Invited Review

Behavioral responses to changing environments

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Humans have brought about unprecedented changes to environments worldwide. For many species, behavioral adjustments represent the first response to altered conditions. In this review, we consider the pivotal role that behavior plays in determining the fate of species under human-induced environmental change and highlight key research priorities. In particular, we discuss the importance of behavioral plasticity and whether adaptive plastic responses are sufficient in keeping pace with changing conditions. We then examine the interplay between individual behavioral responses and population processes and consider the many ways in which changes in behavior can affect ecosystem function and stability. Lastly, we turn to the evolutionary consequences of anthropogenic change and consider the impact of altered behaviors on the evolutionary process and whether behavior can facilitate or hinder adaptation to environmental change.

Key words: adaptation, anthropogenic change, biodiversity, evolutionary rescue, extinction, phenotypic plasticity.

INTRODUCTION

Human activities are having a profound impact on the natural world—from climate change and habitat destruction to overharvesting and the introduction of invasive species (Vitousek et al. 1997; Walther et al. 2002; Parmesan and Yohe 2003; Halpern et al. 2008). Although changes to the environment have been occurring long before the arrival of humans, the often rapid and extensive nature of anthropogenic changes mean that species are confronted with environmental conditions few have encountered previously. In recent years, a growing number of studies are showing that behavior can play a leading role in allowing species to adjust to anthropogenic changes and help to explain why some species are able to survive, or even flourish, under human altered conditions, whereas others flounder (Sih et al. 2011; Tuomainen and Candolin 2011; Candolin and Wong 2012a; Sih 2013).

For many animals, a change in behavior is very often the first response to human-altered conditions. Such behavioral modifications can potentially improve an organism's prospects of surviving and reproducing in a changing world. For example, with the spread of urbanization, some animals have shifted their foraging patterns to avoid humans and vehicles (Dowding et al. 2010; Legagneux and Ducatez 2013), whereas others have altered their vocal signals, so that they can be heard in noisy environments (Slabbekoorn and Peet 2003; Parks et al. 2010). Some species are so adept at adjusting

their behaviors that they are now thriving in our cities (Lowry et al. 2013; Sol et al. 2013) or becoming invasive pests when introduced into new areas (Sih et al. 2010; Chapple et al. 2012; Phillips and Suarez 2012).

Not all behavioral responses, however, are beneficial. Human-altered conditions, for instance, can undermine the reliability of cues used by animals to assess habitat quality, resulting in suboptimal habitat choices that can impact negatively on reproductive success (Schlaepfer et al. 2002; Rodewald et al. 2011; Robertson et al. 2013). Environmental changes can also impair sensory systems (Rosenthal and Stuart-Fox 2012) or interfere with physiological processes (Clotfelter et al. 2004; Zala and Penn 2004; Buchanan and Partecke 2012) and, in so doing, weaken the ability of organisms to mount an appropriate behavioral response. Interference from electromagnetic noise, for example, is disrupting the internal magnetic compasses of migratory birds (Engels et al. 2014), male beetles are mistaking the brown shiny surfaces of empty beer bottles for females (Gwynne and Rentz 1983), and chemical pollutants are affecting social recognition and shoaling behavior in fish (Ward et al. 2008; Brodin et al. 2013).

The purpose of this article is to provide insights into our understanding of how animals adjust their behavior to human-induced environmental change and what the impacts of these behavioral adjustments might be. We focus on what we regard as the main research priorities. We begin by examining the role of behavioral flexibility in determining the success (or failure) of species under anthropogenic change. Recent conceptual insights suggest that

such plasticity is clearly important, but is it always adaptive? And how much plasticity is enough to counter the risk of extirpation? Next, we shift our focus to explore the impact of altered behaviors on population dynamics and discuss the broader ecological and evolutionary implications. Despite studies having now documented a wide range of behavioral changes linked to human activities, we still have only a rudimentary appreciation and understanding of the ecological and evolutionary consequences.

BEHAVIORAL PLASTICITY

Animals can respond to environmental change in 3 key ways: disperse, adjust through phenotypic plasticity, or adapt through genetic changes (Williams et al. 2008; Hoffmann and Sgrò 2011). In the context of anthropogenic change, plasticity is important because opportunities for dispersal and adaptation are often limited. Dispersal between patches, for instance, may not be possible due to physical barriers to movement—a problem that is likely to worsen with the continued destruction and fragmentation of habitats (Chaine and Clobert 2012). Similarly, human-mediated changes are often so rapid that evolutionary processes may simply be unable to keep pace with the changes that are taking place (Gomulkiewicz and Holt 1995; Chevin and Lande 2010; Sinervo et al. 2010). In a meta-analysis, Hendry et al. (2008) showed that phenotypic changes induced by anthropogenic activities are generally greater than those linked to natural environmental variation and that such changes are due largely to phenotypic plasticity rather than genetic evolution.

