Evolution of animal body size: a cautionary note on assessments of the role of energetics

Clinal variation in the body sizes (masses) of animals with temperature, altitude and/or latitude is apparent in many species (e.g. Mayr 1956). Explanations of these phenomena have often been based on the energetic consequences of size (mass) in different thermal environments (e.g. Bergmann 1847; Hesse, Allee & Schmidt 1937; Rensch 1960; Mayr 1963). These early explanations however were principally based on fallacious interpretations of the negative relation between mass-specific energy expenditure and body mass, or the negative relation between mass-specific thermal conductance and body mass (exposed as fallacious arguments by Scholander 1955 and McNab 1971). Although more recent explanations have overcome the objections to the mass-specific approach (e.g. Searcy 1980; Lindstedt & Boyce 1985), these models are also generally flawed.

Despite accounting for costs in relation to the ability to store fat (Searcy 1980; Lindstedt & Boyce 1985) the expressions used to reflect such relationships were mostly based on interspecific comparisons, rather than intraspecific variations in mass, and these different scales are not necessarily comparable.

In a recent paper, Millar & Hickling (1990) have clarified many of the problems with these earlier models. Furthermore they derived several testable hypotheses of the expected direction of selection on size in relation to the predictability in the level of food supply, which may be a covariate of latitude, altitude and temperature. These predictions are based on intraspecific scaling relationships of energy expenditure, and capacity for fat storage to mass, and hence represent an improvement over previous treatments. They suggested, firstly, that larger animals will be selected for in unpredictable environments. This is because the scaling exponent of fat storage to mass is greater than that of energy expenditure to mass, and hence larger animals have greater ‘fasting endurance’ which will make them more able to survive periods of food shortage. Secondly, they suggested that when resources are at low levels but are continuously and predictably available, small size would be favoured because of the lower maintenance costs per individual small animal. Where resources are predictable and abundant then no selection on body size is predicted.

By highlighting the inadequacies in previous models and providing hitherto unavailable data on the intraspecific scaling of energy expenditure and fat storage to mass, Millar & Hickling’s paper represents a useful addition to the literature. Nevertheless there are several problems with the model they present which invalidate the specific hypotheses which were generated. In this forum article several of these inadequacies are discussed.

I shall assume that energetics is the major factor influencing the evolution of body size. This is by no means apparent in natural populations but the principal problems in the model derived by Millar & Hickling do not lie in the fact that energetic arguments might not be important, but rather in the restriction of the interpretation of the exact energetic consequences of body size (mass) to the effects on fasting endurance.

All energetics models for the evolution of body size depend on the consequences of body size for energy balance, and the consequences of energy balance for survival and fecundity. In the scenario of an unpredictable environment, Millar & Hickling (1990) considered only the consequences of body mass on energy balance during periods of food shortage, and hence potential mortality from starvation. Their model predicts selection for increased body size (Millar & Hickling — Fig. 1b) because the intraspecific exponent of the relation between fat storage and mass (averaging 1.45) exceeds the intraspecific exponent relating daily food intake (assumed to be equivalent to energy expenditure) to mass (averaging 1.09). In an unpredictable environment, however, there are also periods when food is available. Millar & Hickling considered these periods, but only to the extent that sufficient food would need to be available during them to replace that used up as fat during the starvation periods. Where this is not the case they suggested survival in the environment would be untenable (Millar & Hickling — Fig. 1d). This interpretation of the role of periods when food is available is too simplistic. Selection on body size may also occur for energetic reasons when food is available, and most importantly the direction of such selection may be reversed when compared with selection during periods of starvation (see below for detailed argument of direction of selection when food is available). In unpredictable environments, therefore, body size will depend not only on the selection for large size during starvation, but rather the directions, intensities and balance of selective forces during periods when food is, and is not, available. There is consequently no unambiguous prediction of the direction of selection on body size in an unpredictable environment as implied by Millar & Hickling (1990). Each environment may have an optimal body size which reflects the trade-off, in these opposing selective pressures, and such optima may vary spatially, leading to size clines, or temporally.

A second potential problem in the starvation
model of Millar & Hickling (1990) concerns the use of scaling exponents which reflect food intake of unstarved animals to derive the cost function. First, this assumes the animals are neither growing nor withdrawing reserves, as intake represents the sum of expenditure and production. However, more importantly, it is well established that during starvation animals compensate by reducing the level of resting metabolism (e.g. Westerterp 1977). The extent to which such responses differ between large and small animals is obscure but may affect the energy cost exponent and hence may compromise the predicted direction of any inferred selection on body size, during periods of starvation.

In a predictable environment, where food is always available, but in restricted quantities, Millar & Hickling (1990) suggest the low costs of maintenance for smaller animals will favour evolution of small size (Millar & Hickling — Fig. 1c). This interpretation, however, fails to take into account the effects of mass on all aspects of the energy budget equation, and hence energy balance. In particular this prediction assumes that capacity for food intake (assimilation or E/T in the model) is independent of mass (b = 0). Such independence is unlikely, since, amongst other things larger animals will have larger alimentary tracts and hence capacity to process food. Moreover, larger animals may also be more capable of competing for or defending resources. The scaling exponent of the relationship between food intake (assimilation) and body mass is of critical importance. Where this exponent exceeds the exponent of energy expenditure in relation to mass, excess energy, which can then be devoted to reproduction, will scale positively with mass and hence large body size will be favoured. Where the exponent sizes are reversed small sizes will be selected for. The exact relationships between mass and energy gains and costs are likely to depend on a wide range of ecological and species-specific factors, and hence there is no unambiguous prediction of the direction of selection on size in an environment with a predictable food supply.

The complex nature of the interactions between energy costs and energy gains and their dependence on body mass, leads to an inability to produce unambiguous predictions of the effects of environmental variables such as temperature, altitude and unpredictability in food supply on body size. This may explain why these variables have no consistent effects on the direction of size clines in wild populations of animals (McNab 1971; Geist 1987). An alternative explanation, however, is that energetics has not been important in the evolution of body size and size clines.

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References

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The fasting endurance hypothesis revisited

The fasting endurance hypothesis to explain the evolution of mammalian body size (Millar & Hickling 1990) suggests that the interplay between food requirements, fasting endurance, and food availability in the environment can explain the evolution of both larger and smaller body sizes. The hypothesis assumes that, within populations, large individuals have, on average, greater food requirements, but also greater fasting endurance than small individuals. If these assumptions are true, then periods of chronic food shortage will select against the smallest individuals first because they have the poorest fasting endurance. Alternatively, if food is always available, but in limited amounts, the largest individuals will be selected against first because they cannot meet their high food requirements. Thus, food shortages can favour large or small individuals, depending on the nature of the food shortage. Of course, smaller sizes can be favoured only if the population does not encounter chronic food shortages for extended