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Adaptedness of behavior

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Synonyms

Adaptive behavior; Behavioral plasticity; Behavioral accommodation; Fitness; Adaptation

Definition

The adaptedness of behavior depends on the effects behavior has on individual fitness, ie, how it influences survival and reproductive success. This hinges in turn on how well suited to environmental conditions the behaviors are.

Introduction

Behavior is a major determinant of fitness. It influences foraging success, the ability to avoid predators, success in the competition for resources, and reproductive success. Similarly to other traits, behavior evolves through natural selection; individuals with behaviors that allow them to produce more viable offspring than other individuals pass more copies of their genes on to the next generations, and thereby also the genes for their behaviors, which then increase in frequency in the population.

Evolution consequently gradually changes the behavior of individuals so that they become better and better adapted to local environmental conditions; lions have evolved a hunting strategy that is efficient in the catching of prey on the savannah, while their prey have evolved escape strategies that increase their possibility of escape in the same habitat. This dependency on environmental conditions implies that changes in the environment can reduce the adaptive value of behaviors (Candolin and Wong 2012; Wong and Candolin 2015). For instance, newly hatched sea turtles use the moonlight reflecting off the ocean to find their way from the beach to the sea. However, artificial lighting from roads and cities are currently disorienting the turtles, which instead of heading towards the sea, are drawn towards the land. Here, dangerous roads take their toll and land predators, such as foxes, dogs and birds, further decimate the population, while the hatchlings that escape these hazards may eventually die from dehydration. Thus, the behaviors that have evolved under past, natural conditions are maladaptive in human-altered environments.

The degree to which behaviors are sensitive to changes in the environment, and the extent to which they remain adaptive or not, depends on their plasticity (or robustness) and on the possibility of evolutionary changes. In the following, I will discuss why behaviors are sensitive to environmental conditions, how they can be altered through plastic responses and evolutionary changes to become better suited to prevailing conditions, and why individuals in a population often differ in their behaviors.

Dependence on environmental conditions

The behavior that an animal adopts in a particular environment depends on its behavioral reaction norm (or response curve), in other words, on the behaviors that a particular genotype expresses across a range of environments (Tuomainen and Candolin 2011; Sih 2013). For instance, the behavioral reaction norm of an animal can induce it to increase its food intake when temperature rises, or to spend less time searching for food when it rains. Thus, reaction norms determine how animals adjust their behavior to variation in the environment. The norms have been shaped by past evolutionary processes and have a genetic basis. They can evolve across generations, similarly to other traits, as well as change during the life span through environmental and epigenetic effects, including parental effects (Figure 1).

