5 Measuring Behavioral Energetics

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1. Introduction

Energy is often regarded as the primary medium of biological exchange between an organism and its environment (e.g., see Townsend and Calow, 1981). Even if energy is not seen as the ultimate determinant of biological interactions, it is surely a factor of significance that an animal must take into account. From a theoretical perspective, an animal may be expected to maximize net energy intake and minimize energy expenditure, thereby maximizing growth and/or reproduction. During predation, for instance, a predator might attempt to capture a prey if the product of the net energetic gain available and the probability of capture exceeds the cost of the capture attempt. As prey are almost always energy-rich in comparison to the behavioral cost of obtaining them, we might anticipate that a predator should always make a capture attempt if only energetic grounds are considered. In comparison, a prey organism, standing to lose everything by being consumed, should be willing to commit any amount of energy to escape successfully.

Such theoretical predictions are not terribly helpful to our understanding of behavioral interactions. In particular, they do not recognize intrinsic (i.e., physiological or anatomical) limitations on energy expenditure in different kinds of organisms (Bennett et al., 1984; Chapters 2, 4, 6). The metabolic systems of some animals, particularly ectothermic animals, place strong constraints on rates of energy utilization and constrain potential behavioral responses (Bennett, 1980; Pough, 1983). Only by actual measurement of energy

expenditure can we know the real cost that animals can and do commit to a behavioral interaction such as predation. This essay examines methodologies available for making such experimental observations. These are discussed with reference to their practicality under both field and laboratory conditions.

The discussion of this topic is divided into the measurement of the energetics of sustainable behaviors, those that can be maintained for long periods of time, and non-sustainable behaviors, in which the animals rapidly tire and sometimes exhaust. This distinction is made because both the methodologies involved and the ecological questions of interest are different for the two intensities of activity. The level of exertion or work that distinguishes sustainable from non-sustainable behavior varies greatly among animals as a function of their capacity for oxygen consumption; sustainable behaviors must be supported aerobically. For instance, sustainable running speeds of mammals are nearly ten times greater than those of lizards (Bennett and Ruben, 1979; Garland, 1982), a reflection of the substantially higher levels of maximal oxygen consumption of the former. When aerobic capacities are exceeded, supplementary anaerobic metabolism is activated. Anaerobic metabolism, for reasons not yet understood, results in rapid tiring and exhaustion. Thus, these behavioral distinctions are largely determined by the type of metabolic energy utilization. The methods for measuring aerobic and anaerobic metabolism are very different and will be detailed in the next two sections.

The questions of energetic interest also are different for these two metabolic modes. For either aerobic or anaerobic metabolism, it is possible to stipulate the cost of a behavioral act, either in joules or high energy phosphate equivalents. For meaningful biological interpretation, this cost must be placed within a broader energetic context for the organism. For aerobic metabolism, it seems to me that there are two important contexts: the total energy budget and the maximal oxygen consumption. In the former case, it is possible to stipulate how expensive a behavior is to the animal as a percentage of its daily energy expenditure. Does it represent a major drain on energy resources or is it a trivial expense? If it is expensive, we might expect physiological, morphological, and/or behavioral adjustments to minimize those costs. If it is cheap, such adaptations might not be expected, at least on energetic grounds alone. Comparisons of actual with maximal oxygen consumption permit us to determine the percentage of an animal's aerobic scope that the behavior entails. If the behavior requires oxygen consumption close to the upper limits of delivery, the animal runs the risk of activating anaerobic metabolism with its ensuing exhaustion. If

rates of oxygen consumption are nearly maximal, the behavior may be an important factor in maintaining maximal oxygen consumption at its present level.

Because of its brevity, anaerobically-supported behavior does not make a significant impact on an animal's total energy expenditure. Even though it may involve rates of substrate utilization and high energy phosphate formation far higher than those of aerobic metabolism (see Bennett, 1978; Gatten, 1985), it is undertaken for such brief periods that it has little significance in terms of an energy budget. The only exceptions are exposure to long-term hypoxia or anoxia, and these are only arguably "behaviors." The questions of interest in regard to anaerobic metabolism are whether it is activated at all and whether it approaches the total possible anaerobic energy delivery (the anaerobic capacity, as defined by Bennett and Licht [1972]) with its consequent exhaustion. We might expect behaviors to be structured such that anaerobiosis might be avoided altogether. If intense activity is required and anaerobic metabolism must be activated, we might expect the behavior to be limited in duration and intensity such that potential exhaustion is carefully avoided.

