REVIEW ARTICLE

The role of behavior in evolution: a search for mechanism

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Abstract Behavior has been viewed as a pacemaker of evolutionary change because changes in behavior are thought to expose organisms to novel selection pressures and result in rapid evolution of morphological, life history and physiological traits. However, the idea that behavior primarily drives evolutionary change has been challenged by an alternative view of behavior as an inhibitor of evolution. According to this view, a high level of behavioral plasticity shields organisms from strong directional selection by allowing individuals to exploit new resources or move to a less stressful environment. Here, I suggest that absence of clear mechanisms underlying these hypotheses impedes empirical evaluation of behavior's role in evolution in two ways. First, both hypotheses focus on behavioral shifts as a key step in the evolutionary process but ignore the developmental mechanisms underlying these shifts and this has fostered unwarranted assumptions about the specific types of behavioral shifts that are important for evolutionary change. Second, neither hypothesis provides a means of connecting within-individual changes in behavior to population-level processes that lead to evolutionary diversification or stasis. To resolve these issues, I incorporate developmental and evolutionary mechanisms into a conceptual framework that generates predictions about the types of behavior and types of behavioral shifts that should affect both micro and macroevolutionary processes.

Introduction

A major question in evolutionary biology is what determines the rate of evolutionary change. Do changes in organismal form merely reflect the rate of external environmental change or are there intrinsic characteristics that differ among taxa that can act as drivers or

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inhibitors of evolution? The traditional view states that the rate of evolution is determined by a combination of mutation rate that generates variation and the intensity of natural selection that sorts this variation (Kimura 1968; Maynard Smith 1976; Barton and Partridge 2000). Changes in the intensity of natural selection are often assumed to be solely a function of the rate of environmental change (Barton and Partridge 2000); however, the intensity of selection is determined by the interaction of an organism with its environment (Lewontin 1983; Odling-Smee et al. 2003). Behavior is at the forefront of this interaction because it determines where organisms live and reproduce and how they obtain resources, avoid predators, choose mates, maintain homeostasis, and respond to conspecific and heterospecific competitors (Bogert 1949; Mayr 1963; Bateson 1988; Wcislo 1989; Huey et al. 2003). Thus, changes in either the environment or an organisms' behavior can alter selection pressures (Plotkin 1988a; Badyaev 2005). This places behavioral change on equal footing with environmental change as a potential cause of evolutionary change (Bateson 1988), but despite the intuitive appeal of this idea, it remains largely unacknowledged in current evolutionary theory (Plotkin 1988a).

Why has it been so difficult to incorporate behavior as a causal force into evolutionary theory? I suggest that lack of clear mechanisms has led to two main problems that impede formal tests of the idea that behavior affects evolutionary change. First, it has led to the unwarranted assumption that high plasticity of behavior is the reason for its special role in evolution. Second, the processes by which behavioral change should lead to micro versus macroevolutionary change are rarely distinguished and thus, there is currently no framework that connects changes in behavior at the level of the individual with population level processes that ultimately lead to evolutionary diversification. Here, I present a conceptual framework that addresses these issues by explicitly incorporating developmental and evolutionary mechanisms.

Behavior as a driver versus inhibitor of evolution

Encompassed within the broader view that behavior is important in evolution are two opposing ideas about how changes in behavior affect the rate of evolution. On the one hand, behavior is thought to generally slow the rate of evolutionary change because behavioral plasticity can shield organisms from strong directional selection by allowing individuals to either exploit new resources (Losos et al. 2004; Sol et al. 2005a) or move to a less stressful environment (Bogert 1949; Huey et al. 2003; Badyaev 2005). On the other hand, behavior is thought to primarily drive evolutionary change because a change in behavior that results in a switch to a new environment or new way of interacting with the environment exposes organisms to novel selection pressures resulting in evolution of morphology, life history and physiology (Mayr 1963; Piaget 1978; Wyles et al. 1983; Plotkin 1988a; Wcislo 1989; Huey et al. 2003; Sol et al. 2005b).

