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Review

Integrating physiology, behavior, and energetics: Biologging in a free-living arctic hibernator☆

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The use of animal-borne instruments (ABIs), including biologgers and biotransmitters, has played an integral role in advancing our understanding of adjustments made by animals in their physiology and behavior across their annual and daily cycles and in response to weather and environmental changes. Here, we review our research employing body temperature (Tb), light, and acceleration biologgers to measure patterns of physiology and behavior of a free-living, semi-fossorial hibernator, the arctic ground squirrel (*Urocitellus parryii*). We have used these devices to address a variety of physiological, ecological, and evolutionary questions within the fields of hibernation physiology, phenology, behavioral ecology, and chronobiology. We have also combined biologging with other approaches, such as endocrinology and tracking the thermal environment, to provide insights into the physiological mechanisms that underlie fundamental questions in biology including physiological performance trade-offs, timing and functional energetics. Finally, we explore the practical and methodological considerations that need to be addressed in biologging studies of free-living vertebrates and discuss future technological advancements that will increase the power and potential of biologging as a tool for assessing physiological function in dynamic and changing environments.

Contents

Abbreviations: ABIs, animal-borne instruments; AGS, arctic ground squirrel; ECG, electrocardiogram; Tb, body temperature; SCN, suprachiasmatic nucleus; T3, triiodothyronine; T4, thyroxine.
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1. Introduction

Determining how individuals function within and interact with their environment is critical to understand behavioral and physiological adaptations and plasticity and by extension, limits to organismal responses to environmental change. The importance of understanding animal–environment interactions and physiological function is evidenced by the emergence of a new field in biology, known as "conservation physiology", which seeks to incorporate this knowledge into ecological models designed to predict population, community and ecosystem-level responses to environmental and land use changes (Cooke et al., 2013). The physiological mechanisms that underlie phenotypic plasticity remain elusive, however, and therefore represent a significant impediment to predicting the ecological effects of a changing climate (Denny and Helmuth, 2009).

Controlled laboratory experiments will always play an instrumental role in environmental physiology, but only by investigating physiological function and behavior in free-living individuals will we be able to fully understand how individuals regulate various aspects of their annual cycle including, as examples, reproduction, migration, molt, and hibernation (Bartholomew, 1986). It is well known that captivity can result in psychological and physiological stresses in animals as evidenced by impaired function of the hypothalamus–pituitary–adrenal axis, depressed immune function, reduced growth rates, and disturbed reproductive cycling (e.g., Romero and Wingfield, 1999; Morgan and Tromborg, 2007; Buehler et al., 2008). Limitations in our ability to replicate natural habitat and natural diets in captive situations constrain the usefulness of data collected in a laboratory setting to develop a thorough understanding of physiological responses to environmental challenges under natural conditions. For these reasons, studies of free-living animals are central to understanding how individuals alter their physiology and behavior across their annual cycle and in response to unpredictable environmental change.

Biologging and biotelemetry, which involve the collection of data from animal-borne instruments (hereafter: ABIs), are advancing our fundamental understanding of physiological adaptation and responsiveness to environmental change. Specifically, this technology allows us to answer questions regarding physiology, behavior, and ecology of free-living animals under natural conditions that would have previously been limited to tests on model organisms under controlled conditions. To date, the greatest impact of ABIs in ecology and environmental physiology has been through the use of devices that enable quantitative measurement of animal movement through space and time, particularly via global positioning systems (GPS), satellite telemetry, and geolocators (Rutz and Hays, 2009; Cagnacci et al., 2010). However, a wide variety of ABIs have been developed that measure a range of physiological, behavioral, and environmental parameters including, but not limited to, body temperature (Tb), heart rate, acceleration, pressure (depth), salinity, light, heat flux, EEG, and PO_2 (Butler et al., 2004; Block, 2005; Vyssotski et al., 2006; McDonald and Ponganis, 2013). Some of these parameters, such as heart rate and acceleration, correlate strongly with metabolic rate which provides insight into how metabolism and daily energy expenditure are influenced by both intrinsic and extrinsic factors, including weather (Green et al., 2009; Halsey et al., 2011). Combining biologging with other techniques, such as endocrinology and immunology, allows for an integrative approach to understanding how physiology mitigates the effects of environmental change and influences behavior, performance, and ultimately lifetime fitness (Wingfield et al., 1997; Semeniuk et al., 2009). Thus, the use and further development of ABIs is critical to understanding the complex interactions between physiology, behavior, climate, and the environment (Evans et al., 2016).

