On connecting behavioral responses to HIREC to ecological outcomes: a comment on Wong and Candolin

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Wong and Candolin (2015) provide a superb review of ideas and case studies on the ecology and evolution of behavioral responses to human-induced rapid environmental change (HIREC). Here, we offer 2 complementary suggestions to help this critically important field move forward.

First, faced with innumerable species, aspects of HIREC and types of behavior, how might one choose what to study? Our impression is that many behavioral ecologists, including ourselves, tend to study what we are familiar with. If, however, our goal is to examine behavioral responses to HIREC that have important ecological consequences, we should let the ecology guide us. If, for instance, a goal is to connect behavioral responses to HIREC to community ecology, we suggest focusing on keystone species or ecosystem engineers. As obvious as this may seem, relatively few studies follow this track: a Web of Science search using “environmental change,” “behavior,” and “keystone species” returned only 3 articles. Our search no doubt missed some relevant articles; still, it appears that looking at behavioral responses to HIREC involving keystone species is a relatively open niche. For population ecology, the classic “limiting factors” tradition asks ecologists to identify (often with experiments) 1) the key limiting factors (here, key aspects of HIREC) that limit success in a given population, 2) in key limiting life-history stages (e.g., using elasticity analyses), and to then 3) focus on the key behaviors that influence variation in individual abilities to cope with those key limiting factors (Sih and Gleeson 1995). We thus suggest that behavioral ecologists may benefit by first focusing on significant behaviors in limiting life-history stages in key species in a community. If HIREC is driven by a combination of 2 factors (e.g., ocean acidification interfering with behavioral responses to an exotic predator), then study behavioral responses to those interacting aspects of HIREC.

We recognize that this advice might be annoying at 2 levels. First, it seems obvious — of course, focus on what is more important — and second, this advice might often be difficult logistically to implement. Still, our sense is that many, including ourselves, might benefit from the reminder to do our best to evaluate ecological importance while choosing a behavior and aspect of HIREC to study, as opposed to simply focusing on what is familiar.

Second, we need theory to explain the observed variation in outcomes. Why do some species respond well behaviorally to HIREC, whereas others do not? Why do some prey respond adaptively to exotic predators, whereas other prey do not? Why have some species (or populations) exhibited a plastic shift to breed earlier in the spring with climate change, whereas others have not? Why have some species fallen into evolutionary traps sometimes involving spectacularly maladaptive behaviors, whereas others have not (Robertson et al. 2013)? Standard behavioral ecology theory based on optimality theory can do a good job of explaining “smart” responses to HIREC but, by definition, might be less well suited for explaining maladaptive responses.

Developing theory on behavioral responses to HIREC starts with a major assumption of optimality theory: past selection pressures have shaped behavioral “rules of thumb” or cue-response systems (as examples of previously adaptive traits). After HIREC, however, organisms may continue to rely on these cues, at least initially. Thus, variation in how well organisms (including humans) respond to HIREC can then be explained by whether novel conditions are evolutionarily matched versus mismatched to past conditions. The call is for explicit theory to formalize this idea (see Sih et al. 2011; Sih 2013). We do not have to entirely reinvent the wheel, though: we can use existing behavioral ecology theory to explain variation in previously adaptive behaviors (e.g., cue-response thresholds) throughout some ecological parameter space, but then extend existing theory to predict how well organisms should respond when they are exposed to new ecological conditions, assuming that at least initially they retain their previously adaptive (but now possibly maladaptive) cue-response systems (e.g., McNamara et al. 2011).

Theory can be further extended to address variation in how behavioral responses to HIREC should affect population and community ecology outcomes. A rich body of existing theory predicts how adaptive behavioral responses should affect population dynamics and species interactions (e.g., Abrams 2010). A valuable addition would be to incorporate the “new behavioral ecology theory,” “predicting both adaptive and maladaptive behavioral responses to HIREC into population/community models. For example, when, according to new behavioral ecology theory do we expect organisms to overavoid humans that actually pose no danger to them, and given predicted negative effects of overavoidance on survival and/or reproduction, how strongly should this impact the population’s performance? With interacting species, a key would be the ability of new theory to predict at least qualitative, among species in their responses to HIREC and how those differences should affect species interactions. For example, with climate change, the goal might be for theory to predict the relative phenological shifts of predators and prey (or 3 trophic levels) and how these would then influence species interactions and, ultimately, ecological dynamics.

