ANNUAL REVIEWS

Annual Review of Ecology, Evolution, and Systematics

A Dual Role for Behavior in Evolution and Shaping Organismal Selective Environments

William T. Wcislo

Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Republic of Panama; email: wcislow@si.edu

Annu. Rev. Ecol. Evol. Syst. 2021. 52:343–62

The *Annual Review of Ecology, Evolution, and Systematics* is online at ecolsys.annualreviews.org

https://doi.org/10.1146/annurev-ecolsys-012921-052523

This is a work of the US Government and is not subject to copyright protection in the United States

ANNUAL REVIEWS CONNECT

www.annualreviews.org

- Download figures
- Navigate cited references
- Keyword search
- Explore related articles
- Share via email or social media

Keywords

behavioral evolution, behavioral drive, behavioral inhibition, phenotypic accommodation, genetic accommodation, sensory drive, plasticity, Baldwin effect

Abstract

The hypothesis that evolved behaviors play a determining role in facilitating and impeding the evolution of other traits has been discussed for more than 100 years with little consensus beyond an agreement that the ideas are theoretically plausible in accord with the Modern Synthesis. Many recent reviews of the genomic, epigenetic, and developmental mechanisms underpinning major behavioral transitions show how facultative expression of novel behaviors can lead to the evolution of obligate behaviors and structures that enhance behavioral function. Phylogenetic and genomic studies indicate that behavioral traits are generally evolutionarily more labile than other traits and that they help shape selective environments on the latter traits. Adaptive decision-making to encounter resources and avoid stress sources requires specific sensory inputs, which behaviorally shape selective environments by determining those features of the external world that are biologically relevant. These recent findings support the hypothesis of a dual role for behavior in evolution and are consistent with current evolutionary theory.

1. INTRODUCTION

Two long-standing, interrelated hypotheses in biology are that (*a*) behavior evolves by descent with modification and (*b*) some behaviors play a role in determining the tempo and mode of evolutionary (and cultural) change by partially shaping selective and developmental environments. The former is noncontroversial and has been extensively documented since Darwin (1871). The latter hypothesis was largely sidelined for over a century since being proposed by Baldwin, Lloyd Morgan, and Osborn, among others; it was well recognized as theoretically important by many architects of the Modern Synthesis (e.g., Schmalhausen 1949; Simpson 1953; Mayr 1963), but data then were scarce on proximate questions relating to behavioral evolution (e.g., references in Wcislo 1989) (Section 2.1). Recent case studies demonstrating the role of behavior in driving evolutionary change come from reviews of genomic, epigenetic, and developmental studies of well-known major behavioral transitions in evolution (e.g., sociality) (Section 3). Comparative studies of species with facultatively and obligately expressed behaviors demonstrate how behavioral novelties can be generated in new physical, biotic, social, and sensory environments, which may change the bases for selection. Other studies, including fossil evidence, show when behavioral novelties originated and how they are evolutionarily elaborated by shaping the evolution of associated traits. Genomic and epigenetic studies document the degree of plasticity, how these reaction norms can evolve, and how novel behaviors evolve by genetic accommodation. Together, these data provide answers to the four complementary proximate and ultimate questions posed by Tinbergen to understand the evolution of behavior (references in Kapheim 2019, Konner 2010); the data also address criteria to demonstrate the relative importance of phenotypic modifications in shaping subsequent evolutionary change (plasticity-first evolution) (reviewed in Levis & Pfennig 2016, 2019).

Revisiting this hypothesis is timely for additional reasons that are further elaborated below. First, recent theoretical models and conceptual syntheses have clarified the conditions under which behavioral and developmental flexibility are expected either to result in stasis at population levels due to stabilizing selection or to facilitate directional evolutionary change. Phylogenetic studies demonstrate the evolutionary lability of many behavioral traits relative to structural ones and document the polarity of change for important behavioral transitions. Behavioral and molecular studies provide abundant evidence that the degree of expression of plastic traits can be modified in response to changes in both internal (genomic and developmental) environmental conditions and external environments—including effects from a social environment (and their interactions)—which may generate novel behavioral variants that influence fitness. Likewise, behavior-induced environmental novelties and external environmental changes are interchangeable in generating new bases for sorting by selection or maintaining the status quo by stabilizing selection. The highly responsive nature of many behavioral traits to changing conditions, and the effects of behavior on external environments, underlie the notion that behavior acts like a "pacemaker of evolution" (Mayr 1988, p. 408). Pacemakers have sensors for rate, not direction, so the simile is incomplete. Adaptive behavioral decisions require tuned sensory inputs and associated neural processing, which partly determine the direction of behavioral change in accord with natural history and preexisting tuned sensory systems.

In this review, I emphasize examples from bees and other invertebrates in which the ancestral and novel behavioral environments can be readily characterized, derived behaviors are facultatively expressed in some taxa and obligately expressed in others with known evolutionary polarity, and behaviors have associated structural traits that are modified to enhance or support the behavior. Comparable roles for behavior and plasticity in shaping many aspects of vertebrate evolution have been reviewed elsewhere (e.g., Levis & Pfennig 2016, 2019), and select comparative examples

are given here when appropriate. A better understanding of the population-level and higher-order consequences of the individual behavior of people has immediate practical consequences for conservation biology and mediating anthropogenic environmental changes, including those involving disease and public health (see Section 5).

2. A DUAL ROLE FOR BEHAVIOR IN EVOLUTION

2.1. History and Status Quo

A hypothesized dual role for behavior in evolution has been reviewed repeatedly (e.g., Crispo 2007, Duckworth 2009, Godfray-Smith 2017, Wcislo 1989, West-Eberhard 2003, Zuk et al. 2014) and primarily dates to work by Baldwin, Lloyd Morgan, and Osborn, which they envisioned as involving the genetic assimilation of initially nonheritable behavioral variation. Huxley, who studied bird behavior and named the Modern Synthesis, was a proponent for behavior as cause and consequence of evolution (sensu Godfray-Smith 2017) (Huxley 1942). Schmalhausen (1949) and Gause (1942) emphasized that natural selection changes the sensitivities of phenotypes to environmental perturbation (reaction norms), with organismal activity generating stabilizing or directional selection. Rensch (1959) expressed astonishment at the similarity of environmental modification and mutation in producing phenocopies and acknowledged his insufficient attention to hypotheses by Lloyd Morgan and Baldwin. Wright (1931) thought that individual adaptability was perhaps the key trait shaped by selection. Roe & Simpson (1958) organized major conferences on behavior and evolution—attended by many architects of the Modern Synthesis—where Simpson argued that behavior was a critical determinant of evolution, despite his earlier skepticism about the importance of the Baldwin effect in evolution, which was partly due to the scarcity of supporting evidence available at the time.

