INVITED PERSPECTIVE

Physiology, Behavior, and Conservation*

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Accepted 3/21/2013; Electronically Published 6/7/2013

ABSTRACT

Many animal populations are in decline as a result of human activity. Conservation practitioners are attempting to prevent further declines and loss of biodiversity as well as to facilitate recovery of endangered species, and they often rely on interdisciplinary approaches to generate conservation solutions. Two recent interfaces in conservation science involve animal behavior (i.e., conservation behavior) and physiology (i.e., conservation physiology). To date, these interfaces have been considered separate entities, but from both pragmatic and biological perspectives, there is merit in better integrating behavior and physiology to address applied conservation problems and to inform resource management. Although there are some institutional, conceptual, methodological, and communication-oriented challenges to integrating behavior and physiology to inform conservation actions, most of these barriers can be overcome. Through outlining several successful examples that integrate these disciplines, we conclude that physiology and behavior can together generate meaningful data to support animal conservation and management actions. Tangentially, applied conservation and management problems can, in turn, also help advance and reinvigorate the fundamental disciplines of animal physiology and behavior by providing advanced natural experiments that challenge traditional frameworks.

Introduction

Global biodiversity and associated ecosystems services are threatened by human activities and human-mediated environmental change (Butchart et al. 2005; Cardinale et al. 2012; Hooper et al. 2012). Conservation practitioners devoted to stemming the loss of biodiversity have had some success, but generally biodiversity continues to decline while threats proliferate (Butchart et al. 2010). For example, 20% of vertebrates are threatened, and that figure is increasing (Hoffmann et al. 2010). Populations of some amphibians (Stuart et al. 2004), mammals (Schipper et al. 2008; Hoffmann et al. 2010), and cartilaginous fishes (Dulvy et al. 2008) have seen dramatic declines, and many species in these groups are at risk of extinction. There is both dire need and abundant opportunity for conservation scientists to understand the factors and processes responsible for population declines of animals and try to work with management authorities and politicians to develop strategies to reverse such trends.

Conservation biology—or conservation science, to reflect its multidisciplinarity—emerged as a crisis discipline in the 1980s

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* This paper was submitted as an Invited Perspective for a Focused Issue on "Conservation Physiology."

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Physiological and Biochemical Zoology 87(1):1–14. 2014. 1522-2152/2014/8701-3006$15.00. DOI: 10.1086/671165

(Soulé 1985, 1986; Kareiva and Marvier 2012), with a goal of trying to stem the loss of biodiversity. Yet because of the inherent complexity of environmental problems, conservation science often requires an interdisciplinary approach, bringing together disparate fields such as social science, biology, law, and resource management (Soulé 1986). As a consequence, a number of new subdisciplines have emerged, some of which have gained significant momentum, such as conservation genetics (Hedrick 2001). An emerging interdisciplinary field is that of conservation physiology (Wikelski and Cooke 2006; Cooke et al. 2013), while another is a behavior-conservation interface called conservation behavior (Sutherland 1998; Buchholz 2007; Blumstein and Fernández-Juricic 2010). Conservation physiology is primarily concerned with animals and, more specifically, vertebrates (e.g., Carey 2005; Tracy et al. 2006; Wikelski and Cooke 2006; Seebacher and Franklin 2012; Cooke et al. 2013; this issue).

Despite clear similarities, conservation physiology and conservation behavior have until now been considered separate entities (although see Cooke et al. 2012; Metcalfe et al. 2012). Yet there is merit in better integrating physiology and behavior to address applied conservation problems. Conservation physiology excels in defining cause and effect relationships (Tracy et al. 2006; Cooke and O'Connor 2010) but often requires behavioral information for practical purposes. Conversely, many targets of conservation behavior (e.g., captive breeding, quantifying human impacts on wildlife, understanding how populations respond to environmental change) would benefit from the mechanistic understanding provided by physiological data. Although a number of reviews have suggested an agenda for both conservation physiology (Wikelski and Cooke 2006; Cooke et al. 2013) and conservation behavior (Sutherland 1998; Buchholz 2007), there are also those that identify a number of challenges with the application of physiology (Cooke and O'Connor 2010) and behavior (Caro 2007; Angeloni et al. 2008) to conservation problems. As such, it seems prudent to explore how aligning and even combining physiological and behavioral approaches might help both contribute to meaningful conservation outcomes.

The review is organized as follows: we start by outlining the development of conservation physiology and conservation behavior, focusing on their strengths and weaknesses (table 1). Next, we consider how these two subdisciplines could benefit from better integration and also provide examples of successful integration. We conclude by considering how to overcome the factors that hinder integration. In addition, we speculate that applied problems can provide an opportunity to better integrate and advance fundamental aspects of animal physiology and behavior.

