Available online at www.sciencedirect.com
SCIENCE DIRECT®
Hormones and Behavior 43 (2003) 16–17
Hormones and Behavior
www.elsevier.com/locate/yhbeh

Commentary

How useful is energy balance as a overall index of stress in animals?

Glenn E. Walsberg

Department of Biology, Arizona State University, Tempe, AZ 85287-1501, USA

Drs. McKewen and Wingfield present a valuable set of messages regarding the concept of stress in physiology. For far too long and much too frequently, as they make clear, the term "stress" has been used in confusing and ambiguous fashions. The conceptual framework subsuming allostasis has the potential to avoid such problems and allow animal function to be analyzed in a more sophisticated and useful manner.

I detect, however, a significant conceptual weakness in the reliance their paper places upon the balance between energy expenditure and intake as a determinant or index of "stress" or allostatic load. Although the authors recognize that this is an oversimplified case, I am concerned that this use may amplify the unfortunately common tendency to take an unrefined view of the balance between energy intake and output as an index of primary biological importance. Such an approach to stress physiology and animal energetics has several large-scale problems, including the following.

(1) Under normal conditions in nature, animals are rarely—if ever—actually in net energy balance except in the context of a very restricted set of time scales.

The typical condition is for food consumption to be episodic and metabolic power consumption to be continuous. Therefore, even the existence of net energy "balance"—much less its significance—depends upon the time scale over which intake and output are averaged. The biologically appropriate time scale varies greatly between taxa. For small endotherms such as many birds which have limited energy storage capacities compared to their high rates of power consumption, the animal may have to approximately balance its energy budget over a 24-h cycle. For ectotherms, in contrast, rates of power use often are so low that they can be supported by body fat stores for many months. For such forms, the annual cycle may be the appropriate time scale for calculation of energy budgets. Negative energy balance for prolonged portions of the annual cycle in many amphibians and reptiles, for example, is the normal condition and an *a priori* assumption of physiological stress would seem unwarranted (e.g., Henen, 1996; Nagy, 1988).

(2) Energetic issues may be of secondary importance to animals and thus energy balance can be of limited utility as an index of physiological stress.

Two examples will suffice. Perhaps the simplest is the classic case of desert mammals, for whom the overwhelming challenge through much of the annual cycle may be the acquisition and conservation of water, and energy balance *per se* is a secondary concern (Walsberg, 2000).

A second example includes animals that are limited during important phases of their life cycle by their dietary intake of nutrients despite ample access to food energy intake. During molt, for example, small birds may be critically limited by their dietary intake not of energy but of sulfur-containing amino acids such as cystine that are required for keratin synthesis. In white-crowned sparrows (*Zonotrichia leucophrys*), diets that are fully adequate for maintenance of energy balance during nonmolting periods produce serious declines in the body mass of molting birds if the food contains inadequate concentrations of sulfur-containing amino acids. This occurs even if food is supplied *ad libitum* (Murphy and King, 1984a,b).

(3) The balance between energy intake and output may be altered greatly in an individual without inducing what is usefully viewed as stress.

Indeed, such shifts may be mechanisms for mitigating or avoiding significant physiological challenges. A familiar

doi:10.1016/S0018-506X(02)00033-8

example is the hyperphagia and great increases in body fat stores characteristic of birds preparing for migration (Biebach, 1996). A second example is the normal use of fasting, and consequent declines in body mass and energy stores, by a variety of animals as a mechanism for mitigating stresses. This includes the classic case of adaptive anorexia in domestic fowl (*Gallus domesticus*; Mrosovsky and Sherry, 1980). Incubating birds are presented with conflicting demands to spend time foraging and attending the nest. Chickens moderate this conflict by reducing their appetite and, thus, time spent foraging. This reduction in appetite means that they lose body mass during incubation, even if food is made so readily accessible that they can feed without having to leave the nest. Thus, a negative energy balance in this case is not an indication of stress but rather a mechanism for coping with a physiological challenge. Similar use of voluntary fasting and negative energy balance for prolonged periods as a mechanism for alleviating competing demands upon the animal is a conspicuous feature of the reproductive biology of a variety of vertebrates (e.g., Ankney et al., 1991; Costa and Williams, 1999).

An incomplete mechanical analogy that illustrates some of the problems of evaluating an animal's status based upon an unadorned accounting of energy balance is to consider the intake and expenditure of chemical potential energy in an automobile. Like animals, vehicles in use refuel periodically yet use energy constantly; only rarely are they in instantaneous net energy balance. The significance of the rate at which fuel is expended or acquired depends upon several variables. Is power consumption limiting the car's ability to meet challenging conditions and continue performing adequately, or is the limit produced by some other mechanical system? What is the quality and cost of the fuel available? How much fuel is stored in the vehicle compared to the distance to the next available refueling? The significance of a high fuel consumption rate differs drastically, for example, between two vehicles if one has fuel reserves of 100 liters and is only 1 km from a fueling station while the other has 1 liter of fuel and is 100 km from a refueling site.

In summary, one cannot assume that the simple balance of energy intake and output is a reliable index of even the energetic stresses on an animal, much less the universe of other physiological challenges or stresses which the organism may face. That is, animals can be faced with simultaneous challenges from limited availability or quality of many types of resources (e.g., energy, time, protein, or micronutrients) and it is not yet possible to express these in a common currency such as energy balance. Such broad-scale problems regarding the context and significance of energy intake and output present, I suggest, difficulties of at least the same magnitude as the concepts of stress and homeostasis discussed by Drs. McEwen and Wingfield.

References

Ankney, C.D., Afton, A.D., Alisauskas., R.T., 1991. The role of nutrient reserves in limiting waterfowl reproduction. Condor 93, 1029–1032.

Biebach, H., 1996. Energetics of winter and migratory fattening, in: Carey, C. (Ed.), Avian Energetics and Nutritional Ecology, Chapman and Hall, New York, pp. 280–323.

Costa, D.P., Williams, T.E., 1999. Marine mammal energetics, in: Reynolds, J., Twiss, J. (Eds.), The Biology of Marine Mammals, Smithsonian Institution Press, Washington, DC.

Henen, B.T., 1996. Seasonal and annual energy budgets of female desert tortoises (*Gopherus agassizii*). Ecology 78, 283–296.

Mrosovsky, N., Sherry, D.F., 1980. Animal anorexias. Science 207, 837–842.

Murphy, M.E., King, J.R., 1984a. Sulfur amino acid nutrition during molt in the white-crowned sparrow. I. Does dietary sulfur amino acid concentration affect the energetics of molt as assayed by metabolized energy? Condor 86, 314–323.

Murphy, M.E., King, J.R., 1984b. Sulfur amino acid nutrition during molt in the white-crowned sparrow. II. Nitrogen and sulfur balance in birds fed graded levels of the sulfur-containing amino acids. Condor 86, 324–332.

Nagy, K.A., 1988. Seasonal patterns of water and energy balance in desert vertebrates. J. Arid Envi. 14, 201–210.

Walsberg, G.E., 2000. Small mammals in hot deserts: some generalizations re-visited. Bioscience 50, 109–122.