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APPENDIX A

Cost of Locomotor Activity

Calculations based on the allometric relations between body mass and minimum cost of transport, daily travel distance and daily energy expenditures in mammals indicated that the "ecological cost of transport" (i.e., percent of daily energy budget spent for covering daily travel distance) is rather low (Garland 1983). The estimates ranged from about 1% in mouse-sized mammals to 15% in large carnivores. If this were true, even a large increase in locomotor activity would cause only a small increase in total energy expenditure.

For several reasons, however, it seems that the above calculations underestimate the real cost of locomotor activity. First, the minimum cost of transport used in the calculations includes only the so-called "incremental" part of the total costs of locomotion (Garland 1983). The total cost of transport is always higher, especially when the speed is low. Second, the estimates of the cost of transport were based on measurements of animals running on treadmills at a constant speed and with a steady-state metabolic rate. When locomotor activity occurs in bursts of several seconds, excess post-exercise oxygen consumption (EPOC) may be responsible for more than 90% of the total cost of the activity (Baker & Gleeson 1998). For both of the above reasons, the estimates of the costs of locomotor activity based on distance travelled can be much lower than the estimates based on the

time of the activity (Koteja *et al.* 1999b).

More direct estimates also show that the cost of locomotion in free living animals can be much higher than predicted from the above allometric comparisons. For example, in the ground squirrel (*Spermophilus saturatus*) the estimated net costs of locomotion amounted to 13% of total daily energy expenditure (Kenagy & Hoyt 1989), 10 times more than predicted from the above allometric comparisons.

In free living African wild dogs (*Lycaon pictus*), the cost of hunting comprises 80% of daily energy expenditures (Gorman *et al.* 1998). If the time spent hunting increased from the observed 3.5 hours/day to 8 hours/day - which does not seem to be an unreasonable time budget (Bunnell & Harestad 1990) - the total daily energy expenditures would be 100% higher. Such a big increase would require an enhancement in the digestive system, with a consequent increase in the resting metabolic rate, and a further increase in the total energy expenditure. Even more convincing are the results obtained in Alaskan sled dogs (Hinchcliff *et al.* 1997). During a 70 hour race the rate of energy expenditure was more than four times higher than the value measured in similarly fit, non-exercising individuals. Moreover, untrained, sedentary dogs had a rate of energy expenditure two times lower than the trained dogs had. Thus, as assumed in the model, the ability to sustain high rates of daily energy expenditure is associated with increased resting metabolic rates.

The results obtained in the canids seem particularly interesting in the context of the evolution of endothermy in mammalian lineage, because Late Permian theriodont therapsids and Triassic cynodonts, the ancestors of mammals, were dog-sized, active carnivores (Ruben 1995).

Comparisons of active-hunters with ambush-predators among reptiles also indicate that the costs of activity are an important part of the energy budget. The former have higher daily energy expenditures and also higher resting metabolic rates (Anderson & Karasov 1981, Huey *et al.* 1984,

Nagy *et al.* 1984, Secor & Nagy 1994). For example, in a widely foraging coachwhip (*Masticophis flagellum*) the costs of movement comprise at least 18% of daily energy expenditures, and other locomotor-related activities (e.g., prey handling, burrowing) - additional 39% of DEE. In a sit-and-wait foraging sidewinder (*Crotalus cerastes*), DEE was 2.5 times lower, and RMR was 40% lower, than in the coachwhip (Secor & Nagy 1994).

Phenotypic Correlations Between BMR, Limits to Energy Budgets, and the Capacity of Visceral Organs

Several authors have suggested that the capacity of visceral organs (alimentary tract, liver, kidneys) sets a physiological limit to long term, sustainable energy budgets (see reviews: Weiner 1992; Hammond and Diamond 1997). Alternatively, it has been suggested that the capacity of viscera is regulated at the level corresponding to current energy needs (e.g. Hammond *et al.* 1994; McDevitt & Speakman 1994; see review: Hammond & Diamond 1997). At any rate, a close correlation between the capacity of the visceral organs and the maximum rate of energy assimilation or maximum sustainable metabolic rate has been observed at the levels of within-individual phenotypic flexibility, variation among individuals, and variation among species (e.g., Daan *et al.* 1990; Hammond & Diamond 1997; Konarzewski & Diamond 1994; Koteja 1996; Speakman & McQueenie 1996; Piersma & Lindström 1997).

The cost of maintaining visceral organs, measured as respiration of the organs, was estimated in a few species of mammals (see review: Wieser 1986; unfortunately, no comparable data are available for reptiles or birds). The cost is indeed very high. For example, in humans 40% of the resting metabolic rate is generated by the viscera, although the organs comprise less than 5% of the body mass. Thus, positive correlations between the size of the organs and BMR, and between BMR

and SuMR, seem warranted. Empirical data, however, do not present a clear picture.

Several studies have shown that at the periods of high energy demand, such as lactation or intensive locomotor effort, the increased capacity for energy processing is accompanied by an increased basal metabolic rate (e.g., Speakman & McQueenie 1996; Piersma *et al.* 1996; Hinchcliff *et al.* 1997). However, cold acclimated mice (*Peromyscus*, *Apodemus*) had an increased capacity for energy assimilation without having their BMR significantly increased compared to non-acclimated individuals (Koteja 1995, 1996). Correlations at the level of phenotypic variation among individuals are also equivocal. In a few species of rodents, the correlations between BMR and: the size of visceral organs, maximum rate of energy assimilation, and energy expenditures of free living animals, were either clear or ambiguous or absent (e.g. Konarzewski & Diamond 1994; Koteja 1995, 1996; Speakman & McQueenie 1996; Meerlo *et al.* 1997). The low correlation coefficients found in these intraspecific studies can be partly explained by the low repeatability of the traits measured. This is particularly true for estimates of energy expenditures of free living animals (Berteaux *et al.* 1996).

Interspecific studies indicated a positive correlation between the size of metabolically active organs (heart, kidneys, liver) and BMR in birds (Daan *et al.* 1990) and in lizards (Garland 1984; Garland & Else 1987). Daily energy expenditures are correlated with BMR in mammals (Koteja 1991; Ricklefs *et al.* 1996), but in birds the correlation is weaker or even not significant (Daan *et al.* 1990; Koteja 1991; Lindström & Kvist 1995; Ricklefs *et al.* 1996). However, both in mammals and in birds the ratio of SuMR to BMR falls in a narrow range of 4 to 7 (Ricklefs *et al.* 1996; Hammond and Diamond 1997), as compared to 6 - 35 or a larger range for the aerobic capacity scope. Thus, as assumed in the model presented in this study, the basal metabolic rate seem to be more tightly related to the capacity for energy assimilation and daily energy expenditures than to a

short-term capacity for aerobic metabolism.

Additional References

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