A Primer on Conservation Physiology

The term "conservation physiology" was first coined by Wikelski and Cooke (2006, p. 38) and defined as "the study of physiological responses of organisms to human alteration of the environment that might cause or contribute to population declines." Although there are no reference or textbooks on conservation physiology per se, in 2013 a journal by the same name was launched in recognition of the growing interest in the topic (for inaugural paper in that journal, see Cooke et al. 2013). In addition, special issues on conservation physiology were published in *Philosophical Transactions of the Royal Society of London B* in 2012 (see Seebacher and Franklin 2012) and *Physiological and Biochemical Zoology* in 2013 (this issue). One of the first examples of conservation physiology comes from Rachel Carson's *Silent Spring* (Carson 1962). The book is famous for highlighting physiological studies that helped to identify the cause-and-effect relationship between dichloro-diphenyl-trichloroethane and reproductive failure of raptors (Pollock et al. 2001). Indeed, there are now many other examples of ecotoxicological studies that have used physiological approaches (see Brouwer et al. 1990) and that led to regulations that protect wildlife and ecosystems, including the listing of species (Fossi et al. 1999). Many others have suggested integrating toxicology and conservation, and these form part of conservation physiology also (e.g., Hansen and Johnson 1999*a*, 1999*b*). Yet conservation physiology has many other facets (Carey 2005; Tracy et al. 2006), including stress biology, particularly the use of glucocorticoid stress hormones to characterize the physiological costs of human activities (reviewed by Wingfield et al. 1997; Busch and Hayward 2009). A further area centers on the reproductive physiology of endangered organisms, for example, by improving captive breeding (Wildt and Wemmer 1999). Finally, in the past decade, broadscale environmental change—such as changing temperatures, levels of precipitation, and ocean acidity—has initiated research using physiological approaches to understand and predict the consequences of perturbations (reviewed in Pörtner and Farrell 2008; Seebacher and Franklin 2012). Physiological knowledge is also increasingly being used to inform resource management of exploited species (Cooke et al. 2012; Metcalfe et al. 2012).

Conservation physiology has several uses in conservation and management. For example, conservation physiology is particularly effective at measuring immediate response of individuals to environmental change or other stressors. Rapid responses are often not evident in other endpoints, such as community structure (Cooke and Suski 2008). Therefore, physiology can provide a mechanistic basis to describe, elucidate, and predict effects of environmental change and human disturbance (Wikelski and Cooke 2006; Seebacher and Franklin 2012). Additionally, many physiological endpoints are also directly relevant to survival or fitness (e.g., ability to recovery from a stressor enabling animals to avoid predators; Costa and Sinervo 2004). With mechanistic understanding, managers can attempt to use strategies that would alleviate or reduce a given stressor and thus modify organismal behavior and/or population biology. Moreover, through controlled experimentation, physiologists are able to define and establish whether, when, and where there is a direct causal link between a stressor and an organismal condition, something that is rarely possible for behavioral ecologists (Tracy et al. 2006; Cooke and O'Connor 2010). Additionally, physiologists have the expertise to delve into the mech-

Table 1: Summary of the key strengths and weaknesses of behavior and physiology, with specific reference to the application of these approaches to conservation problems

Characteristics	Conservation behavior	Conservation physiology
Strengths	Several frameworks (e.g., Tinbergian approach and Berger-Tal et al. 2011) on which conservation problems can addressed	Physiological experiments can be used to identify causal relationships
	Behavior can be a demographic mechanism (Anthony and Blumstein 2000)	Physiological information provides mechanisms underlying observed patterns in behavior or survival
	Behavior is an easily observed and immediate metric of distress for individuals	Physiology provides an objective characterization of animal health and condition
	Behavior integrates the response of an individual to environmental change	Many physiological indicators are linked to stress and fitness
	Behavior is useful for understanding the success or failure of concerted conservation efforts where individuals are known	Physiology can be used to predict organismal responses to environmental perturbations and change
	Behavior can provide an early warning to population decline or habitat degradation before numerical responses are evident	Physiological responses are typically rapid (i.e., compared with changes in organismal abundance or community structure)
	Observable behavior often engenders the human empathy needed to support conservation action	Physiological responses may reveal fitness impacting changes that are not evident from an animal's behavior (e.g., immobility)
		Physiology can be used to characterize the diversity among individuals, populations, and species
		Because of its similarity to medical research, policy makers may find physiological data more convincing or objective than behavioral data alone
Weaknesses	Fails to provide mechanistic explanations (e.g., linked to physiological status, tolerances, and regulata) of observed behaviors	Physiology does not provide information on behavioral responses that could mediate responses to unfavorable environmental conditions or stressors
	Population implications of individual behavior remains tenuous	No common paradigm or underlying conceptual framework for integrating physiology and behavior (although see life history–physiology nexus and performance framework developed by Arnold 1983; also see fig. 2 for proposed framework)
	Some reliance on surrogate species	There is a need to better understand links between physiological indicators and survival/fitness
	There is a need for better integration of behavior in ecological models and conservation/management plans	Population implications of individual physiology remains tenuous
	Conservation managers are often not trained in behavior	Strong reliance on surrogate species
	There is a need for more success stories	There is a need for tools that enable physiology to be studied in the wild
		Some procedures are lethal
		There is a need for better integration of physiology in ecological models and conservation/management plans
		It is difficult to convey physiological concepts to the general public
		Conservation managers often not trained in physiology
		There is a need for more success stories

anisms underlying certain behaviors, from the gathering of sensory information to the processing of information in the brain, which ultimately affects behavioral responses. This level of mechanistic understanding may enhance the success of interventions, such as when managers try to manipulate the behavior of a species (e.g., attraction or repulsion from an area; Sutherland 1998).

Conservation physiology has not been without critics. Cooke and O'Connor (2010) noted that conservation actions tend to focus on populations or species, whereas physiology tends to focus on individuals, cells, or molecules, and they identified the need to expand and validate the tools in the conservation physiology toolbox, particularly those that enable the study of animals in their natural environment (e.g., biotelemetry and biologging, which also yield behavioral information; see Cooke et al. 2004; Block 2005; Ropert-Coudert and Wilson 2005; Cooke 2008; Metcalfe et al. 2012). They also recognized the need to conduct research on threatened taxa rather than relying on surrogates (also a critique of conservation behavior; Caro et al. 2005).

A Primer on Conservation Behavior

Conservation behavior applies knowledge and methods from animal behavior to solve wildlife conservation and management problems (Curio 1996; Blumstein and Fernández-Juricic 2010). It views behavior as a mechanism that influences demographic processes and thus may identify levers that can be applied to manage populations. In the same way that behavior is a mechanism of demography, physiology is a mechanism of behavior. Thus, the integration of these fields is somewhat natural. Indeed, some aspects of physiology—such as endocrine-based motivational changes, sensory neuron sensitivity, and other proximate causes of behavior—have always been considered one of the four behavioral questions posed by animal behaviorists (Tinbergen 1963). As a result, these aspects of physiology were included in the concept of conservation behavior from the very beginning (Clemmons and Buchholz 1997; Wingfield et al. 1997).