Phenotypic plasticity describes the tendency of a particular genotype to produce different phenotypes under altered environmental conditions (Thibert-Plante and Hendry 2011). It allows an animal to adjust behavior to suit the conditions of its immediate environment and, in so doing, increase its fitness (Van Buskirk 2012). Accordingly, a lack of phenotypic plasticity can contribute to the exclusion of species from human-modified environments (Badyaev 2005). For example, some species are able to adjust the structure of their mating calls to compensate for increased background noise from human traffic, whereas others cannot (Lengagne 2008). Most animals, however, exhibit at least some level of plasticity as an evolved response to environmental variation. Thus, for many species, survival in a rapidly changing world will depend on the plasticity of traits that have evolved under past conditions or, in other words, their genetically determined reaction norms (Van Buskirk 2012). Here, there are 2 important questions researchers need to consider. First, are changes ascribed to behavioral plasticity adaptive and, secondly, are they sufficient?

Adaptive versus maladaptive plasticity

There is now a substantial body of research suggesting that plastic behavioral responses are often adaptive. Some of the most compelling come from invasive species and those that have successfully colonized urban environments (i.e., so-called "urban adapters"). In a study using brain size as a proxy for behavioral flexibility, Sol et al. (2002) showed that birds with larger brains were more successful at establishing themselves in new areas—a pattern that has since been observed in invasive amphibians (Ameil et al. 2011) and mammals (Sol et al. 2008). Similarly, urban adapter species often exhibit higher levels of behavioral plasticity compared with their nonurban counterparts (Lowry et al. 2013; Sol et al. 2013). Life in cities is often linked to increased phenotypic variance, and many studies have reported behavioral adjustments in wildlife in response to urban conditions (Dowding et al. 2010; Legagneux and Ducatez

2013). As a reflection of their behavioral flexibility, urban species often exhibit innovative behaviors (Lefebvre 1995; Bouchard et al. 2007). More innovative species are better at learning and solving problems, which are important traits for adjusting to city living (Kark et al. 2007). Learning ability and lack of aversion to novel objects are also valuable for exploiting novel resources. An example of this is seen in black kites (*Milvus migrans*), which have taken to decorating their nests with white plastic rubbish. In a recent article, Sergio et al. (2011) found that kites were using the plastic adornments as an extended phenotypic signal to warn conspecifics about the viability, territory quality, and fighting prowess of the nest builder. Such findings underscore the fact that behavioral plasticity can be adaptive and play a vital role in helping organisms to succeed in novel environments.

Plastic behavioral responses, however, can also be maladaptive. Many species, for example, use indirect cues to assess habitat quality. Changes to the environment can sometimes cause a mismatch between the actual quality of a habitat and the cues used by individuals to assess that quality, resulting in an "ecological trap" (Schlaepfer et al. 2002; Robertson et al. 2013). In such a situation, inappropriate behavioral responses cause animals to make poor habitat choices. A common way in which this can occur is if animals rely on outdated cues and end up choosing a habitat that is lower in quality than nonpreferred alternatives. For instance, northern cardinals (*Cardinalis cardinalis*), attracted by the carotenoid-rich berries of the invasive honeysuckle (*Lonicera maackii*), increase their vulnerability to nest predation by settling in the introduced shrubs (Rodewald et al. 2011). Another way that ecological traps can arise is through the emergence of novel cues that mimic those that organisms traditionally rely on when making their habitat choices. Many aquatic insects, for example, use polarized light reflected off horizontal surfaces to identify ponds suitable for laying their eggs. As a result, misguided insects are also being enticed to oviposit on artificial structures that have the same reflective properties as water bodies, such as dry asphalt roads, cars, and gravestones (Kriska et al. 1998, 2006; Horváth et al. 2007).

Is the level of plasticity sufficient?

