



GRAND CHALLENGES

Behavior as a Key Component of Integrative Biology in a Human-altered World

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Synopsis A major grand challenge in biology is to understand the interactions between an organism and its environment. Behavior resides in the central core of this association as it affects and is affected by development, physiology, ecological dynamics, environmental choice, and evolution. We present this central role of behavior in a diagram illustrating the multifaceted program emphasizing the necessity for understanding this nexus and to fully appreciate the organism in its environment given the ongoing changes affected by contemporary human induced, rapid environmental change (HIREC). We call for the consideration of educational and research focuses to concentrate on the interdisciplinary role that behavior plays in the integration of biological processes.

Introduction

This article is one of a series on Grand Challenges in Organismal Biology. Previous articles in this series have focused on the challenges in comparative endocrinology (Denver et al. 2009), comparative physiology (Mykles et al. 2010), ecomechanics (Denny and Helmuth 2009), migration biology (Bowlin et al. 2010), value of integrative organismal research (Satterlie et al. 2009; Mykles et al. 2010), and organismal biology in general (Halanych and Goertzen 2009; Schwenk et al. 2009). The current article addresses the issues of

behavior and considers how this discipline fits into a multilevel, multiscale, integrated view of organismal biology as discussed previously by Wake (2008) and illustrated in Fig. 1. A key point to which we will return to repeatedly is that behavior interacts reciprocally with other inter-related responses and outcomes. Behavior is influenced by ‘proximate mechanisms’ (e.g., neuroendocrine, endocrine, and physiological states) that are, in turn, influenced by behavior. Behavior affects ecological interactions (e.g., predation, competition) that, in turn, affect behavior. Evolution shapes

behavior and, in turn, behavior shapes the path of evolution. A Grand Challenge for animal behavior is to understand the nature and dynamics of these reciprocal interactions, indicated here by two-way or double-headed, feedback loops (Fig. 1). We also emphasize that a potentially unique and key aspect of behavior is ‘choice’ *per se*. While organisms typically exhibit a broad range of responses (e.g., behavioral, physiological, or induced morphological alterations) that allow them to cope with a current environment, behavior is the one type of response

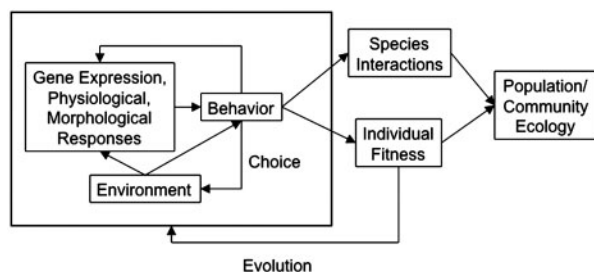


Fig. 1 An integrative view of organismal biology, ecology, and evolution that emphasizes feedback loops between behavioral and other traits, ecology, and evolution. The large box indicates interactions of behavior, expressed by an individual, with physiological, morphological, and genomic traits and the external environment. This portion of the loop includes ways that an individual can, via choice, affect the environment that shapes the expression and development of its own phenotypes. In turn, the behavior expressed by an individual has external impacts by influencing other organisms with which it lives (species interactions and community structure) and, by its effect on fitness, alters the future evolution of behavioral, and other traits.

that provides individuals flexibility for adjusting to the wide range of environments in which they live. A second general Grand Challenge is thus to understand how behavioral choice affects the dynamics of the other feedback loops indicated in Fig. 1. To illustrate, we focus on an issue of particular importance in the modern, human-altered world—the Grand Challenge of understanding behavioral variation and how it underlies variation in ability to cope with contemporary human induced, rapid environmental change (HIREC). We conclude by noting that to address Grand Challenges in behavior, it is timely to put our ‘money where our mouth is’ and support studies that implement Tinbergen’s classic Four (complementary) Approaches to studying behavior that take into account both ultimate and proximate causation. This then suggests the need for training the next generation of behavioral biologists to think and work more integratively than is currently the case.

Grand Challenges for behavior as a key component of integrative biology

Figure 1 outlines our view of how behavior integrates with other systems in organismal biology, ecology, and evolution. Throughout an individual’s lifespan, genes, stimuli from the organism, as well as the surrounding environment, interact reciprocally to affect gene expression in morphological and physiological systems (including aspects of neurobiology, neuroendocrinology, endocrinology, and sensory biology) that influence the behavior and that is expressed at a given age or time (Bateson 2001, 2003; West-Eberhardt 2003; Rutter 2007). Organismal biologists often view behavior as the outcome of morphological and/or physiological traits, such that the current condition of those other traits govern or constrain behaviors (Benca et al. 2009; Leary 2009; McCarthy 2010). In other words, other systems in organismal biology are often viewed as proximate mechanisms that determine behavior. We suggest, however, that since

behavior influences the development and expression of other phenotypic traits, it may be more useful to view behavior as part of an integrated system with ongoing feedback loops. We further suggest that behavior has two key characteristics that allow it to have a unique influence on the dynamics of the overall integrated system.