The term "conservation behavior" was first used in a book review (Blumstein 2001) of an edited volume that integrated behavior and conservation (Gosling and Sutherland 2000). This was just one of several edited volumes (Caro 1998; Festa-Bianchet and Apollonio 2003), substantive reviews (Strier 1997; Sutherland 1998; Caro 1999; Reed 1999; Anthony and Blumstein 2000), as well as two special journal issues (*Oikos*, vol. 77; *Environmental Biology of Fishes*, vol. 55; *Applied Animal Behavior Science*, vol. 102) that followed a pioneering edited book by Clemmons and Buchholz (1997), which emerged from a 1995 symposium at the Animal Behavior Society annual meeting in Lincoln, Nebraska. The first textbook on conservation behavior was published in 2010 (Blumstein and Fernández-Juricic 2010), and there have been additional reviews and conceptual frameworks published recently (e.g., Angeloni et al. 2010; Berger-Tal et al. 2011; Candolin and Wong 2012).

At one level, understanding and managing behavior has always been part of wildlife management (particularly that focused on repelling/attracting animals from certain areas and dealing with captive breeding), but the key contribution in the 1990s was that behavioral biologists could generate novel conservation and management strategies to help manage our biodiversity crisis (Curio 1996). For instance, knowledge of conspecific attraction could be used to help encourage animals to settle (or stay) in places where they were safe (e.g., Ward and Schlossberg 2004). Knowledge of adaptive sex ratio variation (Trivers and Willard 1973) could be used to distort the offspring sex ratio in a desired manner (Robertson et al. 2006). Finally, knowledge of how a species responds fearfully to humans (e.g., Blumstein 2007) could be used to develop setback zones to reduce human impacts on animals (e.g., Fernández-Juricic et al. 2005).

However, conservation behavior has also come in for criticism (Caro 2007). Conservation biology focuses on much larger scales (landscape, ecosystem, biosphere) than the individual focus of animal behaviorists. Caro (2007) suggested that the different approaches of conservationists and behaviorists were evidence of the failure of conservation behavior's theoretical insights to actually be applied to solve conservation problems, and empirical examination concurs (Angeloni et al. 2008). He suggested that conservation problems are driven by habitat destruction, exotics, exploitation, climate change, and pollution—hardly the variables that behavioral biologists study. Buchholz (2007) countered Caro's (2007) criticism with concrete examples of how management has been improved by the integration of behavioral insights about mechanism, ontogeny, adaptive function, and evolutionary history into conservation planning. Interestingly, these relevant academic arguments are sometimes not well rooted in the daily challenges many managers around the world face. Some of these challenges have a central behavioral component because they involve the manipulations of the behavior of individual animals (e.g., lure them to traps for relocation, detract them from breeding in areas with high incidence of predation/brood parasitism). For the correct questions at the proper scale, insights and knowledge gained by those who study behavior can have profound impacts on conservation and management outcomes. Nowadays, however, many recognize that captive breeding, translocation, and reintroduction; creating effective deterrents; and managing and understanding animals' responses to growing populations and urbanization are the areas where behavioral knowledge might be most relevant to management problems (Blumstein and Fernández-Juricic 2010; Candolin and Wong 2012) rather than in in situ conservation programs.

Benefits of Integrating Physiology and Behavior for Conservation Science

The thesis of this article is that the integration of behavior and physiology would generate meaningful understanding to support conservation actions and do so synergistically. Often, questions arise from conservation behavioral studies that are physiological in nature, and vice versa for physiological studies.

Integrating the disciplines would provide simultaneous data and therefore better efficiency and speed in being able to understand causes of population declines and develop strategies to reverse them. Collectively, physiology and behavior move us toward a more complete understanding of individuals and how different drivers could scale up to affect higher levels of biological organization. Even though physiologists and behaviorists are often concerned with different levels of biological organization, they collectively address all of the ways in which stressors can influence biological processes that ultimately will influence population-level processes of great interest to conservation scientists (fig. 1).

Developing a more integrative understanding of target species will improve researchers predictions of individual responses to environmental perturbations, on the basis of exposure and sensitivity (Huey et al. 2012), and thus provide a mechanistic and organismal understanding for changes in populations, distribution shifts of species, and extinctions (e.g., Seebacher and Franklin 2012). Conservation practitioners need predictive demographic models that have specific mechanistic levers identified through physiology and parameterized with behavioral information (e.g., Anthony and Blumstein 2000; Huey et al. 2012). Such knowledge could be used for identifying and applying various management actions that influence animal populations (e.g., leading to increasing populations of endangered animals, reducing populations of invasive species). Extinction probability models can also incorporate behavioral and physiological attributes that influence population persistence rather than focusing solely on population biology (Reed 1999; Blumstein and Fernández-Juricic 2004). From a methodological stance, if we knew more about the correlations between behavior and physiology, we could make more use of quick, inexpensive, and noninvasive behavioral assays to identify target individuals for capture, protection, or aversive conditioning. For example, the field of ethotoxicology uses behaviors as indicators of exposure to toxic chemicals (Parmigiani et al. 1998), and behavioral assays are used to identify rabid individuals, and the same might be true of much more nuanced health states with more investment in the integration of these two fields. With conservation triage inevitable (Bottrill et al. 2009), it would also be worthwhile to identify how physiology and behavior could be used to identify practical conservation priorities. For example, with a growing number of species in need of resource-intensive ex situ conservation, there is a need to identify species/populations that will likely succeed in such environments, an area where the integration of physiology and behavior has the potential to excel.