When considering the role plasticity plays in mediating the impact of human-induced environmental change, it is also important to determine whether the magnitude of the plastic response is sufficient in keeping pace with changing conditions. Surprisingly, only a handful of studies have explicitly addressed this question, and most of these have been in the context of climate change. Many birds, for example, have advanced their egg-laying date with changes to spring temperatures and food availability. In a 47-year population study of British great tits (*Parus major*), Charmantier et al. (2008) showed that individual adjustment to egg-laying date allowed the tit population to keep track of rapidly changing environmental conditions. The extent to which animals are able to adjust their behaviors, however, may not always be enough to counter the effects of anthropogenic change (Van Buskirk 2012). For instance, pied flycatchers (*Ficedula hypoleuca*) breeding in the Netherlands have also shifted their egg-laying date, but unlike the British great tits, the phenological shift observed in this migratory species was found to be inadequate in keeping pace with the changing environment (Both and Visser 2001). More recently, a study looking at the impact of rising temperatures on lizards found that phenotypically plastic adjustments to thermoregulatory behavior increased their vulnerability to extinction (Sinervo et al. 2010). For many species, increased time spent under shelter (although beneficial in helping

lizards to avoid the heat) came at the expense of other fitness-related activities, such as foraging and reproduction—with catastrophic consequences for species persistence (Sinervo et al. 2010). Such examples underscore the need to not only document whether animals have the capacity to adjust their behavior, but more importantly, to invest a greater research effort into determining whether such plastic responses are, in fact, adequate. The latter will be critical if we are to understand the limits of plasticity and, in so doing, forecast the likely fate of populations in response to both current and projected changes.

POPULATION-LEVEL CONSEQUENCES

From individuals to populations…and back

If behavioral responses alter key demographic parameters (birth, death, and migration rates), we can expect the dynamics of populations to also change. For example, animals that are caught in ecological traps end up suffering reduced offspring survival, which can result in population declines. This problem is likely to be exacerbated at low population density, where reduced levels of competition for space can allow more individuals to act on their maladaptive decisions and settle into poorer quality habitat (Kokko and Sutherland 2001). In contrast, responses, such as behavioral innovations that enable organisms to exploit novel resources, could have positive effects on population growth and, in so doing, allow species to flourish in new environments (Phillips and Suarez 2012).

The literature on invasive species is replete with case studies documenting deleterious population-level effects on native species, with behavior often playing a mediating role (Sih et al. 2010). A recent example comes from Crater Lake Apoyo in Nicaragua, where ineffective parental defenses toward a nonnative brood predator, the bigmouth sleeper goby (*Gobiomorus dormitor*), was implicated in the decline of an endemic fish species, the Arrow cichlid (*Amphilophus zaliosus*) (Lehtonen et al. 2012). Cichlid parents, naive to the threat posed by the introduced goby, allow the formidable predator to venture much more closely to their fry compared with native brood predators. Such responses (or lack thereof) point to the fact that many native species simply do not possess the appropriate behavioral responses needed to cope with invasive species, which, in extreme cases, can lead to extinction (Phillips and Suarez 2012).

Changes to sexually selected behaviors, by influencing the quantity and quality of offspring produced, are also expected to have important demographic consequences (Candolin and Heuschele 2008; Candolin and Wong 2012b). Anthropogenic changes, in particular, are predicted to alter the relative costs and benefits of behaviors under sexual selection, which, in turn, can affect female fecundity, the number of females reproducing, and the fitness of offspring, although direct tests of this prediction are still quite rare (but see Candolin et al. 2014). Here, behaviors that are beneficial to the individual can potentially impact negatively on the population as a whole. This is because individual behavior evolves to maximize relative—rather than absolute—fitness (Haldane 1932; Wright 1969). In three-spined sticklebacks (*Gasterosteus aculeatus*), for example, human-mediated changes to visibility in the water column relaxes the intensity of male–male competition, allowing males to signal dishonestly to females (Wong et al. 2007). This increases the chances of females mating with poor quality suitors, which are more likely to cannibalize the females' eggs (Candolin 2000). More generally, conflicts over mating can give rise to circumstances where individuals are able to hinder the reproduction of others and, in so doing, limit the potential for population growth or recovery. For

instance, in the Seychelle's magpie robin (*Copsychus sechellarum*), competition for breeding position within the social group was found to interfere with the reproduction of breeding pairs, significantly prolonging the time it would otherwise have taken for this once critically endangered species to recover (López-Sepulcre et al. 2009)

So far, we have focused largely on how behavioral responses can result in population-level effects. However, it is important to realize that changes to population dynamics can also influence individual behavior (Kokko and López-Sepulcre 2007; Pelletier and Garant 2012). Very low population densities, for example, can disrupt animal mating systems and increase the challenge of finding suitable mates. The reproductive failure of saiga antelope (*Saiga tatarica*) in Russia is a good case in point. Milner-Gulland et al. (2003) showed that poaching of male saiga for their horns resulted in an extremely female-biased sex ratio that led to the subsequent decline in the number of female pregnancies and, eventually, population collapse. The authors speculated that the saiga's demise was probably mediated by changes in reproductive behavior, with dominant females aggressively excluding subdominant females from the few remaining males, thus preventing younger females from conceiving. Although understudied, the interplay between population dynamics and individual behavior is clearly important and can operate through feedback loops that, in turn, entrain further changes. Changes to the demography of one species can also potentially affect others. Next, we consider the influence of altered behaviors on species interactions, communities, and ecosystems.

