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SYMPOSIUM

The Power of Physiology in Changing Landscapes: Considerations for the Continued Integration of Conservation and Physiology

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From the symposium "Physiology in Changing Landscapes: An Integrative Perspective for Conservation Biology" presented at the annual meeting of the Society for Integrative and Comparative Biology, January 3–7, 2015 at West Palm Beach, Florida.

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Synopsis The growing field of conservation physiology applies a diversity of physiological traits (e.g., immunological, metabolic, endocrine, and nutritional traits) to understand and predict organismal, population, and ecosystem responses to environmental change and stressors. Although the discipline of conservation physiology is gaining momentum, there is still a pressing need to better translate knowledge from physiology into real-world tools. The goal of this symposium, "Physiology in Changing Landscapes: An Integrative Perspective for Conservation Biology", was to highlight that many current investigations in ecological, evolutionary, and comparative physiology are necessary for understanding the applicability of physiological measures for conservation goals, particularly in the context of monitoring and predicting the health, condition, persistence, and distribution of populations in the face of environmental change. Here, we outline five major investigations common to environmental and ecological physiology that can contribute directly to the progression of the field of conservation physiology: (1) combining multiple measures of physiology and behavior; (2) employing studies of dose–responses and gradients; (3) combining a within-individual and population-level approach; (4) taking into account the context-dependency of physiological traits; and (5) linking physiological variables with fitness metrics. Overall, integrative physiologists have detailed knowledge of the physiological systems that they study; however, communicating theoretical and empirical knowledge to conservation biologists and practitioners in an approachable and applicable way is paramount to the practical development of physiological tools that will have a tangible impact for conservation.

Introduction

With the alteration of natural landscapes by anthropogenic disturbances and climatic change, organisms are continually faced with new and enduring environmental challenges (Butchart et al. 2010). Conservation physiology represents a toolbox of knowledge, approaches, and techniques that can address the impacts of changing landscapes across scales, taxa, and ecosystems (Wikelski and Cooke 2006; Cooke et al. 2013). A physiological approach to conservation is particularly powerful because it imparts predictive capacity and allows for the assessment of disturbances and of conservation-management practices in a more sensitive and rapid way compared with traditional demographic techniques (Ellis et al. 2012; Cooke et al. 2013). Since conservation physiology also emphasizes determining cause–effect relationships (Carey 2005), the development of solutions (Cooke et al. 2013), and the continuing assessment of employed strategies (Cooke and O'Connor 2010), it has the potential to contribute directly to evidence-based conservation. Although the field of conservation physiology has grown rapidly over the past decade (Lennox and Cooke 2014), researchers and practitioners still point to gaps in the translation of physiological knowledge and data to successes in conservation (Cooke and O'Connor 2010; Cooke 2014; Lennox and Cooke 2014). For example, a recent bibliographical analysis by Lennox and Cooke (2014) indicated that the integration of the fields of conservation biology and physiology still has much room for growth; fewer than 1% of the articles published in major animal and plant

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physiological journals since 2006 contain keywords related to conservation.

The slower than expected integration of conservation and physiology is likely the result of multiple factors, including prior lack of an integrated framework (Coristine et al. 2014), methodological issues related to studying physiology in populations of conservation concern (Lennox and Cooke 2014), previous lack of a dedicated conservation physiology journal (Cooke et al. 2013), and a lack of interest among physiologists to incorporate conservation (Caro and Sherman 2013; Lennox and Cooke 2014). In addition, although there is an enormous existing appreciation of the ecological and evolutionary significance of variation in physiological systems (Martin et al. 2014), many physiologists may still be unaware of the ways in which their current research questions can be of direct applicability to refining techniques for the conservation physiology toolbox. Some of this lack of awareness may be due to the discipline of conservation physiology being viewed primarily as a way for conservation biologists to incorporate new techniques by drawing on existing information and tools in physiology. In this scenario, the flow of information begins with conservation biologists and addresses case-directed endeavors in conservation (Fig. 1A). However, an equally valid and increasingly useful integration begins with the specific generation or re-purposing of information from traditional physiologists with the targeted goal of progressing conservation physiology (Fig. 1B).

