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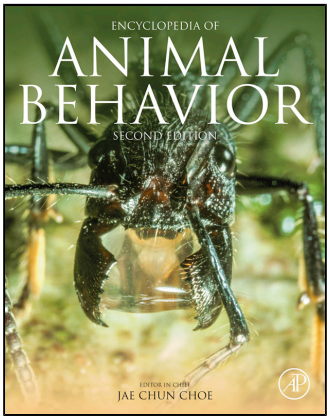

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Evolutionary Behavioral Genetics

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Glossary

Allele One of two or more alternative forms of a gene that arise by mutation and are found at the same place on a chromosome.
CRISPR/Cas9 Is a unique technology that enables geneticists and medical researchers to edit parts of the genome by removing, adding or altering sections of the DNA sequence.
DNA methylation A form of epigenetic modification by which methyl groups are bound to DNA, with effects on chromatin structure and gene expression.
Epigenetics The study of changes in organisms caused by modification of gene expression rather than alteration of the genetic code itself.
Evolutionary developmental biology A comparative approach in biology examining developmental processes across different organisms to determine how they evolved.
Frequency-dependent Selection for the rare form in a mixed population such that two morphs of a species can be maintained in the same populations.
Genetic assimilation The process by which an environmentally induced phenotypic response becomes genetically fixed through a persistent selective environment. After fixation, the originally environmentally induced phenotype persists in the absence of the initial inducing environmental stimulus.
Isoform Any of two or more functionally similar proteins that have a similar but not identical amino acid sequence and are either encoded by different genes or by RNA transcripts from the same gene which have had different exons removed.
Microsatellite A tract of repetitive DNA in which certain DNA motifs are repeated, typically 5–50 times. Microsatellites occur at thousands of locations within an organism's genome.
Phenotype The composite of an organism's observable characteristics or traits, such as its morphology, development, biochemical or physiological properties, behavior, and products of behavior.
Polyphenism Is the phenomenon where two or more distinct phenotypes are produced by the same genotype. Examples of polyphenism provide some of the most compelling systems for the study of epigenetics.
QTL A quantitative trait locus is a section of DNA which correlates with variation in a phenotype. Usually the QTL is linked to, or contains, the genes which control that phenotype.
RNA-interference A biological process in which RNA molecules inhibit gene expression or translation, by neutralizing targeted mRNA molecules. Since the discovery of RNAi, it has become used in the experimental suppression of desired genes.

Abstract

Evolutionary biologists are now able to examine the genetic underpinnings of animal behavior, and how behavior evolves on a genetic level. Genes that underlie behavior can be deeply conserved across animals, but still evolve and contribute to the evolution of new forms of behavior. Behavioral genetics includes the study of behavior at multiple levels, including genomics, epigenetics, endocrinology, neurobiology, and the importance of both genes and environment, and their interaction, in affecting behavior. With the advent of next generation sequencing researchers are extending classical studies using laboratory model organisms to animals in their natural habitats and a diversity of non-model species.

Keywords

DNA methylation; Environmental variation; Epigenetics; Evolutionary developmental biology; Gene expression; Genetic assimilation; Phenotypic plasticity; Social interaction

Introduction

The evolution of animal behavior, like any trait, requires a selective environment in which individuals with different **phenotypes** experience differential fitness, and heritable variation in phenotype. Behavior shows high levels of variation within and between individuals, and this variation has been shown to be moderately heritable (in line with morphological phenotypes). Although it was once assumed that behavioral traits, due to their innately flexible and environmentally responsive nature, are less genetically

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"hard-wired" than other traits, it has now become clear that behavioral traits and their evolution can be studied on a genetic level, just like a physical trait.

Partly due to these perceptions of behavior as refractory to genetic analysis, the study of the evolution of behavior on a genetic level has lagged behind other fields, such as development and morphology. However, researchers have made substantial progress in this area in recent years. Below, we provide an overview of this field, beginning with examples of how genetic variants (of several different types) influence behavior, insights from the application of genetics to the study of behavioral evolution, and future directions in this field, especially as related to the application of new genetic and genomic technologies to the study of behavioral ecology and behavioral model organisms.