First, behavioral responses typically occur faster, and are more rapidly reversible, than are other responses to environmental change. More so than many other traits, behavior depends on past conditions as well as those currently surrounding the individual. As a result, the behavior expressed at a given moment is as much an outcome of the current conditions in the surrounding environment as it is an outcome of the current state of the individual’s physiological and morphological systems. Some physiological traits, such as the endocrine responses to unpredictable stimuli, can also change very rapidly, but most physiological and virtually all morphological responses involve longer temporal lags between changes in the outside world and changes in phenotype. For example, when Hammill et al. (2010) exposed the hypotrich ciliate, *Euplotes octocarinatus*, to odor cues from one of its main predators, *Stenostomum virginianum*, they found that induced changes in movement patterns associated with behavioral defense occurred much more rapidly than did induced changes in body shape. Second, because organisms often exercise choice over their social or physical environments, behavior provides a way for individuals to determine the external stimuli, which will affect the subsequent development and expression of their own morphological,

Table 1 Grand Challenges in behavioral biology

1	To understand how behavior interacts in feedback loops with other types of responses.
2	To build a stronger integrative understanding of 'environmental choice' and how it affects the development, evolution, and ecology of morphological, physiological, and behavioral traits, and correlations among those traits.
3	To better understand, predict, and adaptively manage variation among organisms in their behavioral response to modern, HIREC.
4	To apply Tinbergen's integrative, four-pronged approach to addressing the other three Grand Challenges.
5	To train a new generation of students to best tackle the above Grand Challenges.

physiological, and behavioral traits. Thus, behavior is typically the first response when organisms are confronted by changes in the external environment, and also, via choice of environment, a way whereby organisms can influence the environmental factors that affect the development and expression of all their traits. Behavior thus plays a key role in shaping the development and expression of integrated responses to the environment. Hence, a general Grand Challenge is thus to better understand how behavior interacts in feedback loops with other types of responses to environmental factors to form an adaptive, integrated phenotype and how this integrated response interacts with ecology and evolution (Table 1).

Because behavior is both rapid and reversible, it can play a special role in an organism's overall dynamic response to environmental change, both within its lifetime (within ecological timescales) and across generations (evolutionary timescales). Within one lifetime, a wide range of induced physiological, morphological, and behavioral responses help an individual cope with environmental change. Across generations, a wide array of developmental and heritable mechanisms, including sexual reproduction, parental effects, genomic imprinting, and cultural transmission, can help populations adapt to changing environments. Because it is so labile, however, behavior can affect the expression and the evolution of

the suite of other mechanisms that organisms use to cope with altered or variable environments. Indeed, in the presence of rapid and unpredictable changes in the environment, behavior may provide a means of avoiding or reducing the impact of conditions that would otherwise prove fatal. For example, in the case of severe storms or habitat degradation that reduce opportunities to feed or obtain shelter, organisms may seek a refuge and 'wait it out' or emigrate to other areas, and escape the conditions altogether. If, however, these ploys are unsuccessful and the environmental trauma persists, the neuroendocrine and endocrine systems regulating the initial behavioral response will have devastating effects in the long run on multiple processes, including behavior, immunity, and metabolism, resulting in increased mortality (Wingfield and Ramenofsky 1999; Wingfield and Sapolsky 2003; McEwen 2006). It is thus the initial behavioral reaction to the acute disturbance upon which selection can act. Therefore, organisms may only have an opportunity to express other adaptive responses if the initial response successfully avoided the first perturbation (Wingfield et al. 1998; McEwen 2006). In addition, if dramatic, unpredictable changes in the environment occur within the lifetime of an individual, behavioral responses that are rapidly employed clearly can be critical. Across longer evolutionary time scales,

appropriate, immediate rapid responses to environmental change are often a pre-requisite for the evolution of other traits. Hence, a more specific challenge is to better understand general, fundamental principles about how rapid, reversible behavioral responses integrate with slower changing, less reversible responses to affect the fit between organism and environment.

Behavior plays a key role in ecological dynamics, as it involves reciprocal interactions between organisms and other species with which they share an environment. For example, a meta-analysis found that prey behavioral responses to predators (e.g., reduced prey activity, increased use of refuges, dispersal from habitats with high risk) had as large, or larger, quantitative effects on prey populations (or on the resources consumed by prey) than did actual predation *per se* (Preisser et al. 2005). Clearly, one cannot understand predator-prey interactions unless one understands the behaviors both of predator and prey. Although it is clear that behavioral variation is important in explaining ecological patterns, many conceptual, qualitative, or quantitative models in ecology currently do not include behavior (Gordon 2010). A second specific challenge is to better integrate the feedback loop between ecology and behavioral responses into our understanding of ecological dynamics. Below, we illustrate this point by discussing

how behavior helps explain variation among species in their ability to cope with modern, HIREC.

As suggested above, behavior and evolution have potentially important reciprocal feedbacks with one another. Past evolution has shaped simple behavioral rules (via physiological and cognitive systems) that often result in adaptive behaviors across a wide range of environments (McNamara and Houston 2009). These evolved behavioral rules, however, can also result in maladaptive behaviors in evolutionary novel environments generated as a result of human activities (Schlaepfer et al. 2002). In turn, current behavior can shape future evolution of behavior and of other traits. Although the idea that behavior (or more generally, phenotypic plasticity) has major effects on evolution is more than a century old (Baldwin 1896), the importance of these effects (e.g., via behavioral compensation for maladaptive morphological or physiological traits, or genetic accommodation and the Baldwin effect) remains poorly studied. Given that behavior and evolution likely interact in an ongoing feedback loop, a third-specific challenge is to better understand how past evolution has shaped today's behaviors and how these behaviors, in turn, will likely shape future evolution—of both behavior and other traits.