Although the focus of this symposium is on predator-prey interactions, the techniques discussed here are applicable to a variety of other behavioral activities, such as territorial defense, courtship, or foraging. Hence, the scope of this article is more all-inclusive regarding the measurement of behavioral costs in general.

2. Measuring the Energetics of Sustainable Behaviors

Behavioral energetics may be determined either under natural field or controlled laboratory conditions. Both have their advantages and difficulties. From an ecological point of view, it is always more desirable to undertake measurements under field conditions, where an animal is exposed to its natural environment. However, this situation may place impossible demands on analytical techniques. The artificiality of the laboratory environment must be balanced against opportunities to undertake carefully controlled measurements of energy exchange.

Several methods have been used to determine the costs of sustainable behaviors under field conditions. These involve either direct or indirect measures of gas exchange or measurement of variables correlated with gas exchange. It is generally impractical to collect expired gases from an animal active under field conditions without grossly disrupting its behavior. This has been done successfully on sea

turtles by Jackson and Prange (1979), who were able to measure the cost of egg laying and of routine locomotion in situ on tropical beaches. This was an impressive achievement, but probably says more about the single-mindedness of sea turtles than about the general applicability of the method.

In recent years, gas exchange under field conditions has been successfully measured indirectly with isotopically-labelled water. Injected isotopes of hydrogen and oxygen are removed over time from an animal's body fluids and metabolic rate can be calculated from their differential elimination (see Nagy [1975] for a discussion of the technique). The use of doubly-labelled water has provided considerable information on daily or weekly rates of energy utilization by free-ranging animals. However, the technique generally lacks the resolution required for measurement of the cost of discrete bouts of behavior. There is an insufficient decrease in isotopic concentrations over the short time courses of most behaviors of interest, particularly in ectothermic animals with low metabolic rates. In addition, because the technique measures carbon dioxide production rather than oxygen consumption, measurements over short time intervals can be greatly influenced by respiratory alkalosis or metabolic acidosis. Measured values would not in these instances indicate true metabolic rate. There would, of course, be great problems in obtaining samples of body fluids immediately before and after a desired behavior. Finally, the technique is inappropriate for most aquatic organisms because of the rapid rates of isotopic loss. Its use, therefore, in measuring behavioral energetics is necessarily limited to situations involving prolonged behaviors and high metabolic rates. It has been used to measure the cost of flight in birds (e.g., Flint and Nagy, 1984; Lefevre, 1964) and might be useful to estimate foraging costs of a widely ranging animal over an entire day or night.

Various attempts have been made to estimate metabolic costs by telemetering physiological variables correlated with oxygen transport, e.g., heart rate or breathing rate. Such variables have the advantage of being easily detected in free-ranging animals, and simultaneous visual observations of behavior would permit an estimation of energetic cost. The problem with the method is the lack of tightness of the association of the measured variable and metabolic rate. A close positive association between a variable and oxygen consumption is not sufficient if a large amount of residual variability remains unexplained. The relationship may vary considerably among individual animals and even within a single individual at different times (Hargrove and Gessaman, 1973; Johnson and Gessaman, 1973). On the whole, this approach is

not promising. It requires extensive validation experiments prior to field use without any guarantee that the method can in fact be employed.

None of the previously described techniques holds out much hope for permitting determination of behavioral energetics under field conditions. At present, the outlook for successful and unambiguous studies is bleak unless new methods are developed.

The costs of sustained activity under laboratory conditions are measured by oxygen consumption during either locomotion on a treadmill (or wind tunnel or flow tank) or a staged behavioral event. Both approaches have been very successful in accumulating data on behavioral energetics.

Oxygen consumption increases as locomotor speed increases. Gas exchange is measured by the change in oxygen partial pressure in the respiratory medium as it passes by the animal. The exact form of the relationship between metabolic rate and speed depends on body size, medium, and locomotor mode (see Schmidt-Nielsen, 1984). It is possible to predict from general allometric equations the cost of moving at any speed knowing only the type of animal in question and its mass (see, for example, Taylor et al., 1982). If greater accuracy is desired, experimental measurements can be made on the species or even the individuals of particular interest. Such measurements, made under steady state conditions, should accurately reflect the costs of such sustained behaviors as fish migration or bird flight. Estimated costs may also be used in theoretical models to evaluate the energetic significance of a particular locomotor behavior (e.g., see Garland [1983] regarding the cost of foraging in mammals). The only difficulty in applying this approach is that it is limited to forward locomotion at constant speed, and many behaviors do not take this form.