Genetic Variation in Behavior

The evolution of behavior has been tied to various types of genetic variation, including allelic variation in protein coding genes, variation in gene regulation, **epigenetic** variation, as well as variation in genome structure (Fig. 1). Below, we review examples from a wide variety of animals and behaviors illustrating that behavioral variation and its evolution can stem from a variety of genetic sources.

There are some well-documented cases of protein coding sequences variants within species and populations that are associated with behavioral variation. One famous example relates to foraging behavior in the fruit fly *Drosophila melanogaster* (Sokolowski *et al.*, 1997). There is stable, natural variation within populations of *D. melanogaster* in the extent that larvae move while feeding—some larvae move extensively and are called "rovers", whereas others are relatively stationary and are called "sitters". This variation was found to be closely associated with variants of a cGMP-dependent protein kinase gene, called *foraging*. Individuals with the for^S **allele** have a less active version of the gene and move less on their food, whereas for^R individuals have a more active version of the gene and move more. These versions of the allele appear to be at a stable equilibrium within fly populations in the wild, with both alleles maintained in a **frequency-dependent** manner in the species. The different behavioral types are thought to be

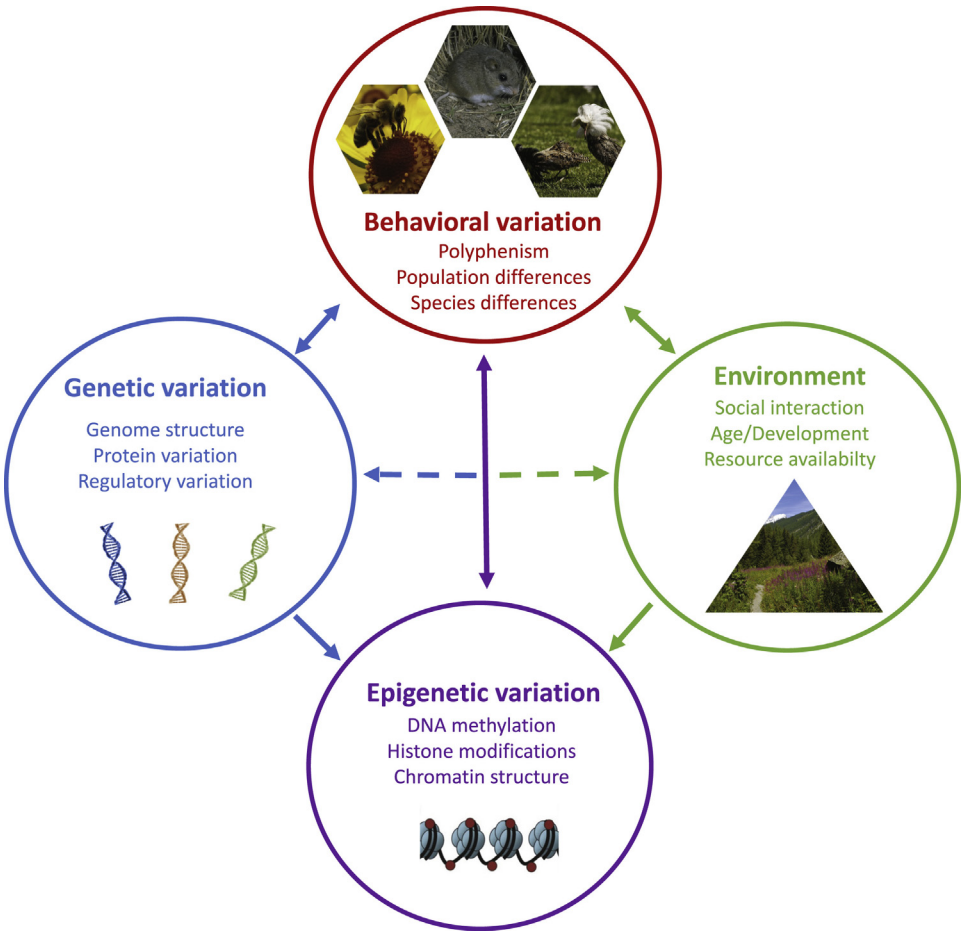

Fig. 1 Conceptual figure showing different forms of genetic, epigenetic and environmental variation and their potential roles in generating behavioral variation.

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maintained within a population and represent different survival strategies, with rovers being more successful under high density conditions.

