

Introduction to the Symposium: Energetics and Animal Behavior¹

JOHN L. GITTLEMAN

*Department of Zoology and Graduate Programs in Ecology and Ethology,
University of Tennessee, Knoxville, Tennessee 37916*

AND

STEVEN D. THOMPSON

*Department of Zoological Research, National Zoological Park,
Smithsonian Institution, Washington, D.C. 20008*

Energy is the currency most often employed in analyses of animal behavior (Townsend and Calow, 1981). Short-term studies of, for example, foraging behavior have mainly dealt with the energetic cost/profit ratios of particular strategies while more evolutionarily oriented studies, for example sex allocation theory, have considered the long-term effects of short-term energetic expenditures. In both types of study, some measure of energy expenditure relative to energy gain is assumed to be positively correlated with fitness (*e.g.*, Clutton-Brock *et al.*, 1982). Thus, behavioral biologists have interests in energy use that converge on those of many physiological ecologists and comparative physiologists (see also Altmann, 1987). Historically, comparative physiologists have been primarily concerned with interspecific differences in energy use that might be attributed to either phylogeny or form and function (*e.g.*, Calder, 1984). Animal behaviorists, on the other hand, have been interested in co-opting physiological data for application to behavioral variation; this has often been with the specific goal of confirming that the time allocated to energetically expensive behaviors is minimized (*e.g.*, Tinbergen, 1951; Hinde, 1960).

In recent years physiological ecology has emerged as a discrete discipline, albeit with its roots still in comparative physiology, focused on the integration of physiology (usually energetics) with the ecology of free-living organisms (Townsend and Calow,

1981; Tracy and Turner, 1982). The physiological ecologist of the 1970s frequently sought to measure and compare the physiology of specific behaviors, measured under controlled laboratory conditions and often evaluated in isolation from the complete behavioral profile. In the 1980s, physiological ecologists are more concerned with gaining a complete understanding of overall energetic strategies. Thus, they now strive to understand the relationships between laboratory and field measurements of energetics and to develop and apply new means of examining the energetics of free-living individuals (*e.g.*, Bennett, 1986). As physiology becomes more field oriented, it is apparent that detailed analyses of physiological strategies, and the relationship between variation in such strategies and fitness, must go hand in hand with detailed studies of behavior.

Parallel to recent developments in the physiological approach to ecology, animal behaviorists have built complex models (*e.g.*, Clutton-Brock *et al.*, 1982; Altmann, 1984; Davies and Houston, 1984) which seem increasingly contingent upon the energetic costs of both general categories of behavior (*e.g.*, locomotion) as well as specific behaviors (*e.g.*, running, trotting, hovering). While many behaviorists are unaware of the capabilities that now exist for measurement of energetics costs of specific behaviors, others have taken such measurements at face value and incorporated them into their models without due consideration of the limitations in the data and the reservations of physiological ecologists. One particular problem is the misleading use of allometric equations to analyze

¹ From the Symposium on *Energetics and Animal Behavior* presented at the Annual Meeting of the American Society of Zoologists, 27-30 December 1986, at Nashville, Tennessee.

physiological parameters. While such equations identify and describe general trends, their predictive value is limited with respect to the precise requirements of most energetic hypotheses. There is great potential for erroneous conclusions arising from extrapolation of allometric trends to species that differ substantially (in behavior, ecology, or phylogeny) from those in the original allometric analyses. The energetic consequences of behavioral events are of extreme importance in our understanding of animal behavior and physiological ecology. At this point in time, one of the more important questions is whether the cost of specific behaviors affects their frequency in nature (*e.g.*, are energetically expensive behaviors minimized?). For example, reproductive behaviors and costs are particularly critical to our understanding of how sex allocation, sexual dimorphism, and mating strategy relate to fitness; yet, for lack of direct measurements, many behavioral and life history models assume that reproduction is very expensive relative to other behaviors. Thus, variation in reproductive patterns (litter size, frequency, and composition) is often attributed to the great expense of reproduction (*e.g.*, Clutton-Brock *et al.*, 1982; Congdon *et al.*, 1982). Although there have been several attempts to describe general relationships between costs and behaviors, the variability in behavioral energetics suggests that for any given species, specific behaviors may pose unique energetic constraints (*e.g.*, Bennett and Houck, 1983 *vs.* Beissinger, 1987).

The papers in this symposium reflect a cross section of approaches and perspectives on the integration of physiological ecology and animal behavior. One of the main themes of the symposium is that behavioral studies supplemented with direct physiological measurements can often lead to results that were initially counterintuitive. In particular, phylogenetically or ecologically similar species may have similar behavioral patterns with drastically different energetic consequences; this may even be true for the same species (or population) between years. We hope

that this symposium will encourage direct testing of the widespread presumptions that energetic data may be readily generalized between species and that behavior patterns are energetically costly.

ACKNOWLEDGMENTS

We are grateful to the Animal Behavior Society for sponsoring this Symposium and to the American Society of Zoologists (particularly Mary Adams-Wiley and Beth Goldfarb) for making the organization run smoothly. Financial support was received from the following sources: American Society of Zoologists; Department of Zoology and Graduate Programs in Ecology and Ethology (University of Tennessee); Department of Zoological Research, National Zoo (Smithsonian Institution).

REFERENCES

- Altmann, S. A. 1984. What is the dual of the energy-maximization problem? *Am. Nat.* 123:433-441.
- Altmann, S. A. 1987. The impact of locomotor energetics on mammalian foraging. *J. Zool.* 211:215-225.
- Beissinger, S. R. 1987. Mate desertion and reproductive effort in the snail kite. *Anim. Behav.* 35: 1504-1519.
- Bennett, A. F. 1986. Measuring behavioral energetics. In M. E. Feder and G. V. Lauder (eds.), *Predator-prey relationships*, pp. 69-80. University of Chicago Press, Chicago.
- Bennett, A. F. and L. D. Houck. 1983. The energetic cost of courtship and aggression in a plethodontid salamander. *Ecology* 64:979-983.
- Calder, W. 1984. *Size, function, and life history*. Harvard University Press, Cambridge.
- Congdon, J. D., A. Dunham, and D. W. Tinkle. 1982. Energy budgets and life histories of reptiles. In C. Gans and H. Pough (eds.), *Biology of the Reptilia*, pp. 233-265. Academic Press, London.
- Clutton-Brock, T. H., F. E. Guinness, and S. D. Albon. 1982. *Red deer*. University of Chicago Press, Chicago.
- Davies, N. B. and A. I. Houston. 1984. Territory economics. In J. R. Krebs and N. B. Davies (eds.), *Behavioral ecology*, pp. 148-169. Sinauer, Sunderland.
- Hinde, R. A. 1960. Energy models of motivation. *Symp. Soc. Exp. Biol.* 14:199-213.
- Tinbergen, N. 1951. *The study of instinct*. Clarendon Press, Oxford.
- Townsend, C. R. and P. Calow (eds.) 1981. *Physiological ecology*. Sinauer, Sunderland.
- Tracy, C. R. and J. S. Turner. 1982. What is physiological ecology? *Ecol. Bull.* 63:340-347.