CONSEQUENCES FOR SPECIES INTERACTION NETWORKS AND COMMUNITIES

Because organisms are connected to each other via linkages within an ecological network, behavioral responses to anthropogenic change can affect the strength and nature of interactions between species, including consumption (predation and herbivory), competition, and symbiosis (mutualism, parasitism, and commensalism) (Hoover and Tylianakis 2012). There are 2 ways in which this can occur. First, behavior can have a direct effect on the interaction itself (Schmitz et al. 2004). An example of this comes from the Arctic, where polar bears (*Ursus maritimus*) have shifted their hunting locations and food habits with the receding ice sheets. Whereas previously bears survived by hunting seals on the ice, they are now being increasingly forced to feed ashore on land-based prey, such as caribou (*Rangifer tarandus*), snow geese (*Chen caerulescens caerulescens*), and the eggs of waterfowl (Gormezano and Rockwell 2013). The second way in which altered behaviors can influence species interactions is to do so indirectly through its effects on population dynamics. For instance, behaviors that lead to population declines in one species are likely to impact on its interactions with others (Hoover and Tylianakis 2012).

A common pathway through which human-induced environmental changes influence species interactions is by altering the spatial and temporal distribution of species and the level of overlap between them. Climate change, for instance, is currently shifting species ranges, which are creating opportunities for new behavioral interactions in areas where species did not previously co-occur (Parmesan and Yohe 2003; Chen et al. 2011; Blois et al. 2013; Ockendon et al. 2014). It is also bringing earlier, established interactions to an end. For example, rising temperatures is predicted to cause a northward shift in the distribution of the snowshoe hare (*Lepus americanus*), which is the primary prey of the Canada lynx

(*Lynx canadensis*). As a result, the persistence of lynx along their southern range edge will depend on the predator's ability to utilize higher proportions of alternative prey (Peers et al. 2014). Climate change is also shifting the timing of behaviors related to life cycle events (e.g., migration to breeding areas) and daily activities (e.g., movement between foraging areas and refuges) (Yang and Rudolf 2010; Ockendon et al. 2014). Such changes can give rise to an ecological mismatch if species differ in the actual timing of their responses to these events. As an example, the earlier arrival of birds to their breeding areas does not always match advancement in the abundance of their food resources (Both et al. 2009).

Environmental changes also influence species interaction networks by altering the size of populations and the diversity of species. For instance, the fragmentation of habitats often results in decreased biodiversity (Fahrig 2003). Not only can this affect the behavior of species inhabiting these areas but also reduce the number of interactions and cause the composition of interaction networks to become homogenized. The conversion of forests to rice fields and pastures in Ecuador, for example, has reduced overall habitat complexity. This, in turn, has improved the ability of parasitic wasps and flies to find their hosts, which has favored some interactions over others, resulting in the parasitoid–host networks becoming more similar across space and time (Laliberte and Tylianakis 2010).

So far, very little attention has been given to the question of how changes in the behavior of one species—because of rapid environmental change—influence species interaction networks. Yet, this is a topic that is calling out for greater research effort, especially as the consequences of environmental change can be far more profound (and complex) than what is revealed from investigating the direct effect on individual species in isolation or simple pairwise interactions.

How are different interactions affected?

The influence of environmental change on species interaction networks can be complex and driven by many different sources of environmental change. How the network is affected depends on the strength and functional importance of the affected interactions, and on the possibility of replacing lost or weakened interactions with novel interactions, or by increasing the strength of existing interactions. In the following section, we outline some common pathways through which environmental changes are influencing species interactions and the consequences that the changes might have for the interaction network.

Consumer–resource interactions

Consumer–resource interactions are sensitive to changes in the environment that modify behavioral interactions directly or alter the size of populations thereby resulting in changes to consumer pressure or resource availability. Habitat destruction and fragmentation, for instance, alter the foraging behavior of herbivores, which can then require adjustments to predator behavior. Similarly, ongoing climate change is expected to have significant effects on consumer–resource interactions by influencing key traits in predator–prey interactions, such as search rate, detection distance, speed, and handling time (Kordas et al. 2011; Dell et al. 2014). The impact of these changes is likely to affect some animals more than others. For example, the behavioral performance of ectotherms is often more sensitive to changes in environmental temperature than those of endotherms, which could influence their relative success at evading predators (Dell et al. 2014).

