



AN APPROACH TO BODY SIZE FLUCTUATIONS IN QUATERNARY CONTINENTAL MAMMALS: THE CASE OF HIPPOPOTAMUSES FROM WESTERN EUROPE

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ABSTRACT: Several paleoenvironmental analyses show that community change over geological time is driven by ecological factors which, in turn, are regulated by climate. To most effectively examine the origin of community change researchers need to single out and track specific paleobiological properties and to see how much they depend on local or more general constraints. A suite of proxies have been used to analyze ecologically based community change. Body size is one of the most sensitive to ecological factors and is therefore deemed to disclose significant information on past environmental conditions. Bergmann's rule proposes a thermoregulatory explanation to the latitudinal gradient of increasing animal body size. Whereas some animals fit the predictions of Bergmann's rule, others do not, or even correlate negatively. Several critical reviews cast doubts on the "thermal" interpretation of Bergmann's rule, and proposed alternative hypotheses for geographic variation in body size based on various physiological, biological and ecological constraints. The Ice Age cycling that was set off by the 2.6 Ma Arctic ice cap expansion led gradually to ever increasing environmental patchiness, and the effects of this habitat fragmentation became particularly evident in the Late Pleistocene and Holocene. Megafaunas progressively split up into metapopulations confined into ever smaller and more isolated habitats. This led numerous large mammals to experience endemic evolution in isolation, and body sizes changed in ways similar to those observed in land mammals distributed on true islands.

Keywords: Body size, Bergman's rule, Mammals, Climate change, Quaternary.

1. INTRODUCTION

The processes that cause community change over geological time have been one of the most investigated topics in paleoecology. To most effectively examine these processes researchers need to single out and track paleobiological properties unaffected by local constraints. Body size is most sensitive to ecological factors and can disclose significant information on past environmental conditions. The pattern and extent of body size change in Quaternary land mammals has often been connected to climatic change (Tchernov, 1968; Davis, 1977, 1981; Klein, 1986). Quaternary is actually characterized by particularly unstable conditions, with long-term cooling trends and glacial cycles of ever increasing amplitude. There are two major, relatively abrupt climate transitions: one just before its onset, around 2.7 Myr ago, of a major northern hemisphere glaciation, the other is the so-called "mid-Pleistocene revolution" (MPR; Berger & Jansen, 1994) when the dominant periodicity of glacial response switched from 41 to 100 kyr.

An equivalence can be established between the body size change of a specific taxon within a community over geological time, on the one hand, and the change of a phenotypic trait of an organism over geological time, on the other. As phenotypic changes reveal specific adaptations, so can body size changes provide information on the environmental modifications that caused them.

Bergmann's rule, pros and contras

Many studies have highlighted the coincidence of climate or latitude change with size changes in various

mammals. Bergmann (1847) observed a latitudinal increase in animal body size and proposed a thermoregulatory explanation to the phenomenon. Climate/latitude-induced size change is often connected to peculiar allometric responses. In 1877 Joel A. Allen gave the fundamentals of what was from then on known as Allen's rule observing that land mammals from colder climates usually develop shorter limbs than their counterparts from warmer climates. Subsequently re-examined and reformulated, the so-called Bergmann's rule (or mechanism *sensu* Meiri, 2011) was found to apply also to poikilotherm vertebrates, as well as to a number of invertebrate taxa (e.g., Ashton, 2002; Makarieva et al., 2005, and references therein), which however are not subject to the heat-conservation mechanisms underlying Bergmann's rule. McLean (1991) believes that large mammals store more heat than smaller mammals, but cannot release it as much easily owing to their relatively small surface/volume ratios. The rapid warming at the transition to an interglacial/interstadial phase causes greater embryogenesis dysfunction in larger mammals than in smaller ones (McLean, 1991). In these periods large mammals may therefore either disappear, experience dwarfing if they are given sufficient time to adapt to the new conditions, or otherwise reduce in size before becoming extinct (Kurtén, 1972; Guthrie, 1984). Meiri & Dayan (2003) reviewed the occurrence of Bergmann's rule in statistical samples of birds and mammals, observing that over 72% of the birds and 65% of the mammals they examined conform to it. Meiri et al. (2007) revised these results finding that the mean variation explained by latitude is 35% for birds and 37% for