In this introductory article to the symposium "Physiology in Changing Landscapes: An Integrative Perspective for Conservation Biology", we outline how five common investigations/approaches in ecological and evolutionary physiology have simultaneous applicability for conservation physiology: (1) combining multiple measures of physiology and behavior; (2) employing studies of dose–responses and gradients; (3) combining within-individual and between-individual approaches; (4) investigating the context-dependency of physiological traits; and (5) establishing links between physiology and fitness. While these opportunities will have the greatest benefit by determining which physiological measures are the best predictors of responses by wildlife to changing environments (both disturbances and conservation-management initiatives), they also hold significant relevance for designing restoration, reintroduction, relocation, or captive-breeding projects (Table 1). We also provide an overview of the symposium's presentations to highlight the diverse ways that physiological investigations currently are benefitting conservation across taxa, scales, systems, and traits. The unifying theme is that an underlying understanding of physiological processes within an ecological and evolutionary context is of paramount importance to progressing the field of conservation physiology.

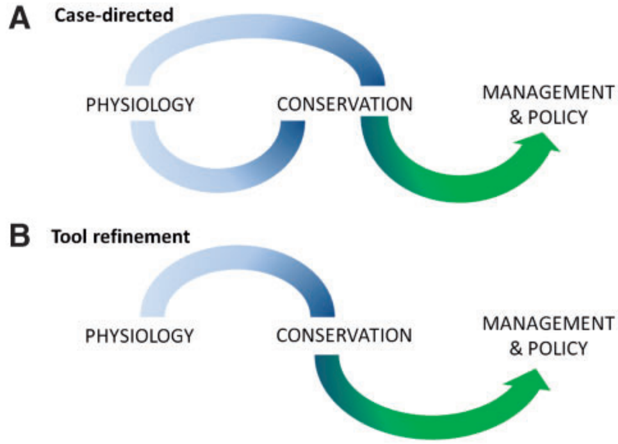

Fig. 1 Potential information flows in conservation physiology. (**A**) A specific conservation question is approached by incorporating existing principles in physiology. In this case, the onus can fall on conservation biologists and managers to identify, assimilate, and apply physiological knowledge to their system. (**B**) Physiology is the starting point and directly provides information on potential tools, their best-suited applications, and considerations for use to conservation biologists and managers. By assimilating knowledge, physiologists can improve the ability for conservation practitioners to choose appropriate physiological tools and potentially decrease the time and costs involved in (A).

Combining multiple measures of physiology and behavior

Ecological and evolutionary physiologists measure multiple physiological traits and behavioral parameters simultaneously to investigate the interactions of physiological systems (e.g., Zuk 1996; Remage-Healey and Romero 2001; Pieterse et al. 2012), explain variation in performance or fitness (e.g., Sinervo et al. 2000; Ahmed et al. 2002; Breuner et al. 2008), investigate the role of physiology in influencing behavioral decisions (e.g., Wingfield et al. 1998, 2006; Ricklefs and Wikelski 2002; McNamara and Houston 2008), and study the evolution of suites of traits (Ketterson and Nolan 1999; Feder et al. 2000; Martin et al. 2014). Physiology and behavior are often tightly linked, directly or indirectly (Dugatkin 2004; Willmer et al. 2005), and therefore both can represent relatively rapid indicators of changes in intrinsic or extrinsic environment compared with demographic measures. As such, investigating how links between physiological traits and behavioral changes lead to optimal (or sub-optimal) performance can

Table 1 Five investigations common to ecological and evolutionary physiology and how they can improve the refinement of tools for conservation physiology (see text for further details)