Alterations in consumer–resource interactions can, in turn, induce cascading top-down effects, where changes in the consumer influence lower trophic levels, or bottom-up effects, where changes in the resource influence higher trophic levels (Pace et al. 1999; Baum and Worm 2009). The eventual effect that these cascading processes can have on the community of species can be difficult to predict due to the complexity of species interaction networks.

Competition

Because animals differ in their optimal niches and tolerance levels, even small changes in the environment can have substantial effects on competitive interactions. For instance, increases in temperature affect agonistic behavioral interactions among 3 invasive species of crayfish in Europe (Gherardi et al. 2013). Under climate change, such behavioral differences are expected to determine which of the 3 species is most likely to outcompete the others and become dominant.

How these competitive outcomes are resolved is also likely to depend on changes in habitat characteristics, as evidenced by behavioral interactions between 2 species of gecko lizards. The common house gecko (*Hemidactylus frenatus*) has invaded islands across the Pacific, where it has successfully displaced many of the resident gecko species, including the mourning gecko (*Lepidodactylus lugubris*). An experimental study revealed that the larger and more aggressive house gecko was able to outcompete the mourning gecko in more open habitat and when the distribution of their insect prey was clumped (Petren et al. 1993). However, when the habitat was more complex and the distribution of prey was more even, the effect of competition disappeared (Petren and Case 1998).

Parasitism and mutualism

Anthropogenic activities can influence host–parasite interactions by affecting the search behavior of parasites and the avoidance behavior of their hosts (Budria and Candolin 2014). For instance, increased use of insecticides in pest management has impaired the search behavior of parasitic wasps by reducing their activity and life span (Desneux et al. 2007). Changes in the avoidance behavior of hosts can, in turn, affect their likelihood of coming into contact with potential parasites (e.g., through choice of nesting or foraging habitats) as well as the probability of the parasite gaining hold once contact has occurred (e.g., removal of parasites through cleaning and grooming behaviors; Okuno et al. 2012).

Mutualistic interactions are particularly sensitive to environmental change because negative effects on one species are expected to adversely affect the other partner(s) in the relationship. An example of this is seen in the African savanna, where the loss of large herbivores in some areas has led to the breakdown of ant–*Acacia* mutualisms (Palmer et al. 2008). *Acacia* trees support ants by offering nectar and shelter. In return, the ants defend the trees against insect and mammalian herbivores (Palmer et al. 2008). Exclusion of large herbivores shifts the community structure and competitive relationships among different ant species, altering the mutualistic relationships between ants and trees—and leaving the *Acacia* more susceptible to attack from insect pests (Palmer et al. 2008).

ECOSYSTEM-LEVEL CONSEQUENCES

Changes in the strength and nature of species interactions are expected to have important ecosystem-level effects (Schmitz et al. 2008; Palkovacs and Dalton 2012). This is because ecosystems consist of integrated abiotic and biotic components, which are linked,

both directly and indirectly, to one another. As a result, changes in one part of the system can drive changes throughout, which can then alter ecosystem function and stability. Yet, in spite of this, we have only a basic understanding of how behavioral responses in one species, through its effects on others, might alter ecosystem processes.

The main mechanisms by which altered behaviors influence ecosystem processes is through effects on consumption and the spatial distribution of nutrient (Palkovacs and Dalton 2012). Changes in these can, in turn, influence the stability of ecosystems and, in so doing, fundamentally alter the structure and function of the ecosystem.

Effects arising from changes in consumption

Behavioral responses that influence consumption often underlie ecosystem-level changes (Pace et al. 1999; Schmitz et al. 2004). This is because consumer–resource interactions govern how energy and material flow through systems, which then determines the length and structure of food chains and food webs. Changes in nutrient input or primary production, as a result of human activities, can induce bottom-up processes, whereas changes in the abundance or behavior of apex predators (or in the perceived risk of predation in prey) can induce top-down processes. A classic example of the latter comes from Western Alaska where anthropogenic changes to the offshore oceanic ecosystem were linked to an increase in killer whale (*Orcinus orca*) predation on sea otters (*Enhydra lutris*). This, in turn, resulted in the precipitous decline of sea otter numbers, which allowed their primary food source, herbivorous sea urchins (*Strongylocentrotus* spp.), to flourish and decimate vast tracts of kelp forests (Estes et al. 1998).