Another example of allelic variation underlying natural behavioral variation is found in the burrowing patterns between species of *Peromyscus* mice (Weber *et al.*, 2013). Deer mice (*Peromyscus maniculatus*) dig short, simple burrows, while old-field mice (*Peromyscus polionatus*) dig deeper, more elaborate burrows with escape tunnels. Based on breeding studies and quantitative trait locus (**QTL**) mapping, differences in burrow structure (and the behavioral programs that produce them) have been linked strongly to heritable genetic variation. These studies indicated that derived more elaborate burrows are the result of dominant genetic loci acting on different modules of burrow formation (e.g., length and presence of an escape tunnel), and appear to have evolved through sequential changes in multiple genomic regions. In particular, they uncovered three genetic loci associated with tunnel length, and only a single locus associated with the presence of an escape tunnel. Although the exact nature of this genetic variation (e.g., whether protein coding or regulatory) remains to be discovered, the results "suggest that complex behaviors — this case, a classic 'extended phenotype'—can evolve through multiple genetic changes each affecting distinct behavior modules" (Weber *et al.*, 2013).

Variation in gene expression, in the absence of any protein sequence variation can produce profound phenotypic differences. Differences in the level, timing, localization, and **isoform** expression of individual genes can have important functional consequences for organismal traits. Within species, there are some striking examples of gene expression mediated changes in behavioral traits associated with polyphenisms. One dramatic example is in the migratory locust, *Locusta migratoria*, which shows distinct phases depending on the level of crowding in the environment. Under low density conditions, these locusts develop into cryptically colored, solitary individuals that do not tolerate others. Under high density conditions, these locusts develop into brightly colored, gregarious individuals that are attracted to others and form massive migratory swarms. The genetic basis of this trait is complex, with hundreds of genes differentially expressed in association with the transition from solitary to gregarious, and vice versa. Overexpression of two classes of genes in the head and antennae, chemosensory proteins (*CSP* family) and the odorant binding protein *Takeout 1*, are highly predictive of the gregarious and solitary states, respectively (Guo *et al.*, 2011). These genes also appear to be causally related to the phase switch, as gene knockdown experiments demonstrate *CSP*3 knockdown leads locusts to become more solitary and repulsed by the odors of others, whereas *TO1* knockdown results in the opposite phenotype. The locust phase shift represents a prime example in which a strong selection pressure in the environment (crowding and food resource availability) drive the evolution of a developmental switch in the genome regulating distinct behavioral states.

Variation in gene expression can also result in behavioral differences between species. One classic case is the occurrence of monogamy in prairie voles *Microtus ochrogaster*, in which males pair bond with females and assist in the care of young. Most vole species, including another North American species the meadow vole *Microtus pennsylvanicus*, have a promiscuous mating system. There is variation in the length of a **microsatellite** in the promoter region of the vasopressin receptor gene *V1aR* between the species, with long allele prairie voles showing enhanced *V1aR* expression in the ventral pallidum of the forebrain (Donaldson and Young, 2008). This enhanced expression may be the cause of increased partner preference and pair bonding behavior, as injections of *V1aR* into the ventral pallidum of montane voles shifted their behavior towards enhanced partner preference (Lim *et al.*, 2004). It has thus been suggested that variation in the length of this microsatellite in a regulatory region allowed for the evolution of monogamy in prairie voles.

Another source of heritable variation in behavior can stem, not from changes to the genome sequence itself, but from epigenetic variation that can affect chromatin structure and gene expression. Epigenetic variation can result from environmental influences, especially during early development, that result in long-lasting changes in gene expression as a due to various forms of chemical modification of DNA. Commonly studied epigenetic marks include methylation of DNA nucleotides (usually cytosines), and acetylation and methylation of histone structural proteins that hold DNA together into chromatin. A classic example of epigenetic influence on behavior relates to maternal care behavior in rats (Champagne *et al.*, 2006). Rat pups receiving high levels of maternal care (licking, grooming, and arch-backed nursing) show higher levels of maternal care themselves upon reaching adulthood. This is associated with decreases in methylation in promoter regions of the glucocorticoid and estrogen receptors in specific regions of the rat brain, associated with higher levels of receptor expression. Because **DNA methylation** patterns can be inherited across generations, this sets up the potential for social environmentally determined changes in gene expression and behavior to be inherited epigenetically. Thus, experiences in one generation have the potential to have multigenerational effects on the behavior of descendants. In an evolutionary context, stable, epigenetic variants could be targets for evolutionary change in behavior (Dias *et al.*, 2015).