Examples of Successful Integration to Advance Conservation

While advocating the integration of behavior and physiology to improve conservation outcomes, we acknowledge that some examples already exist. Here we summarize some successful cases of integration of behavior and physiology that span environments, taxa, and conservation problems in an attempt to illustrate the benefits to advancing conservation. A common feature of success is an interdisciplinary team or individuals that walk the line between behavior and physiology (i.e., integrative biologists, behavioral physiologists). Successes are evident in documenting problems and developing conservation solutions in both ex situ and in situ contexts.

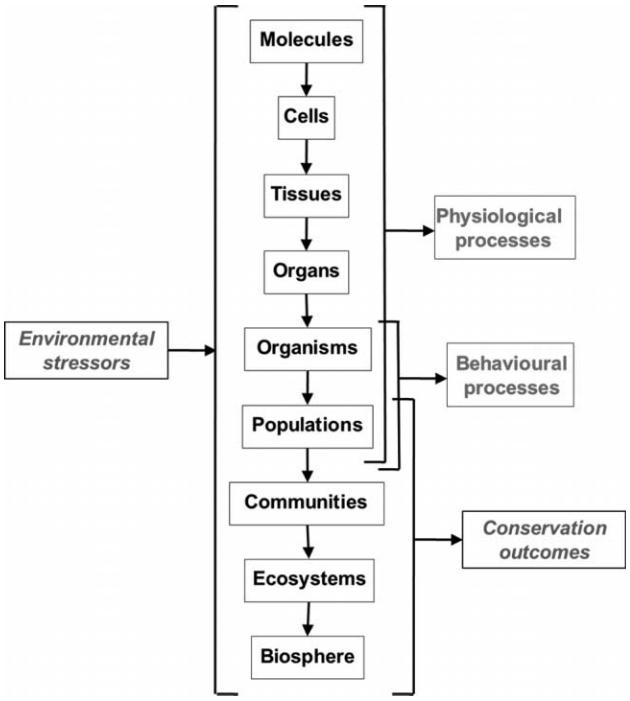

Figure 1. Hierarchical levels of biological organization illustrating where behaviorists, physiologists, and conservation practitioners typically focus their efforts. Note that environmental stressors affect multiple levels of biological organization and that failure to combine physiology and behavior to address conservation-oriented perspectives would mean that there is an incomplete understanding of the biological processes that ultimately determine the state of animal populations, ecosystems, and conservation outcomes. A color version of this figure is available online.

*Hoatzin (*Opisthocomus hoazin*) and Ecotourism*

As noted above, the effects of human disturbance on wildlife are often studied using either behavior or physiology, rarely both. In South America and elsewhere, ecotourism operators seek to provide tourists with opportunities to view birds and other wildlife in their natural environment. Müllner et al. (2004) studied hoatzin in areas with low and high ecotourism and recorded adult flush distance, nest success, chick development, and glucocorticoid stress responsiveness (baseline and maximal) of chicks. The behavior and fitness endpoints (survival) were alone meaningful and indicated that birds were impacted by tourist activity. However, the physiological component identified the mechanism by which mortality was occurring (i.e., high levels of corticosterone, which impeded growth), and identified that the impact was greatest on juveniles before fledging. The notion of differential sensitivity to tourist stress across developmental stages provides managers with potential opportunities for using temporal and/or spatial restrictions on ecotourism to protect sensitive species.

Ungulate Responses to Airplane Noise

Noise from anthropogenic activities is regarded as a form of pollution. Weisenberger et al. (1996) studied the effects of simulated low-level military jet aircraft noise on mule deer (*Odocoileus hemionus*) and mountain sheep (*Ovis canadensis*) in outdoor desert enclosures. Heart rate telemetry and behavioral observations both revealed evidence of disturbance. Heart rate showed a positive relationship between cardiac response and the decibels of the noise disturbance. Both heart rate and behavior, although altered, returned to predisturbance levels within several minutes following the end of the disturbance. Both metrics also showed evidence of habituation when exposed to repeated flyover simulations. Others have taken such work further and modeled the energetic consequences of disturbance (e.g., on wandering albatross [*Diomedea exulans*] relative to human disturbance; Weimerskirch et al. 2002).

*Pacific Salmon (*Oncorhynchus *spp.) and Climate Change*

Climate change and associated warming river temperatures are expected to have detrimental consequences on Pacific salmon. Studies using biotelemetry to study survival, behavior (e.g., entry timing, migration speed), and physiology (e.g., tissue samples of telemetered animals, parallel laboratory cardiorespiratory studies) reveal that there are stock-specific thermal thresholds and clear relationships between impaired migration behavior (including failed migration and subsequent death) and physiological status (Cooke et al. 2012; Hinch et al. 2012). The cardiorespiratory capacity of Pacific salmon is constrained such that fish are unable to migrate beyond a given stock-specific thermal threshold (Farrell et al. 2008; Eliason et al. 2011). The behavioral and physiological disturbances are magnified when other stressors are added, such as when fisheries interactions (e.g., bycatch) coincide with high temperatures (e.g., Gale et al. 2011). The combination of approaches (in lab and field, behavior and physiology) used in this coordinated research program (summarized in Cooke et al. 2012) have generated data for management adjustment models (i.e., restricting harvest when water temperatures warm) allowing adequate numbers of adults reach spawning grounds, and they have also led to the development of best handling practices for those that capture and release salmon.