The idea that behavior is important in evolution has a long history which has been reviewed in detail elsewhere (see Plotkin 1988a; Wcislo 1989; Huey et al. 2003). Here, I focus on delineating the similarities and differences between these two opposing views of the role of behavior in evolution. Although each view predicts a different evolutionary outcome, they largely converge in underlying processes. For example, both views emphasize that the critical novel step in the evolutionary sequence is a behavioral shift, i.e., a change in behavior (Fig. 1, Boxes 1a and 2b). In addition, they both propose that the immediate consequence of this shift is that an organism either moves to a new environment or changes its interaction with the current environment (Fig. 1, Boxes 2a, 3a, 3b, and 4b).
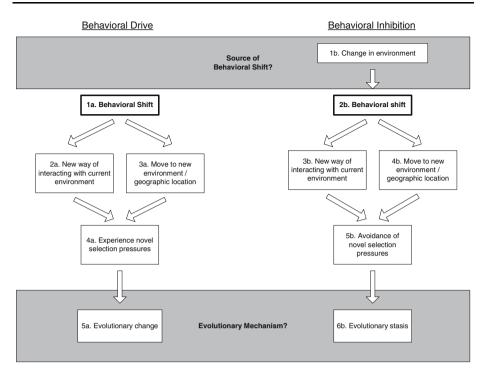
Fig. 1 Path diagram summarizing current view of the role of behavior in evolution. In the view of behavior as a driver of evolutionary change, behavioral shifts (outlined in bold) are the starting point in the evolutionary sequence and their causation is not considered (Box 1a), whereas, in the behavioral inhibition hypothesis, a behavioral shift occurs as a response to changes in external environmental conditions (Box 2b). Both of these views propose that the immediate consequence of the behavioral shift is either a new way of interacting with the current environment (Box 2a and 3b) or a move to a new environment/geographic location (Box 3a and 4b). Both views also propose that behaviors affect evolutionary processes by altering selection pressures (paths to and from 4a and paths to and from 5b). The gray boxes highlight two areas where mechanisms have not been made explicit

Finally, both views propose that behavioral shifts affect evolutionary processes through changes in selection pressures (Fig. 1, Boxes 4a and 5b). Yet, where they most clearly diverge—in their initial and final steps (Fig. 1, Boxes 1a and 1b, 5a and 6b)—is also where the underlying mechanisms are most difficult to discern. In the initial step, both views are vague about the origins of behavioral shifts and in the final step they are unclear about the specific evolutionary mechanisms that would lead to diversification or stasis (Fig. 1). Explicit recognition of mechanism at both of these steps not only points out unwarranted assumptions of the hypotheses, but also emphasizes where they converge conceptually which enables their unification into a single coherent framework. In this review, I fill in the gaps that have not been made explicit in previous discussions of the role of behavior in evolution and by doing so attempt to clarify assumptions and generate testable predictions for new empirical advances in this area. I conclude with suggestions for future work.

Is behavior special?

In the introduction to his edited book, Plotkin (1988a) points out that for behavior to play a special role in evolution, it must differ in some important way from other aspects of the

phenotype. Otherwise, "since every phenotypic attribute relates to every other, we would be back to the undifferentiated question of the role of the phenotype in evolution. But the intuition...is that it *is* important to distinguish behavior from other phenotypic attributes" (Plotkin 1988a, p. 8; emphasis in original). What, then, distinguishes behavioral traits from other aspects of the phenotype? And what accounts for its special role in evolution?

Behavior is often defined as the activity or movement of an organism (Tinbergen 2005; Plotkin 1988a) and many have emphasized the active role of behavior in enabling an organism to respond to and modify its environment and suggest that this is what accounts for its special role in evolution (Waddington 1960; Piaget 1978; Lewontin 1983; Bateson 1988; Plotkin 1988a). Through behavior, organisms determine where to live and reproduce, which resources to use, which mates to select, and how to respond to competitors and predators. In contrast, others have emphasized the high plasticity of behavior as the key to its central role in evolutionary processes (Wyles et al. 1983; Wcislo 1989; Huey et al. 2003; West-Eberhard 2003; Sol et al. 2005b). The focus on behavioral plasticity reflects the widely held assumption that behaviors are generally more labile than morphological or physiological traits (Pigliucci 2001) and consequently, that a behavioral shift can occur faster than an adaptive change in morphology or physiology and thus should take the lead in evolution (West-Eberhard 2003). The idea that behaviors are more plastic than other traits seems intuitive but it does not capture how behavioral plasticity differs from plasticity of other traits. For example, there are many different types of plasticity and many morphological, physiological and life history traits are also highly plastic. Is any type of plasticity important and behavior is simply plastic more often or is behavior plastic in a different way than other traits? To gain a better understanding of how exactly behavior differs and ultimately, why behavior plays a special role in evolution, it is important to critically evaluate what is meant by behavioral plasticity.