In addition, as discussed in more detail below, behavioral choice of environments (niche-picking) can help buffer individuals from some types of environmental change, allow individuals to maintain themselves in different social or physical environments at different ages or life stages, and allow different individuals in the same population to maintain themselves in different environments at the same age

and life stage. To the extent that these processes provide control over the conditions in which organisms live and develop, they can encourage suites of behavioral, physiological, and morphological traits that are profoundly different from those expected if individuals had no control over environmental factors that vary over short spatial or temporal scales (Stamps and Groothuis 2010b). Hence, a fourth-specific challenge is to understand how behavioral choice of environments affects the development and expression of integrated suites of morphological, physiological, and behavioral traits.

Some of the points outlined above have been discussed, or at least touched upon, in earlier articles in the Grand Challenges series (Satterlie et al. 2009; Schwenk et al. 2009; Denny and Helmuth 2010). This is hardly surprising, given the close links between behavior and the research areas discussed in those articles. Other points considered in earlier articles in this series are not discussed here, but apply equally well to behavior. For instance, genomics and other 'omics' are currently generating great excitement in many areas of biology, but since issues and challenges associated with the 'omics' revolutions have been addressed in earlier Grand Challenges papers (Satterlie et al. 2009; Schwenk et al. 2009), we will not repeat them here. With respect to behavior, genomics (and the other 'omics') are powerful tools that provide a way to study multiple genes (gene networks), patterns of gene expression, and physiological systems that affect the behaviors that individuals express under a given set of conditions, following a given set of prior experiences, at a given age and time. However, it is important to note

that because behavior is the outcome of a complex series of contingent, 'reciprocal' interactions between genes and experiential factors that occur over the course of development, 'omics' methods alone cannot fully answer many of the most important questions about behavior. Studying 'omics' without considering these interactions is likely to produce results of limited relevance to free-living organisms, especially if experimental subjects are raised and tested under laboratory conditions that differ substantially from those in which they evolved in nature (see also Satterlie et al. 2009).

Environmental choice—a unique challenge for animal behavior

As noted earlier, although many systems allow organisms to cope with changes in environment and improve function in a current environment, behavior, in the form of 'environmental choice' uniquely provides a way for an animal to change the current conditions in which it exists. In nature, the abiotic (e.g. temperature, humidity, light, chemical contaminants) and biotic (e.g., food, competitors, predators) conditions in which an individual lives and develops over the course of its lifetime critically depend upon its choices of habitat and microhabitat. Similarly, the social environment experienced by an individual depends on its choice of neighborhoods, groups, sex ratios, mates, and other individuals with whom that individual interacts on a regular basis. As depicted in Fig. 1, choice plays a dominant role in selection of the environment. This involves both spatial decisions (e.g., where to forage, whether to join a large foraging group or a small one), and

temporal decisions (e.g., at what time of day to forage, when to leave a juvenile flock and acquire a territory in a neighborhood of adults). Because the other boxes in Fig. 1 (physiology, ecology, evolution) all depend on the environments experienced by organisms, environment choice is crucial in determining how the overall integrative dynamics play out. Environmental choice has thus aptly been termed behavioral ‘niche picking’ (Plomin 1977, see also Stamps and Groothuis 2010a).

Although environment choice clearly can play a critical role in an integrated view of the ecology and evolution of a wide range of phenotypic traits, not just of behavior but also of other traits, our understanding of choice remains curiously fragmented. We do know that different individuals presented with the same array of choices consistently make different choices, and a few studies indicate that preferences for habitat features (Barker and Starmer 1999) or social group size (Serrano and Tella 2007) are similar in parents and their offspring, although the extent to which genes, parental effects and other factors contribute to the heritability of these preferences is currently unclear. We also know that the choices that individuals make are not only related to their behavior, but also to their physiological and morphological traits. For instance, within a population of three-spine sticklebacks (*Gasterosteus aculeatus*) individuals that preferred a stream habitat had morphological features adapted to that type of habitat, while individuals that selected a lake habitat had morphological features better suited to that type of habitat (Bolnick et al. 2009). However, although it is clear that free-living animals often have a choice of

environments in which to live and develop, and although we suspect that an individual’s choice of physical or social environments earlier in life encourages the development of suites of behavioral, physiological, and morphological traits suited to those environments, thus far we lack experimental studies that address this question. Indeed, to our knowledge, no one has simultaneously studied the choices made by different individuals and how those choices affect the development of multiple phenotypic traits in those same individuals.

In principle, at least, environmental choice could have profound effects not only on the development of a wide range of morphological, physiological, and behavioral traits, but also on the evolution of those traits. In the parlance of quantitative genetics, if variation in preference of environments has a genetic basis, choice can generate gene–environment correlations (systematic differences among genotypes in the environments that shape their own development). In turn, systematic differences across genotypes in preferred developmental environments would encourage the development of integrated phenotypes (including behavioral, physiological, and morphological traits) suited to those respective environments. That is, if animals are permitted to exercise environmental choice, variation in environmental preferences could generate phenotypic correlations involving a wide range of traits, without requiring genetic correlations among those traits. Over longer periods of time, these sorts of links between environmental choice and phenotypic adaptation to the chosen environment could pave the way for the subsequent evolution of genetic correlations between

morphological, physiological, and behavioral traits, and to the types of divergent specialization to different environments that can ultimately lead to speciation. Although this logic seems compelling, for most aspects of environmental choice and most phenotypic traits, including behaviors, potential links between environmental choice and the development and expression of phenotypic traits have not been well studied. A second Grand Challenge is thus to build a stronger integrative understanding of environmental choice and how it relates to the development, evolution, and ecology of morphological, physiological, and behavioral traits, as well as to correlations among those traits (Table 1).