Questions regarding the causal roles for behavior and plasticity in evolution address two related phenomena. Do behavioral traits play a disproportionate role in plasticity-first evolution? And to what extent do behavioral traits shape selection on other traits? There is consensus that both are theoretically plausible, with open questions concerning the empirical support (e.g., Crispo 2007, Duckworth et al. 2018, Futuyma 2017, Levis & Pfennig 2016, Scott-Phillips et al. 2014). Despite suggestions that new data call for revisions to evolutionary theory (reviewed in Odling-Smee et al. 2003, Scott-Phillips et al. 2014), as seen from the brief historical sketch above, the findings from studies on the evolution of behavior neither require any significant revisions to current evolutionary theory nor point to some new factor in evolution.

Using modern terms to paraphrase the original formulations, gene-based plasticity of individuals in changed environments may enable population persistence (see Section 3.3). Persistence maintains the status quo, as individuals behaviorally compensate for changed environments and alleviate any stressors, with such traits under stabilizing selection. Behavioral variants in new environments expose any previously unexpressed genetic variation to selection (Schlichting & Wund 2014). If recurrent in a given direction, any variants create new demands for associated structural, physiological, and behavioral traits; any chance variants, including those that affect the breadth of reaction norms, that are favorable increase in frequency by directional selection.

2.2. Theoretical Models

Population genetic and neural network models of phenotypic plasticity (including learning) specify conditions under which trait plasticity may enhance rates of evolutionary change, result in stasis, or modify directional selection. Moderate amounts of adaptive phenotypic plasticity are optimal for evolving in novel environments by enhancing population persistence under an additive genetic

variance model and by producing phenotypic responses that translocate populations on an adaptive landscape (Price et al. 2003). As discussed in Section 2.3.3, behavioral traits vary along a broad spectrum from highly plastic, often with strong influences from early experience and learning, to highly consistent and nearly insusceptible to external influences. Depending on the topography of the adaptive surface, this shift may result in faster or slower directional selection to a new peak or result in stasis, assuming there is additive genetic variation for traits aligned with the direction of the peak (Berdal & Dochtermann 2019). An increase in the number of behavioral options also results in a more rugged fitness landscape (Stewart et al. 2016). Increasing the number of needs that organisms must satisfy also increases the roughness of the fitness landscape (Niklas 2004). Rates of environmental change matter as well, with volatility favoring plasticity (Ancel 1999). Interplay between the evolution of behavior and morphology has been modeled for resource specialization (Rueffler et al. 2007) and choice of habitat and mates, showing how it shapes the direction of natural and sexual selection, with potential for adaptive diversification (Uy et al. 2018, West-Eberhard 2003).

2.3. What Is Behavior, and Why Is It Special?

2.3.1. Inside-outside interface. Behavior serves as the interface between what Bates (1960, p. 11) called "skin-in" biology—genomics and epigenetics, development, physiology, and where applicable, neurosensory biology and cognitive psychology—and "skin-out" biology, the outside world of ecology and physical and biotic environments. For motile animals especially (Lotka 1925), behavior is primary in seeking out favorable habitats and other necessary conditions (Porter & Akcali 2020), including choice of food, mates, or hosts, and avoidance of predators, parasites, or competitors (e.g., Streelman & Danley 2003; see Godfray-Smith 2017).

2.3.2. Organisms respond selectively to their external world. In developing his mathematical theory of ecology, Lotka (1925, pp. 338–39) noted that use of an energy source with a heterogeneous distribution requires sensors and behavior in order to respond to the external world to maximize encounters with resources while minimizing encounters with stress sources. He emphasized that the physiological mechanisms by which "*behavior is adapted to circumstances*" (italics in original) are "not an incidental detail . . . but must occupy the very center of attention" to understand how organisms accommodate to their ecological environments. Encountering new resources is contingent on successful exploratory behavior, while avoiding stress sources, favors conservative behaviors that maintain homeostasis (Huey et al. 2003, Waddington 1975). These adaptive behaviors require tuned sensors to specify inputs for processing and preventing information overload (Bernays & Wcislo 1994) while minimizing energetic costs from expensive neural tissue for processing, which vary according to body size and allometric grade, and behavioral needs (Eberhard & Wcislo 2011). Accordingly, excess capacity is screened by selection, constraining behavior to specific sensory modalities, enhancing selection for related traits that rely on information from those sensors (see Section 3.2).

2.3.3. Response thresholds and evolutionary change. The time delay between gene expression and expression of the resulting phenotype during development is important for understanding how behavior shapes evolution (Foster 2013; Ghalambor et al. 2010; Konner 2010; West-Eberhard 2003, 2019; Zuk et al. 2014). Structural traits are often plastic (Whishaw et al. 1998) but tend to respond to environmental cues early in ontogeny and, once determined, are less likely to be transient or reverse later in life (Emlen & Nijhout 2000, West-Eberhard 2003). In contrast, many behavioral and some physiological traits are determined later in ontogeny (i.e., with a shorter time lag between expression and use) and are often readily reversible, and modules can be recombined

to quickly generate novel behaviors (Ghalambor et al. 2010; West-Eberhard 2003, 2019; Zuk et al. 2014).

Responsiveness to changing environments is a universal attribute of phenotypes (West-Eberhard 2019). It underlies the hypothesis that behavior plays a dual role in evolution (e.g., Ghalambor et al. 2010, West-Eberhard 2003, Zuk et al. 2014). Some phenotypes are more responsive than others, which is evolutionarily significant due to a truism and tautology (West-Eberhard 2003): In a population of individuals with modular phenotypic traits that vary in responsiveness, the trait most sensitive to specific environmental influences is first to be changed when circumstances change. Any "fitness-affecting variants thereby produced are subject to selection" (West-Eberhard 2003, p. 180). The key point that variants must be fitness affecting is sometimes overlooked. Some proponents for the evolutionary importance of niche construction construct a large umbrella for their term to cover disparate behaviors and socio-environmental modifications (e.g., Odling-Smee et al. 2003), some of which covary with fitness and some of which do not, confounding evolutionary analyses (Brodie 2005, Futuyma 2017).

