Ecophysiology and conservation: The contribution of energetics—introduction to the symposium

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Synopsis

Animal physiologists have begun making contributions to conservation biology based on their knowledge of endocrinology, immunology, and sensory biology. Contributions to this symposium use the perspective of energy and mass balance to examine questions about habitat usage, activity times, competition, foraging, reproduction, and body condition. Physiological constraints or requirements sculpt the behavioral and life history choices of individuals and provide mechanistic linkages with population processes and conservation policies.

Introduction

Preventing the loss of biodiversity is one of the great challenges facing humanity today (Wilson 2002). The earth is currently experiencing its sixth great mass extinction, but unlike the previous events this one is uniquely caused by human-related activities (Leakey 1996). Overharvesting (Flannery 2002; Martin 2005) was the initial driver, but today anthropogenic-induced climatic change, habitat loss, toxic substances, and invasive species (including novel diseases) all contribute (Vitousek and others 1997; Lubchenco 1998; McMichael and Kovats 2000; Wilson 2002). Cultures around the world have had complex relationships with nature, and no single cause is at the root of environmental degradation and loss (Diamond 2005). The growth economy of present-day modern societies (Daly 1996) shows that society as a whole does not value the vital role of the environment, especially ecosystem services (Daily 1997). However, across organizational scales from the local to the global, individuals, NGOs, and governmental agencies are focusing on critical environmental problems such as climatic change, invasive species, habitat loss, water shortages, and pollution. Efforts by these organizations are underway to link scientific understanding to policy (Ludwig 2001; Ludwig and others 2001; Folke and others 2005). Scientists are key participants in these organizations and they have responded to the global environmental degradation with the creation of several new disciplines including environmental toxicology, global change studies, sustainable development, and conservation biology.

Conservation biology is a nascent, applied science, born in the late 1960s (Carson 1962; Ehrenfeld 1970) out of a pragmatic desire to stem the loss of our natural heritage. The Society for Conservation Biology, now a worldwide organization with 10,000 members, was officially founded just 20 years ago. The development of conservation science has focused at the genetic, population, landscape, and ecosystem levels (Meffe and Carroll 1997; Hunter 2001; Soule and Orians 2001; Primack 2006). Curiously, conservation practice has placed less emphasis on the individual organism and how it is affected by environmental change, despite the tools available from decades of ecophysiological research. Recently, however, physiologists, especially reproductive physiologists, have been making contributions (Clemmons and Buchholz 1997; Berger and others 1999; Gordon and Bartol 2004; Carey 2005; Stevenson and others 2005; Wikelski and Cooke 2006). For instance, in the past 3 years the Society for Integrative and Comparative Biology has sponsored 4 symposia that have related organismal level studies to conservation biology (2004—EcoPhysiology and Conservation: The Contribution of Endocrinology and Immunology; 2005—Zoo-based Research and Conservation; 2006—Ecological Immunology: Recent Advances and Applications for Conservation and Public Health; and this symposium) (for program listings see meetings link at the society Web site, www.sicb.org/).

It is no surprise that an energetics perspective would be of help in conservation biology because energy is needed to sustain life and energetics is used as an organizing perspective in many areas of biological research. The study of energy flows, sources, and sinks, across levels of biological organization...
provides useful insights into organization and function. An energetics approach allows scientists to rank the quality of habitats or to ask how individual time and energy budgets translate into population changes. Studies may be focused—such as asking if there is sufficient energy for reproduction—or may be more expansive—such as examining coupled material and energy flows to assess tradeoffs between reproduction and survival. This symposium provided a diverse and rich set of examples. The articles cover topics about reproductive energetics, migration, feeding ecology, metabolic rates, thermoregulation, and water loss. In addition, presentations covered a diverse range of taxa including fence lizards, wood frogs, Atlantic bluefin tuna, honeybees, Monarch butterflies, the Hawaiian po‘ouli, and desert tortoises. Most are case studies providing linkages between physiology and population processes, while contributions from McNab and from Stevenson and Woods are more comparative and synthetic. Techniques span many levels of biological organization from genetic analysis to biogeography. The following section provides more detail about each article.