Changes in the spatial distribution of nutrients

Behavioral responses can impact on the spatial distribution of nutrients by altering where consumption, excretion, and decomposition occur (Vanni 2002; Palkovacs and Dalton 2012). This can influence bottom-up processes and, hence, the length and structure of food webs. For instance, migratory Pacific salmon (*Onchorhynchus* spp.) carry with them marine-derived nutrients from the ocean when returning to their natal streams and lakes to spawn. The nutrients, which are released into the freshwater ecosystems, come from the salmons' gametes and the decomposition of their carcasses after spawning. This nutrient subsidy, in turn, has a substantial impact on the structure and function of the ecosystem (Janetski et al. 2009). Moreover, bears (*Ursus* spp.), wolves (*Canis lupus*), and scavenging birds that feed on the eggs and carcasses of the salmon help transport the nutrients into the terrestrial realm (Schindler et al. 2003; Field and Reynolds 2013). Changes in the abundance and behavior of salmon and the scavengers—because of overexploitation, barriers to migration, habitat degradation, and climate change—can, therefore, alter the nutrient status of both freshwater and adjacent terrestrial ecosystems (Hocking and Reynolds 2011).

Effects on the stability of ecosystems

Altered behaviors that change the network structure of species interactions are expected to influence ecosystem stability (Berlow 1999; Hoover and Tylianakis 2012; Rooney and McCann 2012). Reduced diversity of species and the homogenization of species interaction networks can reduce the resilience of the ecosystem and thereby increase the risk of drastic perturbations of the ecosystem. A dynamically variable interaction network, on the other hand, with species interactions that are changeable in both presence and strength, can buffer the ecosystem against such perturbations and maintain stability. This influence on ecosystem stability emphasizes the importance of determining how behavioral responses alter species interaction networks. Specifically, the effect of environmental change on ecosystem stability may not be evident when inspecting only pairwise interactions.

Nevertheless, it is important to also point out that some human-induced changes appear to have a positive effect on ecosystem stability. For instance, the introduction of species into new areas can improve stability if it gives rise to novel interactions. An example of this comes from the Galápagos Islands, where introduced insect pollinators were found to visit more plants than either their native or endemic counterparts (Traveset et al. 2013). Importantly, by increasing the complexity of the network structure, these novel interactions may act as a buffer against secondary extinctions (Traveset et al. 2013).

Complexity of effects

Ecosystems usually face a multitude of human-induced stressors at the same time, which can work in a variety of ways to influence species interactions. A well-known example comes from Lake Victoria in East Africa, where a decline in water clarity as a result of eutrophication has eroded the visual signals important in maintaining reproductive isolation among closely related cichlid species (Seehausen et al. 1997). The resultant impact on the Lake's cichlids has been exacerbated by predation pressure from introduced Nile perch (*Lates niloticus*), which has kept cichlid densities low, thereby hampering their recovery—even when water quality started to improve (Witte et al. 2013). More generally, because species are embedded in complex communities, any behaviorally mediated changes to a specific interaction will depend on how other interactions are affected. This complex interplay between species and the environment can make it exceedingly difficult to predict exactly how human-induced changes to behavior will influence the structure, function, and stability of ecosystems.

Furthermore, because of eco-evolutionary feedbacks, environmentally mediated changes to behavior can also affect evolutionary processes and, in so doing, generate further ecological change (Estes et al. 2013). An example of this is seen in Trinidadian guppies (*Poecilia reticulata*), which inhabit streams associated with different predatory fish communities. Guppies adapted to life in high- and low-predation sites have evolved differences in diet. In a study highlighting the dynamic nature of the feedback between ecological and evolutionary processes, Bassar et al. (2010) showed that such diet differences alter the ecosystem directly by influencing species composition and primary production. In the next section, we focus more specifically on the evolutionary consequences of environmentally mediated changes to behavior and consider the potential role that evolution plays in facilitating responses to altered conditions in the longer term.

BEHAVIORAL RESPONSES AND THE EVOLUTIONARY PROCESS

Changes in abiotic and biotic factors that influence behavior can affect evolutionary processes either by inducing behavioral responses that impact on the processes themselves or by bringing about evolutionary changes in behavior (Sih et al. 2011; Tuomainen and Candolin 2011). The introduction and subsequent spread of invasive cane toads (*Rhinella marina*) across Australia provides a good

example. Cane toads are highly toxic to snake predators, resulting in strong selection pressure on native snakes to evolve behaviors that help them to avoid devouring the toxic toads (Phillips and Shine 2006). Selection has played a pivotal role in shaping the behavior of the invader too, with cane toads evolving longer legs to facilitate their rapid dispersal across the landscape (Phillips et al. 2006). Evolutionary-induced changes to behavior could also be important in ameliorating the impacts of climate change (Pulido and Berthold 2010). In black caps (*Sylvia atricapilla*), birds that overwinter closer to their breeding grounds avoid the high cost of migrating over longer distances and are able to rapidly adjust the timing of reproduction to food availability. Because the phenotypic changes in migratory behavior reflect actual genetic shifts in the population, it would appear that resident populations have the capacity to very rapidly evolve to changing conditions (Pulido and Berthold 2010). But is this always the case?