2.3.4. Genetic variation and behavioral repeatability. Novel fitness-affecting behavioral variants are generated by genomic and environmental factors that can be interchangeable in shaping phenotypic expression (LaFreniere & MacDonald 2013, West-Eberhard 2003). Individual behavioral performance is repeatable (Bell et al. 2009), and behaviors have heritable additive genetic variation in accord with other traits (Dochtermann 2011, Dochtermann et al. 2019). Behavioral norms of reaction vary in breadth, which can evolve (e.g., Edgell et al. 2009, Foster 2013, Renn & Schumer 2013, Schlichting & Wund 2014, West-Eberhard 2003). Genes do not specify behaviors directly, but genic variation modulates metabolic and developmental networks, receptor cell function, and neuronal circuitry, shaping the expression of behavior (Niepoth & Bendesky 2020). The genomic bases for behavior can be polygenic and epigenetically complex, as in assimilated aggressive behavior in Africanized lines of European honey bees (*Apis*), with individuals showing a stable molecular brain signature associated with aggression, regardless of whether the behavior was induced by genetic, ontogenetic, or social factors (Alaux et al. 2009). Other behavioral innovations involve simple genetic mutations (Niepoth & Bendesky 2020), indirect genetic effects subject to both natural and sexual selection (Bailey et al. 2018), and genetic accommodation [~20% of roughly 150 publications tabulated by Schlichting & Wund (2014) provide evidence for genetic accommodation of behavioral traits] (see Section 3).

2.4. Lability of Behavior in Ontogeny and Phylogeny

2.4.1. Ontogeny. Some behaviors are conditioned on phenotypic traits such as body size that, once determined, do not change much (e.g., Emlen & Nijhout 2000, Whishaw et al. 1998). Others are responsive to changes in both internal and external environments, and expression is transient or reversed as circumstances change (e.g., Duckworth et al. 2018, Konner 2010, Snell-Rood & Steck 2019, West-Eberhard 2019). Individual variation in the development of neural circuitry generates nonheritable variation in behavior (Levis & Pfennig 2019, Linneweber et al. 2020). Early experience often has significant long-lasting effects in organisms ranging from humans and other vertebrates (Konner 2010) to caterpillars (Blackiston et al. 2008). Phenotypic correlations between behaviors reliably estimate the direction of underling genetic relationships but give relatively imprecise information regarding the magnitude of genetic correlations (Dochtermann 2011).

2.4.2. Phylogeny. Comparative analyses of different kinds of traits that test for strength of phylogenetic signal show that behavioral traits generally are more labile than other traits (Blomberg

et al. 2003). Above the species level, however, some behavioral traits are highly conserved and provide a reliable phylogenetic signal (Blomberg et al. 2003), including nocturnality [stable in some vertebrates for ~350 million years (Anderson & Wiens 2017)] or high-level dietary preferences [e.g., carnivory, stable >850 million years (Román-Palacios et al. 2019)]. At the tips of phylogenetic trees, however, traits relating to diet and resource gathering, or temporal patterns of activity, can evolve rapidly (see Section 3).

2.4.3. Molecular bases for evolutionary lability of behavioral traits. A review of the genetic architecture of traits in nine behavioral categories for 30 species from five classes supports Bates' (1960) claim that food and sex make the world go around (York 2018; also Zuk et al. 2014). Indeed, the ionotropic chemoreceptor IR84a links them in *Drosophila melanogaster*, as it is activated by food odorants and also increases levels of male courtship behavior (Grosjean et al. 2011, Joseph & Carlson 2015). The distribution of effect sizes for the behavioral genetic data indicates that courtship and feeding behaviors each explained significantly more phenotypic variance than the other categories of behavior combined, with up to threefold stronger mean effect sizes; most behaviors are determined by many loci of moderate to small effect (York 2018). Genomic analyses for 87 behavioral traits from different *Drosophila* lines also showed that courtship and feeding behaviors explain significantly more genetic variance than other behavioral traits (York 2018).

In fruit flies, the release of behavior by chemoreception is governed by the activities of more than 180 receptors for odorants of food, mates, aversive stimuli, and tastants (Joseph & Carlson 2015). Molecular studies provide evidence for both adaptive evolution in different habitats (e.g., enhanced receptor diversity following colonization of land by animals and secondary reductions with reversions to marine habitats) and transitions to a social system based on complex chemical communication (e.g., Wittwer et al. 2017). The cockroach *Blattella germanica* shows how sensory system plasticity facilitates adaptive responses to rapid environmental changes. Most cockroaches are attracted by sugars and deterred by bitter compounds, which are detected when sugar– or bitter–gustatory receptor neurons (GRNs) are stimulated, respectively (Mullins 2015). An environmental change from widespread use of glucose as a phagostimulant in poisonous baits has led to the evolution of glucose-averse roach populations, due to changes in the peripheral sensory system: Bait-averse roaches have sugar-GRNs with reduced sensitivities to glucose, while glucose also stimulates bitter-GRNs, changing its valence from attractive to aversive (Wada-Katsumata et al. 2013).

3. BEHAVIORAL DRIVERS AND IMPEDIMENTS TO EVOLUTIONARY CHANGE

3.1. Empirical Criteria and Tests

For the purposes of showing that behavior evolves, Darwin (1871) did not need to resolve the question of whether behavior changed first and then structural enhancements evolved, vice versa, or both evolved simultaneously (see Crispo 2007, Wcislo 1989, West-Eberhard 2003). With regard to a dual role for behavior in evolution, however, fossil or phylogenetic evidence for the repeated evolution of novel, modified structures prior to their use in adaptive behavior would negate any hypothesis involving behavior as a pacemaker of evolution (Lister 2014, Wcislo 1989). Behaviors that are little modified by the environment and those that are flexible also potentially shape selection on other traits. For the latter category, a role for behavior in shaping how selection acts on other traits is a specific case of plasticity-first evolution, and evaluating the hypothesis similarly requires data on (*a*) the phylogeny and ontogeny of a focal trait, confirming it is behaviorally

induced in lineages that serve as proxies for ancestral states; (*b*) patterns of expressed behavioral variation under varying environments and its underlying genetic variation; and (*c*) the phenotypic and genetic changes that occur in a derived lineage in form, function, and regulation to enhance or elaborate the behavioral function (cf. Levis & Pfennig 2016, 2019, which review evidence for plasticity-first evolution, and 10 of 21 tabulated examples meeting most or all of these criteria involve behavioral traits; for examples from social insects, see Jones & Robinson 2018, Kapheim 2019, Kapheim et al. 2020). Ideally, an especially strong case for the importance of phenotypic plasticity in shaping adaptive evolution to a new niche would involve those species with a mix of traits that are relatively plastic (e.g., many behaviors) and relatively nonplastic (e.g., many structural traits) (Price et al. 2003).