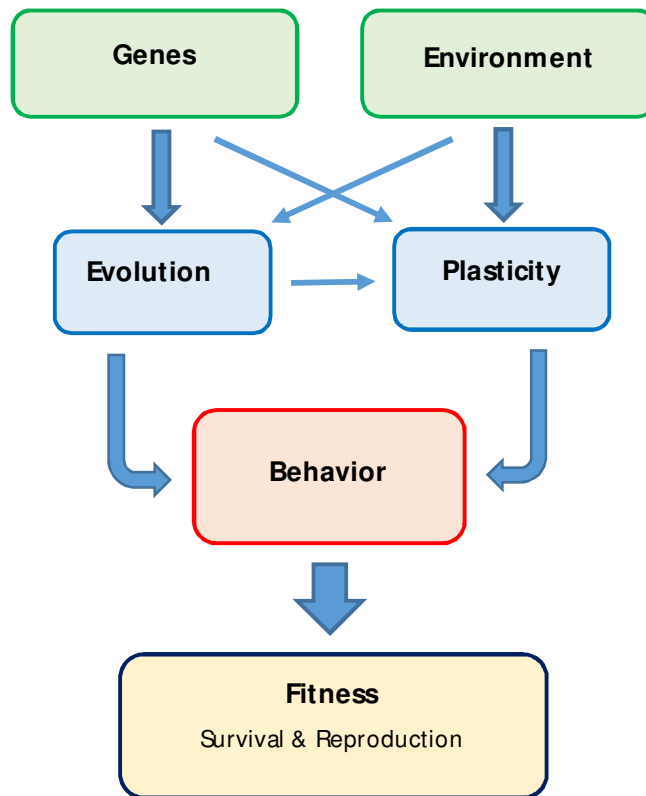


Figure 1. Behaviors are determined by both genes and the environment. These determine the evolution of behavior and its degree of plasticity, which then influence the survival and reproductive success of individuals and, hence, their fitness.

Because behavioral reaction norms have evolved in the past, under the conditions that then prevailed, they can be maladaptive under altered conditions. Thus, species that encounter conditions that they have not encountered in their recent evolutionary past may not have reaction norms suited to the altered conditions (Figure 2). For instance, many animals have evolved migration strategies that are timed so that reproduction coincides with the peak availability of critical food resources for offspring. However, climate change is currently altering the phenology of food organisms, which is disrupting the timing between arrival at breeding grounds and food availability. An example is the long-distance migratory pied flycatcher (*Ficedula hypoleuca*) that migrates from overwintering sites in Africa to breeding grounds in Europe. The species rely on a short burst of caterpillar availability each spring to feed its young. However, the caterpillars have been emerging earlier as temperature in spring has risen. Because the flycatchers use their endogenous timing mechanisms to determine when to migrate, they have not been able to advance their arrival date to the same extent as spring has advanced at the breeding grounds. This has resulted in a phenological mismatch between the hatching of the nestlings and the availability of caterpillars (Both and Visser 2001).

When animals decide on the behavior to adopt in a given situation or environment, they generally use various cues to evaluate the environmental conditions. For instance, many animals in seasonal habitats use day length as a cue for when to start reproductive activities, such as defending a territory, building a nest or attracting mates. These cues are usually reliable indicators of current conditions. However, when the environment suddenly changes, either naturally or because of human activities, the cues may become unreliable indicators of environmental conditions. For instance, artificial lighting along beaches does not

indicate the position of the sea to newly hatched sea turtles. The earlier evolved behavioral strategy then becomes maladaptive and causes an 'evolutionary trap', with sea turtles orienting towards the artificial light on land. Other examples of evolutionary trap are aquatic insects laying their eggs upon asphalt or glass because these reflect polarized light in the same manner as the water surface, and jewel beetles copulating with discarded beer bottles because the surface of the bottles resembles that of females (Robertson et al. 2013).