*Kakapo (*Strigops habroptilus*) Supplemental Feeding and Captive Breeding*

The kakapo is a critically endangered bird endemic to New Zealand. While early studies focused more on behavior and demography of kakapo, aggressive conservation efforts have begun to include supplementary feeding to increase chick survival and improve breeding frequency. This has led to a demand for more knowledge of nutritional physiology. The research team hypothesized that there was a minimum weight threshold below which the birds would be incapable of reproducing (Harper et al. 2006) but also recognized that too much supplemental feeding seemed to reduce breeding (Elliot et al. 2001). Detailed nutritional physiology studies followed that examined the nutrient composition of kakapo diets in the field (Cottam et al. 2006), estrogenic activities of foods (Fidler et al. 2000), and gut microbiology (Waite et al. 2012) to inform supplemental and captive feeding. Experimental feeding with food formulations revealed that nutritional quality was the problem with diets, not energy content (Houston et al. 2007). A recent thesis (Cottam 2010) further explored the chemical compounds in key fruits in an effort to identify triggers to reproduction. Research continues to unravel whether reproductive cues are visual or directly related to ingestion of compounds.

Ultraviolet B Effects on Amphibians

Amphibians are experiencing dramatic population declines and extinctions. Although it is common for the causes of population declines to be multifactorial, this concept is exemplified in the amphibians in which ultraviolet (UV) radiation has synergistic effects with a variety of environmental (e.g., water temperature, pH, nitrates) and biotic (e.g., disease, predation) factors (see Bancroft et al. 2008; Alton et al. 2010, 2012). After initial observations of deformities and population declines thought to be mediated by UV light, both physiologists and behaviorists became involved in attempting to understand the influence of UV light on amphibians and identify its relevance to different conservation strategies. One of the first studies to link physiological tolerances to behavior in a field environment revealed that because of parental oviposition behavior, the embryos of the most UV-sensitive species experienced the least UV-B radiation (Palen et al. 2005). Palen and Schindler (2010) combined surveys of the incubation timing, incident UV-B, optical transparency of water, and oviposition depth and light exposure of embryos at various sites to further reveal that exposure to lethal levels of UV-B was minimal in a natural heterogeneous landscape. Collectively, these studies suggest that maintenance of natural heterogeneous habitats is essential for providing opportunities for amphibians to avoid UV-B. However, even when UV-B is itself not lethal, in the presence of other stressors (especially disease and predation pressures; Alton et al. 2011; Blaustein et al. 2012), it is important to maintain good water quality and minimize human disturbances associated with development. Much work is currently underway on understanding disease development and immune function (e.g., Richmond et al. 2009), which is highly relevant to understanding the effects of multiple stressors on amphibian populations.

Bycatch Reduction of Cetaceans and Turtles

Bycatch in marine fisheries is a global conservation problem. Early studies focused on developing strategies to reduce bycatch and documented the behavior of nontarget taxa around fishing gear. It became evident that where the target of the fishery and the nontarget species overlapped, bycatch was inevitable. Researchers then began to incorporate knowledge and studies of sensory physiology in an attempt to identify means of deterring animals from approaching fishing gear. For example, pingers (acoustic harassments devices) that are used to alert cetaceans, especially dolphins, to nets and other fishing gear (e.g., Barlow et al. 2003) have been developed according to physiological and anatomical hearing capacities of cetaceans (e.g., Tyack et al. 2003; Nowacek et al. 2007). Similarly, visual, olfactory, and auditory cues can be used as determents to bycatch for sea turtles approaching baited long-line gear (Southwood et al. 2008). Spectral capacity of sea turtles differs from most target species, and visual deterrents have been developed and tested; in particular, use of light sticks and LEDs show promise (Wang and Swimmer 2007; Wang et al. 2007). Laboratory studies combined with field trials using both behavior and physiology (for examples, see Southwood et al. 2008) have already yielded tools to reduce bycatch.

Impacts of River Damming on Bimodally Respiring Turtles

The damming of river systems can significantly alter the physiochemical conditions, including loss of pool-riffle sequences, reduced water flow, and increased water depths; these changes typically culminate in altered temperature profiles and decreased aquatic oxygen levels. In Australia, many of the river systems that are dammed are home to species of freshwater turtles that can respire aquatically via cloacal respiration, including some species that can acquire a significant amount (>70%) of oxygen via this route (Priest and Franklin 2002; Gordos et al. 2007). Studies looking at the diving behavior and physiology of bimodally respiring turtles, such as the Mary River turtle (*Elusor macrurus*) and the Fitzroy River turtle (*Rheodytes leukops*), found that elevated temperatures and reduced oxygen levels reduce submergence time and that these species have little capacity to acclimate to these conditions (Gordos et al. 2006; Clark et al. 2008, 2009). For hatchlings, this may lead to an elevated predation risk as a consequence of increased surfacing. These findings have resulted in greater scrutiny of the impacts of dams on these vulnerable species, including the cancellation of the Traveston Dam on the Mary River.

Impacts of Diffuse Pollutants on Atlantic Salmon

A recent joint physiological and behavioral study of the impact of the herbicide atrazine (a contaminant that salmon are exposed to in the wild and that modifies parr-smolt transformation) on Atlantic salmon (*Salmo salar*) smolts during their transition from fresh to sea water (Moore et al. 2008) showed that exposure to low but environmentally realistic levels of atrazine in freshwater over a 72-h period significantly reduced gill Na^+-K^+-ATPase activity. Subsequent transfer to 33‰ saltwater resulted in 100% mortality after 72 h. No mortality occurred in control fish on transfer to saltwater. On the other hand, tracking studies showed that both atrazine-treated and control fish successfully migrated across freshwater, out of the estuary, and into marine coastal waters over similar periods of time (Moore et al. 2008). In the tracking component of this study, fish were held in freshwater for 6 d after atrazine exposure before being released to the wild, so it may be that the fish had at least partially recovered from the physiological effects of atrazine exposure, suggesting that its physiological effects can be reversed. This approach of using both physiological and behavioral studies, together with the development and application of life-history models, has been used to assess the potential impact of diffuse pollutants on salmon populations in the United Kingdom, and the results form the basis of advice to the government.