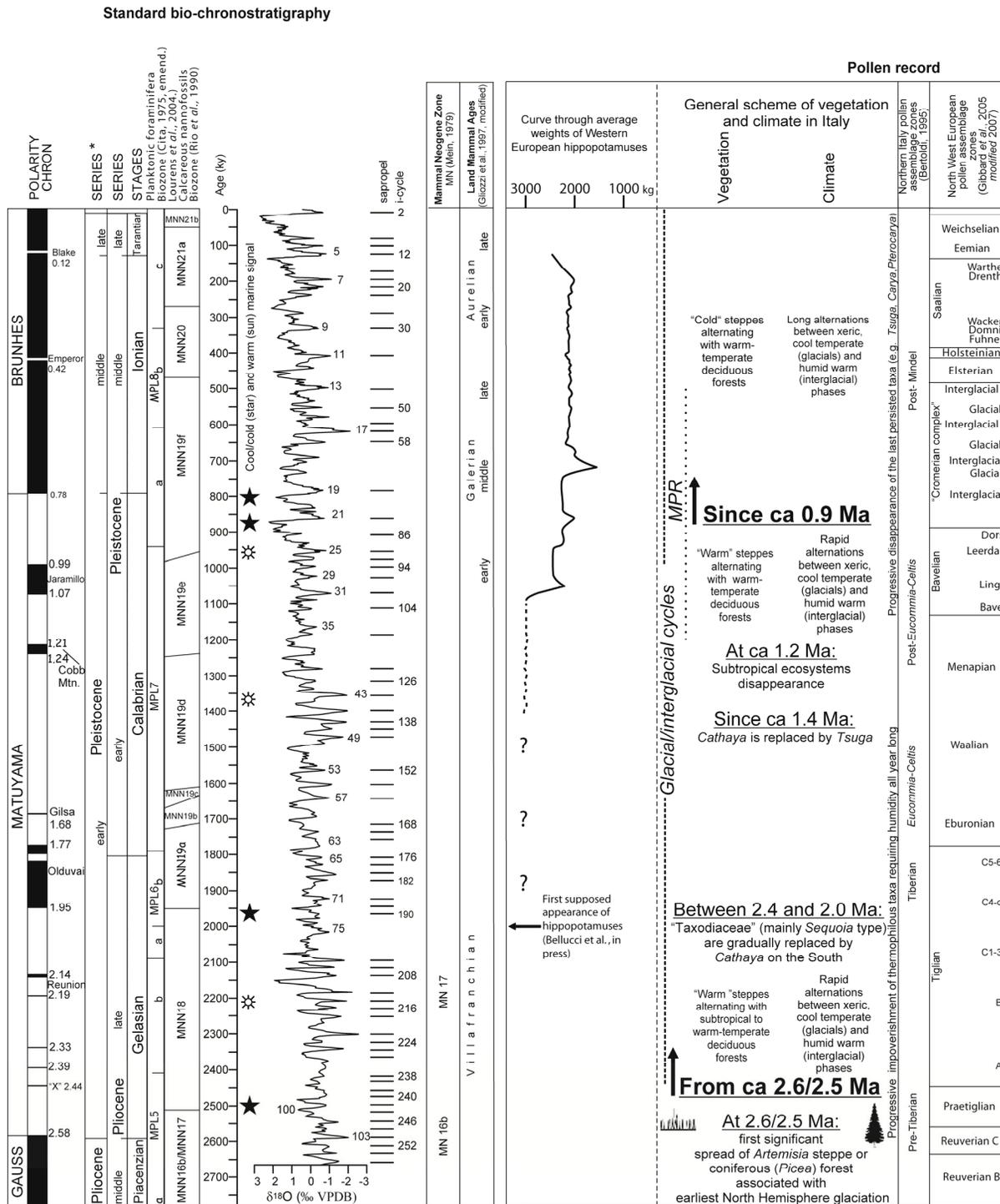


Fig. 1 - Curve through estimated average weights of Western European hippopotamuses, obtained from odontometric and osteometric data, as well as by using allometric scaling techniques (analysis in progress by the writers). Stratigraphic scheme modified from Bertini et al. (2010).

mammals. Meiri & Dayan (2003) had also found that birds tend to adhere to Bergmann's rule whatever their size, while smaller mammals (<500 g) conform significantly less than larger ones. The latter observation is consistent with the conclusions drawn by McDonald (1984), Martin (1984), Merilees (1984), and Ashton et al.