Behavior and variation in ability to cope with HIREC

Several previous papers in the Grand Challenges series have stressed the critical importance of understanding how organisms respond to the global environmental change that we refer to here as HIREC. Major aspects of HIREC include alterations of the habitat (loss, degradation, and fragmentation of habitat), spread of exotic species and diseases, harvesting by humans, pollutants (chemical, noise, and other abiotic alterations), and climatic change. Importantly, although some organisms are doing badly in the face of HIREC (e.g., threatened or endangered species, species of concern for conservation), others are doing better than ever (e.g., invasive pests, urbanized species). A key question is how to explain variation among species, or among significant subsets of individuals within species, in their ability to cope with HIREC. Given that HIREC is often very

rapid, behavior is clearly a key first step in an organism's overall response. Some organisms appear to 'get it' and respond well behaviorally to humans and the environmental changes we cause, while others do not (see Sih et al. 2010; Tuomainen and Candolin 2010, for reviews). For example, some animals avoid humans even when we pose no threat, whereas others are compatible with us (Frid and Dill 2002). Some prey exhibit appropriate anti-predator behavior in response to exotic predators, but others do not and thus suffer heavy mortality (Sih et al. 2010). Some herbivores thrive on exotic plants that we provide (crops, ornamental plants) but most have not adopted these new resources even though they could (Bossart 2003). Some organisms are shifting the seasonal timing of key events (onset of migration or reproduction) and thereby accommodate climatic change, but others are not (Zlakevicius et al. 2006; Rubolini et al. 2007; Van Asch et al. 2007; Lyon et al. 2008; Both et al. 2009; Reed et al. 2009). Also, while some animals cope well with habitat change, others appear to exhibit strikingly maladaptive habitat use in a human-altered world; e.g., some are attracted to novel, poor habitats ('ecological traps') where they have low fitness (Schlaepfer et al. 2002; Gilroy and Sutherland 2007). Why do some species exhibit appropriate behavioral responses to HIREC while others respond inappropriately? Perhaps the most pressing Grand Challenge facing behavioral biologists is to better understand, predict, and even adaptively manage variation among organisms in their behavioral response to HIREC (Table 1).

HIREC is not only a pressing problem in its own right, but it

provides an excellent way to illustrate the reciprocal interactions between behavioral and other traits, and between behavior, ecology, and evolution discussed earlier in this article. For example, one approach to predicting responses to HIREC is based on the feedback loop between past evolution, current traits, and future species' persistence and evolution, mentioned earlier in this article. We begin here with the intuitively attractive assumption that a species' current and future evolutionary response to HIREC might depend on the extent to which novel, modern environments match 'the environment' in which that species evolved (Cox and Lima 2006; Sih et al. 2010). In practice, this might involve studying the behavior of species in a 'pristine' environment, chosen to represent the environment in which that species evolved, and to which it is presumably well adapted (e.g. Boinski et al. 2005). One problem with this approach, however, is that for as long as there have been humans, there has been HIREC. Although the current extent of HIREC may be unprecedented, HIREC *per se* is not new. Humans have been altering ecosystems for as long as we have evidence. Anthropogenic fire and clear cutting have been used everywhere to manage plant and animal communities, agricultural and urban environments altered the landscape in ways that favor and disfavor particular organisms, and selective predation by humans has altered faunas and community structure before any biologists began to measure them. Humans and the organisms that cohabit with us have been adapting to human-induced changes for tens of thousands of years now, as have humans themselves. Even before hominids had

significant effects on ecosystems, the ancestors of any species on earth today experienced rapid and dramatic changes in environmental conditions. Hence, although contemporary rapid changes in climate and ecosystems have generated new interest in the study of how animals respond to environmental change, these changes also remind us that the world has always been dynamic, and that the ancestors of extant species were able to persist across millennia despite major temporal and spatial fluctuations in their environments. Thus, instead of simply viewing responses to HIREC as a result of a mismatch between contemporary environments versus a single 'past environment', it may be helpful to consider phenotypic traits in current species which allowed them to utilize a range of environments in the past. That is, not only are we challenged to understand how current organisms respond to environmental change, but also to understand how variation in environments in the evolutionary past of a given lineage led to the evolution of mechanisms that may, or may not, enable current members of that lineage to cope with contemporary environmental change.

A simple idea based on this perspective is that organisms that have experienced more variable, unpredictable environments in the past should be more ready (perhaps by being flexible generalists) to cope with HIREC. The notion that generalists and more flexible organisms should be better able than inflexible, specialists to cope with novel environments is part of conventional wisdom (Colles et al. 2009). For example, both detailed experimental work contrasting congeners (Rehage et al. 2005) and broad comparative surveys

(Sol 2005; Sol et al. 2008) support the notion that invasive or urbanized species tend to have more flexible and innovative behaviors, associated perhaps with having a more complex nervous system (in vertebrates, including a larger neocortex or neostriatum), as well as distinct neuroendocrine and endocrine responses to stress (Bonier et al. 2007), reduced parasite loads (Geue and Partecke 2008) and changes in migratory tendencies (Partecke and Gwinner 2007). Along similar lines, there is evidence that species that, on average, respond well to HIREC might have a ‘personality type’ or behavioral syndrome (flexible, exploratory, bold, or aggressive behavioral tendencies) that make them particularly well suited to cope with novel conditions (Sih et al. 2004; Cote et al. 2010).