3.2. Sensory Biology Shapes Selective Environments Generated by Behavior

Some structures must antedate the evolution of behaviors: "You cannot move an arm until you have one" (West-Eberhard 2003, p. 180), and likewise, there is no point in waving unless a receiver can detect the movement. Such movements antedate the evolution of numerous secondary sexual traits (West-Eberhard 2003). Sensory bias applies to interspecific interactions as well. The evolution of plant behavior is beyond the scope of this review (see Trewavas 2014), but many examples show how plants exploit the sensory biases and needs of animals to facilitate the dispersal of pollen or seeds. Fruit and flower colors, for example, are related to the evolution of color vision in seed dispersers (Lu et al. 2019) and pollinators (Chittka et al. 1999), respectively. Given the learning capabilities of insects (Chittka et al. 1999, Papaj & Lewis 1993), plant traits should evolve to be easily learned by pollinators and difficult to learn by herbivores (Jones & Agrawa 2017).

Across the Tree of Life, the stunning diversity of sexually selected behaviors and associated structures—including songs and vibrations and the brilliant coloration and baroque adornments, movements, or weapons used to court mates or contest rivals (**Figure 1**)—are phylogenetically concentrated in 12% of animal phyla; further, within the Chordata, Mollusca, and Arthropoda, they are restricted to a small number of classes (Wiens & Tuschhoff 2020). This pattern is likely related to the restricted phyletic distribution of different sensory modalities. Hearing with ears is restricted to Chordata and Arthropoda; vision with eyes and lenses occurs in four phyla (though photoreceptors are more widespread) (Wiens & Tuschhoff 2020). Chemoreception is widespread, but airborne olfaction is more restricted (Joseph & Carlson 2015, Yohe & Brand 2018). In addition, moveable appendages with tactile receptors are also phyletically restricted (e.g., Boxshall 2004). Fossil evidence also suggests new sensory modalities are sometimes associated with innovation and diversification (see Section 4).

3.3. Behavior Buys Survival Time That Facilitates Population Persistence

Determined relatively late in ontogeny, behavioral flexibility may buffer physiology against changes in the physical environment (e.g., temperature) and promote stabilizing selection (e.g., Huey et al. 2003). In an anole (*Anolis cristatellus*) individuals along an elevational (temperature) gradient change their microhabitat preferences, allowing them to maintain their body temperature near their preferred optimum despite large differences in ambient temperature (Huey et al. 2003). High-elevation lizards on Hispaniola shift perching preferences from branches to boulders to increase exposure to sunlight; this habitat preference selected for changes in limb dimension and cranial structure, showing how the same behavior can impede or drive evolutionary change in different traits (Muñoz & Losos 2018).

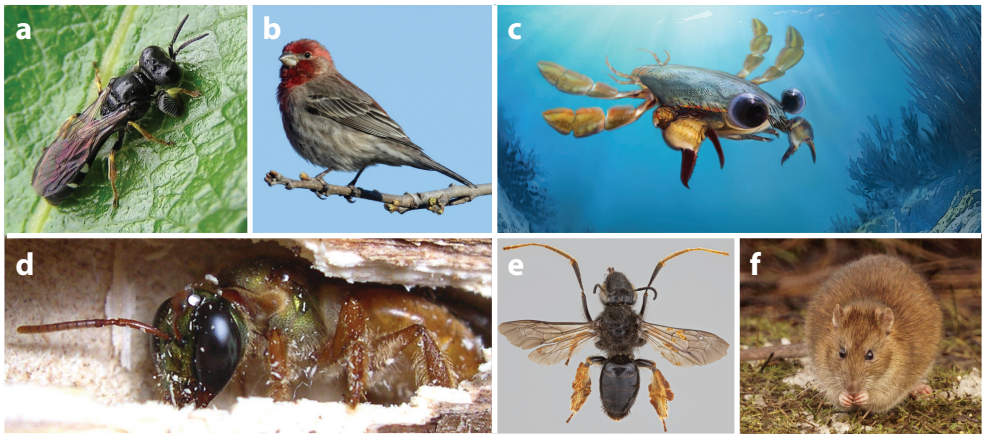

Figure 1

(*a*) Male digger wasp (*Crabro*) with modified forelegs used to place over the compound eyes of prospective mates before and during mating. (*b*) House finch (*Haemorhous*) that evolved suites of traits by organic selection on behavioral and phenotypic plasticity. (*c*) Mid-Cretaceous predatory crab (*Callichimaera*) with paddle-like legs supporting a novel gait. (*d*) Nocturnal bee (*Megalopta*) with enlarged simple and compound eyes to invade a new temporal niche. (*e*) Oil-bee (*Rediviva*) with elongate forelegs for harvesting oil from highly specialized floral resources. (*f*) A rat (*Rattus*) with its dexterous generalized forelimbs (and superb learning abilities). Panel *a* adapted from **https://commons.wikimedia.org/wiki/File:Crabro_scutellatus.jpg**, copyright Teppo Mutanen; panel *b* adapted from **https://www.flickr.com/photos/13836948@N04/3504416570**, copyright John Benson (CC BY 2.0); panel *c* adapted with permission from C. Jaramillo; panel *d* adapted with permission from C. Ziegler; panel *e* adapted from **https://commons.wikimedia.org/wiki/File:Rediviva_longimanus_FEM_65mm_1x_ZS_PMax.jpg**; and panel *f* adapted from **https://commons.wikimedia.org/wiki/File:Rattus_norvegicus,_Hatchpond,_Poole,_Dorset_(8395418976).jpg**), copyright Ian Kirk (CC BY 2.0).

Plasticity as a coping mechanism to deal with changing environments helps promote the persistence of populations (Britton & Badyaev 2020). Populations of relatively light-colored side-blotched lizards (*Uta stansburiana*) live on light-colored soil in southern California; one dark-colored population resulted from the recolonization of a dark-colored Pisgah Lava Flow (Corl et al. 2018). Coloration is phenotypically plastic according to substrate, but Pisgah individuals are darker than off-flow ones when exposed to the same dark substrate. Genomic data indicate relatively low genetic differentiation among this population and surrounding light-colored ones, with the exception of genes important for coloration; simulations indicate those genes arose postcolonization of the lava flow. The change in coloration is due to new gene variants and not to selection on exposed cryptic genetic variation, as derived variants were not found in nearby populations [as expected from a plasticity-first hypothesis (compare with Levis & Pfennig 2016)]. Innovation is a kind of plasticity that also promotes persistence. Bird species with individuals that are more likely to be innovative (and have associated neural traits; see Section 3.8), for example, are more likely to survive rapidly and radically changing environments, again showing how individual activities have evolutionary consequences in terms of population persistence (Ducatez et al. 2020, Socolar et al. 2017).