(2000), who found that large land mammals had been more sensitive to the climatic oscillations than smaller ones. Meiri et al. (2004) obtained a significantly positive correlation between skull length and latitude in 50% of 44 carnivore species they examined, and a significantly negative correlation in 11% of those species. Diniz-Filho

Species and specimens	Ortona	Colle Lepre	Valdarno	Colle Curti	Untermaßfeld	<i>H. gr. H. antiquus</i> (= <i>H. tiberinus</i>)	Incarcal I	<i>H. amphibius</i> (Barrington included)
upper M2 (Janis, 1990)	length x breadth (cm)	28.75		30.66				
	log	1.46		1.48				
	min length x breadth (cm)			22.56	25.3	23.04		18.49
	log			1.35	1.4	1.36		1.26
	max length x breadth (cm)			30.24	30.36	34.16		32.48
lower M2 (Janis, 1990)	length (cm)	5.48						
	log	0.74					6.32	
	min length (cm)			5	6.6	5.2		0.8
	log			0.7	0.82	0.71		
	max length (cm)			6.4	7	5.9		
	log			0.8	0.84	0.77		
Femur (allometric scaling: Schmidt-Nielsen, 1984; Reitz and Quitmyer, 1988; Prange et al., 1979)	DC (cm)	9.5				11.7		
	log	0.98				1.07		
	DC min (cm)			9.5	9.5	8.7		7.4
	log			0.98	0.98	0.94		0.87
	DC max (cm)			10.8	10.2	9.3		8.6
	log			1.03	1.01	0.97		0.93
Fifth metatarsal (allometric scaling: Schmidt-Nielsen, 1984; Reitz and Quitmyer, 1988; Prange et al., 1979)	length (cm)		9.92				9.3	
	log		0.99				0.97	
	min length (cm)			9.5	10	9.9	10.3	
	log			0.98	1.00	0.99	1.01	
	max length (cm)			11	10.7	10.8	10.9	
	log			1.04	1.03	1.03	1.04	
estimated weights (kg)	1000-2100	2200	2100-2750	2100-2600	2200-3200	1700-2750	2000	1260-3000

Tab. 1 - Body weight estimates

et al. (2007) have also analyzed patterns of body size geographic variation in European carnivores. Rodríguez et al. (2006) observed nonlinear relationships between body size and temperature, finding a strong association in northern Europe, and virtually none in the south. Kurlén (1968) and Huston & Wolverton (2011) propose the idea that mammal size is primarily connected with the amount and nature of food resources. Barnosky (2005) actually showed that most body-size reductions at the last glacial/interglacial transition were ecophenotypic rather than genotypic changes. Teplitsky et al. (2008) reached similar conclusions. In the light of these results, many authors have cast doubt on the "thermal" interpretation of Bergmann's rule, finding that body size is controlled by many other factors rather than just temperature. Some authors advocate various physiological, biological and ecological constraints [(1) vascular control and fur insulation (Scholander 1955; Steudel et al., 1994); (2) food availability (Huston & Wolverton, 2011);