**Symposium articles**

In the first article, O’Connor and colleagues apply biophysical models at the landscape level. The approach of biophysical ecology combines micrometeorological data with thermal properties and physiological data of organisms, linked by mass and thermal balance equations, to predict locations of animals or sources of water and food in the environment (Gates 1980). O’Connor and colleagues present 2 case studies. In the first they address questions about the impacts of climatic change on the canyon lizard (*Sceloporus merriami*). They use extensive field data to show that a site of intermediate elevation has the highest rate of reproductive success based on modeling balance of thermal and chemical energy. The predicted body temperatures of the lizards determine energy expenditure and the thermal environment constrains both the length of daily activity and foraging time and thus access to food. Calculations suggest that the thermal sensitivity of digestive rates may be very important. In the second example, O’Connor and colleagues studied the impacts of habitat alterations on activity and population dynamics of the wood frog (*Rana sylvatica*). Here, biophysical models show that frogs can be active in rainy periods but under drier conditions leaf litter provides a refuge from dehydration. Frogs cannot be active but they maintain water balance. Calculations show that during extended droughts frogs could dehydrate even under leaf litter.

Harrison and colleagues presented an integrative overview of the invasion of the European and African honeybees, summarizing genetic, behavioral, and physiological data. There are several ecotones between the Africanized races (which now are dominant throughout the neotropics) and the European bees (which are dominant in the temperate zone). The authors ask what individual genetic, behavioral, and physiological traits contribute to the success of each group. They suggest that bees of strictly European origin have an advantage in cooler climates because of a behavioral preference for honey over pollen that enhances their energy stores and increases the probability of survival over winter. They also suggest that increased winter survival is linked to the higher hemolymph vitellogenin levels found in European bees. In warmer climates Africanized bees are the better competitors because of (1) a preference for pollen over nectar, which increases nutrient uptake and brood production, and (2) their larger and more energetically costly flight relative to body size, which makes them better fliers and thereby increases their foraging intake, mating success and dispersal. Using distributional patterns and climatic data from South America, Harrison and colleagues forecast that hybrid bees will invade about 200 km further north to where maximum January temperatures are 15–16°C.

For many years Lincoln Brower and his colleagues have documented one of nature’s greatest spectacles—the migration of Monarch butterflies from Mexico to the United States and Canada and back. They have unraveled much of the behavior and ecology of these migratory populations, and documented several of the threats to their continued survival, especially the loss of the high elevation forests in 12 or so overwintering sites in the Sierra Madre Oriental Mountains of Mexico. We know that during their winter resting period, butterflies do not feed but instead metabolize fat reserves for their energy source. In this article, Brower and colleagues update the energetic aspects of migration and overwintering biology of the Monarchs, analyzing fat data from 17 published and unpublished sources. They concluded that Monarchs are optimistic fuelers during migration (fat levels between 0 and 150 mg) and that they do not gain large amounts of fat (150–250 mg) until they spend more time feeding on nectar in Texas or northern Mexico, just before reaching the overwintering sites. Brower and colleagues worry that changes in nectar-producing plants across the landscape will reduce nectar-producing individuals.
The analysis by Brower and colleagues implies that conservation of this long-distance migratory species requires more emphasis on energetics and stopover ecology.

Porter and colleagues apply the same biophysical modeling approach as O’Connor and colleagues to investigate the potential distribution of the Hawaiian po’ouli (*Melamprosops phaeosoma*), a bird that inhabited Maui. This species was only discovered in 1974 and is now thought to be extinct. Archeological records indicate that po’ouli historically lived at sea level but that the most recent distribution was limited to elevations close to 2100 m. The thermal balance model predicts that at sea level the required foraging rates (grams wet weight) are 3–4 times greater for snails, the po’ouli’s historical prey, than for insects, their most recent prey. Foraging rates on both diets were higher at 2100 m but the ratio remained about the same. There was little seasonal effect in the model calculations because the climate is relatively constant, but in April and May, during the reproductive season, foraging rates need to increase to meet reproductive energy requirements. Porter and colleagues also predicted discretionary energy for the birds. The calculations suggest that low metabolic costs at low elevations increase discretionary energy, and that when the gut cannot process bulky food fast enough to meet the reproductive demand for energy, a diet of snails reduces discretionary energy. These models demonstrate the interrelationships of metabolism and water balance on activity times, diet, and the potential for growth and reproduction.