3.4. Behavior Shapes Conditions of Life for Offspring

Many behaviors are conserved, and the canalized way of life is the phenotypic path of least resistance (with little evidence of more additive genetic variation in that direction; see Section 2). Most females selectively seek specific locations to lay eggs or give birth under conditions favorable for

the growth and development of offspring. These preferences can sometimes lead to highly exaggerated structural traits, such as the extremely long proboscis of a weevil, used to drill holes in fruits for oviposition, which has been shaped by natural selection associated with pericarp thickness (Toju 2009). These evolved or learned parental preferences initially determine the physical, and sometimes social, environments in which progeny develop, the possible choice of foods, and other conditions to which they are exposed and to which they must accommodate themselves (Snell-Rood & Steck 2019, Wcislo 1989). These maternally imposed environments also influence ecological interactions and conditions for processes such as selection and drift. House finch females (*Haemorhous mexicanus*) (**Figure 1*b***), for example, are highly flexible in their egg-laying and brooding behavior in response to changing environments, which shapes thermal conditions for their developing embryos. Females in a far northern population flipped the order of laying male or female eggs (and their exposure to cooler temperatures), with significant consequences for shaping subsequent behavioral and structural evolution via organic selection (Baldwin effects) (Britton & Badyaev 2020). Such behavioral capabilities potentially have significant ecological consequences. Across an altitudinal gradient in the Andes, the nesting preferences of females of different bird species result in behavioral interactions and resource competition among individuals of different species, with behavior influencing range limits and patterns of coexistence (Freeman et al. 2019).

Most of the ~20,000 species of bees (Apiformes) are solitary and are intolerant of social interactions (except mating), although caste-based social behavior has evolved (and been lost) repeatedly in this monophyletic clade (Danforth et al. 2013, Wcislo & Fewell 2017). In some species, females in several families facultatively express solitary behavior or live in social groups as a member of the reproductive or nonreproductive caste. In the latter case, the novel social environment entrains new bases of selection on socially relevant phenotypic variation (Kapheim 2019, Konner 2010, West-Eberhard 2003). In facultatively social *Megalopta* bees (**Figure 1*d***), for example, plasticity in ancient developmental pathways for regulating life-stage or sexual differences in solitary bees provides the variation with which evolution tinkers to generate new social phenotypes via genetic accommodation in reproductive and nonreproductive castes (Kapheim et al. 2020; also Jones & Robinson 2018, Renn & Schumer 2013, Schlichting & Wund 2014). Signatures of selection on gene expression patterns show that variation in developmental plasticity expression patterns (resulting in solitary or social behavior) also shapes the selective environment for subsequent molecular evolution of other traits, with strong selection shaping socially relevant traits, especially in neural and reproductive tissues (Kapheim 2019, Kapheim et al. 2020, Rubenstein et al. 2019).

In some bee species, relevant social traits can be induced experimentally in solitary forms by forcing multiple bees to live together, revealing unexpressed genetic variation in a novel environment (Jones & Robinson 2018, Kapheim 2019, Wcislo & Fewell 2017). With a transition from solitary to social living, selection results in genomic refinements for caste-biased genes, which evolve faster and are subject to stronger selection than noncaste-biased genes (Kapheim 2019, Kapheim et al. 2020). The specialized phenotypes of many derived social bees, wasps, and ants are highly differentiated in structure, behavior, and physiology, with derived genomic architectures (references in Kapheim et al. 2020, Opacheloemphan et al. 2018) similar to vertebrate taxa (Rubenstein et al. 2019).

3.5. Behavior Facilitates the Invasion of New Environments

Habitat choice and behavior have been emphasized repeatedly by Mayr (Mayr 1988) and others as playing central roles in the invasion of a new ecological niche (references in Wcislo 1989).

3.5.1. Low-oxygen environments. Many organisms evolved lifestyles with high energetic demands fueled by aerobic respiration (Vermeij 2017). A transition to low-oxygen environments requires changes in behavior and respiratory physiology to accommodate to these new conditions.

3.5.1.1. High elevations. *Homo sapiens* used behavior and culture to invade new, extreme physical environments. In some cases, these changes led to new bases for natural selection. For example, colonizing high-altitude environments on three continents resulted in positive selection on genes in a cascade associated with facultative compensatory phenotypic responses to low oxygen levels, followed by genetic accommodations to hypoxic conditions (Niepoth & Bendesky 2020, Schlichting & Wund 2014). Analogous genetic adaptations to these low-oxygen environments evolved in many other vertebrates with lowland ancestors that moved into highland habitats (Storz et al. 2010).

3.5.1.2. Deep-sea diving. A danger of hypoxia occurs in other environments. A shift in fishing behavior led the indigenous Bajau people of Southeast Asia to practice long-breath diving to gather deep-water marine resources as part of their food-gathering traditions (Ilardo et al. 2018). This behavioral modification entrained natural selection on gene variants for traits promoting hypoxia tolerance, enabling them to spend more time underwater due to a suite of phenotypic changes that result in an increased supply of red blood cells. Today, some members of this culture, regardless of current occupation, express a number of gene variants at a relatively high frequency, and these variants are usually not expressed in people from the nearest linguistic group on nearby islands that never regularly engaged in deep-diving fishing behavior. Convergent genetic adaptations occur in many obligate marine mammals, which also behaviorally invaded an environment for resource gathering that resulted in prolonged exposure to oxygen stress (Hindle 2020).

3.5.2. Dim-light environments. Niche differentiation between diurnal and nocturnal behavior is ancient (Anderson & Wiens 2017). By their behavior, organisms may access new resources by invading new temporal niches, with multiple independent switches in light environments between nocturnal and diurnal lifestyles, including recent ones and reversals; similarly, organisms may colonize caves and other dim-light habitats (Anderson & Wiens 2017, Tierney et al. 2017, Wcislo & Tierney 2009). The vast majority of bees are diurnal and are active throughout the day, with some variation in timing due to preferences for specific floral resources, social needs, and ecological specializations (Wcislo & Tierney 2009). Bees have apposition compound eyes for a high-acuity visual system that is light demanding, so a dim-light environment represents an extreme ecological niche for them (Wcislo & Tierney 2009). Nevertheless, many otherwise-diurnal bees facultatively forage in dim light at dawn, dusk, and night (see Section 3.5.3); when recurrent, these behavioral changes entrain selection on traits associated with sensory ecology in the new environment (Tierney et al. 2017, Wcislo & Tierney 2009).