These simple ideas, however, ignore the ‘devils in the details’ on which specific characteristics of novel environments and their match to specific aspects of a range of past environments might matter. Addressing these devilish details brings us back to the general challenge discussed earlier, of understanding how behavior interacts with other responses to form an integrated response to environments that are changing on varying time scales. Because behavior can respond more quickly than do many other responses to environmental change, behavior is the key initial reaction that can guide subsequent developmental and evolutionary responses. In turn, to explain behavioral responses when organisms are first exposed to a novel environment, we need to know about the cue–response relationships that they use to evaluate and respond to environments, new or old. The organism’s evolutionary history

may provide insights into the structure of these cue–response relationships. If the ‘new’ environment is fundamentally similar (in the ‘eyes’ of the organism) to a range of past environments, then the organism should respond well to HIREC. Whether this is the case depends both on the similarity of new versus past environments *per se*, and on how the organism ‘sees’ the environment. The challenge is to convert this intuitive idea into a quantitative science. A specific challenge is thus to better understand the sensory/cognitive ecology of organismal responses to HIREC. What simple behavioral rules do organisms use to guide their behavior (McNamara and Houston 2009)? How have those rules been shaped by their evolutionary history, and how do those rules explain their responses to HIREC?

For example, to understand why some prey respond well to an exotic predator while others do not, we not only need to know how similar the ‘exotic’ predator is to the range of predators with which that species evolved, but also the cues that prey use in evaluating danger. Even if the exotic predator is not similar to the native predator, if prey use very general cues (rules) to evaluate risk (e.g., avoid any large, moving animal), they might respond better to a novel predator than if they rely on more specific cues (e.g. olfactory cues from particular taxa). Similarly, to explain why an herbivore might feed on an exotic plant, or why a parasite might adopt a new host, we need to know how similar the new plant (or host) is to past plants (or hosts), and we need to know the cues that herbivores (or parasites) use in evaluating suitability of hosts. Along similar lines, to explain why some organisms are

shifting the timing of many life-history stages such as migration and reproduction, as well as less discreet events, such as species interactions, in response to climatic change (Yang and Rudolf 2010), it is vital to know what cues organisms use for timing such events (e.g. photoperiod, temperature, a combination of photoperiod \times temperature, other sets of environmental cues, or endogenous rhythms). Notably, many of these potential behavioral responses to novel environments involve environmental choice, in space (e.g., choice of habitats or microhabitats) or time (e.g., via shifts in phenology). That is, the Grand Challenge of understanding environmental choice is a key part of understanding variation within and among populations and species in response to HIREC.

If individuals respond well enough to survive an initial exposure to HIREC, then they may be able to develop the many changes in behavior subsumed under the general category of ‘learning’. In addition, in some taxa, including humans of course, learning from others (social learning) may allow individuals to cope sufficiently well to novel challenges without directly suffering costs associated with a poor initial response. Another specific challenge is thus to determine whether species’ differences in learning can help explain inter-specific variation in responses to HIREC. In turn, this requires that we have a better understanding of how organisms learn (individually or socially) to cope with specific aspects of HIREC, and how the species’ evolutionary history has shaped their learning tendencies (Garcia et al. 1966). Even more generally, a challenge is to understand how behavior develops (in coordination with other phenotypic traits) to cope with complex

and dynamically changing abiotic and biotic environments. Finally, if individuals respond well enough within a generation, then the species has the opportunity to ‘evolve’ a more adaptive response to HIREC. Hence, research focusing on HIREC provides an opportunity to explore one of the general challenges for behavioral biology: building a stronger, theoretical, and empirical framework to understand how behavioral changes that occur within an animal’s lifetime influence the evolution of behavioral, and other, traits. All of the above responses become yet more complex when we acknowledge that organisms often face multiple stressors associated with multiple aspects of HIREC. For example, amphibian declines have been associated with loss of habitat, numerous exotic enemies (predators, diseases, and parasites), chemical contaminants, elevated UV light, and climatic change (Hayes et al. 2006; Lips et al. 2006; Blaustein and Bancroft 2007). These environmental stressors often likely have synergistic negative effects. For example, while some amphibians can cope well with either predators or low concentration of pesticides, when they are exposed to both, they show very

low survival (Relyea and Mills 2001; Rohr et al. 2006). Similar negative synergistic impacts were recently seen for predators and for acidification of the oceans, where coral reef fish exposed to projected, elevated levels of acidification exhibited poor anti-predator behavior that resulted in very high-predation rates (Dixon et al. 2010). Also, it is valuable to appreciate the complexity of predator–prey relationships. For example, high risk of predation by lynx (*Lynx canadensis*) affected foraging efficiency in the prey, snowshoe hares (*Lepus americanus*). Time budgets devoted to vigilance reduced feeding opportunities and maintenance of health, resulting in obvious measures of chronic stress in the hares and ultimately increased mortality (Boonstra et al. 1998). Given that animals face multiple stressors, both novel and familiar, that select on multiple traits, we expect animals exposed to HIREC to often exhibit a mix of adaptive and maladaptive behavioral responses. The more complex challenge is thus to understand how these interact to determine variation in ecological persistence and future evolution.