McNab used allometric and comparative analyses of metabolic data to make inferences about populational processes in birds and mammals. He summarized the basic pattern that small mammals have higher metabolic rates per unit body mass and faster growth rates than do large mammals. Based on analyses of the residuals of metabolic rate, he suggested that animals of the same body mass but with higher metabolic rate have higher reproductive rates. When comparing eutherian with marsupial mammals, McNab argues that basic limits of reproductive physiology in marsupials limit growth rates of young, implying that selection for high reproductivity drives selection for increasing relative basal metabolic rate of eutherian mammals. Recent analyses among birds suggest that they might show a similar pattern. His conclusion is that the species with relatively low fecundity (large size and relatively low metabolic rates) are more prone to extinction. High-energy species have flexibility in their reproductive outputs, whereas low-energy species are inflexible in theirs, making low-energy species more vulnerable. Comparisons of the outcome of competition between species with high and low fecundity support his conclusions. McNab used his fecundity rule to make some useful predictions for conservation biologists. Marsupial and island species generally are at a competitive disadvantage and need isolation, whether on islands or in otherwise protected habitats, if they are to survive.

Stevenson and Woods reviewed approaches to judging the health of individuals, especially their energetic status. They provided an introduction to a very large literature (over 200 citations) on condition indices that have been widely used in studies of humans, agricultural and zoo animals, and other vertebrates in the contexts of resource management, ecology, and conservation biology. The review suggests that specific condition indices are used because of historical precedent rather than having been proven to be a good measure for animal health. The human and fisheries biologists have had the most active discussions, and it would appear that more effort to standardize approaches would be prudent for the scientific community. Stevenson and Woods also reviewed the variety of advanced technologies used to measure body composition directly and nondestructively. These methods are diverse and often require specialized machinery, but several hold promise for becoming more usable in the field and for validating traditional morphological metrics. Finally, Stevenson and Woods identified 2 common views of how body mass changes among animals. The cargo model assumes that structural components of the body are fixed and that changes result from taking on loads. The dynamic models meet the more complex biological reality in which “structural materials” including digestive tissue and flight muscle mass can be regulated to accommodate the immediate ecological needs of an animal.

Tracy and colleagues discussed basic feeding biology and the relationship between stress, disease, and population ecology of an endangered species, the desert tortoise, a species originally listed as threatened because of die-off from respiratory illness. Desert tortoises occur mainly in Nevada and California where a variety of anthropogenic factors including habitat loss from agriculture and military maneuvers, off-road vehicles, and grazing competition from burros and horses negatively impact them (Berry 1997). Four resource acquisition hypotheses (the nutritional wisdom hypothesis, the optimal diet hypothesis, the optical digestion hypothesis, and the cost of switching hypothesis) have been used to explain tortoise foraging patterns. Foraging observations and plant nutritional data are consistent with the last
3 hypotheses, but the authors find no support for the nutritional wisdom hypothesis that was based on (1) balancing the calcium, phosphorus, and magnesium acquisition for bone and shell growth or (2) avoiding excessive phosphorus because of the lack of extrarenal salt glands and the potential negative consequences of storing high concentrations in the urine. Tracy and colleagues also discuss the immune system function of tortoises. They make the novel suggestion that at high densities (as many as 200–250 animals per hectare) aggressive behaviors can lead to increased testosterone levels. Higher levels of testosterone imply increased levels of corticosterone, because both are regulated by the same globulins, and increased plasma titers of corticosterone would reduce the effectiveness of the immune system. Their hypothesis is that this linkage could lead to the outbreak of disease and become the driving mechanism for population cycles on the scale of decades.

Final comments

Hopefully this collection of articles, along with others such as those by Jones and colleagues (2004) and Wallace and colleagues (2005), will serve to stimulate conversations about the role of physiological energetics in conservation biology. For environmental physiologists, I believe they demonstrate how their own cutting-edge science can simultaneously inform conservation biology. For nonphysiologists, I believe these articles specifically demonstrate how physiologists can help explain the mechanical underpinnings of changes at the population level. The role of energetics at the individual level and its application in ecology is currently undergoing a transformation led by the efforts of Brown and colleagues (2004). Their scaling relations (also see Marquet and others 2005) provide a big-picture perspective such as the specific examples McNab presents here. These observations suggest that energetics, as a branch of conservation physiology, will continue to make fruitful contributions to an understanding of how to preserve biodiversity.

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References