The spectacular radiation of flowering plants is associated with biotic pollination (Hernández-Hernández & Wiens 2020). Bees are their primary pollinators and also underwent a spectacular radiation (Danforth et al. 2013). Most plants have diurnal flowers, so most bees are diurnal (Wcislo & Tierney 2009). Nocturnal flowering evolved repeatedly (Borges et al. 2016), and 18 bee lineages transitioned from diurnal to dim-light foraging behavior (with one reversal), especially in xeric temperate regions and the tropics (Wcislo & Tierney 2009). Biologically relevant features of the ancestral and novel environments, such as light levels and temperature, can be quantified precisely. A Neotropical clade of sweat bees (Augochlorini) includes several lineages of bees that shifted >20 Mya to a dim-light environment and nocturnal foraging behavior (with a likely reversal to secondarily diurnal foraging). A behavioral transition to a dim-light environment led to

stabilizing selection on a long-wavelength opsin in dim-light augochlorine bees, while in the lineage leading to the most diverse radiation (*Megalopta*), this opsin gene has point mutations under directional selection, though the functional significance for the chromatophore-binding structure is not known (Tierney et al. 2012).

Megalopta bees orient using visual information and fly in the forest understory to visit flowers at light levels up to 100 million times dimmer than those experienced by diurnal relatives. This behavioral transition resulted in numerous structural changes suited for the novel light environment, including enlarged photoreceptors and eyes (ocelli and ommatidia), with neural rewiring to enhance sensitivity and enable night vision using neural summation (Tierney et al. 2017, Wcislo & Tierney 2009). These optical changes degrade visual acuity, which has behavioral consequences in that bees compensate by flying slower than diurnal relatives to obtain visual information on flight direction and speed (Baird et al. 2011).

The constraints from sensory biology on flight behavior with reduced flight speed modify selection on wing structure in nocturnal forms. The shape and vein structure of insect wings are expected to be strongly canalized (Waddington 1975), which is why they are often highly reliable taxonomic characters. A general trend among Hymenoptera (bees, wasps, ants) is that, as body size increases, there is a more distal extension of wing vein elements, a decrease in relative stigma area, and a proximal shift in the centroid of wing area, and aspect ratios are higher, all influencing drag (references in Wcislo & Tierney 2009). The exceptions are obligate dim-light taxa in diverse taxa; the larger-bodied dim-light species have wing morphologies similar to small-bodied diurnal species. Further, the wings of dim-light bees are characterized by an increased number of wing hooks (hamuli, which join hind- and fore-wings into a functional unit) relative to diurnal species (Wcislo & Tierney 2009), making a stiffer wing surface, putatively related to their slow flight speeds.

3.5.3. First steps into darkness. In many bee species, especially larger-bodied ones that have relatively large eyes and eye facets, some individuals regularly or occasionally fly at dusk and dawn, as well as during the day; this behavior is presumably associated with resource competition (e.g., Wcislo & Tierney 2009), but nothing is known of the proximate mechanisms underlying this facultative behavior.

In fruit flies (*Drosophila*) there is extensive standing genetic variation for eye size and related cephalic modifications (Gaspar et al. 2020), which may relate to variation in diel behavioral activity under differing light levels. In the laboratory, *Drosophila melanogaster* exhibit bimodal (crepuscular) locomotor activity during a 24-hour period, but a survey of 272 natural population strains from 33 regions in Europe and Africa revealed substantial genetic variation segregating in natural populations for preference in diel activity, ranging from diurnal to nocturnal (Pegoraro et al. 2020). Relative to a heterogeneous crepuscular control group, artificial selection experiments produced highly diurnal or nocturnal lines within 10 generations; the response was asymmetrical with heritability being higher in diurnal than nocturnal lines ($h^2 = 37.1\%$ and 8.4%, respectively), though nocturnal females lived longer and had more offspring than diurnal ones. The genetic bases for these changes involved both circadian and noncircadian genes relating to sensory perception. As in deep cave environments without light that result in the evolution of sightless organisms (Tierney et al. 2017), artificially depauperate visual environments can also result in reduced investments in vision. The compound eyes of *D. melanogaster* reared in culture vials are smaller in flies from those cultures that have been kept longer in captivity (Tan et al. 2005), and eye structures degrade completely in flies from cultures kept for decades in constant darkness where vision is impossible (e.g., Özer & Carle 2020).

3.6. Escape from Predators

Successful accommodations to new environments are contingent on any naive prey detecting and evading novel predators. These invasions provide natural experiments to explore the evolution of predator-avoidance behavior, and limb morphology that subserves the behavior. For example, long limbs are favored in fence lizard (*Sceloporus*) populations that cooccur with invasive fire ants (*Solenopsis)*, and the lizards twitched and jerked their limbs in novel ways to shake off the ants (Langkilde 2009; see Zuk et al. 2014 for other examples). Other lizards, such as *Anolis sagrei*, spend time foraging on the ground or perching in shrubs to escape from predators, and body size and limb length influence performance in these two habitats (Bailey et al. 2018). An experimental introduction of a predatory terrestrial lizard (*Leiocephalus carinatus*) to a naive population of brown anoles (*A. sagrei*) initially resulted in directional selection favoring increased running speed and limb length (references in Lapiedra et al. 2018). Subsequently, a behavioral shift in habitat preference (from terrestrial to arboreal behavior), with individuals perching on more slender branches, reversed selection on limb length. Several species of anoles exhibit plasticity in hindlimb length relative to perch diameter, with longer limbs in response to broader substrata (and vice versa) and limb length relating to running speed; these traits likely evolved in a common ancestor of *Anolis*. An experimental study comparing small cays with and without predatory lizards showed that repeatable individual behavioral differences in exploratory behavior varied independent of structural differences. When predators were present, selection favored anoles that spent less time exposed on the ground and were smaller in body size, facilitating a shift to spending more time in shrubs. This shift is costly, and the strength of selection depended strongly on context, because those shrub-dwelling females were in poorer condition (comparing weight:length ratios) than females on predator-free islands that spent more time foraging on the ground.

3.7. Behavior Is What Animals Do with Their Structures

A role for behavior in evolution is reflected in adaptive morphological modifications to enhance particular functions or to acquire new functions. Appendages, for example, are modified in many taxa to enhance locomotion, but when used in other contexts such as courtship, mating, or gathering resources, they may be modified in numerous other ways (Emlen & Nijhout 2000). Male *Crabro* wasps have highly modified forelegs, figured by Darwin (1871), who incorrectly hypothesized they secondarily evolved a function as structures to clasp females. Instead the translucent and flexible leg extensions (**Figure 1*a***) are used to cover the compound eyes of females during courtship behavior (Low & Wcislo 1992). Once particular structures have evolved and are used for specific functions, the timing of trait expression during ontogeny (see Section 2.3.3) suggests that, to evolve a new function, behavior generally should change first before structure due to an asymmetry between activity and anatomy. This asymmetry arises because most mutations are expected to be abnormal, and therefore selected against unless preexisting behaviors can compensate for them, but preexisting structures cannot rescue a deviant behavioral phenotype (Ewer 1960), though they may be useful in other contexts. Structural changes are not always expected to follow from behavioral innovations. No consequent changes are expected if (*a*) behavior is not enhanced by further structural change, as with learning; (*b*) behavioral modules recombine so frequently that the same conditions are unlikely to recur; (*c*) structural changes are constrained by other uses; or (*d*) there is no standing genetic and phenotypic variation for these other traits (West-Eberhard 2003).