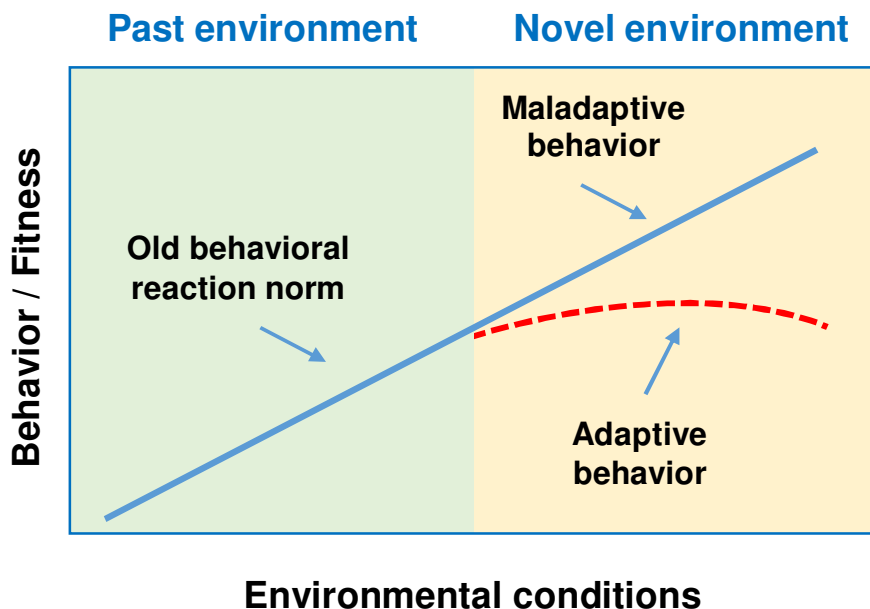


Figure 2. When the environment changes, animals respond to the changes according to their old behavioral reaction norms, which have evolved under past environmental conditions. However, these may not be adaptive under the altered conditions and result in maladaptive behaviors. Evolutionary changes of behavioral reaction norms may be needed for individuals to behave adaptively in the new environment.

Maladaptive behaviors in altered environments can cause the decline of populations. In the worst case scenario, this can result in their eventual extinction of the population, and perhaps even of the species. A population decline is especially likely when the environmental change is rapid and there is not enough time for evolutionary adaptation. For instance, juvenile African penguins (*Spheniscus demersus*) use cold surface water with high chlorophyll levels as a cue of high fish abundance. However, overfishing by humans has drastically decreased fish stocks in areas where these conditions apply, while climate change has caused remaining fish to move southward. This has resulted in the penguins now selecting feeding areas where forage fish are scarce. They are thus caught in an ecological traps, which is decimating the population (Sherley et al. 2017).

Species that are especially likely to show maladaptive behaviors in changing environments are species from habitats that have been highly stable in the past. These species are usually less plastic and less able to phenotypically adjust to altered conditions. This is because plasticity has not been needed in the past environment and, hence, has not evolved. Similarly, species that encounter novel conditions, which they have not encountered in their recent evolutionary past, may lack reaction norms that are adaptive under the altered conditions. Genetic adaptation and the evolution of behaviors suited to altered conditions are in turn less likely in species with longer generation time, as these may evolve too slowly to keep track with the changes. Small populations may again lack the genetic variation needed to genetically adapt to changing environments.

Plasticity of behavior

The degree of behavioral plasticity that an individual expresses depends on its reaction norms for the behaviors, as well as on how these norms have been molded by environmental factors, parental effects, and learning during the life span (Tuomainen and Candolin 2011). Thus, both genes and experiences during development influence behavioral responses and their plasticity.

Behavioral responses to environmental change can largely be divided into three different forms: 1) The behavioral response may be more or less fixed so that an animal always responds in a particular way to a stimuli, such as attacking a prey when detecting it. 2) The behavioral response may be plastic and the animal adjust its behavior to the exact nature of the stimuli, according to its reaction norm. For instance, a predator may adjust its attack behavior to the size or escape ability of the prey. 3) The behavioral response may change during the life span, depending on the conditions that the individual encounters during its lifetime, as well as on its ability to learn new behaviors or improve its skills. For instance, a predator may acquire more advanced hunting skills with age and, hence, attempt to catch prey it would not have aimed at when younger and more unexperienced.

The degree and form of behavioral plasticity is generally adaptive in the natural, undisturbed environment, within the constraints that arise because of other traits (discussed in more detail later). This is because selection across generations have promoted the evolution of behavioral plasticity that maximizes fitness in a particular habitat or context.

Early life experience and development

Experiences during early development can have persistent effects on behavior into adulthood, through parental effects as well as through direct effects of the environment on the developing individuals. Parental effects arise when the conditions that the parents encounter during their lifetime affect the offspring. This can be through the quality of parental care, the transfer of hormones and nutrients via egg yolk, placenta and milk, or through transgenerational epigenetic effects that alter the expression of the genes encoding for behavior. Parental effects usually improve offspring fitness and are adaptive. This is because improved offspring fitness increases also the fitness of the parent, which selects for beneficial parental effects. For instance, breeding western bluebirds (*Sialia mexicana*) influence the aggression and dispersal behavior of their offspring by biasing the birth order of the offspring by sex. When population density increases and the availability of resources declines, females produce more aggressive, dispersive sons. These disperse and colonize new areas where competition for resources is lower and conditions more favorable (Duckworth et al. 2015).