A second approach, which is less dependent on steady state locomotor activity, is the direct measurement of oxygen consumption during a behavioral event. This is usually done with the animal or animals in a chamber that is big enough to permit unrestrained behavior but small enough to permit a measurable decrement in oxygen partial pressure. If the chamber is completely sealed, samples of the medium can be removed immediately before and after the behavior and analyzed for total oxygen consumption during the event. In this case, care should be taken to avoid hypoxia, and instantaneous rates of oxygen consumption are not obtained. If the medium is monitored and recirculated through the sealed chamber, hypoxia remains a potential problem but instantaneous rates can be determined (Bartholomew et al., 1981). A flow-through system avoids potential hypoxia, but requires

a sufficient decrement in oxygen partial pressure to permit accurate determination of oxygen consumption. This situation often requires such low flow rates that the response of the system is too slow to permit discrete analysis of metabolic costs. A closed system is usually recommended.

The chamber approach has obvious limitations that exclude behaviors of animals of large body size (e.g., cost of combat by male elk) or behaviors that require considerable space (e.g., flight costs for birds). However, for small animals that will perform behaviors in small, enclosed quarters, the technique can be highly successful. It has been used, for example, to measure the cost of burrowing in toads (Seymour, 1973) and gophers (Vleck, 1979); calling by frogs (Bucher et al., 1982; Taigen and Wells, 1985), katydids (Stevens and Josephson, 1977), and cicadas (MacNally and Young, 1981); pre-flight warmup in moths (Bartholomew et al., 1981); courtship and aggression in salamanders (Bennett and Houck, 1983); and construction of foam nests by frogs (Bucher et al., 1982; Ryan et al., 1983). In my opinion, this technique has been underutilized in studies of behavioral energetics. Its technical problems have already been solved and numerous, interesting problems remain to be investigated. These include, for example, the cost of singing by birds, territorial aggression in fish, prey consumption by snakes, and territorial displays by lizards, to name only a few.

3. Measuring the Energetics of Non-sustainable Behaviors

Intense activity demands rates of energy utilization above the capacity of the aerobic metabolic systems. Supplementary anaerobic metabolism provides for that energy delivery but results in endproduct accumulation and ultimate and often rapid fatigue. Anaerobic metabolic pathways vary in different taxa (Bennett, 1978; Hochachka and Somero, 1984). Lactic acid production, for instance, is restricted to chordates, crustaceans and some arachnids and annelids. Among molluscs, bivalves accumulate a variety of endproducts during anoxic exposure, including succinate and proprionate; cephalopods form octopine during activity. Insects do not use anaerobic metabolism, at least in their flight muscles.

Most measurements of anaerobic metabolism during activity have been undertaken on vertebrates, although a parallel series of observations is now being made on crustaceans (e.g., Burke, 1979; Full and Herreid, 1984; McMahon et al., 1979) and spiders (e.g., Prestwich, 1983). These have usually involved determination of lactic acid

accumulation, lactic acid being the principal anaerobically-formed endproduct in all these animals. Depletion of high energy phosphate stores may also contribute to anaerobic energy production but this is more difficult to analyze and has not often been attempted: a significant depletion of phosphocreatine was found in tadpoles during burst swimming (Gatten et al., 1984) and changes in total high energy phosphate pools have been demonstrated by nuclear magnetic resonance in an active lizard (Smith and Schmidt, 1983). The latter technique, while potentially promising for in vivo metabolic measurements, currently has substantial difficulties in quantification of compound interconversions and in excessively long sampling times. Lactate, in contrast, is easily measured in either body fluids or tissue samples by spectrophotometric techniques. For use in the measurement of anaerobic energetics, it is best to analyze the accumulation of lactate in the entire body of the animal (Bennett and Licht, 1972). Due to the compartmentalization of lactate formation and elimination, sampling only one body compartment (e.g., blood) is definitely less desirable and involves many assumptions about lactate distribution. Measurements of total body lactate formation involve determination of the lactate content of a group of animals before a behavioral event and the content of another group that has engaged in the behavior. An alternate design might involve measurement of a series of post-active groups after different durations or intensities of behavior. The technique has two primary difficulties. First, pre- and post-active determinations cannot be done on the same individual animals. Consequently, careful attention to pre-active controls is necessary. Second, the method is restricted to animals of small body size (i.e., under 1 kg). For larger animals, blood sampling is an inferior but still feasible technique as long as the limitations on estimating total lactate formation are recognized.