(3) basal metabolic rate (Steudel et al., 1994); (4) energy costs (Thompson, 1942); (5) size and nature of food (Teplitsky et al., 2008); (6) dominance in a community (Hansson & Jaarola, 1989); (7) competition (Simberloff & Boecklen, 1981); (8) mating success (Lande & Arnold, 1983)]. Others suggest additional climatic factors, such as moisture levels, demonstrating that small body size is associated with hot and humid conditions while larger size is connected to cooler and drier circumstances (Rosenzweig, 1968; James, 1970). Yom-Tov & Nix (1986) and Yom-Tov & Geffen (2006) observed that body size correlates with moisture and precipitation, and thus with primary production, better than with temperature. Blois & Hadly (2009) linked body sizes to climate-change-related responses of vegetation and primary productivity. During the last decade, a wealth of studies analyzed the empirical validity of ecogeographic rules (Blackburn & Gaston, 1998; Blackburn et al., 1999; Angilletta & Dunham, 2003; Cruz et al., 2005; Millien et

al., 2006; Rodríguez et al., 2006, 2007; Gaston et al., 2007; Meiri & Gavin, 2007; Meiri et al., 2007; Aragón et al., 2010; Gardner et al., 2011). Many of these factors suggested as alternatives to Bergmann's rule could be more or less directly correlated, or at least influenced, by the environmental and climatic changes that occurred over the last 2 million years. Quaternary climate instability caused changes in the vegetation (e.g., Lang, 1994; Bertini, 2003, 2010; Tzedakis, 2003, 2007; González-Sampériz et al., 2010; Rodríguez-Sánchez et al., 2010; Joannin et al., 2011; Magri & Palombo, 2012), as well as the progressive fragmentation of the ecosystems, with consequences on the fauna that are described further on.

2. BODY SIZE CHANGE IN QUATERNARY HIPPOPOTAMUSES: A WESTERN EUROPEAN EXAMPLE

In Western Europe, the significant changes in temperature and precipitation ensuing from the maximum expansion of the Arctic ice cap that set off the Ice Age cycling caused the progressive demise of tropical and subtropical forest taxa, while altitudinal arboreal taxa and herbs spread, with the creation of new competition patterns (e.g., Suc et al., 1995; Bertini, 2010, Bertini et al., 2010; Fig. 1). Vegetational modifications clearly reflect substantial paleoecological and paleoclimatic reorganizations. Most commonly, but not exclusively (e.g., Bertini, 2010), *Artemisia* and *Ephedra*-dominated open vegetation alternated with interglacial forests characterized by deciduous taxa, such as *Quercus*, *Carya*, *Carpinus*, *Pterocarya*, *Ulmus* and *Zelkova* in response to the Early Pleistocene 41 kyr climatic cycling. A ca. 100 kyr (eccentricity) cycling, which started since the transition to the Middle Pleistocene, intensified the glacial phenomena, but also seasonality and aridity. This had disrupting consequences on both flora and fauna. Many resident animal taxa became extinct, whereas others were replaced by new incomers from eastern Europe, central Asia, and Africa. Some of the Western European inhabitants seem to have changed size in coincidence with climatic variations. Hippopotamuses might represent a good example (Fig.1). If the body sizes of European Quaternary hippopotamus are estimated from stratigraphically controlled remains, it seems that these pachyderms grew smaller from the Jaramillo subchron onwards (Table 1). During the second half of the Middle Pleistocene these suiforms turned progressively rarer, especially during the coldest phases of this interval (MIS 8, 6). At the beginning of the Late Pleistocene, during the very warm MIS 5e, large to very large hippopotamuses dispersed as far north as the British Isles. It is worth noting that Western European hippopotamuses grew smaller in coincidence with the MPR (~1.2±0.5 Ma) and just after the disappearance of the subtropical vegetal ecosystems from the Mediterranean area, around 1.2 Ma (e.g. Combourieu-Nebout & Vergnaud-Grazzini, 1991; Bertini, 2010). The great modifications in the structure and composition of vegetal formations induced by the long lasting glacial phases (up to 85 ka) and short interglacial phases (up to 15 ka) of this time period had significant consequences on the type and availability of food for the fauna. In a working hypothesis in preparation by the writers, hippopotamus-

es turned smaller under the prevalently cooler Middle Pleistocene conditions, in contrast to Bergmann's predicted pattern, as an indirect response to climatic change, owing to the unsteadiness in food availability. This would fully agree with Kurtén's (1968) and Huston & Wolverton's (2011) idea that mammal size is primarily connected with the amount and nature of food resources.