Physiological investigation	Description	Application(s) to conservation physiology
1. Combining multiple measures of physiology and behavior	Investigating how multiple physiological traits and behavioral metrics covary and interact	Information on how environmental change is translated into measureable impacts on wildlife
		Determination of which physiological variables represent the most rapid and cost-effective measures of disturbance
		Development of rapid behavioral assays of individual health or condition
		Targeting of physiological variables to specific disturbances or management strategies
2. Employing dose–response and gradient studies	Determining how different levels of a physiological trait produce changes in organismal function, behavior, health, or fitness	Determination of physiological thresholds to limit disturbances based on time-period, duration, or intensity
	Determining how gradients of environmental variables relate to physiological traits	Determination of susceptibility of certain populations or species to specific environmental changes
		Information on how gradual versus unexpected environmental changes influence populations of interest
		Delineation of critical components of habitat-quality
		Improve the design of reserves and restorations
		Increase success of releases and translocations
		Improve captive-breeding programs
		Determination of whether management activities improve health or condition of target populations
3. Combining within-individual and between-individual approaches	Quantifying variation in physiological traits between populations, between individuals, and within individuals	Determination of whether average levels of a physiological trait can be interpreted as a population-level indicator of disturbance, health, condition, or degree of success in management
	Determining consistency of physiological traits under static and changing environmental conditions	
4. Considering the context-dependency of physiological traits	Determining whether intrinsic (e.g., age, sex, life-history stage/strategy) and extrinsic factors (e.g., predation pressure, temperature, availability of food) influence levels of physiological traits	Determination of which intrinsic and extrinsic variables must be taken into account when interpreting levels of a physiological trait as an indicator of condition, health, or disturbance
		Tailoring of approaches to certain species, time-periods, age classes, or sexes
5. Linking physiology to fitness	Investigating whether physiological variables relate to survival and/or reproductive success, and under what conditions	Determination of which physiological traits link measures of individuals to the viability and persistence of populations
		Establishing whether the predictive capacity of certain traits is limited to particular time-periods, age classes, or sexes

provide conservation physiologists with detailed information about how environmental disturbances are translated into measureable impacts on wildlife populations. In a conservation setting, cost and rapidity of assessment are of paramount importance; determining which physiological variables represent the most logistically feasible measures for on-the-ground assessments will therefore be of major importance for expediting their effective use in conservation. Specifically, investigations that identify covariation among physiological traits and behavioral measures can lead to the identification of proxies of health, condition, or environmental change (Cooke et al. 2014). Similarly, directed investigations into how different disturbances (e.g., social conflict, limited food, human interaction, changes in suitability of habitats) manifest as physiological and behavioral alterations will help to target different physiological techniques for specific species, times, or locations (Cooke et al. 2014).

To illustrate the power of combining physiological techniques and behavioral assays for conservation-management, Cooke et al. (2014) highlighted a collective body of work completed on the Mary River

Turtle (*Elusor macrurus*). By studying the physiological capacity of this species to acclimate to elevated temperatures and reduced levels of oxygen, researchers were able to determine that the conditions associated with the installation of a dam would lead to increased mortality through influences on diving behavior (Clark et al. 2008, 2009). Importantly, this work carried through to the implementation of a management decision, resulting in the cancellation of a dam (Cooke et al. 2014). Overall, applying ecological and evolutionary studies focusing on the links between physiological systems and behavior to conservation can provide a holistic understanding of environmental impacts and refine how disturbances and management initiatives can best be monitored in wildlife populations (Cooke et al. 2014).

Employing studies of dose–responses and gradients

Experimental physiologists have borrowed the toxicological concept of determining the concentrations at which a physiological parameter produces effects on organismal functioning, behavior, health, or fitness (Peek et al. 2002; Romero et al. 2009; Costantini et al. 2010), hereafter designated as dose–response relationships. Conversely, natural and experimental studies of gradients can help physiologists determine which level of environmental conditions (e.g., temperature, salinity, and resource availability) cause changes in physiological functions (Willmer et al. 2005). Within the context of ecological and evolutionary physiology, investigations of gradients and of dose–response relationships have generated information on patterns of distribution and diversity of organisms (macrophysiology) (Chown and Gaston 2008), detected trade-offs in life-history traits (Ricklefs and Wikelski 2002), and contributed to our understanding of whether and how organisms can adapt or acclimate to changing environmental conditions (Sieck 2014).