Opportunities Lost?

Conservation Physiology

A number of opportunities to improve conservation and management outcomes have been lost because physiological studies have not fully incorporated behavioral approaches. For example, the oxygen limitation hypothesis proposed by Pörtner and Farrell (2008) postulates that organismal performance (activity metabolism and survival) will be impaired in the face of stressors such as climate change that reduce aerobic scope. However, field studies that combine physiology and behavior are needed that directly test this idea and evaluate potential thermoregulatory responses to mediate such effects. Indeed, some preliminary work on that topic (i.e., Mathes et al. 2010) suggests that fish may seek thermal refuge in deep, cooler lake waters when possible. This is not intended to be critical of the oxygen limitation hypothesis; rather, to date, field studies that incorporate behavioral and physiological aspects have been limited yet are needed to test the validity of this interesting hypothesis.

Stress physiology is also particularly pertinent in this regard (Tarlow and Blumstein 2007). Hundreds of studies have examined the glucocorticoid response of a variety of vertebrates to stress (reviewed in Walker et al. 2005; Busch and Hayward 2009), yet there are few studies that have integrated behavioral aspects. For example, recent work on the effects of ecotourism on glucocorticoid responses of orangutans (Muehlenbein et al. 2012) focused solely on physiological endpoints, but we do not know whether or how these physiological stresses translated into fitness consequences. Tarlow and Blumstein (2007) noted that there is no single optimal method to quantify the effects of anthropogenic stressors on wildlife, emphasizing the potential benefits of integrating behavioral, physiological, and ultimately demographic endpoints. Given the direct interaction between hormones and behavior and the potential for animals to mediate stress responses through behavioral alterations, it would seem sensible to study both simultaneously. There are exceptions where both behavior and hormones were measured simultaneously, often leading to unexpected results (e.g., Butler et al. 2009).

Conservation Behavior

Behavior has been applied successfully to understanding the success or failure of concerted conservation efforts where individuals are known, such as in captive breeding programs, relocation efforts, and monitoring wild individuals in the field. But here too, as with conservation physiology, there still appear to be some lost opportunities. For example, Wielebnowski (1998) noted the need to integrate physiology and behavior in captive breeding of endangered fauna. Specific examples include the testing of enrichment for breeding giant pandas, where physiology could be used to test whether management techniques can reduce glucocorticoid stress hormones (Swaisgood et al. 2000). Another example would be characterizing the feasibility of captive-breeding Strombidae conch, which focused on trying to breed animals in captivity without understanding environmental and physiological tolerances and nutritional needs of the animals (Shawl and Davis 2004). For some threatened species, physiological data could aid in manipulating sex ratios (such as the Australian brush turkey and various sea turtles; e.g., Robertson et al. 2006). Another suite of examples of where physiology and behavior could together inform management decisions relates to animal-environment interactions and sensory physiology (Appleby and Hughes 1993). These include understanding how individuals decide which habitats to use (Cooke 2008) and the consequences of doing so (Huey 1991), where to settle, crossing gaps in fragmented habitats (Fahrig 2007), and deterring individuals from unsuitable habitats (Blumstein and Fernández-Juricic 2010). For instance, when using nest boxes to increase the breeding densities of a given species, researchers rarely consider the sensory attractiveness of the boxes. Incorporating physiology by designing nest boxes that are attractive to the visual system of the target organism (e.g., arboreal marsupial, cavity nesting birds) yet do not attract predators could lead to higher breeding success. The same sensory principles can be applied to artificial stimuli that managers develop to repel birds from a given area, such as airport runways, airplanes, wind turbines, or windows (e.g., Blackwell et al. 2012).

One particular example of a lost opportunity stands out. Physiology could be combined with behavior to address key questions related to the effects of human disturbance on wildlife populations. First, how can we promote the spatial and temporal coexistence of recreationists and wildlife within protected areas? Addressing this problem has obvious educational benefits and requires a good understanding of how different species respond behaviorally to different levels of recreationists (Blumstein et al. 2005; Rodríguez-Prieto and Fernández-Juricic 2005). Second, can human disturbance negatively affect populations or species? This necessitates understanding more than behavioral responses of a species to a given source of disturbance (e.g., visual, auditory). Buchholz and Hanlon (2012) reviewed studies of wildlife disturbance and found that most of them did not link behavioral change to fitness indicators (but see Beale and Monagham 2004), even though a framework for doing so exists (Gill et al. 1996; Houston and McNamara 1999; Frid and Dill 2002). They noted that integrating physiological measures, such as glucocorticoids or heart rate, into studies on whether human disturbance harms animal populations would make results (whether positive or negative) more believable and thus better support effective decision making (e.g., Bisson et al. 2008). Indeed, many behavioral studies alone would fail to meet the evidentiary requirements in a legal context if a regulator were to attempt to press charges related to some form of human disturbance. However, with a physiological understanding that is worked out well, behavioral indicators could be robust indicators of disturbance.

Opportunities to Advance Fundamental Knowledge

If physiologists and behaviorists could work together to address conservation problems, we believe that their disciplines would thrive better as a result of the integration, potentially reinvigorating and advancing both disciplines. In recent years, there have been more scientists combining physiological and behavioral techniques and theories (see Gilmour et al. 2005; Cabanac 2011), and conservation problems could serve as an opportunity to increase the level of integration further and would help attract trainees. Possibilities for integration include (1) the use of genomic physiology to understand physiological pathways and genomic connections between behavior and genes (Ryder 2005) and (2) the integration of behavior and physiology to yield measures or proxies of organismal fitness, such as elevated cortisol being a marker for reproduction and fitness in organisms subject to human activity.