The conditions that the offspring encounter during development can similarly influence behaviors expressed in later life (Sachser et al. 2013). For example, western black widow spiders (*Latrodectus hesperus*) experiencing poor food conditions during development mature at a smaller size and are more aggressive than well-fed spiders (Di Rienzo and Montiglio 2016). These small, aggressive spiders build webs that differ in structure from those of well-fed spider; they are lighter and more efficient in catching prey, but less safe. The lower safety implies that poor condition spiders take higher risks in favor of larger food intake. This is probably an adaptive adjustment as the impact of foraging on fitness increases with deteriorating body condition, while the investment into avoiding predators may not improve fitness when body condition endangers survival. Interestingly, if the body condition of the spiders improves in later life, the spiders start building denser and safer webs. However, the webs are still less safe than those of spiders well-fed during development, which indicates that the web-building behavior cannot be fully adjusted to changes in body condition later in life - some degree of maladaptation may still occur.

The influence of environmental conditions on behaviors is often mediated by effects on the development of morphological and physiological characteristics, such as body size or the functioning of the endocrine system. Poor environmental conditions usually result in a small body size, which in turn can impinge on behaviors such as aggression and reproductive behavior. For instance, the larvae diet of dung beetles

determines their body size and horn size as adults and, hence, their reproductive tactic. Well-fed males of *Onthophagus acuminatus* develop large horns that they use in the fight for females. Small males, on the other hand, who have experienced poorer food conditions, develop tiny horns, or no horns at all, and attempt to steal fertilizations by sneaking on pairs of mating beetles (Emlen 1994).

The timing of maturity can influence the mating tactic adopted, as it determines the size of the individual during reproduction. In the coho salmon (*Oncorhynchus kisutch*), males that mature precociously at a small size become 'jacks' that sneak on the spawning grounds, while males that mature at an older age when larger become 'hooknoses' that fight for females (Gross 1985). A further possibility is that the behavioral tactic adopted changes over the life span of the individual as it grows. In the Azorean rock-pool blenny (*Parablennius parvicornis*), males adopt a sneaking or satellite tactic when small and switch to a nesting, courting tactic when larger (Oliveira et al. 2001). Satellite males are males that are attached to the territory of a nest-holder and help this in defending the territory in exchange for occasional matings.

The adoption of different reproductive tactics is generally adaptive in the natural environment; it maximizes the fitness of individuals that differ in condition and in prerequisites for various fitness linked behaviors (Gross 1996). However, if conditions change, the adaptedness of the different tactics may change as well.

Population characteristics

The density and structure of the population can influence the behavior of the individuals in the population. The impact may be mediated through competition for resources and mates. For example, elks (*Cervus canadensis manitobensis*) adopt a more generalist habitat selection strategy when population density increases; they choose their preferred habitat - mixed forests - less often when density is high, and their home ranges are smaller (van Beest et al. 2016). These changes are likely to be adaptive, as generalist strategies usually yield the greatest fitness return at high densities, while specialist strategies are more favorable when density is low and the competition for preferred resources weak. Thus elks appear to be able to adaptively alter their habitat choice in response to changes in population density.

Changes in the operational sex ratio (OSR) - the ratio of fertilizable females to sexually active males - can alter the intensity of competition for mates and, hence, mating behavior. For example, male guppies (*Poecilia reticulata*) decrease their courtship activity when the OSR becomes more male biased and fewer females are available to mate with. Instead males start interfering with the courtship behavior of other males, with the aim to disrupt their mating attempts and, in so doing, make the females available as mates. This may increase the mating success of dominant males in relation to subdominant males. Female guppies, in turn, are more selective when more males are available to choose among; they show a stronger preference for colorful males, as the color generally indicates male quality (Jrotkul 1999). Thus, changes in the OSR in guppy populations influence both male-male competition and female choice.