Concluding remarks—invoking Tinbergen’s four approaches

Many of the topics discussed above and listed in Table 2 re-invoke Tinbergen’s four complementary approaches to studying behavior (Tinbergen 2005): development, immediate causation, functional significance (current utility), and evolutionary history. Although Tinbergen’s four approaches are often taught to students as a fundamental part of an introduction to animal behavior, many research fields and most research programs have not felt a need to actually integrate and apply them. For instance, behavioral ecologists usually focus on questions about function and sometimes consider recent evolution. However, many rarely consider the physiological and morphological mechanisms that generate behavior, and even more rarely consider how genes and experiential factors interact to contribute to the development of behavior. The same, of course, is true of other fields in behavioral biology, in particular, and organismal biology in general. Although some behavioral geneticists, physiologists, and endocrinologists have championed a

Table 2 Specific challenges in behavioral biology

1	To better understand how rapid, reversible behavioral responses integrate with slower changing, less reversible responses to affect the fit between organism and environment.
2	To better integrate the feedback loop between ecology and behavioral responses into our understanding of ecological dynamics.
3	To better understand how past evolution has shaped today’s behaviors and how these behaviors, in turn, will likely shape future evolution—of both behavior and other traits.
4	To understand how environmental choice affects the development and expression of integrated suites of morphological, physiological, and behavioral traits.
5	To better integrate new methodologies (e.g., new ‘omics’, new computational methods) into studies of behavior.
6	To better understand not only behavioral responses to modern environments, but also how the mechanisms responsible for those changes have been shaped evolutionarily by both past environments and past patterns of environmental change.
7	To better understand the sensory/cognitive ecology of organismal responses to HIREC.
8	To determine whether species’ differences in learning can help explain variation in responses to HIREC.
9	To better understand behavioral responses to multiple, conflicting environmental stressors.

more integrative view of their fields (Gwinner 1986; Sapolsky 1997; Wingfield 2008), most researchers focus, naturally enough, on narrower topics within their own areas of training and expertise. In contrast, we suggest that many of the Grand Challenges that pertain to behavior as well as to other phenotypic traits will benefit from perspectives that integrate all four approaches. Thus one could say that the Fourth Grand Challenge is to finally, regularly apply Tinbergen's four questions to attack other Grand Challenges in behavior and other traits in organismal biology (Table 1).

Ideally, this should be done using the full range of both traditional and modern 'sexy' tools including field studies, laboratory experiments, molecular methods, agent-based models, system models, and other sophisticated computational methods. While some studies will follow Krogh's Principle to identify, develop and focus on model systems best-suited to a particular question, the need to understand diversity will almost certainly require parallel study of non-model organisms. In part, this is because a model species that is ideal for studying one of Tinbergen's four questions need not be amenable for studies of the other three. As noted by earlier Grand Challenges papers, a practical first challenge will be to both train a new generation and re-tool the current generation of behavioral scientists (Denver et al. 2009; Halanych and Goertzen 2009; Bowlin et al. 2010). However, we stress here that these new scientists should be trained to understand and fully appreciate the importance of all of Tinbergen's four questions, so that they can engage more fruitfully and productively

in interdisciplinary, integrative studies. Simultaneously, we need to build a stronger intellectual social network of collaborations and bridges across sub-disciplines. More than ever, having a strong, interdisciplinary, intellectual infrastructure, as well as financial support from granting agencies, will facilitate the exciting work of making progress on the critically important and challenging demands of understanding the organism in its environment. Thus, we see the fifth and final Grand Challenge as a call to train a new generation of students to best tackle the above issues with success as the goal (Table 1).

Acknowledgments

We wish to thank the individuals who contributed to the preliminary discussions of the first rendition of Grand Challenges in Animal Behavior. George S. Bakken, Peggy Hill, Vladimir Pravosudov, and John C. Wingfield initiated this effort and offered many helpful suggestions in the second generation of the project. Our colleagues in the Animal Behavior Graduate Group at UC Davis included Rick Grosberg, Gaby Nevitt, Gail Patricelli, and Brian Trainer as well as Zoltan Németh were instrumental in helping to formulate and develop the ideas presented here.

Funding

Development of many of the ideas and writing of this manuscript were facilitated by National Science Foundation Grants IOS #0920791 to M.R. and #0951232 to A.S.

References

Baldwin JM. 1896. A new factor in evolution. *Am Naturalist* 30:441–51, 536–53.