Expanding these approaches to conservation physiology has the potential to contribute both to improved monitoring and to conservation planning. For example, just as LD_{50} (the dose of a toxin, radiation, or pathogen required to kill 50% of a tested population) has been a useful threshold indicator of a species' or a population's sensitivity (Landis and Yu 2003), determining whether physiological thresholds exist in relation to different anthropogenic disturbances could allow managers to better limit activities (e.g., construction, noise, use by humans) based on intensity, time-period, or duration. Similarly, comparing the physiological sensitivities of different populations or species can provide information on the susceptibility of certain organisms to anthropogenic influences, allowing for more tailored management strategies for the protection of species (Cooke et al. 2013). In particular, studies of gradients have the potential to help determine whether there are specific environmental changes that may be more detrimental than others for specific populations or species, and allow for the comparison of gradual versus unexpected anthropogenic stressors (Fokidis et al. 2009; Ellis et al. 2012; Zhang et al. 2011; Grunst et al. 2014). Overall, studies of this nature can also indicate critical components of habitat (Homyack 2010; Bourbonnais et al. 2014) and provide valuable information in the context of the design of reserves and restorations (Cooke and Suski 2008), translocations and releases (Besson and Cree 2011; Tarszisz et al. 2014), and captive-breeding programs (Brown 2000; Schwarzenberger 2007). Finally, a comprehensive understanding of how gradients of environmental quality influence physiology also has direct applicability to the monitoring of conservation-management activities, allowing managers to assess whether habitat-restoration techniques improve the health or well-being of targeted populations (Cooke and Suski 2008; Cooke et al. 2013).

Combining within-individual and between-individual approaches

Evolutionary physiologists have long appreciated variation among and within individuals because investigating the evolution of traits requires the calculation of repeatability and heritability (Conner and Hartl 2004). In addition, physiology has been studied extensively within the context of phenotypic flexibility and plasticity, necessitating the use of repeated-measures analyses, reaction norms, and the direct assessment of within-individual variation to understand acclimation and adaptation (Stearns 1989; Pigliucci 2001; Williams 2008; Kingsolver et al. 2011). While many investigations in conservation physiology have considered whether two or more populations with varying levels of disturbance differ in the average level of a physiological trait (Busch and Hayward 2009), few studies have examined how the same individual responds physiologically to varying levels in the quality or disturbance of habitat. However, considering the degree of variation in a physiological trait within individuals is of paramount importance to assessing the capacity of that trait to act as a population-level biomarker of disturbance or habitat quality (Madliger and Love 2014). Specifically, a highly variable trait at the level of the individual (i.e., individually-specific

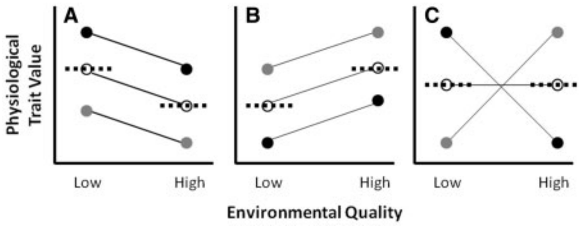

Fig. 2 Within-individual variation in a physiological trait in relation to changing environmental quality. Each shade of color represents an individual. Dashed lines indicate physiological averages in each environment. In (**A**) and (**B**), all individuals adjust their physiology in the same way in response to the environmental change. Average values of traits are therefore representative of the overall change in the population. In (**C**), physiology responds in an individually-specific manner. Solely measuring population averages would suggest that the change in environmental quality does not affect physiology, while a within-individual consideration indicates many individuals may indeed be impacted by the environmental change.

responses to environmental change) increases the difficulty of using that trait to assess between-population differences (Fig. 2).

Two types of within-individual investigations can provide critical information about whether a given physiological trait will be useful for monitoring population-level disturbance. First, the trait must show consistency within individuals when environmental conditions do not change (Cooke and O'Connor 2010; Madliger and Love 2014). Second, the trait should ideally show the same relative change within all individuals in the face of a given environmental change (i.e., all individuals increase or decrease) (Dantzer et al. 2014; Madliger and Love 2014). A combination of laboratory and field studies can best determine these characteristics, and appropriate investigations rely on the multiple-regression and mixed-effect modeling techniques traditionally employed by evolutionary biologists (e.g., Nussey et al. 2007; Dingemanse et al. 2010; Kluen and Brommer 2013). Recently, such techniques have become much more accessible to behavioral ecologists and physiologists (Nussey et al. 2007; Dingemanse and Dochtermann 2013), providing an easier extension to conservation physiology.

Considering the context-dependency of physiological traits

The highly labile nature of physiological traits related to condition, health, reproduction, growth, and energetic metrics, and their sensitivity to extrinsic and intrinsic conditions, are two of the primary reasons physiology is so appealing for application to conservation (Seebacher and Franklin 2012). However, many physiological traits are also sensitive to other conditions that can influence their levels beyond the disturbances or management actions that are the focus of assessment. For example, ecological and evolutionary physiologists have long appreciated contexts related to underlying population structure or season, such as age, life history or reproductive stage, or sex (Zera and Harshman 2001; Romero 2002; Love et al. 2008; Hau et al. 2010). In addition, other contexts may represent components of the environment that may or may not be consequences of the focal change under study, such as weather (e.g., temperature), competition, social structure, parasite load, predator pressure, and availability or quality of food or water (Fitter and Hay 2001; Willmer et al. 2005).