Changes in population size or structure can influence the degree to which individuals help and support each other and, hence, their social behavior. Change in relatedness (kinship) among individuals is particularly likely to influence cooperation. This is because individuals are expected to favor close relatives to gain inclusive fitness benefits; helping relatives with shared genes to reproduce can increase the number of copies of their own genes (or alleles) that are passed on to the next generations. Cooperation is therefore most beneficial among related individuals. If the degree of kinship changes, cooperative behaviors may change as well. For instance, flocks of long-tailed tits (*Aegithalos caudatus*) show more helping behavior during breeding when the flock contains closer related individuals (Napper and Hatchwell 2016).

Learning

The ability of animals to learn new behaviors, or modify existing ones, can increase the adaptive value of their behavioral repertoire. Learning occurs as a result of an individual's experience and practice. The ability varies among species as well as within species, depending on genetically determined capacities, as well as on environmental and parental effects. Learning requires that the individual can perceive its behaviors and change them. The changes may occur through habituation to the conditions, such as the

presence of humans that pose no predation risk in urban areas, or by adopting new behaviors, such as learning to capitalize on the food found in garbage cans.

New behaviors may be adopted through associative learning, such as through trial-and-error or by imitating other individuals. Young zebra finches (*Taeniopygia guttata*), for instance, learn how to build nests by observing nest building by familiar conspecifics (Guillette et al. 2016). Interestingly, the finches don't learn new skills if observing unfamiliar conspecifics. This indicates that the use of social information depends on familiarity. Such group-dependent learning of new behaviors can promote the cultural transmission of information within a social group.

However, learning is not always adaptive. For instance, the imitation of the behavior of others may not benefit imitators that differ in other characteristics. An individual in poor condition that copies the behavior of an individual in good condition may expend more energy on the behavior than it can afford, or the behavior may expose it to increased risk of predation or attacks from other individuals. Thus, learning is under selection and can evolve as other traits.

Optimal behavior: trade-offs and constraints

Trade-offs among behaviors limit plasticity. For example, the need to watch out for predators restricts the rate at which an individual can forage, while the opportunity to mate can reduce vigilance for predators. The optimal balancing of investments among various behaviors depends on their fitness benefits. Because being killed by a predator has a larger impact on fitness than a slight reduction in food intake, animals may forgo foraging opportunities for safety. Similarly, the possibility to reproduce may surpass the benefit of prolonging life by evading predators, particularly in animals with only a few possibilities to mate during their lifetime.

The fitness benefits of behaviors can vary depending on life-history stage, body condition and environmental factors, and influence the investment into them. A young animal may invest in safety rather than in reproduction if more reproductive opportunities are available at an older age when larger and more experienced. An old individual, on the other hand, that nears the end of its lifespan and, hence, have few future reproductive opportunities, may invest in current reproduction rather than in safety and in extending its lifespan. For example, male threespine stickleback (*Gasterosteus aculeatus*) take larger risks towards the end of their single breeding season: they are more likely to engage in conspicuous reproductive activities in the presence of predators, and develop more bright nuptial coloration that attract predators as well as females (Candolin 1998; Candolin 2000).

Changes in environmental conditions that alter the costs and benefits of behaviors can similarly influence the investment into them. For example, the hunting of top predators that reduces their abundance decreases predation risk for smaller species. These may then spend less time watching out for predators and instead increase their foraging rate. Such behavioral adjustments are usually adaptive and improve fitness. However, adjustments can be maladaptive when novel environmental conditions are encountered and the behaviors have not been shaped by evolution to suit these. The adaptedness of behavioral adjustments depends on the ability of the animal to perceive the changes as well as to respond adaptively to these. Species may fail to perceive the changes, or they may lack reaction norms for responding adaptively to these. For instance, many species reduce their normal activities when encountering humans, although the humans pose no risk (Frid and Dill 2002). For instance, birds are less likely to establish breeding territories and reproduce in forests where they are disturbed by walking humans (Botsch et al. 2017).