3.7.1. Food-related behavior. Examples of host shifts and other behavioral feeding innovations are numerous (Wcislo 1989, West-Eberhard 2003), and recent studies identify how the latter modify selective gradients. Floral oils have evolved repeatedly as a novel resource for pollinators

(28 times in 11 angiosperm families; ~1,500–1,800 species) (Renner & Schaefer 2010). For bees, this environmental change resulted in the repeated evolution of oil-collecting behavior (~350 species of bees in two families), with structural modifications to the legs and setae on the forelegs for retaining oil, which do not occur in non-oil-collecting bees (Policarová et al. 2019, Renner & Schaefer 2010). The South African endemic *Rediviva* bees (~26 species; Melittidae) collect oil from diverse species of four plant families with elongate oil-bearing spurs that vary in length. Among bee species the forelegs are differentially elongated (**Figure 1*e***). An interaction network for each bee species defined the selective environment by using the average spur length for the plant species visited, weighted by frequency of visits to that plant (Pauw et al. 2017). Phylogenetic contrasts show that the evolution of foreleg differences is related to the relative strengths of the selective environment that arises from behavioral decisions of bees to visit plant species with different spur lengths.

3.7.2. Locomotory behavior. Evolution of limb structures illustrates how behavioral innovations drive the evolution of adaptive modifications to limbs and also provide functional constraints on structural modifications because of the original function. The foraging behavior of many pigeons and doves (Columbiformes) is readily characterized as terrestrial or arboreal, though some species are generalists (Lapiedra et al. 2013). Evolutionary transitions from terrestrial to arboreal foraging were associated with accelerated rates of morphological evolution, resulting in shorter tarsi and longer tails in arboreal species in short periods of time (Lapiedra et al. 2013). The behavioral change likely drove the structural evolution and not the reverse; phylogenetic models of morphological evolution following Brownian motion models, with correlated behavioral change, had weak explanatory power. Rodent taxa evolved fossorial, semifossorial, semiaquatic, and arboreal behavior, invading habitats around the world with diverse feeding behaviors and ecologies, and they all use forelimbs for locomotion and grasping food (except for guinea pigs) (Whishaw et al. 1998) (**Figure 1*f***). Despite their extensive diversity in behavior and morphology, rodents retain a generalized forelimb structure (except fossorial species) due to constraints on locomotory and food-handling behaviors (Hedrick et al. 2020).

3.8. Neurosensory Capabilities and Behavioral Innovation

Another way of measuring how behavioral change shapes subsequent morphological diversity is to compare rates of morphological evolution among lineages with species that differ in behavioral capabilities or proxies for them (e.g., brain size) or sensory capabilities (e.g., color vision). Within grades, metrics of brain size are correlated with behavioral flexibility and capability for innovation in birds and primates, including use of tools (e.g., Lefebvre et al. 2004, Reader & Laland 2002), and predict problem-solving capabilities in mammalian carnivores (Benson-Amram et al. 2016). Brain size in birds is correlated with the degree of subspecific diversification (Sol et al. 2005) and with numbers of species per clade (Nicolakakis et al. 2003). For 120 families of birds, mean brain size accounts for a significant fraction of body-size diversification rates within families, independent of numbers of species in the clade, geographic range, or other traits associated with speciose taxa (Sol & Price 2008). Accelerated rates of speciation are associated with color and plumage polymorphisms in birds, and behavior with color vision plays a critical role in incipient speciation (Price 2006; Uy et al. 2018) among other taxa.

4. PALEOBIOLOGY AND BEHAVIORAL EVOLUTION

Some fossils preserve behaviors as well as structures (Lister 2014). Various lineages of African proboscideans shifted their diets through the Miocene to Quaternary, apparently associated with

the spread of C_4 grasses (Lister 2014). Following this behavioral shift to grass grazing, there was a significant time lag before the evolution of dental innovation (hypsodonty) that is seen only in later lineages. A comparison of 17,000 Phanaerozoic marine invertebrate genera, with and without visual capabilities, showed that sighted taxa diversified more strongly than blind genera (with higher extinction rates in the latter) (Aberhan et al. 2012). Vision is one of the traits that helps account for differences in diversification rates among metazoan phyla (Jezkova & Wiens 2017), although within some taxa, the evidence is equivocal (Müller et al. 2018), and a model without vision explains almost as much variation in diversification (Jezkova & Wiens 2017). Vision enables new levels of activity and movement, as seen in a predatory brachyuran crab (*Callichimaera*) (**Figure 1*c***) from the mid-Cretaceous that evolved large compound eyes and paddle-like legs for active swimming with a novel gait (Luque et al. 2019). Colonization of land by animals was a major behavioral achievement with significant consequences for subsequent behavioral evolution and ecological escalation (Vermeij 2013). Movement and activity (behaviors) are less constrained in air than water: The majority (nine of twelve) of high-performance evolutionary innovations originated on land after the Ordovician, and for animals, eight of nine of these innovations are behavioral ones [e.g., vertebrate herbivory; farming; aerial locomotion; eusociality; botanical payments to animals to behave as guards, pollinators, or seed dispersers; echolocation; and collective construction behaviors (Vermeij 2017)], highlighting behavior's role in driving evolution.

5. HUMAN BEHAVIORAL ENVIRONMENTS

The natural and cultural histories of *Homo sapiens* provide outstanding examples of how the behavior of individuals within species has evolutionary consequences (Konner 2010). A rigorous understanding of the role played by behavior in coping with novel environmental conditions is of increasing practical importance, due to the directionality and intensity of human behavior-induced environmental changes relating to loss of biological and cultural diversity and to the emergence of infectious diseases (Seitz et al. 2020, Wilson et al. 2014).

5.1. Domestication and Pathogen Pressure

Human behavior has generated artificial environments that create conditions for artificial selection on desirable traits of plants and animals. Analyses of archaic hominin genomes show many examples of adaptive genetic evolution resulting from behavioral innovations and environmental modifications relating to agriculture and diet, invasions of new physical environments, and increased exposure to pathogens (Marciniak & Perry 2017, Niepoth & Bendesky 2020). These changes in turn shaped human physiology and behavior, including resiliency during child development (Konner 2010). An inevitable consequence of social success is increased risk of disease transmission with complex evolutionary trade-offs and population-level consequences relating to patterns of disease transmission and public health strategies (Seitz et al. 2020).