Changes in genome structure and composition may also have consequences for behavioral variation and evolution. These include gene and genome duplication, gene family expansion and contraction, as well as major genome rearrangements such as chromosomal inversions. There has been increasing interest in the potential for genome rearrangements to mediate complex suites of traits, including behavioral traits, in species showing distinct behavioral types or morphs. "Supergenes" are stretches of chromosomes containing multiple, linked genes held together by a lack of recombination, which may be the result of large chromosome level mutations such as chromosomal inversions. Such "supergenes" may serve to cluster alleles that regulate coadapted suites of traits, e.g., coloration, physiology, and behavioral variants. One prominent example of a supergene in behavioral variation has been identified in *Philmachus pugnax* ruffs (Küpper *et al.*, 2016), in which populations consist of three different male morphs, differing in plumage, coloration, and behavior—these are aggressive "independents", satellite males, and female mimicking "faeders". Morph type was recently found to be linked to a supergenic region, resulting from an inversion on chromosome 11 containing 125 genes, associated with autosomal inheritance of suites of traits related to coloration, behavior, and reproductive physiology. Another example relates to the occurrence of single queen vs multi queen colony structure in fire ants *Solenopsis*

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invicta (Wang *et al.*, 2013). Colony type is associated with the presence of a Y-chromosome like "supergene" containing multiple genes with potential roles in regulating various aspects of queen and worker behavior, physiology, and chemosensation. Supergenic control of suites of correlated, complex traits including behavior, may be more common than previously assumed.

Given the great diversity of genetic variants and their potential for influencing behavior and its evolution, both within and between populations and species, which type of genetic variation is most important in behavioral evolution? Some have proposed gene regulatory evolution to be a prime mover in behavioral evolution, while others suggest a combination of protein coding change and regulatory change (Robinson and Ben-Shahar, 2002). And how common are supergenes and other major genomic changes in the regulation of behavior? The relative importance of different forms of genetic variation in behavioral evolution remains to be seen, our understanding will undoubtedly improve in the near future, with the increasing development of genomic resources for a wider variety of species with striking behavioral variation and traits. It is likely that the type of genetic variation underlying a behavior and its evolution will depend on the type of trait (simple, complex, modular, or part of a correlated suite), evolutionary distance (recent vs. ancient origins), etc.

Evolutionary Conservation of Genes and Behavior

The field of *evolutionary developmental biology*, or "evo-devo" has demonstrated deep conservation of genes involved in organismal development, morphology, and body form (Carroll, 2005). Changes in the regulation of deeply conserved genes, such as the *Hox* (homeobox domain transcription factor) genes have been demonstrated, time and time again, to be involved in the evolution of novel developmental and morphological traits. This has led to the designation of a "genetic toolkit" for development, consisting of deeply conserved genes regulating organismal development across a wide variety of animal taxa. Is the same true for behavior?

Although behavior is more environmentally responsive than morphology, and appears to be more evolutionarily labile as well as more variable between individuals, it is now becoming clear that genes for behavior can be deeply conserved, like those for physical traits. For example, the serotonin system is known to have an influence on aggressive behavior in both vertebrate and invertebrate animals. However, the exact serotonin system genes (i.e. receptors, transporters, etc.) involved and the direction of regulation can vary widely (e.g., lower serotonin is associated with aggression in mammals, whereas higher serotonin is associated with aggression in crustaceans, Edwards and Kravitz, 1997). A recent study comparing brain gene expression patterns across honey bees, stickleback fish, and mice found significant similarities in the brain gene expression patterns associated with territorial aggression, implicating some of the same deeply conserved brain transcription factors in all three, highly evolutionarily distinct lineages (Rittschof *et al.*, 2014). Another study used comparative neuroanatomy and measurements of brain gene expression to study the evolution of the social decision making network in vertebrate brains, surveying numerous species, from fish to reptiles, to mammals (O'Connell and Hofmann, 2012). This study revealed deep conservation in the expression of neuroendocrine ligands and receptors across hundreds of millions of years of vertebrate evolution. These findings of deep evolutionary conservation of the genetic underpinnings of behavior lends validity to the use of "model organisms" to study the genetic basis of human behavior.