Do behavioral responses facilitate adaptation?

It has been suggested that behavioral responses to environmental change can facilitate evolutionary changes by preventing drastic population declines, which are critical in buying much-needed time for genetic changes to accrue (The Baldwin effect; Pigliucci 2001; West-Eberhard 2003; Crespi 2007; Ghalambor et al. 2007). Behavioral responses can also expose hidden genetic variation to selection, thereby increasing the probability of adaptive genetic changes (Grether 2005). In so doing, it has been suggested that behavior has the potential to promote the evolutionary "rescue" of populations (Barrett and Hendry 2012).

However, an organism's behavior can also hinder evolutionary responses by masking any underlying genetic variation (Huey et al. 2003; Ghalambor et al. 2007; Duckworth 2009). For instance, plastic adjustments to the timing of migration in response to climate change can potentially conceal the genetic variation that selection could otherwise be acting on to bring about adaptive genetic changes. An evolutionary response may thus be delayed until individuals have reached the limits of their plasticity and genetic variation is finally exposed to the powers of selection. This can drastically shorten the time available for genetic changes to accrue, which may hinder evolutionary rescue. This is particularly true for human-mediated environmental changes, which, as we have already discussed, are often much more rapid than nonanthropogenic sources of change (Hendry et al. 2008). Whether the behavioral response will facilitate or hinder genetic adaptation depends on the degree to which the response is sufficient in adjusting to the altered conditions and on the existence of genetic variation in the direction of selection when the behavioral response is not sufficient (i.e., on the presence of standing genetic variation and the input of new variation through mutations and gene flow; Barrett and Hendry 2012).

In the context of sexual selection, environmental changes can affect not only the evolution of sexually selected traits but also the costs and benefits of sexually selected behaviors (Candolin and Wong 2012b). Consequently, an important issue is whether sexually selected behaviors, such as mate choice and mate competition, should help or hinder adaptation to environmental change (Candolin and Heuschele 2008). On the one hand, changes to the environment that increase the fitness costs of mating behaviors (e.g., costs of conspicuous courtship displays or mate sampling; Jennions et al. 2001) can result in population decline—and thus, one might predict that sexual selection could operate to prevent or hinder adaptation. On the other hand, sexually selected behaviors that are adaptive under

novel conditions could have the capacity to promote the good genes process and accelerate adaptation (Lorch et al. 2003). If environmental change weakens sexual selection (e.g., by hampering mate choice or mate competition), then genetic variation could essentially increase. This is because strong sexual selection is expected to otherwise suppress the amount of genetic variation within a population (Kirkpatrick and Ryan 1991). As genetic variation is crucial in adapting to novel selection pressures, a weakening of sexual selection with changing environments might, therefore, improve the possibility of adaptation (Wilson et al. 2006). This is clearly a contentious area that desperately warrants further investigation.

Influence on hybridization and speciation

Environmentally mediated changes to mating behaviors can shape the course of evolution by breaking down barriers to reproductive isolation. We earlier discussed the well-known example of the cichlid fishes of Lake Victoria in East Africa and how eutrophication has undermined the visual signals critical in preventing matings between heterospecifics (Seehausen et al. 1997). Chemical pollution of the aquatic environment has also been implicated in the disruption of olfactory communication in swordtail fish (*Xiphophorus* spp.), resulting in hybridization between 2 closely related, sympatric species (Fisher et al. 2006). Both examples underscore how human-induced changes can lead to the erosion of species isolation mechanisms and, ultimately, the loss of biodiversity.

Environmentally induced changes in mating behavior, however, can also promote the mechanisms underpinning speciation. In particular, altered conditions can favor the evolution of novel behaviors, which, over time, may facilitate population divergence. For instance, human disturbance of the African rainforest has caused divergence in the song of little greenbuls (*Andropadus virens*) inhabiting habitats that differ in the level of human disturbance. The divergence of song between habitat types is probably due to differences in signal propagation in the disturbed and undisturbed sites (Smith et al. 2008). Such changes, over time, have the potential to lead to reproductive isolation among the different populations through divergent selection.