Piersma and Drent (2003) suggested the terms "phenotypic flexibility" and "life cycle staging" for types of plasticity that are reversible and "developmental plasticity" and "polyphenism" for types of plasticity that are irreversible. Although these distinctions are helpful, they are not mutually exclusive categories, at least in relation to behavioral traits. Behavioral traits are always reversible, yet their level of expression can nevertheless be highly consistent in adulthood such that the expression of a particular behavior can be at once reversible and developmentally plastic (Fig. 2; Boake 1989; Sih et al. 2004). For example, in birds, aggressive behavior is reversible in the sense that it is only displayed in response to a specific stimulus (e.g., territorial intrusion by a conspecific competitor), but at the same time, it can be developmentally plastic if an individual's level of aggression (e.g., the rate at which they attack the intruder) is highly consistent in adulthood because it was determined early in ontogeny (e.g., based on the amount of testosterone they were exposed to in the egg). Behaviors are reversible because they are only expressed in response to an appropriate internal or external cue (Fig. 2A), and without the cue, a particular behavior is not perceptible (e.g., parental behavior in the absence of offspring). Thus, reversibility of behavior is distinct from the question of whether the level of expression of a behavior is developmentally plastic or not. In contrast, morphology (of determinant growers, at least) is relatively stable in adults because, in most cases, it is not immediately reactive to a cue except during ontogeny (however, see Piersma and Lindström 1997; Piersma and Drent 2003; West-Eberhard 2003). Behavioral traits are plastic in the sense of their reversibility—what I will refer to here as their *reactivity*—but similar to morphology, physiology and life history traits, they vary widely in the extent of developmental plasticity (West-Eberhard 2003).
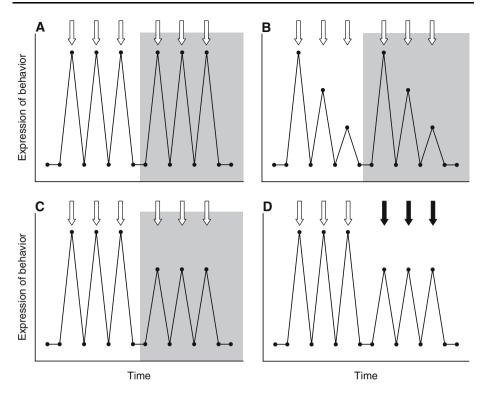
Fig. 2 Illustration of reactivity versus plasticity in the level of expression of behavior within an individual. In (**a**), the level of expression of behavior is highly consistent within as well as across environmental contexts (indicated by white and gray areas). Reactivity of behavior is indicated by the response of behavior to a cue (arrows) that can be either an internal or external signal. In (**b**), the level of expression is not affected by environmental context, but does change over time. This can be due to habituation, learning, or age-dependent life history strategies. In (**c**), the level of expression is highly consistent within contexts, but changes between contexts. An example is the expression of parental behavior in the presence or absence of a nest predator. Finally, in (**d**), the level of expression is consistent toward a specific cue, but when the cue changes (indicated by white versus black arrows), the level of expression changes. In this case, the change in expression may indicate two functionally different behaviors (e.g., conspecific versus heterospecific aggression) even when the category of behavior is the same (e.g., aggression). All of these scenarios illustrate a situation in which behavioral plasticity is limited in some way, yet, in each scenario it is still possible that expression of behavior is also developmentally plastic if it was modified during ontogeny by environmental context. Thus, more complex shifts in the level of expression or reactivity of behavior due to different combinations of developmental plasticity, behavioral flexibility, and learning are also possible

The reactivity of behavior results in an animal shifting among its repertoire of behaviors (Gordon 1991), is an integral part of any behavioral response, and is not plasticity in the sense that is commonly discussed in the morphological literature. By distinguishing "reactivity" from "level of expression" it becomes apparent that, similar to morphology, behaviors can be highly stable in their level of expression. Recent studies show that behaviors are often highly repeatable when assessed in response to an identical stimulus (Dingemanse et al. 2002; Schwagmeyer and Mock 2003; Forstmeier and Birkhead 2004; Duckworth 2006a), highly consistent when measured across contexts (Dall et al. 2004; Sih et al. 2004; Bell 2005; Duckworth 2006a), and highly intercorrelated with other behavioral traits (Dingemanse et al. 2003; Sih et al. 2003; Johnson and Sih 2005; Duckworth and Badyaev 2007). Finally, similar to morphological plasticity, the extent of plasticity of

behavior depends on both its phylogenetic history and current function (Slikas 1998; Mahler and Tubaro 2001; Suhling et al. 2005). These observations emphasize that behavior, like any other aspect of the integrated phenotype, can be limited in plasticity (Dall et al. 2004; Merilä and Björklund 2004; Sih et al. 2004). Thus, it is not warranted to classify all behavior as "generally more plastic" than other traits (Pigliucci 2001) except in reference to their reactivity and it is this reactivity of behavior that distinguishes it from morphological traits.

By distinguishing different types of behavioral plasticity, it is evident that the two views of why behavior is special—"behavior as the activity of an organism" and "the high plasticity of behavior"—are related. Behavior is more plastic than other traits in its high reactivity and this reactive nature of behavior is what enables organisms to actively interact with their environment. In this way, behavior influences selection pressures by determining which aspects of the environment are relevant to an organism (Lewontin 1983). The theory of niche construction proposes a similar view of the active role of organisms in evolution except proponents of niche construction do not limit their focus to behavioral traits and suggest that any aspect of an organism that modifies the environment creates novel evolutionary dynamics (Odling-Smee et al. 2003). However, it is clear that behavior plays a prominent role in the theory of niche construction and many of the examples used to illustrate niche construction are of behavioral traits (Odling-Smee et al. 2003, Chap. 2).