The detailed knowledge of how intrinsic and extrinsic conditions influence physiological traits that comparative, evolutionary, and ecological physiologists have been amassing for decades can provide a meaningful database allowing for the inclusion of relevant covariates in statistical analyses of applied questions. This information will indicate whether other variables related to environmental conditions or intrinsic factors must be collected to accurately interpret changes in physiology in the context of conservation monitoring. Finally, information on context-dependency can provide conservation physiologists with a means of determining which physiological traits may be easiest to measure in relation to certain disturbances (i.e., tailoring approaches), and to decide whether certain traits may be best-suited for particular species, time-periods, or age classes. For example, while it is possible to acquire fecal samples from large ungulates or marine mammals that can provide information on sex, reproductive hormones, glucocorticoid levels, and metabolism to take into account how reproductive state or availability of food influence levels of stress hormones when interpreting them in the context of disturbance (Rolland et al. 2005; Wasser et al. 2011; Ayres et al. 2012; Escribano-Avila et al. 2013), it is not possible to acquire a large enough sample non-destructively to take into account these contexts for a small species of amphibian.

Linking physiology to fitness

While physiologists investigate traits in relation to survival and reproductive success to determine the mechanistic underpinnings of variation in performance and fitness (Harshman and Zera 2007; Williams 2012), and to study the evolution of physiological systems (Feder et al. 2000; Zera and Harshman 2001), linking physiological measures to fitness is also necessary if physiological traits are to be employed as predictive biomarkers for monitoring populations (Wikelski and Cooke 2006; Cooke and O'Connor 2010; Cooke et al. 2012). Although this concept is straightforward, quantifying relationships between physiology and fitness can require large sample sizes and extensive longitudinal studies (Feder 1987). In addition, to fully understand a given physiology–fitness relationship, it is important to investigate within different taxa, life stages, ages, and sexes to determine whether the relationship is context-dependent (Breuner et al. 2008; Bonier et al. 2009; Kimball et al. 2012; Madliger and Love 2014). For example, by determining cadiorespiratory thresholds for thermal tolerances in different stocks of Pacific salmon, Cooke et al. (2012) provided a method for managers to predict stock-specific and sex-specific success in migration, and to provide justification for restricting fishing effort at certain times, based on the temperature of rivers.

Finally, the physiology–fitness relationship may vary depending on the fitness metric investigated, necessitating the measurement of multiple metrics of fitness (i.e., longer-term measures of survival and shorter-term measures of reproductive success). For example, for one of the most heavily proposed biomarkers, baseline glucocorticoids, the relationship often is opposite for survival compared with reproductive success (Bonier et al. 2009), due to the important role of glucocorticoids in the management of daily, seasonal, and life-history-related energetic demand (Romero 2002; Landys et al. 2006; Crespi et al. 2013). This complexity once again reinforces the vital importance of appreciating physiological variation in the light of life-history theory (Zera and Harshman 2001; Ricklefs and Wikelski 2002). As a result, meta-analyses will be extremely useful in determining which physiological traits will be best suited to predicting changes in populations in the face of environmental alteration, and establishing whether use of certain physiological measures may be limited to certain circumstances (e.g., age classes, times, or sexes).

Summary of the symposium

The symposium was comprised of speakers that represented a strong cross-section of work in conservation physiology in terms of taxon, scale, type of ecosystem, and physiological system. Presenters linked their work to the themes outlined above, while also providing an indication of the diversity of ways that physiological approaches can be employed to accomplish a variety of conservation goals. Steven Cooke and colleagues (2015, this volume) focused on the merits of combining physiological and behavioral assessments, outlining how this approach has led to improved management of endangered coho salmon (*Oncorhynchus kisutch*) in the Fraser River, British Columbia, Canada, by providing improved estimates of mortality for individuals incidentally caught in fishing nets and contributing to best-practices guidelines for fisheries. This talk also highlighted that linking physiology to metrics of behavior can provide simple, cost-effective strategies for the assessment of wildlife in the field. Craig Willis (2015, this volume) also outlined the merits of combining physiology and behavior, using measures of energetics and activity level to determine how white-nose syndrome leads to mortality during hibernation in little brown bats (*Myotis lucifugus*). He also illustrated the importance of taking into account social context and structural components of the habitat when providing directions for management. Kevin Hultine and colleagues (2015, this volume) similarly stressed the importance of considering investigations in conservation physiology within the context of entire ecosystems. Their work suggests that accurately determining the impact of invasive *Tamarix* spp. on desert cottonwood trees (*Populus fremontii*) necessitates the consideration of soil properties, symbiotic fungal associations, carbon storage, growth, and interactions with agents of biocontrol.

