



The natural selection of metabolism and mass selects allometric transitions from prokaryotes to mammals



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ABSTRACT

The exponents of inter-specific allometries for several life history (metabolism, lifespan, reproductive rate, survival) and ecological (population density, home range) traits may evolve from the spatial dimensionality (d) of the intra-specific interactive competition that selects net assimilated energy into mass, with $1/4$ exponents being the two-dimensional (2D) case of the more general $1/2d$ (Witting, 1995). While the exponents for mass-specific metabolism cluster around the predicted $-1/4$ and $-1/6$ in terrestrial and pelagic vertebrates, the allometries of mobile organisms are more diverse than the prediction. An exponent around zero has been reported for protists and protozoa (Makarieva et al., 2005, 2008), and the exponent appears to be strongly positive in prokaryotes with a value of about $5/6$ (DeLong et al., 2010).

I show that the natural selection of metabolism and mass is sufficient to explain exponents for mass-specific metabolism that decline from $5/6$ over zero to $-1/6$ in 3D, and from $3/4$ over zero to $-1/4$ in 2D. These results suggest that mass-specific metabolism is selected as the pace of the resource handling that generates net energy for self-replication and the selection of mass, with the decline in the metabolic exponent following from a decline in the importance of mass-specific metabolism for the selection of mass. The body mass variation in prokaryotes is found to be selected from primary variation in mass-specific metabolism, while the variation in multicellular animals is selected from primary variation in the handling and/or densities of the underlying resources, with protists and protozoa being selected as an intermediate lifeform.

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1. Introduction

It is difficult to overestimate the evolutionary importance of body mass allometries as they reveal the joint evolution of the life history with mass across the tree of life. The most well-known allometry is Kleiber (1932) scaling in multicellular animals, with a negative $1/4$ exponent for the dependence of mass-specific metabolism on mass. Yet, the real value, or rather values, of the exponent is still debated (e.g., McNab, 2008; White et al., 2009; Isaac and Carbone, 2010), and it is also uncertain whether the relationship between the two traits is a straight allometric line or a slightly bent curve (Hayssen and Lacy, 1985; Dodds et al., 2001; Packard and Birchard, 2008; Kolokotronis et al., 2010; Deeds, 2011; Ehnes et al., 2011; MacKay, 2011).

A value around $-1/4$ is though in general agreement with the average exponent for the basal (BMR) and field (FMR) metabolic rates across a wide range of vertebrates (e.g., Peters, 1983; Savage et al., 2004; Glazier, 2005; Duncan et al., 2007; Kabat et al., 2008; Capellini et al., 2010), and the exponents for BMR and FMR are statistically indistinguishable in most lineages of mammals (Capellini

et al., 2010). It is therefore reasonable to assume that a value close to $-1/4$ is acting as an attractor for the natural selection of the allometric relationship in many taxa, and that the value may vary somewhat with variation in the underlying mechanism of natural selection.

It is important to recall that the metabolic allometry is only one of several essential allometries, with the empirical exponents in many studies approximating $1/4$ for lifespan and reproductive periods, $-1/4$ for the rate of exponential population growth, $-3/4$ for the density of populations, and 1 for the area of the home range (Bonner, 1965; Schoener, 1968; Turner et al., 1969; Fenichel, 1974; Damuth, 1981, 1987; Peters, 1983; Calder, 1984). This existence of related exponents across several traits indicates that the evolution of allometries may be determined by a selection that involves not only a variety of life history traits, but also ecological traits like the density of the population and the home range of its individuals.

Allometries, however, are often studied for a single trait only, and the correlation between metabolism and mass is not only the most studied allometry empirically, it is also the most studied theoretically (reviewed by e.g. Glazier, 2005; White and Kearney, 2013). The widespread view has seen the allometry as a consequence of the physiology, where a physiological optimisation of

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metabolism in relation to resource transportation networks is the cause of the metabolic exponent (e.g. West et al., 1997, 1999a,b; Banavar et al., 1999; Dodds et al., 2001; Dreyer and Puzio, 2001; Rau, 2002; Santillán, 2003; Glazier, 2010). This explanation, however, suffers from a circular argument of contingency (Witting, 1997, 2008): as the overall physiology is optimised by natural selection it is *in principle* impossible to infer evolutionary causality from an observed physiological correlation. While it might be the metabolic exponent that evolves from the constraints of the evolved resource transportation network, it might just as well be the transportation network that is optimised to follow a metabolic allometry that reflects the primary selection of metabolism and mass (Witting, 1998).

The physiological hypothesis is also insufficient from another natural selection point of view, as it does not show how the primary selection of metabolism and mass is causing the evolution of the allometric relation between the two traits, and nor does it select the allometric exponents of other traits. Even if the allometric relation is seen to be naturally selected by a physiological optimisation that operates relatively independently of the natural selection of mass, it is essential to show that the allometric hypothesis is consistent with the natural selection of mass. But the selection of mass that has been connected with the physiological cause for the metabolic allometry (Brown and Sibly, 2006) is generally inconsistent with the inter-specific allometries of other traits. The assumed frequency-independent selection selects for an increase in average fitness [as given by the rate of exponential increase in population (r), or by the carrying capacity (K , denoted n^* in this paper)] with an increase in mass, but r and K are typically declining with mass across natural species (see Witting, 2017 for more details).

