$\iota^{**}=7/3\psi$

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Body mass allometries caused by physiological or ecological constraints?

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Two recent papers[1,2] on allometries have received much attention in Nature[3], Science[4], and most recently in TREE[5]. Non of these five articles[1−5] reefer to other recent studies[6,7] that question the conclusions in (1) and (2). I briefly describe some of the problems with the two studies.

Kozlowski and Weiner[1] argue that interspecific allometries are secondary relations resulting from body mass optimisation and intraspecific allometries. West et al.[2] deduce the 3/4 exponent of the interspecific metabolic allometry from the physiological constraints associated with branching vascular systems arguing that ecological allometries, like that of population density and homerange, are secondary relations following from more fundamental physiological constraints. These studies are contrasted by Witting[6,7] that deduce the exponents of 4 physiological (metabolic rate, lifespan, lifetime reproduction, and intrinsic growth rate) and 4 ecological (population density, homerange, biomass, and population energy use) interspecific allometries together with the exponent of one intraspecific allometry (lifetime reproduction) from the foraging process in mobile organisms. This deduction shows that interspecific allometries can be more fundamental than intraspecific allometries, that the evolutionary equilibration of the body mass optimisation process can be determined by the interspecific allometries, and that physiological allometries, like that of metabolism and lifespan, can follow from more fundamental ecological constraints.

Kozlowski and Weiner's explanation, that interspecific allometries follow from intraspecific allometries, suffers from a chicken and egg problem: the intraspecific allometries from which they calculate the interspecific allometries are given by assumption instead of being deduced from first principles. Hence, they do not shown that the intraspecific allometries can exist independently of the interspecific allometries, and therefore it seems a bit premature to conclude that intraspecific allometric relations are more fundamental than interspecific allometries. The studies of West et al.[2] and Witting[6,7], on the other hand, deduce interspecific allometries from first principles showing that they can exist independently of intraspecific allometries suggesting that interspecific allometries are more fundamental than intraspecific allometries.

However, physiological hypotheses, as proposed by West et al., imply that interspecific and intraspecific allometries are expected to be identical[1,7]. This is not supported by evidence where, e.g., the allometric exponent for lifetime reproduction is different at the two levels[7]. This difference is explained by Witting's ecological framework, where the intraspecific exponent for reproduction follows from the evolutionary equilibration of the selection gradient on body mass, a gradient that ultimately is determined by the interspecific allometries[7].

Another problem with the physiological hypothesis is that the branching pattern of vascular systems is a phenotypic trait that is evolutionarily plastic because it is evolutionarily determined. Hence, we may expect that the branching of vascular systems is so evolutionarily flexible that it contains no evolutionary constraints that can determine the allometric exponents. Would it not be more obvious if the branching pattern had evolved so that it obeys allometric laws imposed by constraints that cannot evolve, e.g., because they lie outside the phenotype of the organism. Witting[6] proposes such a model by deducing the allometric exponents from ecological constraints.

One important fact supports the ecological hypothesis at the cost of the physiological hypothesis: The ecological hypothesis predicts that the 3/4 exponent for the metabolic rate and the 1/4 exponent for lifespan apply only across organisms that forage in two spatial dimensions, while these exponents are 5/6 and 1/6 for organisms foraging in three dimensions. This pattern is not expected from the physiological hypotheses, but the prediction holds for mammals where the exponent is 0.25 $\pm$0.04 (SE) among 195 species of terrestrial mammals (that forage in two horizontal dimensions) while it is 0.16 $\pm$0.02 (SE) among 40 species of pelagic mammals

(that forage also in the extra vertical dimension)[6,7]. Further data[6,7] suggests that the allometric distinction between two and three dimensional foragers is a general principle separating terrestrial from pelagic organisms. Hence, it seems to be the ecology that drives the physiology, and not the other way around as assumed since 1883 where Rubner proposed the first explanation for the metabolic allometry.

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