Unlike behaviors such as aggression and mating, which are found in most animals, other specialized behavioral traits, such as specific forms of anti-predator behavior and extreme forms of cooperation like eusociality, are highly derived and have evolved independently multiple times. These "natural experiments" allow researchers to ask the question: how repeatable is the evolution of behavior on a molecular level? The idea of genetic toolkits for behavior, summarized above, suggests that some deeply conserved genes could be utilized repeatedly during evolution to generate behavioral novelty. Some recent studies indeed suggest there is some repeatability to behavioral evolution on a genetic level. A comparative transcriptomic study across lineages of eusocial insects (bees, ants, and wasps) suggested some of the same molecular pathways and functions, such as genes related to mitochondrial energy metabolism, though not exactly the same genes, underlie the evolution of queen and worker caste differences (Berens *et al.*, 2014). In rodents, the vasopressin system was demonstrated to have a role in aspects of parental behavior in species of both *Peromyscus* field mice as well as in *Microtus* voles (Bendesky *et al.*, 2017). Although the vasopressin system is implicated in both, the exact mechanisms differ; the vasopressin receptor *V1aR* was found to be related to pup licking and grooming in male voles, whereas in mice the ligand vasopressin was related to nest building aspects of parental care. Within stickleback fish populations, there has been repeated evolution of suites of physical and behavioral traits associated with freshwater adaptations to either benthic or limnetic forms (e.g., pelvic spine reduction, schooling behavior, and feeding strategy). Quantitative trait locus (QTL) studies revealed some of the same genomic regions in independent populations are associated with morphological changes during the repeated evolution of convergent traits. QTL for behavioral traits such as schooling have also been identified (Greenwood *et al.*, 2015), but comparisons across multiple independently evolved populations have not yet been conducted. Although QTL studies do not permit pinpointing the exact genes or sequence variants associated with the traits, the data suggest similar genes or suites of genes may be targets for selection during the repeated evolution of these traits. The mostly likely explanation for this repeatability is that the trait evolved from standing genetic variation present in the ancestral marine population, with previously rare allelic variants being selected and eventually fixed, multiple independent times, in benthic and limnetic forms in lake populations, likely due to similar selection pressures such as reduced predation (Peichel and Marques, 2017).

Together, these studies suggest there is some repeatability to behavioral evolution on a genetic level. However, it is important to note that all of the aforementioned studies involve comparisons within a fairly limited taxonomic range (within stickleback fish, rodents, or hymenopteran insects). Thus, while the aforementioned studies have uncovered some similarities in the molecular basis of these convergent behaviors, it is important to consider the possibility that such similarities may be absent at greater evolutionary

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distances. In addition, while there were some similarities in the molecular basis of these traits, i.e., genes possessing similar functions or involved in related molecular pathways, all of the studies pinpointed different specific genes within these pathways. Therefore, although certain genes and pathways appear to be more likely targets for the evolution of particular types of behavioral traits, there is likely to be multiple specific genetic routes to evolving a particular behavior or set of behaviors.

Evolutionary Perspectives on Genes and Behavior

The role of a gene or gene network in behavior can be considered on multiple timescales (Robinson *et al.*, 2008). On a physiological timescale, a gene can have rapid effects on a behavior, e.g., an immediate early gene expressed in neurons that peaks in expression just a few minutes after a stimulus. On a developmental timescale, the expression of a gene can show gradual changes over the lifetime of an individual, e.g., expression of a hormone and/or its receptor associated with sexual maturation and associated reproductive behaviors. Finally, a gene can have an impact at an evolutionary time scale, with genetic variants being selected over many generations and contributing to behavioral diversity within a species or between species. Some compelling examples suggest genes can maintain related functions across multiple time scales. For example, the *period* gene in *Drosophila* fruit flies was one of the first genes to be studied for effects on behavior, and was shown to not only regulate circadian rhythms across the course of a day, but also regulate the rhythm of male courtship songs on a second to second basis. Even more intriguingly, evolutionary differences in the sequence of the *period* gene are associated with species differences in the courtship song rhythm, showing this gene has impacts on behavioral differences across evolutionary and physiological time scales (Greenspan and Ferveur, 2000). Another example is the *foraging* gene, discussed above in *Drosophila* fruit flies. In addition to its role in regulating behavioral differences between individuals within flies (evolutionary time scale), the gene also regulates behavioral differences on a developmental time scale within the lifetime of individual honey bee workers, increasing in expression as bees age and transition from hive work to foraging behavior (Ben-Shahar *et al.*, 2002). These observations suggest that because gene function related to behavior can be conserved across deep evolutionary time, natural selection can act on variation in a gene to generate behavioral diversity within the lifetime of a single individual, between individuals, and even between species.