- Barker JSF, Starmer WT. 1999. Environmental effects and the genetics of oviposition site preference for natural yeast substrates in *Drosophila buzzatii*. *Hereditas* 130:145–75.
- Bateson P. 2001. Behavioural development and Darwinian evolution. In: Oyama P, Griffiths P, Gray R, editors. *Cycles of contingency*. Cambridge, MA: MIT Press. p. 149–66.
- Bateson P. 2003. The promise of behavioural biology. *An Behav* 65:11–17.
- Benca R, Duncan MJ, Frank E, McClung C, Nelson RJ, Vicentic A. 2009. Biological rhythms, higher brain function, and behavior: gaps, opportunities, and challenges. *Brain Res Rev* 62:57–70.
- Blaustein AR, Bancroft BA. 2007. Amphibian population decline: evolutionary consideration. *Bioscience* 57:437–44.
- Boinski S, Kauffman L, Ehmke E, Sche S, Vreedzaam A. 2005. Dispersal patterns among three species of squirrel monkeys (*Saimiri oerstedii*, *S. boliviensis* and *S. sciureus*): I. Divergent costs and benefits. *Behaviour* 142:525–632.
- Bolnick DI, Snowberg LK, Patenia C, Stutz WE, Ingram T, Lau OL. 2009. Phenotype-dependent native habitat preference facilitates divergence between parapatric lake and stream stickleback. *Evolution* 63:2004–16.
- Bonier F, Martin PR, Wingfield JC. 2007. Urban birds have broader environmental tolerance. *Biol Lett* 3:670–73.
- Boonstra R, Hik D, Singelton GR, Tinnikov A. 1998. The impact of predator-induced stress on the snowshoe hare cycle. *Ecol Monog* 79:371–94.
- Bossart JL. 2003. Covariance of preference and performance on normal and novel hosts in a locally monophagous and locally polyphagous butterfly population. *Oecologia* 135:477–86.
- Both C, Van Asch M, Bijlsma RG, Van Den Burg AB, Visser ME. 2009. Climate change and unequal phenological changes across four trophic levels: constraints or adaptations? *J Animal Ecol* 78:73–83.

- Bowlin MS, et al. 2010. Grand Challenges in migration biology. *Integr Comp Biol* 50:261–79.
- Colles A, Liow LH, Prinzing A. 2009. Are specialists at risk under environmental change? Neocological, paleoecological and phylogenetic approaches. *Ecol Lett* 12:849–63.
- Cote J, Clobert J, Brodin T, Fogarty S, Sih A. 2010. Personality-dependent dispersal: characterization, ontogeny and consequences for spatially structured populations. *Philosophic Transact Linnean Soc*.
- Cox JG, Lima SL. 2006. Naiveté and an aquatic-terrestrial dichotomy in the effects of introduced predators. *Trends Ecol Evol* 21:674–80.
- Denny M, Helmuth B. 2010. Confronting the physiological bottleneck: a challenge from ecomechanics. *Integr Comp Biol* 49:197–201.
- Denver RJ, Hopkins PM, McCormick SD, Propper CR, Riddiford L, Sower SA, Wingfield JC. 2009. Comparative endocrinology in the 21st century. *Integr Comp Biol* 49:339–48.
- Dixon DL, Munday PL, Jones GP. 2010. Ocean acidification disrupts the innate ability of fish to detect predator olfactory cues. *Ecol Lett* 13:68–75.
- Frid A, Dill L. 2002. Human-caused disturbance stimuli as a form of predation risk. *Conserv Ecol* 6:1.
- Garcia J, Ervin FR, Koelling RA. 1966. Learning with prolonged delay of reinforcement. *Psychonomic Sci* 5:121–2.
- Geue D, Partecke J. 2008. Reduced parasite infestation in urban Eurasian blackbirds (*Turdus merula*): a factor favoring urbanization? *Can J Zool* 86:1419–25.
- Gilroy JJ, Sutherland WJ. 2007. Beyond ecological traps: perceptual errors and undervalued resources. *Trends Ecol Evol* 22:351–6.
- Gordon DM. 2010. The fusion of behavioral ecology and ecology. *Behav Ecol*.
- Gwinner E. 1986. Circannual rhythms. Endogenous annual clocks in the organization of seasonal processes. Berlin: Springer.
- Halanych KM, Goertzen LR. 2009. Grand challenges in organismal biology: the need to develop both theory and resources. *Integr Comp Biol* 49:475–9.
- Hammill E, Kratina P, Beckerman AP, Anholt BR. 2010. Precise time interactions between behavioural and morphological defences. *Oikos* 119:494–9.
- Hayes T, et al. 2006. Pesticide mixtures, endocrine disruption, and amphibian declines: are we underestimating the impact? *Environ Health Perspect* 114:40–50.
- Leary CJ. 2009. Hormones and acoustic communication in anuran amphibians. *Integr Comp Biol* 49:452–70.
- Lips KR, Brem F, Brenes R, Reeve JD, Alford RA, Voyles J, Carey C, Livo L, Pessier AP, Collins JP. 2006. Emerging infectious disease and the loss of biodiversity in a Neotropical amphibian community. *PNAS* 103:3165–70.
- Lyon BE, Chaine AS, Winkler DW. 2008. Ecology – a matter of timing. *Science* 321:1051–2.
- McCarthy MM. 2010. How it's made: organizational effects of hormones on the developing brain. *J Neuroendocrinol* 22:736–42.
- McEwen BS. 2006. Protective and damaging effects of stress mediators: central role of the brain. *Dial Clin Neurosci* 8:367–81.
- McNamara JM, Houston AI. 2009. Integrating function and mechanism. *Trends Ecol Evol* 24:670–5.
- Mykles DL, Glalambor CK, Stillman JH, Tomanek L. 2010. Grand Challenges in comparative physiology: integration across disciplines and levels of biological organization. *Integr Comp Biol* 50:6–16.
- Partecke J, Gwinner E. 2007. Increased sedentariness in European blackbirds following urbanization: a consequence of local adaptation? *Ecology* 88:882–90.
- Plomin R, Defries JC, Loehlin JC. 1977. Genotype-environment interaction and correlation in analysis of human behavior. *Psychol Bull* 84:309–22.
- Preisser EL, Bolnick DI, Benard MF. 2005. Scared to death? The effects of intimidation and consumption in predator-prey interactions. *Ecology* 86:501–9.
- Reed TE, Warzybok P, Wilson AJ, Bradley RW, Wanless S, Sydeman WJ. 2009. Timing is everything: flexible phenology and shifting selection in a colonial seabird. *J Animal Ecol* 78:376–87.
- Rehage JS, Barnett BK, Sih A. 2005. Foraging behaviour and invasiveness: do invasive *Gambusia* exhibit higher feeding rates and broader diets than their noninvasive relatives? *Ecol Freshwater Fish* 14:352–60.
- Relyea RA, Mills N. 2001. Predator-induced stress makes the pesticide carbaryl more deadly to gray treefrog tadpoles (*Hyla versicolor*). *Proc Natl Acad Sci USA* 98:2491–6.
- Rohr JR, Kerby JL, Sih A. 2006. Community ecology as a framework for predicting contaminant effects. *Trends Ecol Evol* 21:606–13.
- Rubolini D, Møller AP, Rainio K, Lehikoinen E. 2007. Assessing intraspecific consistency and geographic variability in temporal trends of spring migration phenology among European bird species. *Clim Res* 35:135–46.
- Rutter M. 2007. Gene-environment interdependence. *Dev Sci* 10:12–18.
- Sapolsky RM. The trouble with testosterone and other essays on the biology of the human predicament. New York: Touchtone Books, Simon and Schuster.
- Satterlie RA, Pearse JS, Sebens KP. 2009. The black box, the creature from the black lagoon, August Krogh, and the dominant animal. *Integr Comp Biol* 49:89–92.
- Schlaepfer MA, Runge MC, Sherman PW. 2002. Ecological and evolutionary traps. *Trends Ecol Evol* 17:474–80.
- Schwenk K, Padilla DK, Bakken GS, Full RJ. 2009. Grand challenges in organismal biology. *Integr Comp Biol* 49:7–14.
- Serrano D, Tella JL. 2007. The role of despotism and heritability in determining settlement patterns in the colonial lesser kestrel. *Am Naturalist* 169:E53–67.
- Sih A, Bell AM, Johnson JC, Ziemba RE. 2004. Behavioral syndromes: an integrative overview. *Quart Rev Biol* 79:241–77.