Changes in the level of expression (how organisms react) and reactivity (i.e., what organisms react to) both have the potential to influence evolutionary change, but it is only the latter aspect of behavior that clearly distinguishes it from morphological traits. Therefore, part of the challenge to elucidating whether behavior plays a unique role in evolution relative to changes in other phenotypic traits is to determine to what extent changes in these different aspects of behavior either drive or inhibit evolutionary change. Moreover, distinguishing between reactivity and the level of expression of behavior enables a more rigorous analysis of sources of variation in behavior and enhances the ability to determine when, at what frequency, and what types of behavioral shifts occur (Fig. 2; Table 1). As I will discuss below, such distinctions are crucial to understanding whether or not a specific behavioral shift has the potential to influence evolutionary processes.

Evolutionary mechanisms: causes of divergence versus stasis

A major problem with both views on the role of behavior in evolution—whether as a driver or inhibitor—is that mechanisms by which behavioral shifts impact micro versus macro-evolutionary change are rarely distinguished despite the implication that behavioral shifts should be important in influencing both processes (Mayr 1963; Wcislo 1989; Nicolakakis et al. 2003; Odling-Smee et al. 2003; West-Eberhard 2003; Sol et al. 2005b). Most discussions allude to a mechanism for how behaviors affect microevolutionary change—behavioral shifts alter selection pressures on other aspects of the phenotype by changing the way an organism interacts with its environment—but do not explicitly link behavioral changes that occur within an individual to population level processes. In this section, I discuss how incorporating of modes of speciation and developmental mechanisms underlying behavioral shifts provides insight into the types of behavioral shifts that lead to evolutionary diversification or stasis.

Incorporating of modes of speciation (e.g., allopatric versus sympatric) emphasizes the distinction between behavioral shifts that cause an animal to move to a new environment

Table 1 Types of behavioral shifts

Type	Source of variation	Examples	Citation
Reaction to new cue: because an animal behaves continuously (see Gordon 1988) it is constantly shifting among its repertoire of behaviors in response to internal and external stimuli. This type of "life cycle staging" is an integral part of the behavioral response.	Environmental	Seasonal shifts from territorial to parenting behavior in male birds	Wingfield (1987)
		Temporal changes in activities of the harvester ant, *Pogonomyrmex barbatus*	Gordon (1986)
Developmental plasticity: behavior that is modified by environmental variation before an individual reaches adulthood.	Environmental	Changes in mate preferences due to imprinting in two species of tits (*Parus*)	Slagsvold et al. (2002)
		Changes in sexual behavior of offspring due to maternal effects in zebra finch, *Taeniopygia guttata*	Forstmeier et al. (2004)
Behavioral flexibility: in an adult, behavior is modified by environmental context.	Environmental	Changes in provisioning rate of nuthatches (*Sitta*) in response to predators	Ghalambor and Martin (2002)
Learning: incorporation of information gathered through experience or observation that enables modification of behavior. This describes a specific mechanism of behavioral change that can occur under the more general categories of developmental plasticity or behavioral flexibility.	Environmental	Changes in foraging behavior with experience in honeybees, *Apis mellifera*	Hammer and Menzel (1995)
		Changes in song repertoire of indigo buntings (*Passerina cyanea*) as a result of cultural evolution	Payne (1996)
Frequency shift: population level changes			
Gene flow	Genetic	Changes in climbing behavior of dear mouse (*Peromyscus maniculatus*) populations	Thompson (1999)
Selection	Genetic	Disappearance of song in a parasitized population of field crickets, *Teleogryllus oceanicus*	Zuk et al. (2006)
Developmental plasticity (population level consequence of plasticity listed above)	Environmental	Changes in frequency of carnivorous and omnivorous behavior in spadefoot toad (*Spea*) populations	Pfennig et al. (2006)

Table 1 continued

Type	Source of variation	Examples	Citation
Founder's effect	Genetic	Only aggressive western bluebird (*Sialia mexicana*) males colonize new populations	Duckworth (2008)
	Cultural	Disproportionate effect of single immigrant male large ground finch (*Geospiza magnirostris*) on song type of population	Grant et al. (2001)
Mutation	Genetic	Variation in foraging behavior in *Drosophila melanogaster*	Pereira and Sokolowski (1993)

versus behavioral shifts that cause an animal to change the way it interacts with the environment but essentially remain in the same location (Fig. 3). This distinction is rarely drawn, yet is important because, in the former case, a change in behavior is the first step in the process of allopatric or parapatric speciation (Fig. 3, paths from Box 4 to 8), whereas, in the latter case, a behavioral shift that results in novel selection pressures would have only micro-evolutionary consequences unless it leads to evolutionary diversification through sympatric speciation (Fig. 3, paths from Box 3 to 7). Moreover, although discussions of behavior driving evolution focus almost exclusively on changes in behavior
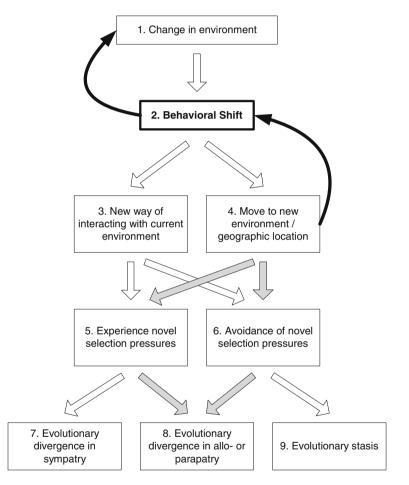