The utilization of anaerobic metabolism under free-ranging field conditions can be determined by measuring lactate concentrations in post-active animals. Blood samples are sufficient if only a qualitative result is desired; total body content is better if the specification of the quantity of joules or high energy phosphate equivalents is required. Samples taken under field conditions must be preserved immediately on collection by freezing in liquid nitrogen or by homogenization in a protein-precipitating acid. Measurements of anaerobic metabolism under free-ranging conditions have not been made frequently. This is another area in which a considerable amount of work remains to be done. Significant lactate accumulation has been found in lizards during natural activity and staged territorial encounters in the field (Bennett et

al., 1981; Pough and Andrews, 1985a), in frogs in a breeding chorus
(Pough and Gatten, 1984; but see also Ryan et al., 1983 and Taigen and
Wells, 1985), in crocodiles during escape behavior (Bennett et al.,
1985), in sea turtles during egg laying (Jackson and Prange, 1979), and
in hibernating turtles (Gatten, 1981). Many natural behaviors thus
appear to entail some anaerobic metabolism. It does not appear to be a
system that is restricted for use only under desperate circumstances but
rather one that is frequently used as a supplement to aerobic energy
provision. However, the amount of lactate formed is usually low in
comparison with the animal's capacity for lactate formation. Animals
appear to structure their behavior to avoid extensive anaerobiosis with
its consequent fatigue. Surprisingly, the circumstance in which
anaerobic metabolism does appear to be avoided by free-ranging
animals is that in which it was first described under laboratory
conditions: diving. Most freely-diving animals undertake relatively short
dives that can be supported by aerobic metabolism, reserving
anaerobiosis only for extended dives or underwater emergencies
(Kooyman et al., 1981; Seymour, 1982).

The use of anaerobic metabolism during a behavioral sequence can
also be determined in the laboratory. This can be done under
unrestricted conditions allowing free behavior. This approach has been
used to measure the anaerobic energetics of a predator-prey encounter
between garter snakes and salamanders (Feder and Arnold, 1982). Both
animals have significant amounts of lactic acid formation and the
salamanders approach fatiguing levels during their escape attempts.
Newborn garter snakes also use their full anaerobic capacity during
escape attempts (Arnold and Bennett, 1984). Measurements of lactate
formation and oxygen consumption may be made simultaneously on
animals active in closed chambers (as described previously). In this
circumstance, the relative importance of aerobic and anaerobic
energetic inputs can be measured simultaneously and the total cost of
the behavior determined. This approach has been used to analyze the
cost of courtship and aggression in a salamander (Bennett and Houck,
1983), nest construction, including fertilization and oviposition, by
frogs (Ryan et al., 1983), and feeding by a lizard (Pough and Andrews,
1985b). Anaerobic metabolism does occur under these circumstances,
but its energetic contribution is very small in comparison with that of
aerobic metabolism. Again, it seems to me that these approaches have
much to contribute to our understanding of the energetics of and
metabolic support for behavior. They should be more widely utilized
than they are.

4. Conclusions

We cannot trust our intuitive sense of how expensive a behavior might be. Some activities are surprisingly costly. Who, for example, would have anticipated that a calling frog raises its metabolic rate 400 to 2400% above resting levels (Bucher et al., 1982; Taigen and Wells, 1985)? Conversely, other expenses may seem low. Daily levels of free-ranging energy utilization exceed standard or basal levels by only 100 to 200% in a variety of different animal groups (King, 1974; Nagy, 1982). We might have anticipated that the costs of natural behavior, thermoregulation, growth, etc., would be considerably higher than these values indicate. It is simply not acceptable to assign metabolic costs by sheer guesswork (e.g., Orians' [1961] supposition of the cost of bird song and its subsequent incorporation into energy budget models, such as that of Schartz and Zimmerman [1971]). Additionally, the source of metabolic support may be poorly anticipated. The avoidance of anaerobic metabolism by diving animals (Seymour, 1982) and its use by calling frogs (Pough and Gatten, 1984) are both surprising findings. The study of behavioral energetics must be an empirical exercise until we know considerably more than we presently do.

Our capacity to investigate behavioral energetics under natural conditions in the field is greatly handicapped by our inability to measure or estimate oxygen consumption over short time intervals. The anaerobic contribution can be determined but is of minor energetic significance. I currently see no way of making desired energetic measurements of behavior on free-ranging animals under field conditions. We must rely instead on extrapolations from measurements on aerobic and anaerobic contributions to different behaviors that can be undertaken under laboratory conditions. This situation is not ideal, but it is better than nothing.

Acknowledgments

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