In some ways, the rapid human-caused environmental change serves as a large-scale experiment that provides opportunities to understand physiological and behavioral reactions to environmental change (Carey 2007; Candolin and Wong 2012). Such work will also yield a better understanding of the proximate and ultimate explanations behind how organisms interact with each other and their physical environment, an outstanding big question in ecology and one that demands integration (May 1999). Referring to fundamental behavioral questions, Owens (2006, p. 360) stated that "many of these new [behavioral] questions are of a subtly different type and require a more detailed understanding of the genetic and physiological mechanisms that underlay behavioral traits," emphasizing the need for integration to advance fundamental scientific questions. Similar perspective articles on the future of physiological ecology (Feder and Block 1991) and comparative physiology and biochemistry (Mangum and Hochachka 1998; Somero 2000) all identified the need and opportunity to further embrace research outside of the laboratory, using new models and, where relevant, integrating other techniques and disciplines, such as behavior. Collectively, these advances in fundamental knowledge would contribute to better predictive abilities in basic biology (e.g., developing predictive models of mechanistic diversity that link to fitness) as well as integration of information into large ecological and evolutionary models.

In terms of advancing fundamental knowledge, behavior and physiology both require comparative data, yet disappearing spe-

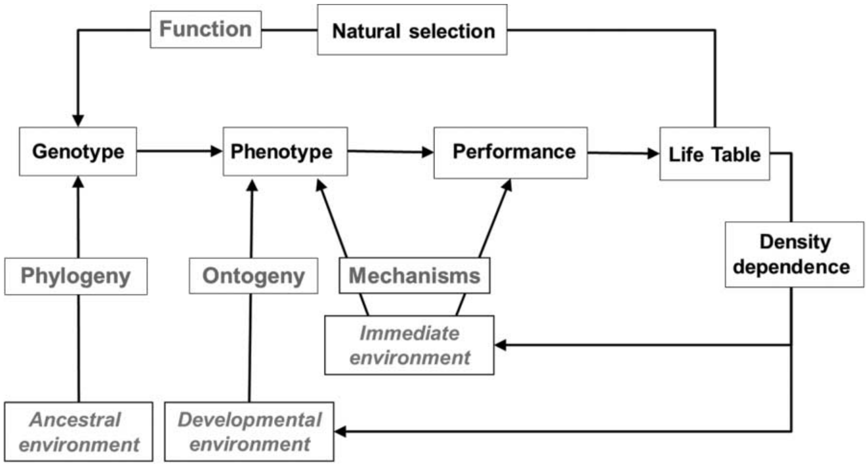

Figure 2. Adaption of the physiology–life history nexus (Ricklefs and Wikelski 2002) to incorporate Tinbergen's concept that questions can be approached in a complementary way using phylogenetic, ontogenetic, functional, and mechanistic approaches (Tinbergen 1963). This framework emphasizes the connections among behavior, physiology, and population-level and evolutionary processes. A phylogenetic approach can be used to understand variation in both behavior and physiology within and among species, while ontogenetic approaches can be used to understand the influence of anthropogenic stressors in the developmental environment on behavioral and physiological phenotypes. Perhaps the most common approach in conservation biology, a mechanistic approach can be used to understand the influence of anthropogenic stressors in either the developmental or the immediate environment on physiological and behavioral aspects of performance. In this case, physiological tools can also be used as a mechanistic tool to understand differences in behavioral performance. Finally, a functional approach to understanding ultimate causes of variation in genotypes and phenotypes helps connect individual to evolutionary processes. Key to applying this framework to conservation issues is to connect variation in performance to population-level processes whenever possible.

cies will increasingly prevent us from using the comparative approach in physiology and behavior (Caro and Sherman 2011). For example, the gastric breeding frog *Rheobatrachus silus* and *Rheobatrachus villinus* raised tadpoles in its stomach but became extinct before the mechanism was identified. This likely led to an irreversibly lost opportunity for treating peptic ulcers, since these frogs secreted substances that inhibit acid and pepsin secretions (Chivian and Bernstein 2008). Furthermore, as populations disappear, so do unique behaviors (Caro and Sherman 2012). In other words, there is merit in behaviorists and physiologists contributing to conservation science inasmuch as it also may help to ensure that they have the most diverse suite of animals available for fundamental research.

Practical Challenges

Conceptual Challenges

Researchers tend to consider issues within a specific research sphere and theoretical framework. The manner in which physiologists and behaviorists approach questions can be quite different. Behaviorists tend to work within the framework of Tinbergen's four questions, even when addressing conservation problems (Anthony and Blumstein 2000; Blumstein and Fernández-Juricic 2004; Berger-Tal et al. 2011). Yet this framework provides an explicit entrée for the study of physiological mechanisms. While there is not a similar unifying theme or framework in physiology (or conservation physiology), the life history–physiology nexus (Ricklefs and Wikelski 2002; Young et al. 2006; also see Spicer and Gaston 1999 for some discussion of such integration) has strongly influenced many conservation physiologists, and it provides an explicit entrée for the study of the adaptive basis of some behavioral traits (fig. 2). Nonetheless, frameworks can be constraining.

Another conceptual challenge is that physiology and behavior operate on different timescales, even though both are mechanisms underlying demography. Many physiological responses occur much more slowly than (neurologically based) behaviors (especially those related to seasonal acclimation, energetics, growth, or reproductive preparedness), yet the consequences of a seemingly ephemeral behavior (e.g., eating a toxic food, winning a contest with a higher-ranking individual) can be long lasting. There is a need for integrating these timescales.

