurm, H. 1982. Über die Schwankungen der durchschnittlichen Körperhöhe im Verlauf der deutschen Geschichte und die Einflüsse des Eiweißanteils der Kost. *Homo* 33:21–42.
- Wurm, H. 1984. The fluctuation of average stature in the course of German history and the influence of the protein content of the diet. *Journal of Human Evolution* 13:331–334.
- Yokoyama, M., K. Kaji, and M. Suzuki. 2000. Food habits of sika deer and nutritional value of sika deer diets in eastern Hokkaido, Japan. *Ecological Research* 15:345–355.
- Yom-Tov, Y., and E. Geffen. 2006. Geographic variation in body size: the effects of ambient temperature and precipitation. *Oecologia* 148:213–218.
- Yom-Tov, Y., and H. Nix. 1986. Climatological correlates for body size of five species of Australian mammals. *Biological Journal of the Linnean Society* 29:245–262.
- Yom-Tov, Y., S. Yom-Tov, and G. Jarrell. 2008. Recent increase in body size of the American marten *Martes americana* in Alaska. *Biological Journal of the Linnean Society* 93:701–707.
- Zedrosser, A., B. Dahle, and J. E. Swenson. 2006. Population density and food conditions determine adult female body size in brown bears. *Journal of Mammalogy* 87:510–518.

#### SUPPLEMENT 1

Data on skull length for 44 species of carnivores and sources for the data used in Table 3 (*Ecological Archives* M081-014-S1).

#### SUPPLEMENT 2

Data and references for human height data used in Fig. 4B and F (*Ecological Archives* M081-014-S2).

#### SUPPLEMENT 3

Table of data and sources for information from large marine areas (LMEs) used in Figs. 8 and 10 and Table 7 (*Ecological Archives* M081-014-S3).

#### SUPPLEMENT 4

Unpublished data analysis of Missouri Raccoon study by Virginia Lee Sharpe, approximately 1943 (PDF of original report) (*Ecological Archives* M081-014-S4).

#### SUPPLEMENT 5

Additional material for terrestrial eNPP: Fig. 1, global natural forest aboveground eNPP, and Fig. 4A, global natural vegetation aboveground eNPP (excluding managed vegetation and wetlands) (*Ecological Archives* M081-014-S5).