A more parsimonious explanation, where allometric exponents are selected by the natural selection of mass, was proposed as the theory of Malthusian Relativity prior to the physiological hypothesis (Witting, 1995, 1997). This mass selection hypothesis is parsimonious in the sense that it does not involve separate selection hypotheses for the selection of mass and the selection of allometries. The hypothesis assumes energy conservation and density-dependent population growth, where individuals meet more frequently in interactive competition as the abundance of the population increases. The interactive competition produces a density-frequency-dependent bias in resource assimilation in favour of the larger and competitively superior individuals, and this generates a population dynamic feed-back selection that selects the net energy that is obtained by foraging into non-negligible body masses. The assimilated net energy that is obtained by foraging is the essential component that drives the population dynamic feed-back selection of mass, with all of the above-mentioned allometric exponents following from the geometrical constraints (spatial dimensionality) of a foraging process that is optimised for a trade-off between the local resource exploitation of the individual and the density-dependent interactive competition between the individuals in the population.

With the predicted exponents following directly from a selection that is imposed by population growth and the conservation of energy, the mass selection hypothesis is deterministic in the sense that it avoids the circularity of contingent arguments (see review by Witting, 2008). There is no chicken and egg dilemma, where we somewhat arbitrarily need to choose one component of the phenotype (like the metabolic exponents) as an evolutionary function of another component (e.g., resource transportation networks). Apart from the life history constraints from population growth and energy conservation, and some initial conditions that does not affect the prediction, the mass selection model includes only the phenotypic properties that evolve directly from the natural selection of mass. And with the predicted exponents following from

the ecological geometry of foraging, their values are dependent on the spatial dimensionality (d) of foraging, with $1/4$ being the two-dimensional case of the more general $1/2d$. The $1/4$ value is replaced by $1/6$ for species that forage and interact in three dimensions, with a $1/4 \rightarrow 1/6$ like transition being observed quite commonly between terrestrial and pelagic animals (Witting, 1995, 1997).

The observed metabolic exponent is though more diverse than the predictions of the ecological mass selection model. The empirical exponent varies at least to some degree with mass (Kolokotronis et al., 2010), among major taxa and phylogenetic lineages (Peters, 1983; Glazier, 2005; Duncan et al., 2007; White et al., 2007a,b, 2009; Sieg et al., 2009; Capellini et al., 2010), and it is also dependent on the activity level of individuals (Darveau et al., 2002; Weibel et al., 2004; Glazier, 2005, 2008, 2009; Niven and Scharlemann, 2005; White et al., 2007a,b).

More recent studies have found that the exponent tends to change across the tree of life. Instead of being negative, it is strongly positive in prokaryotes with an apparent value around $5/6$ (DeLong et al., 2010), and it has been reported to be zero in protozoa (Makarieva et al., 2008; DeLong et al., 2010) and on the macro evolutionary scale across all non-sessile organisms (Makarieva et al., 2005, 2008; Kiørboe and Hirst, 2014).

This variation is not explained by Witting (1995, 1997) where the selection of mass is dealt with independently of the primary selection of mass-specific metabolism. I extend the mass selection model with primary selection on mass-specific metabolism to examine if the joint selection of metabolism and mass will explain the wider set of allometries that is observed across the tree of life.

2. Basic selection relations

The proposed model is developed to explain the evolution of metabolism, mass, and exponents of inter-specific allometries as they are selected by the intra-specific interactive ecology between individuals in populations. The basic assumptions are the conservation of energy, the demography of age-structure, and the unfolding of interactive competition from the density-dependent growth of the population. Deviations in the interactive ecology from the assumed may select for alternative allometries, but this is not studied directly in the paper.

I will not attempt to explain absolute trait values, but only the selection response of the life history and the ecology to the primary selection of mass-specific metabolism and mass. This is done by two processes that I refer to as metabolic-rescaling and mass-rescaling selection. Metabolic-rescaling is associated with the primary selection of metabolism that generates net energy for the selection of mass, and mass-rescaling is the selection response of the life history and the ecology to the evolutionary changes in mass. Both selection responses are described by the first partial derivatives of the evolving traits with respect to the selected changes in metabolism and mass, with the integrals over mass being the inter-specific body mass allometries.

This level of explanation resembles the Newtonian tradition in physics, where we can explain the acceleration of an object, but not its absolute speed, from the action of a force. In order to use the proposed model to “predict” e.g. an absolute rate of reproduction, we will have to include an observed survival rate as an assumption. The explanation is then no longer deterministic, but contingent upon the observed life history.

To show that the allometric exponents follow from the primary selection of metabolism and mass I define all the exponents with unknown values. The allometries with unknown exponents are then included in a mathematical formulation of the selection process on metabolism and mass, with the resulting equations

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