Here, we review our use of ABIs that measure temperature, light, and acceleration in a free-living semi-fossorial hibernator, the arctic ground squirrel (hereafter: AGS; *Urocitellus parryii*). First we provide a brief overview of the practical and methodological issues associated with the use of these particular ABIs. Then, we use our work on AGSs as an example to illustrate the diversity of physiological and ecological questions that can be addressed using these relatively simple devices. We also demonstrate how combining biologging with endocrinology can provide insight into the functional mechanisms that underlie individual differences in behavior and physiology. The promise and power of ABIs is enormous and continued technological advancements of ABIs will undoubtedly provide for a more integrative understanding of the physiological and behavioral mechanisms that underlie vertebrate responses to environmental change.

2. ABIs — practical and methodological considerations

According to "Moore's law", which is actually an empirical observation, the number of transistors on an integrated circuit doubles approximately every 18 months and this has important implications for processing speeds and memory (Schaller, 1997). Battery technology is also improving, though at a much slower rate, such that the battery has become the greatest limiting technical factor in terms of continuing to reduce the size, mass and lifespan of ABIs. Nevertheless, the combined evolution of processing speed, storage capacity and battery technology has resulted in modern devices that are much smaller and better performing than their predecessors of just a few years ago. As a result, technologies that were once only suitable for deployment on relatively large animals, such as accelerometry, are now being used on increasingly smaller organisms (Rutz and Hays, 2009; Brown et al., 2013). This has led to widespread use of ABIs, but there are a variety of practical and methodological considerations that need to be addressed when initiating an ABI-study. These considerations include cost and robustness of the device, sampling resolution, method of attachment, capture/handling effects, effects of the device itself, and methods of analysis. Despite the continued progress in miniaturizing and improving ABI technology, the commercial demand is relatively small and thus further development/refinement of this technology requires continued support from funding agencies. The high cost of cutting-edge ABIs also means that many researchers continue to use older, more affordable technologies. Selection of an appropriate sampling interval, resolution and method of analyses is also very important and dependent on the question being addressed; this subject is too lengthy to discuss here, but see Ropert-Coudert and Wilson (2004).

Whether an ABI is worn externally or implanted is an important consideration. In general, we suggest following the taxon-specific guidelines provided by various societies (birds: Fair and Jones, 2010; fish: Q4 Q5
Nickum, 2004; mammals: Sikes and Gannon, 2011; reptiles and am- Q6
phibians: Beaupre et al., 2004). Physical characteristics of the device such as its size, shape, mass, and buoyancy require important consideration and are dependent upon the size and ecology of the species; drag and buoyancy, for example, are much more important than mass for aquatic animals (Ponganis, 2007). Mass is much more important for flying birds and bats than it is for animals that use terrestrial locomotion (Barron et al., 2010; Rojas et al., 2010; O'Mara et al., 2014). It should also be noted that even within a particular taxonomic group, some species may be more sensitive to capture/handling stress and/or carrying the ABIs, and therefore attempts should be made to validate a lack of deleterious effects on natural physiology and behavior of a given species (e.g., Whidden et al., 2007; Jepsen et al., 2015). In some cases the decision regarding implantation or external-mounting will depend on the ABI itself. ABIs that measure environmental parameters (e.g., light) will obviously need to be mounted externally whereas some ABIs that measure physiological variables (e.g., PO2) must be implanted; however, many ABIs can be either mounted externally or implanted. One should not assume that external devices are necessarily preferred simply because they avoid invasive surgeries as some externally-affixed ABIs may be more likely to cause negative behavioral effects (Saraux et al., 2011). In a recent meta-analysis of biologging effects in birds, White et al. (2013) found that externally attached, but not implanted ABIs, were consistently detrimental to the birds. They concluded that

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