Fig. 3 Illustration of a unified framework with behavior as both a driver and inhibitor of evolutionary change. In this conceptual diagram, a change in the environment precedes most forms of behavioral shifts (with random mutation the only exception). Whereas, in Fig. 1 the paths linking behavioral shifts to evolutionary divergence and stasis occur as alternate pathways, here, they can occur simultaneously. For example, a behavioral shift leading to Box 3 can simultaneously cause and animal to experience novel selection on one trait (path from Box 3 to 5) while avoiding selection on another (path from Box 3 to 6). Gray arrows indicate continuation of paths originating from Box 4. Shifts that cause a move to a new environment (Box 2–4) are unique in that novel selection pressures are not necessary for evolutionary divergence. The black arrows indicate potential feedback loops between environmental and behavioral changes

that result in novel selection pressures, explicit incorporation of modes of speciation shows that speciation can occur without novel selection pressures if movement to a new environment leads to evolutionary divergence through stochastic processes such as a founder's effect or genetic drift (Wares et al. 2005). Finally, integration of the two views emphasizes that the role of behavior in driving and inhibiting evolution are not always mutually exclusive alternatives but may often be distinct stages in an evolutionary sequence (Huey et al. 2003; Losos et al. 2004). For example, a move to a new environment can result in behavioral inhibition on a short time scale by allowing the organism to avoid novel selection pressures in the old environment (Fig. 3, path from Box 4 to 6) whilst driving evolutionary change on a longer time scale by setting the stage for allopatric speciation (Fig. 3, path from Box 6 to 8) or by exposing the organism to a different set of novel selection pressures in the new environment (Fig. 3, path from Box 5 to 8).

Integrating developmental and evolutionary mechanisms enables us to bridge the gap between changes in behavior that occur within the individual and population level processes that ultimately lead to evolutionary diversification or stasis. There are two necessary requirements to bridge this gap. First, for a change in behavior to have long-lasting consequences on the evolution of other traits, it must occur in a large enough subset of the population so that there is substantial variation on which novel selection pressures can act. Some types of behavioral shifts are more likely to meet this requirement than others. These include (1) developmental plasticity where different individuals within a population share a similar reaction norm and are exposed to the same environmental variation (West-Eberhard 1989, 2003; Badyaev 2005, 2007), (2) learning, but only if the learned trait is culturally transmitted (Irwin and Price 1999; ten Cate 2000; Price 2007), (3) selection, because it can shift the behavioral phenotype of the entire population (Duckworth and Badyaev 2007; Zuk et al. 2006), and (4) a founder's effect because it can result in the reduction of a population's behavioral repertoire through the loss of both genetic and cultural diversity and this can influence the evolutionary trajectory of the founding population (Grant et al. 2001). The diverse types of behavioral shifts listed above (see also Table 1) emphasize that the source of the behavioral shift (whether environmental or genetic) is less important than the proportion of the population experiencing the behavioral shift. For example, a change in habitat preference due to either plasticity or selection, by affecting the expression of behavior in many individuals at once, will change the selective environment for a large proportion of the population whereas, a mutation which creates a unique habitat preference in one or a few individuals will create a small, isolated subpopulation that has a high chance of going extinct.

Second, for a behavioral shift to change the evolutionary trajectory of a population, the change in behavior must persist across several generations. Behavioral shifts due to genetic changes, although usually not discussed, have at least as much potential for affecting the evolutionary trajectories of other traits as purely phenotypic shifts. For example, Losos et al. (2006) showed that when *Anolis sagrei* is introduced on islands with predators, they shift their microhabitat preference by moving to higher perches where they are out of reach of the predator. This change in habitat use has led to differential selection on limb length on islands with predators compared to islands without predators. Presumably, the behavioral shift here is purely phenotypic and if the predators are removed from all islands *A. sagrei* would move back to the ground and the difference in selection on limb length among islands would disappear. However, if variance among individuals in perch preference is underlain by genetic variation and predation favors individuals with innate preferences to perch higher, then, even if predators are removed, *A. sagrei* should continue to perch high and the difference in selection on limb length among populations could

remain for several generations. This example illustrates two points. First, for a change in behavior to be relevant on an evolutionary time scale, it must last long enough for selection to act on and produce an evolutionary response *in other traits*. Second, the emphasis solely on plastic changes in behavior is not warranted given that genetic changes in behavior can also have evolutionarily important consequences.