Various constraints may further limit the degree to which behaviors are expressed. For instance, an animal may not be able to increase its foraging rate because of its hunting tactic, long handling time or slow metabolism. For instance, butterflies that feed on nectar from deep-tubed flowers cannot increase their suction time by developing longer proboscides (elongated mouthparts). This is because the length is constrained by manipulation times per flower; the longer the proboscis the more time the butterfly has to spend handling the flower, and this functional cost limits elongation and nectar intake (Bauder et al. 2015). In addition, the perpetual coevolution between interacting species can prevent behaviors from reaching

maximal optimality. For instance, predators continually evolve traits that make it more difficult for prey to detect them, while prey evolve counter adaptations that improve their ability to detect the predators, such as improved hearing or smelling. This eternal coevolution may result in neither species behaving completely optimally at any time.

Because of various trade-offs and constraints, most behaviors are not maximally expressed, or expressed in the most profitable way. They are instead expected to evolve towards an optimal state under prevailing conditions, considering the various constraints and the trade-offs that limit their expression. Foraging rate, for example, is a compromise among hunger level, body condition, the necessity to avoid predators, and the constraints imposed by morphological and physiological characteristics. Changes in environmental conditions that disrupt the behaviors from their optimal state may require the animals to adjust their behaviors accordingly to maintain their high fitness. If plastic adjustments are not possible, because of various constraints and the lack of adaptive reaction norms, selection for evolutionary alterations in behaviors will strengthen. In the following section, I will discuss the likelihood that animals can evolve better adapted behaviors when phenotypic plasticity is not enough.

Evolution of behavior

The evolution of behavior depends on the strength of selection and on the existence of genetic variation in the direction of selection, as well as on the influence of epigenetic effects on the expression of genetic variation. When the environmental change is gradual, as is usually the case during natural changes, animals may gradually adapt their behavior to the new conditions. The evolution may occur through beneficial mutations spreading in the population, ie, through selective sweeps, as well as through immigrants bringing new genetic material into the population, ie, through gene flow. Moreover, hybridization between species can incorporate new genetic material into their gene pools. Such gradual changes are usually adaptive, with natural selection favoring genes and alleles that improve the fitness of individuals. Increased fitness of individual may in turn increase the viability of the population.

Behaviors can change also through random evolutionary changes - genetic drift - particularly in small populations or when a new population is founded by only a few individuals with limited genetic variation (founder effect). Thus, the split of a population into smaller subpopulations because of habitat fragmentation can result in the subpopulations evolving in random directions. For instance, the small and relict population of brown bears in the Italian Apennine Mountains differs in aggressiveness from other bear populations because of random genetic drift. It became separated from other populations by farming and forest burning in Neolithic times, and developed reduced aggressiveness through high inbreeding and random fixation of alleles (Benazzo et al. 2017). Such random changes may not necessarily be adaptive. However, populations with maladaptive behaviors are expected to be quickly wiped out. In the case of the Apennine brown bear, the population has survived despite reduced aggressiveness, as the number of competitors has decreased, and also because the less aggressive temperament allows co-existence with humans.

When only a few individuals survive a change in environmental conditions, a population bottleneck occurs that can drastically decrease the amount of genetic variation in behavior. The bottleneck can either increase or decrease the fitness of the population, depending on the stability of the environment after the bottleneck. Bottlenecks can increase population viability by selecting for individuals best adapted to current conditions, as only the best fit individuals, with behaviors well suited to the conditions, are expected to survive. On the other hand, bottlenecks can decrease population viability by impeding adaptation to further changes in the environment, as genetic variation is lost.