Evolutionary biology is moving towards a more integrative, "eco-evo-devo approach", which extends the modern synthesis of Mendelian and population genetics to include recent insights from developmental biology and ecology. The main tenets of this approach include: 1) a deeper understanding of developmental plasticity and its role in phenotypic variation, and 2) the role of environmentally induced changes in gene expression and epigenetic variation as fuel for evolutionary change (Abouheif *et al.*, 2014). This approach may be especially important in considerations of behavioral evolution, because behavior is highly environmentally responsive by nature. Related to this, an evolutionary process that is receiving attention in the field of evolutionary behavioral genomics is genetic assimilation (Bell and Robinson, 2011). This refers to a process by which an environmentally-induced change in behavior that begins as phenotypic plasticity (with associated patterns of brain gene expression, e.g., as in locust phase change discussed above) becomes genetically hard-wired over evolutionary time.

As an example, consider the case of highly defensive behavior in some subspecies of honey bees, for example the east African subspecies *Apis mellifera scutellata*. Most honey bee subspecies show extensive plasticity in their aggressive, antipredator defense of stinging behavior, i.e. the behavior is rarely exhibited, but can be induced and increasingly sensitized to sting in the face of a strong and constant predation threat. It has been suggested that highly aggressive behavior in *A. m. scutellata* evolved through genetic assimilation, spurred by environmental change. The hypothetical scenario is as follows (**Fig. 2**). First, the environment changed to a high predation state, leading bees to show a heightened aggressive response (accompanied by induction of aggression related gene expression). Second, over generations, accommodating mutations arose, e.g., in regulatory regions of genes related to aggressive behavior, that led this aggressive response to be constantly induced. Third, if the environment remained in the new, high predation state, these accommodating mutations would be selected for and spread throughout the population. Finally, this led to a change in the genetic background of the bees so that they now all constantly showed heightened aggression (and associated patterns of aggression-related gene expression). Therefore, even in the absence of the inducing high predation environment, these bees would remain in a constant state of high aggression. Through this process of **genetic assimilation**, phenotypic plasticity has been lost, but its initial existence served as a first step to fuel the evolutionary change observed. Although the scenario above is hypothetical, a recent study on gene brain gene expression patterns in honey bees descended provides some empirical support. This study examined bees from the genetic background of *Apis mellifera scutellata* (the so-called "killer" bees invading the Americas). This study found that brain gene expression patterns in these aggressive genotypes overlaps with the environmentally-induced changes in gene expression in a docile European subspecies of honey bees in response to an environmental disturbance (Alaux *et al.*, 2009). These data provide indirect evidence in support of the idea that processes such as genetic assimilation could play role in behavioral evolution. However, there are no direct studies demonstrating this process, and thus its importance in behavioral evolution remains unresolved, and deserving of further study.

Future Directions

The number of studies of the genetic basis of behavior and its evolution have exploded in recent years, fueled by advances in DNA sequencing technology and functional genomics. With many initiatives for sequencing dozens, hundreds, or thousands of genomes