Although plastic responses are typically not transferred across generations, an important exception is cultural transmission of learned behavior. There are several reasons that, among highly plastic behaviors, learned behaviors should have particular importance in affecting evolutionary processes. First, learning enables immediate and adaptive responses to environmental variation (e.g., by improving foraging ability or predator avoidance) which is particularly important for both colonizing novel environments and adapting quickly during periods of rapid environmental change (Plotkin 1988b; Rosenzweig 1995; West-Eberhard 2003; Sol et al. 2005a). Second, in species with high cognitive abilities, learned behaviors can be rapidly culturally transmitted, which can result in alteration of the selective environment for many individuals at the same time (Wyles et al. 1983; Jablonka and Lamb 1995; Avital and Jablonka 2000; West-Eberhard 2003). Finally, two specific types of learning, cultural transmission of behaviors within families and imprinting can facilitate the persistence of novel behaviors across generations (Lewontin 1982; Grant and Grant 1996; Laland et al. 2000; Price 2007).

For these reasons, proponents of the idea that behavior drives evolutionary change often focus primarily on behavioral shifts due to learning (Wyles et al. 1983; Plotkin 1988b; Sol et al. 2005b; Price 2007). Yet, while cultural transmission of learned behaviors may give them a high potential to affect selection pressures, there is no a priori reason to expect them to always drive evolutionary change (Odling-Smee et al. 2003). Evolution of lactase in humans of western cultures is an oft-cited example of behavioral drive (e.g., Wyles et al. 1983) in which a physiological adaptation (ability to digest lactose) evolved in response to a behavioral/cultural change (shift to farming and use of domesticated livestock). However, cultural transmission of behavior may provide just as many examples of behavioral inhibition. Humans inhabit a wide range of climates and habitats, yet further morphological adaptations are likely inhibited by cultural transmission of technologies that make it possible for humans living in distinct climatic conditions to nevertheless experience similar environments. In one of the few empirical studies on this topic, Wyles et al. (1983) showed that large brain size, a surrogate for behavioral flexibility, was associated with faster rates of anatomical divergence supporting the idea that the high levels of behavioral flexibility speed up evolutionary diversification. However, this causal interpretation was criticized by Lynch (1990) because it did not account for variation in lineage age and this may have confounded measures of evolutionary rates.

These theoretical and empirical examples are mainly concerned with adaptive evolutionary changes in traits which may or may not lead to higher rates of speciation. How might learning affect rates of evolutionary diversification in terms of species richness? Species with high cognitive abilities have been shown to produce novel innovative behavior at a high rate (Lefebvre et al. 1997; Reader and Laland 2002) and this has been suggested to influence patterns of species richness in two ways. First, a higher rate of innovation could lead to a niche shift opening up new ecological opportunities which potentially can initiate an adaptive radiation (Mayr 1963; Schluter 2000; Sol et al. 2005b; Price 2007). Second, species with higher behavioral flexibility are more likely to survive if they colonize a novel environment (Sol et al. 2005a; Price 2007)—a crucial first step in allopatric models of speciation. Recent tests of these ideas found that behavioral flexibility as measured by brain size is associated with higher species richness in birds (Nicolakakis et al. 2003; Sol et al. 2005b) and is also

linked to invasion success supporting the idea that behavioral flexibility enhances coloni-zation ability of animals (Sol and Lefebvre 2000; Sol et al. 2002). While these studies suggest that high behavioral flexibility associated with learning can influence patterns of species diversification, it will be important to test these ideas in other taxa to determine whether this is a general pattern or is limited to avian species.

Role of behavior in evolution: behavior as both evolutionary cause and consequence

Explicit recognition of developmental and evolutionary mechanisms enables the integra-tion of behavior as both a driver and inhibitor of evolution into one comprehensive framework (Fig. 3). This integration produces several novel insights into the role of behavior in evolution. First, acknowledgement of diverse developmental mechanisms underlying behavioral shifts makes it evident that the difference in starting points of the two hypotheses—a behavioral shift in the behavioral drive hypothesis (Fig. 1, Box 1a) and a change in the environment in the behavioral inhibition hypothesis (Fig. 1, Box 1b)—is not warranted. This difference reflects the association of behavioral innovation with behavioral drive (Sol et al. 2005b; Wyles et al. 1983) and adaptive behavioral plasticity with behavioral inhibition (Huey et al. 2003). Implicit is the idea that when behavioral shifts are an adaptation to the current environment they maintain evolutionary stasis; whereas, when behavioral shifts produce novel behavior they are more likely to drive evolution. Thus, whether a particular behavior pattern is the cause or consequence of adaptive evolutionary processes is the central question of behavior's role in evolution (Piaget 1978) and investigating the developmental origin of novel behavior is essential for evaluating the potential for behavior to lead in evolution. Yet, the developmental origin of novel behavior patterns is often dismissed in discussions of behavior's role in evolution (Plotkin 1988a, b; Bateson 1988). This may stem from the insistence of separating behavioral and environmental change in order to give behavioral rather than environmental changes a lead role in evolution. However, the origin of novel behaviors cannot be understood outside the environmental context in which they are produced. Acknowledging that behavioral and environmental changes are intimately interconnected does not diminish the role of behavior in evolution, but instead emphasizes the need to understand of sources of behavioral change in order to evaluate the relative importance of behavioral and environmental changes in driving or inhibiting evolution. This is illustrated in the feedback loop that connects behavioral and environmental changes (Fig. 3, path from Box 2 to 1) reflecting that, not only do most changes in behavior originate in response to environmental change (Gottlieb 2002), but that behavioral change can also be critical in producing environmental change (Laland et al. 1999; Odling-Smee et al. 2003).