These conceptual challenges would best be addressed by training the next generation of integrative animal biologists not only in the fundamentals of behavior and physiology but also in their convergence and applicability to conservation. In reality, few academic programs cover behavior and physiology in depth.

Methodological Challenges

Another significant challenge to the integration of behavior and physiology is methodological. This is somewhat influenced by the fact that for conservation problems, much of the research needed is best done in the wild. Yet there are a growing number of technological tools to integrate physiology and behavior in field environments (see Costa and Sinervo 2004), particularly related to biotelemetry and biologging, which incorporate various sensors (e.g., heart rate, temperature, pressure, acceleration; Cooke et al. 2004). Indeed, new technologies enable the tracking of both behavior and physiology at the same temporal scale and at a scale that is relevant to the animal. Unfortunately, there are still many animals for which these tools cannot be readily applied, given the small size of the animals (e.g., most insects) or extreme environments (e.g., deep sea fishes).

Finding tools that themselves do not alter the behavior of the animal being studied or impart physiological costs is a common problem for behaviorists and physiologists and one that influences data quality and ethical concerns (Cuthill 1991), particularly when working with endangered animals (Putman 1995). Analytically, there can also be different expectations of what good data are (e.g., treatment of outliers, biological significance) and the type of analyses involved. For example, and in stark contrast to behavioral studies, there are few examples of multivariate techniques or other advanced statistical approaches applied to physiological data aside from bioinformatics. Several books have been written on analyzing behavioral data (e.g., Russo 2003; Blumstein and Daniel 2007; Martin and Bateson 2007), and some animal behavior journals (e.g., *Animal Behaviour*) provide authors with extensive guidelines of acceptable statistical practice. The integration between physiology and behavior will increasingly require that researchers on both sides acquire strong analytical skills and develop novel statistical methods for a variety of data sets.

Communication and Institutional Challenges

There is still poor communication between behavioral and physiological experts related to the different research traditions. Joint meetings, integrative books and journals, and—most importantly—identifying questions or problems that simply demand integration (such as many animal conservation problems) could help to overcome these challenges. Communication is increasing, and there have been several syntheses on the behavior-physiology interface (albeit typically written by those working more from physiological perspectives and in physiology journals, including *Physiological and Biochemical Zoology*; see Gilmour et al. 2005); outlets such as *Hormones and Behavior* and *Physiology and Behavior* are both positioned around the interface and have been focused on fundamental research for decades (albeit largely in a laboratory setting). Another barrier is that funding structures do not overtly require integrating input (knowledge and research capability) from managers, conservationists, ecologists, and behavioral and physiological biologists. A more interdisciplinary research approach where such projects are encouraged would be useful.

Conclusion

Although conservation physiology and conservation behavior have been considered separate entities, there is merit in better integration in regard to applied conservation problems from both pragmatic and biological perspectives (fig. 3). Both disciplines struggle to extend their findings to meaningful conservation outcomes (Caro 2007; Angeloni et al. 2008; Cooke and O'Connor 2010; Cooke et al. 2013). This is particularly the case for conservation physiology, which excels in defining cause and effect relationships but often requires behavioral information related to how animals interact with their environment for results to be made relevant to the natural world (Cooke et al. 2013). Clearly, an animal's physiology modifies its behavior and vice versa. Here we have highlighted some examples where the two disciplines achieved meaningful conservation outcomes that benefited imperiled animal populations or improved resource management. Indeed, there are certainly examples of where physiology and behavior have been integrated for some time to address basic and applied issues. We also provided examples where there were opportunities lost from applying physiology and behavior in isolation to conservation problems. There are many complementary aspects to physiology and behavior (table 1) that collectively can lead to conservation successes. Together, behavior and physiology can generate meaningful data to support conservation actions, and applied conservation problems are an opportunity to better integrate and advance the fundamental disciplines of animal physiology and behavior as well.

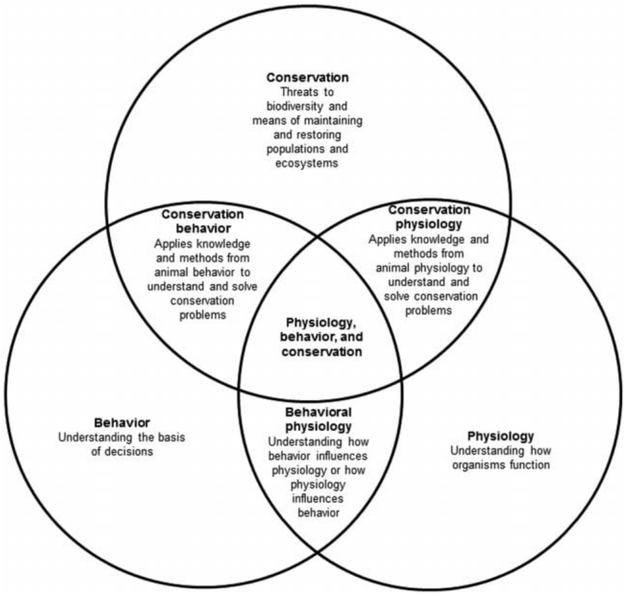

Figure 3. Schematic diagram of the possible links between conservation, behavior, and physiology. We argue that there is inherent overlap between behavior and physiology when either one is integrated with conservation. A color version of this figure is available online.

Acknowledgments

S.J.C. was supported by the Canada Research Chairs Program and the Natural Sciences and Engineering Research Council of Canada. C.M.O. was supported by an E. B. Eastburn Postdoctoral Fellowship from the Hamilton Community Foundation. C.E.F. is supported by funding from the Australian Research

Council. R.B. is supported by the National Science Foundation (NSF) and the University of Mississippi. D.T.B. and E.F.-J. are supported by the NSF. W.J.S. is funded by Arcadia.

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