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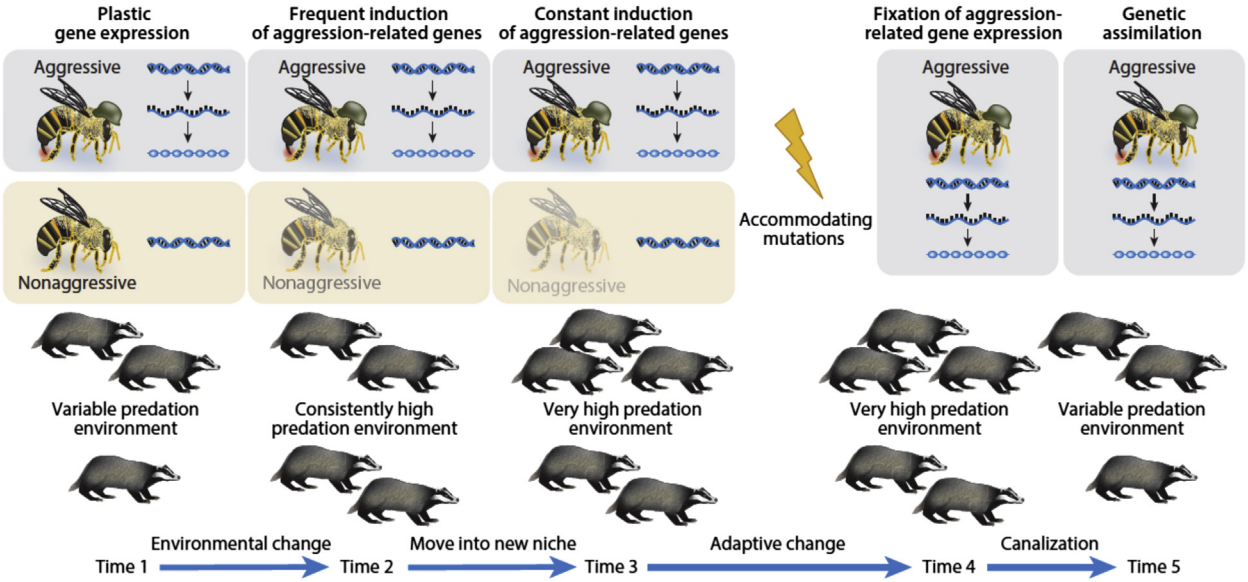

Fig. 2 Scenario of genetic assimilation, as applied to the evolution of aggression in honey bees. Initially individual phenotypic plasticity provides an adaptive response to variable environmental stimuli, e.g., aggressive response to predation pressure (time 1). Subsequently, with an environmental change (time 2) such as increased predation pressure, the gene expression pattern inducing the aggressive response is more often exhibited compared to the non-aggressive response. This *may* allow aggressive colonies to move into previously unoccupied niches in the environment (time 3), such as very high predation environments. Over time, environmentally-induced responses in gene expression and aggressive phenotype can become fixed differences due to the accumulation of accommodating mutations (time 4). The response then becomes canalized, resulting in a loss of plasticity, and individuals are fixed for the aggressive phenotype, and associated gene expression, even in the absence of the high predation environmental stimulus (time 5). Figure from Toth, A.L., Rehan, S.A., 2017. Molecular evolution of insect sociality: An Eco-Evo-Devo perspective. Annual Review of Entomology 62, 419–442.

on the horizon, behavioral geneticists will have expanded opportunities to work in a wider variety of species, exhibiting many diverse and varied forms of behavior. Such advances have already spawned studies of the comparative genomics of behavior, in which large genomic datasets from a range of species varying in behavior can be compared to understand the genomic changes associated with behavioral evolution. With multiple genomes, researchers can examine which types of genetic changes occur across species comparisons during evolutionary transitions in behavior.

One deficit of most studies to date on the genomic basis of behavior and its evolution is that most studies have been correlative. The use of functional genomics for validation of candidate genes and their roles in behavior has not yet widely extended from laboratory, model organisms (such as mice, rats, flies, and worms) to ecologically relevant systems. Functional validation is extremely important, as many uncovered gene-behavior associations may only be correlational. Also, behavior is highly context-dependent, so functional validation in a realistic, field-relevant setting is critical. New methods of functional validation are now being increasingly employed in behavioral model organisms, including the use of **RNA-interference** to knock down expression of target genes, as well as gene editing technologies such as **CRISPR/Cas9**, which is being applied increasingly more to non-model organisms and to the assessment of behavioral phenotypes (Trible *et al.*, 2017). Functional genomics remains an important frontier area in behavioral genetics, and expansion of this work to numerous species will be critical for furthering our understanding of the processes that govern behavioral evolution.

See also: **Genes and Behavior:** Behavioral genetics of dog breeds; The Oxytocin System: Single Gene Effects on Social Behavior Across Species.

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