The synthesis of the two hypotheses also illustrates the place of the Baldwin effect within the more general framework of behavior's role in evolution (Fig. 3, feedback loop from Box 4 to 2). This idea, which has often been proposed as a mechanism of behavior as a driver of evolution (Wcislo 1989), emphasizes the role of behavioral plasticity in enabling colonizers of new environments to survive through phenotypic accommodation before adaptive evolution has time to occur (Baldwin 1896; West-Eberhard 2003). In this view, behavioral flexibility is thought to be crucial for enabling organisms to persist under novel environmental conditions (West-Eberhard 2003; Pigliucci et al. 2006; Badyaev 2007). Ultimately, a behavioral shift in this context can lead to evolutionary change by

enabling population persistence in a novel environment long enough for either stochastic processes or selection to produce divergence from the source population.

Finally, this framework makes specific predictions about the types of behavior that are likely to play a key role in evolution. For example, a change in migratory patterns or habitat selection that causes an organism to move to a novel environment or new geographic location should be particularly important in affecting rates of diversification (Holt 1987; Berthold et al. 1992; Clobert et al. 2001; Wiens 2004; Bearhop et al. 2005; Phillimore et al. 2006). In contrast, changes in mating preferences and resource use could potentially lead to sympatric speciation or ecological divergence without causing reloca-tion to a new environment (Schluter 1996; Dieckmann and Doebeli 1999; Via 2001). Behavioral changes involved in maintaining homeostasis that are adaptations to the current environment, such as thermoregulatory behavior, are more likely to inhibit evolutionary change by preventing ecological divergence of populations that inhabit a broad environ-mental gradient (Huey et al. 2003). Finally, when an organism encounters a new environment either through chance events or because of previous behavioral changes, flexibility in food preferences, predator recognition, reproductive investment, and mating behaviors could all enhance an individual's ability to survive and reproduce in the new environment (Wcislo 1989). Thus, this framework makes specific predictions about the types of behaviors that are most likely to be involved in allopatric versus sympatric speciation and in evolutionary divergence versus evolutionary stasis.

Future directions

A critical analysis of the mechanisms underlying the alternative views of behavior as a driver versus inhibitor of evolution points to several areas where further study is needed. First, more attention needs to be given to the developmental basis of behavioral variation. Investigating whether changes in behavior are purely phenotypic, underlain by genetic variation, or are culturally transmitted will enable predictions about their ability to produce a stable change in selection on other traits. Although behaviors are often difficult to study within a rigorous evolutionary genetic framework (Arnold 1988, 1994; Roff 1994), captive breeding programs as well as long-term studies of marked populations have enabled evaluation of genetic versus environmental sources of variation in behavior in a growing number of wild populations (Hedrick 1994; Dingemanse et al. 2002; Drent et al. 2003; MacColl and Hatchwell 2003). Studies on repeatability of behavior (e.g., Boake 1989) and investigations of correlations among different types of behaviors or of the same behavior to different stimuli (Sih et al. 2004; Duckworth 2006a) are needed to evaluate what consti-tutes a behavioral "trait"—a functional unit that is the target of selection (Wagner 2001). Once patterns of correlation among behaviors are identified, studies on the development, heritability, and function of variation can be used to understand which behaviors share developmental pathways and consequently the likelihood that correlated behaviors can evolve independently (Cheverud 1982; Nijhout 1994; Duckworth 2006a; Badyaev 2004, 2007). These studies can provide insight into the kinds of behavior that are more likely to change due to plasticity and those that are more likely to change in response selection. In turn, this can shed light on the frequency with which new behaviors originate, which is crucial for investigating behavior as a driver of evolution (Wyles et al. 1983).