- Sih A, Bolnick DI, Luttbeg B, Orrock JL, Peacor SD, Pintor LM, Preisser E, Rehage J, Vonesh JR. 2010. Predator-prey naivete, antipredator behavior, and the ecology of predator invasions. *Oikos* 119:610–21.
- Sih A, Ferrari MCO, Harris DJ. 2010. Evolution and behavioural responses to human-induced rapid environmental change. *Evolution Appl.*
- Sol D, Bacher S, Reader SM, Lefebvre L. 2008. Brain size predicts the success of mammal species introduced into novel environments. *Am Naturalist* 172:S63–71.
- Sol D. 2005. Big brains, enhanced cognition, and response of birds to novel environments. *Proc Natl Acad Sci USA* 102:54–60.
- Stamps J, Groothuis TG. 2010a. The development of animal personality: relevance, concepts and perspectives. *Biol Rev* 85:301–25.
- Stamps J, Groothuis TG. 2010b. Developmental perspectives on personality: implications for ecological and evolutionary studies of individual differences. *Philos Transact R Soc B*.
- Tinbergen N. 2005. On aims and methods of Ethology. *Animal Biol* 55: 297–321.
- Tuomainen U, Candolin U. 2010. Behavioural responses to human-induced environmental change. *Behav Rev.*
- Van Asch M, Tienderen PH, Holleman LJM, Visser ME. 2007. Predicting adaptation of phenology in response to climate change, an insect herbivore example. *Global Change Biol* 13:1596–604.
- Wake M. 2008. Integrative biology: science for the 21st Century. *Bioscience* 58: 349–53.
- West-Eberhardt MJ. 2003. Developmental plasticity and evolution. New York: Oxford University Press.
- Wingfield JC, Breuner C, Jacobs J, Lynn S, Maney D, Ramenofsky M., Richardson R. 1998. Ecological bases of hormone-behavior interactions: the “emergency life history stage”. *Am Zool* 38:191–206.
- Wingfield JC, Ramenofsky M. 1999. Hormones and behavioral ecology of stress. In: Balm PHM, editor. *Stress physiology in animals*. Sheffield, UK: Sheffield Academic Press. p. 1–51.
- Wingfield JC, Sapolsky RM. 2003. Reproduction and resistance to stress: when and how? *J Neuroendocrinol* 15:711–24.
- Wingfield JC. 2008. Comparative endocrinology, environment and global change. *Gen Comp Endocrinol* 157:207–16.
- Yang LH, Rudolf V. 2010. Phenology, ontogeny and the timing of species interactions. *Ecol Lett* 13:1–10.
- Zlakevicius M, Bartkeviciene G, Raudonikis L, Janulaitis J. 2006. Spring arrival response to climate change in birds: a case study from Eastern Europe. *J Ornithol* 147:326–43.