3. THE "INSULARIZATION" OF QUATERNARY CONTINENTAL MAMMALS

The MPR caused increasing habitat fragmentation (Simakova, 2001; Markova et al., 2001; Zazula et al., 2003), whose effects became particularly evident in the Late Pleistocene and Holocene. The mosaic evolution of plant communities, as habitats grew smaller and more isolated, turning into habitat islands (Lister & Bahn, 1994; Ward, 1997; Reumer, 2007), affected the evolutionary relationships between herbivores and the vegetation (Graham & Lundelius, 1984). Megafaunas progressively broke down into metapopulations.

As interbreeding became ever more infrequent, subpopulations were increasingly exposed to the effects of inbreeding, genetic drift as well as morphological change. When the intensity of interbreeding turned excessively low, evolutionary change tended to resemble that of insular settings (Schmidt & Jensen, 2003). Numerous mammals grew smaller (e.g., edentates, mastodons, wild boar, gazelle, goat, aurochs, bison, deer, fox, wildcat, spotted hyena, beech marten, burrowing mole rat, hedgehog, porcupine: Kurtén, 1965; Tchernov, 1968; Frenkel, 1970; Heller, 1970; McDonald, 1981; King & Saunders, 1984; Martin, 1993; Martin & Barnosky 1993; Wilson, 1996; Barnosky et al., 2003; Blackburn & Hawkins, 2004; Rodríguez et al., 2006, Cooper & Purvis, 2010; Saunders et al., 2010), with results somewhat fitting the predictions of the so-called Island Rule (Foster, 1964; Sondaar, 1977). Insular populations, both in true and ecological islands, are in fact under the control of strict genetic and ecological constraints (Lomolino et al., 2010).

As in true islands, in isolated ecosystems population densities are bracketed between a maximum number of individuals, determined by the carrying capacity of the environment, and a critical minimum number of individuals to prevent extinction. Large-sized animals seems to be left with no other choice but to decrease their size to lower selective pressure in insular isolation.

4. CONCLUSIONS

Because mammal body size is most sensitive to ecological factors, size changes are often considered as a useful proxy indicator to monitor climatic changes, not only in the past. In fact, declining body size has recently been considered the third universal response to climate, together with changes in phenology and distribution of species (Gardner et al., 2011). In his pioneer contribution Bergmann (1847) stirred debate over the relation between temperature and body size. The controversy peaked over the years, with convinced supporters and opponents both with shrill and convincing arguments on the merits or shortcomings of Bergmann's rule. Many

studies have admirably shown that mammalian body size is governed by, and responds to, a number of factors, which include temperature, precipitation and moisture, physiologic constraints, basal metabolic rate and energy costs, environmental carrying capacity (food availability), degrees of environmental stability, interspecific competition, predator-prey interaction, just to mention some. A body size that is thought to be diagnostic of a particular environmental situation may actually arise for different reasons, being the result of the interplay of an array of factors which may be, to various degrees, interdependent. Researchers involved with these issues are therefore confronted with a tangled network of related variables, which imposes to inquire each instance individually, on a case-by-case basis: model ("Rule") generalization is not easy to achieve. Today, researchers could have the unprecedented opportunity to test the effects of global warming on fast-reproducing animals (e.g., Gardner et al., 2011). Paleoclimatological analysis and oxygen isotope curves clearly show that, with the outstanding exceptions of particularly warm episodes (e.g., MIS 47, 37, 11, 9, 5e), Earth's climate has been progressively deteriorating over time, trending towards increasingly cooler and somewhat drier conditions. The escalating environmental patchiness during the Quaternary translated into habitat fragmentation, and this in turn caused the splitting up of populations into subpopulations or metapopulations. Owing to this parcelling of habitats and biotas, body size has been ever more under the influence of factors (e.g., food availability) that may not always operate or be accessible latitudinally, but rather areally, in accordance with the habitat specificity of the species (Meiri et al., 2007). Countless studies show that mammal body size change is a most effective sign of some ecological change, of whatever kind and degree (Aragon et al., 2010). And possibly even a predictor of environmental instability. Deepening our knowledge and understanding of this phenomenon can therefore be a promising direction for future research aimed at environmental monitoring.

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