Empirical studies are also needed to test the prediction that behavioral shifts will alter selection pressures on other aspects of the phenotype and to test the idea that behavioral shifts can influence rates of speciation and extinction. Only a few studies have explicitly

linked behavioral changes to natural selection on other aspects of the phenotype and already these studies suggest that a simple relationship between a behavioral shift and a change in selection is unlikely (Losos et al. 2004, 2006; Duckworth 2006b). For example, shifts in behavior may inhibit selection on some traits while simultaneously enhancing selection on other traits (Fig. 3; Huey et al. 2003; Losos et al. 2004). Similarly, studies that link behavioral shifts to rates of species diversification are also rare. Recent advances in methods of estimating rates of speciation and extinction should enable more precise testing of the mechanisms underlying the links between behavioral shifts and patterns of species richness (Sanderson and Donoghue 1996; Maddison et al. 2007).

Close examination of evolutionary mechanisms suggest that changes in dispersal, migratory, and habitat selection behavior should be particularly important in driving evolution. This is because shifts in these behaviors may cause an animal to colonize a novel environment and can lead to diversification through multiple pathways (Fig. 3, paths from Box 4 to 8). There is some evidence to support this view. In avian species, novel migratory routes have been linked to population divergence and this has potentially set the stage for speciation (Berthold et al. 1992; Bearhop et al. 2005) and diversification rate has been shown to be higher in families that are highly migratory (Phillimore et al. 2006) presumably because they have more opportunities to colonize new areas (Rosenzweig 1995; Lester et al. 2007). In contrast, Belliure et al. (2000) found a higher rate of diversification at the subspecific level in less migratory species. These opposing results may indicate that different processes (e.g., extinction versus speciation) are responsible for the patterns of diversification at different taxonomic levels because rates of species accumulation often decline with lineage age (Schluter 2000). Thus, investigation of the link between behavioral changes and diversification at different taxonomic levels may provide insight into the mechanisms that generate patterns of species richness.

Finally, further development of theory investigating how different types of behavioral shifts affect evolutionary change is also needed. Studies on niche construction, indirect genetic effects and the role of plasticity in evolution have begun to tackle the issue of how variation in behavioral traits might affect evolutionary change. For example, Laland et al. (1996, 1999) have shown that niche construction, in which organisms actively modify their environment, can simultaneously weaken selection on some traits while creating new evolutionary trajectories for other traits. Wolf et al. (1998, 1999) have documented that behavioral modifications that result in a predictable covariance of traits among social partners is, as originally suggested by West-Eberhard (1983), a powerful source of selection. Finally, models by Price et al. (2003) and Behera and Nanjundiah (1995) suggest that the most extreme levels of phenotypic plasticity can inhibit or slow evolutionary change. While these models provide an important start to understanding behavior's role in evolution, more explicit comparisons of how different types of behavioral shifts affect the stability of subsequent evolutionary changes are needed. In addition, incorporation of reversible versus irreversible behavioral plasticity (e.g., Gabriel et al. 2005) into the models is likely to provide important new insights.

Conclusions

There are two re-occurring themes that point to current conceptual difficulties in incorporating behavior as a causal force in evolution. First, the focus on high plasticity of behavior has diverted attention from the investigation of developmental mechanisms that underlie behavioral shifts which is crucial for detecting novel behavior patterns. Second,

lack of clear evolutionary mechanisms has hindered our understanding of how changes in behavior that occur within individuals can affect population level processes. In this review, I have suggested that an explicit incorporation of both developmental and evolutionary mechanisms allows us not only to resolve these issues, but to move beyond the question of whether behavior primarily drives or inhibits evolution and to ask how and under what circumstances behaviors affect evolutionary processes.

Implicit acknowledgement that behaviors are important in evolutionary processes is common in current evolutionary theory. Recognition that behavior can affect evolutionary change is evident in models which are the basis for population genetics (e.g., Hardy–Weinberg equilibrium), such as in the assumptions of random mate choice and absence of emigration and immigration. Moreover, gene flow, a central concept in evolutionary biology (Endler 1973; Slatkin 1985), is essentially a genetic description of organismal movement. Implicit in all of these concepts and models is an active organism—one that chooses where it will live and who it will mate with, and one that responds to changes in its environment. The motivation behind emphasizing behavior's role in evolution is to make the active organism an explicit part of evolutionary theory (Bateson 1988; Ho 1988; Wcislo 1989).

The foundation for arguments that behavior plays a unique role in evolution—whether that role is as a driver or as an inhibitor of evolutionary change—is that behavioral traits are distinct from other aspects of the phenotype (Plotkin 1988a). I suggest that it is not high developmental plasticity which makes behaviors unique but instead is their reactive nature. Active organisms are shaped by their environment and these same organisms also shape their environment (Lewontin 1982; Laland et al. 1999, 2000). Yet, recognizing that behavior can play a causal role in evolution does not mean that all types of behavior and all types of behavioral shifts should affect evolutionary processes in the same way. Instead, the challenge for future studies in this area is to determine how different types of behaviors (e.g., social behaviors versus habitat selection) and different types of behavioral shifts (e.g., shifts due to learning versus shifts due to selection) affect selection pressures in the short term to ultimately impact the rate of evolutionary diversification.

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