Kathleen Hunt and colleagues (2015, this volume) provided an overview of how the measurement of multiple fecal hormones in critically endangered North Atlantic right whales (*Eubalaena glacialis*) is contributing to the understanding of reproductive health, overall condition, and susceptibility to anthropogenic influences such as shipping noise and entanglement in lobster lines. She stressed the importance of longitudinal datasets to allow for the measurement of hormonal changes within individuals, linking physiological parameters to vital rates and thereby allowing for the assessment of population effects, and the importance of appreciating the contexts of age and sex when interpreting hormonal levels. Samuel Wasser (work presented by Kathleen Hunt) continued the discussion of the value of measuring multiple physiological traits by reviewing how fecal samples from killer whales (*Orcinus orca*) can provide a non-invasive overview of health. His work reinforced that physiological assessments can expose the causal mechanisms behind population decline. By linking nutritional limitation to reproductive failure, and the availability of prey to different levels of toxin, it became evident that the focus of killer whale conservation should be on the recovery of prey.

Brent Sinclair and colleagues highlighted the power of physiological approaches to conservation at large spatial scales and in the context of modeling. Using information on temperature and water balance to predict the distribution of insect populations under different scenarios of climatic change, he illustrated how physiological modeling could foster proactive conservation and the delineation of protected areas, especially when data are limited. Jason Rohr continued the theme of modeling physiological responses to change and variability in climate by discussing how metabolism can predict susceptibility of amphibian species to infectious disease. In addition, he highlighted that pairing a modeling approach with experimental studies in the laboratory can provide greater accuracy in predicting how changes in climate have caused, and will cause, species' declines through influences on disease. Erica Crespi and colleagues (2015, this volume) incorporated multiple spatial scales and a consideration of life history to assess stress and disease ecology in wood frogs (*Lithobates sylvaticus*). By taking a physiological approach to wildlife disease, they were able to use the current physiological variation across the species' range to predict how changing anthropogenically-induced environmental conditions may influence this species, and the consequences this could have for the persistence of populations. Finally, Cory Suski and colleagues (2015, this volume) demonstrated that physiology can link organisms to landscape-level properties and habitat quality, thereby placing emphasis on how anthropogenic changes can affect multiple physiological systems simultaneously. Through the study of two species of freshwater fishes, they were able to ascertain which aspects of stress physiology, metabolism, nutrition, and oxidative status are associated with a gradient of habitat types, providing information on habitat requirements, tailoring monitoring protocols, and potentially guiding future restoration.

Conclusions: why integrate?

The integration of conservation and physiology is often viewed as a way for conservation biologists to expand their toolbox. However, we have argued that there are a number of opportunities for physiologists to contribute to, and incorporate principles in, conservation biology, many of which do not necessitate working within an endangered system. Importantly, this approach can have direct benefits to the ecological, evolutionary, and comparative physiologists who choose to undertake it. Viewing physiological function and diversity through the lens of conservation can lead to unexpected opportunities and collaborations, and can foster new interpretations and generate new directives for research. Since physiologists already work diligently to refine the tools they employ to assess variation in physiology, applying this approach to conservation can greatly broaden the impact and appeal of physiological research. In a more practical sense, most modern ecological researchers work within systems impacted to some degree by human perturbation; studying physiological mechanisms and responses within altered or threatened systems can provide knowledge that otherwise could be lost if ignored. Finally, as individuals whose research is dependent on wildlife, many physiologists have a vested practical interest in the natural world; addressing conservation issues can provide a way to invest in the perpetuity of the systems we rely upon so heavily (Caro and Sherman 2013).

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