Alterations of mating behavior in changing environments can consequently both promote and undermine biodiversity. In this regard, the likely outcome will depend on whether the behavioral responses improve fitness in the changed environment, the presence of species with which hybridization may occur, and the existence of genetic variation that makes evolutionary divergence possible.

Constraints on the evolution of behavior

Research indicates that most responses to anthropogenic disturbances are individual-level behavioral or plastic responses and, in fact, few examples of population-level evolutionary responses exist, including the evolution of behavior (Barrett and Hendry 2012; Merilä and Hendry 2014). This could be a consequence of limited genetic variation in the direction of selection, in which case populations are forced to wait for gene flow or mutations to provide the needed variation. Mutations take time to arise and increase in frequency, which emphasizes the importance of standing genetic variation in fuelling evolutionary rescue (Futuyma 2010). The existence of favorable standing genetic variation depends, in turn, on the evolutionary history of the species and, in particular, whether the species has encountered similar conditions in the past and whether it has maintained alleles that are suitable under the new conditions (Hendry et al. 2011; Sih et al. 2011). A long history of

being subjected to rapid environmental changes can also maintain genetic variation that can allow species to swiftly adapt to novel conditions or favor the evolution of traits that permit rapid evolutionary changes, such as the evolution of shorter generation times (Hendry et al. 2011; Sih et al. 2011).

Even when additive genetic variation in the direction of selection already exists, it is important to realize that genetic correlations among traits can prevent selection from moving populations in the appropriate direction (Walsh and Blows 2009). For instance, genetic correlations due to behavioral syndromes can constrain adaptation (Sih et al. 2004). As an example, an individual that is bold while mating might benefit from being shy while foraging to avoid predators, but a switch in boldness across the 2 contexts might not be possible if genetic correlations link the behaviors together into behavioral "types." Similarly, evolution may be constrained by allocation trade-offs between different traits. For example, in wing-dimorphic insects, such as the cricket (*Gryllus firmus*), investment into constructing and maintaining large flight muscles leads to a lower reproductive output, which limits selection for improved flight ability (Roff et al. 2002).

Human activities often reduce standing genetic variation, particularly through habitat fragmentation and reductions in population size. The prospects of species adapting to rapid environmental changes through genetic changes may, therefore, be limited. Such prospects only increase the importance of the plastic behavioral responses we discussed at the start of our article. More research is needed to determine the ability of populations to adapt to rapid human-induced environmental changes and the role that behavior could play in facilitating or hindering this process. In particular, do populations harbor enough genetic variation in the direction of selection for evolutionary responses to occur—and will there be enough time for these responses to play out? Or are populations forced to rely on phenotypic plasticity and behavioral responses alone?

CONCLUSIONS: BEHAVIORAL ECOLOGY FOR A CHANGING WORLD

Anthropogenic disturbance and its impacts on biodiversity pose an urgent challenge to biologists. Given the unprecedented pace and scale of human-induced changes to ecosystems worldwide, it is critical to understand whether and how organisms will cope in an increasingly human-dominated world. Here, there is much that behavioral ecologists can do.

As we have emphasized throughout this review, behavior is clearly important and, in most cases, is very often the first response when conditions are altered. Behavioral plasticity, in particular, appears to be vital in helping moderate the impacts of human-induced environmental changes on populations, especially where other options, such as genetic evolution, are limited. However, as we have discussed, behavioral responses are not always adaptive. Nor is the plasticity of behavior necessarily sufficient to counter the magnitude of the changes that are taking place, even when the behavioral response appears to be beneficial. More work, in this regard, is clearly needed, and understanding the limits of plasticity itself will be an important avenue for future research.

The interplay between individual behavior and population dynamics also is in urgent need of further research attention, particularly as our knowledge is still limited when it comes to understanding the nature of the associated feedback between behavior and population-level processes. This is important, not the least because changes in the demography of one species can affect others—with consequences for communities and ecosystems. Here, a

major obstacle to comprehending how behavior will influence the structure, function, and stability of ecosystems will be to disentangle the complexity of the interactions that exist between species and the environment.

Lastly, further work is needed to expand our knowledge of how behavior mediates the evolutionary responses of organisms to environmental change and, in particular, the circumstances under which behavior might facilitate (or even hinder) adaptation. In this regard, it would be important to determine how behaviorally induced changes in evolutionary processes will, in turn, alter the ecosystem, resulting in feedback loops connecting behavioral responses with evolutionary and ecological processes. Such knowledge will be crucial in allowing us to forecast the likely fate of species in the longer term and, where possible, to take the remedial actions necessary to counter the loss of biodiversity.

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