The key point is that an explicit set of theory on behavioral responses to change should generate predictions on conditions when we expect organisms to respond well or not to HIREC. Case studies can then test predictions that serve to further tune the theory, moving us toward not just a case-by-case, system-specific understanding of responses to HIREC but, potentially, a general understanding that can ideally be used to identify, a priori, situations where organisms are likely to be more versus less vulnerable to HIREC.

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Integrating behavior into life-history theory: a comment on Wong and Candolin

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In their nice review, Wong and Candolin (2015) convincingly argue that understanding behavioral responses is essential to forecast the impact of rapid human-induced environmental changes (HIREC) on populations, communities, and ecosystems. Here, we will elaborate on this by remarking that behavior is part of a broader adaptive complex through which animals respond to HIREC and that building a more general theory requires to integrate behavior into life-history theory.

As Wong and Candolin (2015) argue, the fate of animals exposed to environmental alterations is essentially driven by population dynamics (i.e., the balance between births and deaths). Because the rates of birth and death are ultimately determined by how organisms allocate their limited time and energy into reproduction and survival, the species’ life history will largely affect this fate (Saether et al. 2013). Indeed, life-history theory proposes a variety of mechanisms of response to changes, including growing fast in numbers to avoid demographic stochasticity, skipping a reproductive event when conditions are unfavorable, and reducing the risk of reproductive failure by distributing the reproductive effort in many attempts (e.g., Sol et al. 2012).

The above mechanisms can act in concert, either synergically or antagonistically, and their relative importance primarily depends on the evolved combination of life-history traits (Saether et al. 2013). Organisms exhibit an enormous diversity of life-history strategies, which largely reflect trade-offs that limit their performance under altered conditions. For example, growing fast in numbers is only possible with a fast-lived strategy in which reproduction is prioritized over survival while skipping a reproductive event is more beneficial for slow-lived species that have more opportunities to breed again in the future (Sol et al. 2012). Nevertheless, the response also depends on the nature of the alteration, which determines the route toward extinction (i.e., stochastic accidents vs. negative population growth). For example, if the altered environment implies an adaptive mismatch, reflecting the absence of appropriate adaptations, extinction can occur by negative population growth. Likewise, if the alteration undermines the reliability of cues to assess habitat quality, resulting in suboptimal choices, this can also lead to a negative population growth (Wong and Candolin 2015). In both circumstances, a slow-lived strategy may afford advantages by reducing the fitness cost of a reproductive failure.

Our argument to suggest that behavior is also essential to understand how life history affects population dynamics in changing environments is based on 3 observations. First, behavior can be plastically modified to improve performance under altered conditions. Although Wong and Candolin (2015) do a good job convincing us that this is the case, it is important to remark that there are 2 types of behavioral plasticity: activational and developmental (Snell-Rood 2013). Activational plasticity reflects the expression of a prewired genetic program and is central in habitat choice, a mechanism that allows reducing adaptive mismatches and environmental uncertainties. Although activational plasticity is often insufficient to deal with new challenges and can even lead to ecological traps, behavior can also be plastically modified by learning, which involves developing new nervous connections that alter motor responses. Learning allows animals to devise innovative behavioral responses or to improve already established behaviors instead of consistently expressing the same behavior to a particular stimulus. It is this type of plasticity to which Wong and Candolin (2015) seem to refer to in their review although it is worth noting that activational and developmental plasticity often act in concert.

Second, behavioral plasticity affects, and is affected by, life history, which implies that both are part of a same adaptive strategy. The fast–slow continuum, for example, reflects a differential need to collect and use information (Sol 2009). Animals at the “slow” extreme of the fast–slow continuum tend for instance to explore more accurately and often exhibit better performance in problem solving and learning. Thus, when we examine how life history affects invasion success, we are also inevitably considering behavioral mechanisms as well.

Finally, behavior can directly mediate some of the mechanisms by which life history influences the response to HIREC (Sol et al. 2012). For example, the decision between breeding or not under unfavorable conditions is itself a behavioral response that may benefit slow-lived animals directly by reducing reproductive costs and indirectly by leaving individuals more time for exploration and learning. Behavior may thus change the predictions of classic life-history theory, making its integration essential for the development of a more predictive theory regarding extinction risk associated with HIREC.

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