In general, the ability of a population to evolve behaviors better suited to altered environmental conditions depends on the rapidity of the change in relation to the generation time of the individuals, and on population size and the magnitude and direction of genetic variation. Species with longer generation time, typical for larger top predators, are less likely to adapt their behavior to rapid environmental changes.

Small populations, or populations that have not encountered similar conditions in the past, may again lack the genetic variation needed to adapt. In addition, mutations may be too slow to arise to rescue small populations, and immigration of individuals with beneficial alleles may be unlikely if rarer species. When populations are not able to adapt by evolving behaviors better suited to altered conditions, the populations may decline and eventually go extinct (Reed 1999).

When the requirements for evolution is fulfilled, in terms of suitable genetic variation and ample time for evolutionary changes, evolution may still not occur because of various constraints. Trade-offs among traits are particularly common causes of restricted evolution. For instance, a population that has the genetic variation needed to evolve a foraging tactic that reduces predation risk, may not evolve the tactic because it would have negative effects on foraging rate. Similarly, various morphological and physiological constraints may limit evolution, such as the evolution of faster escape speed, as this is limited by physiological, energetic and biomechanical factors. Thus, the evolution of behaviors is constrained by correlations with other traits and by various genotypic and phenotypic limitations.

Interaction between plasticity and evolution

Phenotypic plasticity – the ability of an individual to alter its characteristics in response to changes in the environment - can influence the evolution of behaviors, by either facilitating or constraining evolutionary changes. Plasticity in behavior can facilitate evolution by promoting the persistence of a population in a changing environment, as this allows more time for selection to act on heritable variation. Plasticity can also reveal hidden genetic variation that selection can act on and thereby also facilitate evolution. Alternatively, plasticity can constrain evolution by hiding genetic variation.

Whether plasticity reveals or hides genetic variation depends on how it influences the distribution of phenotypes in relation to genotypes in the population. If plasticity results in different genotypes producing the same phenotype, this hides genetic variation, which constrains evolution. On the other hand, if plasticity increases phenotypic differences among genotypes (while maintaining the correlation between phenotype and genotype), this improves the detectability of genetic variation, which can facilitate evolution. An example of behavioral plasticity constraining evolution by hiding genetic variation is the response of the reef fish *Acanthochromis polycanthus* to elevated CO₂ levels. Chronic exposure of juveniles to high CO₂ reduces their variation in behavioral response to chemical alarm cues of predators (Welch and Munday 2017). This masks genetic variation in anti-predator behavior, which reduces its heritability. Reduced heritability decreases in turn the potential of the species to genetically adapt to elevated CO₂ levels. Because the plastic responses are maladaptive - the fish become less responsive to chemical alarm cues – the species may not be able to adaptively adjust to rising CO₂ levels in the ocean, neither through plasticity, nor through evolutionary changes.

Behavioral plasticity can influence evolution also by moving the phenotypes in the same or opposite direction to selection, depending on whether plasticity is adaptive or maladaptive. If the phenotypes are moved in the same direction as selection (adaptive plasticity), so that the phenotypes come closer to the optimum phenotype, selection will relax, which constrains evolution. If plasticity is maladaptive and moves the phenotypes further from the optimum, in the opposite direction to selection, selection will strengthen, which can promote evolution. However, whether maladaptive plasticity promotes evolution depends also on its effects on genetic variation. In the above example with reef fishes responding to elevated CO₂ levels, the maladaptive plastic responses hide genetic variation, which constrains evolution.

Phenotypic plasticity can be lost over evolutionary time through genetic accommodation, or assimilation. The phenotype originally produced through plasticity then becomes genetically encoded via natural selection. It is then fixed and can no longer change with environmental conditions. For instance, the production of alternative, diet-induced, larval ecomorphs of spadefoot toads is replaced by the production of only one ecomorph when several species compete for food. When the species occur separately, in allopatry, they produce two ecomorphs; omnivores that eat detritus, and carnivores that specialize on

shrimp and other tadpoles. When two species are brought together and occur in sympatry and, hence, have to compete for detritus, one of the species loses the plasticity and becomes nearly fixed for producing carnivores only. The loss of plasticity occurs through genetic accommodations, whereby the ecomorph becomes genetically canalized. The loss of plasticity is caused by changes in the regulation of gene expression (Levis et al. 2017).

Variation among individuals

Within a population, there is often large variation among individuals in their behavior. This within-species variation can be adaptive and improve individual fitness, or, alternatively, be maladaptive if some individuals are not able to behave adaptively because of various constraints or past experiences or evolutionary processes (the ghost of selection past). The variation in behavior can be genetically determined or the results of phenotypic plasticity, or a combination. Most often the variation is a combination of the two, with environmental conditions and intrinsic properties of individuals modifying genetically determined behavioral reaction norms. For instance, during invasions into new areas, individuals at expanding range edges often differ in their behavior from individuals in the range core: they are often bolder and more exploratory and aggressive. These differences in behavior can have a genetic basis but also be modified by experience. For example, cane toads (*Rhinella marina*) at invasion fronts are bolder and take more risks than toads in range cores. These individual differences have a genetic basis but can be modified by individual experiences of environmental and demographic conditions (Gruber et al. 2017).

Within-population variation in social and reproductive behaviors is often adaptive and promoted by selection. For instance, individual great tits (*Parus major*) follow alternative social strategies depending on their behavioral characteristics. Proactive great tits - which are fast-exploring individuals - form weak associations with a great number of conspecifics and move between foraging flocks, while reactive tits - which are slow-exploring birds - form stronger and more stable relationships with a few conspecifics (Aplin et al. 2013). These social strategies are adaptive and maximize individual fitness as well as the social organization of the population.

Adaptive, alternative reproductive behaviors are common in species where individuals attempt to monopolize mates. Individuals in poor condition, who are not able to acquire mates through the dominant tactic, such as by establishing a territory and courting females, may adopt an alternative mating tactic, such as sneaking. The alternative behavior is then a conditional strategy that improves the fitness of the individual compared to attempting to reproduce through the dominant strategy. Alternative reproductive behaviors can be also genetically determined and have equal fitness that is maintained through frequency-dependent selection. In the lek-breeding ruff (*Philomachus pugnax*), three genetically determined reproductive tactics occur; territorial 'independent' males with dark plumage that defend courts on leks, white satellite males that join the territorial males on courts and compete for matings by co-displaying to attract females, and small, female-mimicking faeders that visit the courts of territorial males and attempt rapid copulations when females solicit matings from displaying males (Jukema and Piersma 2006).

Maladaptive behaviors are especially common when individuals are not adapted to prevailing environmental conditions. In particular, when conditions are changing rapidly because of human activities, some individuals may behave maladaptively because their reaction norms are not suited to the novel conditions. Such individuals will eventually be wiped out from the population. However, if the environment continues to change, the population may never be composed of mostly well adapted individuals and, hence, become well adapted to local conditions.

Conclusion

The behavior that an animal expresses in different situations is a major determinant of its fitness. It influences foraging success, predator avoidance, social interactions, dispersal, and reproductive success. Behaviors are determined by genetically determined reaction norms, which can be influenced by environmental factors, early life experiences, and learning. Behaviors are usually more or less adaptive in the natural environment. However, sudden environmental changes, particularly those induced by human activities, can seriously disrupt their adaptive value. Because behavioral responses are usually the first response to altered environmental conditions, they can have a decisive impact on the success of populations in disturbed environments.

The influence that behavioral responses have on populations in changing environments is an emerging research field. In particular, considering the rate at which humans are altering environments, and the fact that biodiversity is seriously declining in many areas of the world, more information is needed on the factors that influence the fate of populations in disturbed environment. Important topics in need of more attention are the degree to which behaviors contribute to the decline or growth of populations, and how behaviors can be considered in conservation and management practices to improve population viability.

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