5.2. Behavioral Responses to Rapid Human-Induced Environmental Change

The human ability to manipulate physical and social environments has significant knock-on consequences for life on Earth. Phenotypic plasticity rather than immediate genetic evolution accounts for many phenotypic changes in response to rapidly changing environments, though the degree of plasticity may evolve as well (Hendry et al. 2008). Core problems relating to biodiversity conservation or species invasions all involve behavior (e.g., home-range size, sustaining pollinators and seed dispersers). A predictive science would have obvious advantages for better understanding

how animals will respond by behavior to future human-modified environments and which traits are associated with resiliency (e.g., Derryberry et al. 2020, Socolar et al. 2017). The fact that many behaviors are highly sensitive to environmental change sometimes leads to maladaptive behavioral responses, such as sensory traps causing individuals to respond inappropriately to anthropogenic changes, which modify selection on other phenotypic traits, entraining negative feedback (Cotto et al. 2019). These anthropogenic examples show how the maladaptive expression of evolved behavior can also take the lead in shaping the evolution of related phenotypic traits.

6. CONCLUSIONS

Extensive new data on proximate mechanisms for the development and expression of behavior show how these mechanisms help shape ultimate processes for the evolution of behavior. Animals have different behavioral needs, and to meet them, some traits are highly conserved, while others are highly labile and responsive. Behavior is the interface between internal and external conditions and is therefore responsive to all environmental changes, no matter the source. Recurrent behaviors potentially modify environmental conditions that covary with fitness. Genomic studies reveal that feeding and courtship behaviors are especially important, as is locomotion (or other uses for appendages). Reciprocal evolution involving novel behavior often results in selection for modified morphologies. Reviews on behavioral evolution provide evidence of plasticity-first evolution and genetic accommodation. Behavior potentially shapes selective environments to either drive evolution in a particular direction or remain near an adaptive peak. The outcome hinges on the natural history of the organism, especially the sensory biology. Higher-order effects on ecological interactions and the evolution of adaptive radiations are observed in rates of morphological diversification and speciation. Empirical results, along with new models, fully support conclusions from Modern Synthesis–era symposia on behavior and evolution: The general theory of behavior is evolution, and behavior is an essential determinant of evolution in animals.

DISCLOSURE STATEMENT

The author is not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

I am grateful to T. Price, B. Crespi, M.J. West-Eberhard, W. Eberhard, and E. Leigh for reading an impossibly rough draft and providing helpful ideas and to D. Futuyma for helpful suggestions on a later draft; P. Galgani helped compile bibliographic references.

LITERATURE CITED

Aberhan M, Nürnberg S, Kiessling W. 2012. Vision and the diversification of Phanerozoic marine invertebrates. *Paleobiology* 38(2):187–204

Alaux C, Sinha S, Hasadsri L, Hunt GJ, Guzmán-Novoa E, et al. 2009. Honey bee aggression supports a link between gene regulation and behavioral evolution. *PNAS* 106(36):15400–5

Ancel LW. 1999. A quantitative model of the Simpson-Baldwin effect. *J. Theor. Biol.* 196:197–209

Anderson SR, Wiens JJ. 2017. Out of the dark: 350 million years of conservatism and evolution in diel activity patterns in vertebrates. *Evolution* 71:1944–59

Bailey NW, Orleach LM, Moore AJ. 2018. Indirect genetic effects in behavioral ecology: Does behavior play a special role in evolution? *Behav. Ecol.* 29:1–11

Baird E, Kreiss E, Wcislo W, Warrant E, Dacke M. 2011. Nocturnal insects use vision for flight control. *Biol. Lett.* 7:499–501

Bates M. 1960. *The Forest and the Sea*. New York: Random House

Bell AM, Hankison SJ, Laskowski KL. 2009. The repeatability of behaviour: a meta-analysis. *Anim. Behav.* 77(4):771–83

Benson-Amram S, Dantzer B, Stricker G, Swanson EM, Holekamp KE. 2016. Brain size predicts problem-solving ability in mammalian carnivores. *PNAS* 113:2532–37

Berdal MA, Dochtermann NA. 2019. Adaptive alignment of plasticity with genetic variation and selection. *J. Heredity* 2019:514–22

Bernays EA, Wcislo WT. 1994. Sensory capabilities, information processing, and resource specialization. *Q. Rev. Biol.* 69:187–204

Blackiston DJ, Silva Casey E, Weiss MR. 2008. Retention of memory through metamorphosis: Can a moth remember what it learned as a caterpillar? *PLOS ONE* 3(3):e1736

Blomberg SP, Garland T Jr., Ives AR. 2003. Testing for phylogenetic signal in comparative data: Behavioral traits are more labile. *Evolution* 57(4):717–45

Borges RM, Somanathan H, Kelber A. 2016. Patterns and processes in nocturnal and crepuscular pollination services. *Q. Rev. Biol.* 91:389–418

Boxshall G. 2004. The evolution of arthropod limbs. *Biol. Rev.* 79(2):253–300

Britton SE, Badyaev AV. 2020. Adaptation and adaptability in the house finch (*Haemorhous mexicanus*) biology. In *Invasive Birds: Global Trends and Impacts*, ed. CT Downs, LA Hart, pp. 149–54. Wallingford, UK: CABI Publ.

Brodie ED III. 2005. Caution: niche construction ahead. *Evolution* 59:249–51

Chittka L, Thomson JD, Waser NM. 1999. Flower constancy, insect psychology, and plant evolution. *Naturwissenschaften* 86:361–77

Corl A, Bi K, Luke C, Challa AS, Stern AJ, et al. 2018. The genetic basis of adaptation following plastic changes in coloration in a novel environment. *Curr. Biol.* 28:2970–77

Cotto O, Sandell L, Chevin LM, Ronce O. 2019. Maladaptive shifts in life history in a changing environment. *Am. Nat.* 194(4):558–73

Crispo E. 2007. The Baldwin effect and genetic assimilation: revisiting two mechanisms of evolutionary change mediated by phenotypic plasticity. *Evolution* 61:2469–79

Danforth BN, Cardinal S, Praz C, Almeida EAB, Michez D. 2013. The impact of molecular data on our understanding of bee phylogeny and evolution. *Annu. Rev. Entomol.* 58:57–78

Darwin C. 1871. *The Descent of Man, and Selection in Relation to Sex*. London: John Murray

Derryberry EP, Phillips JN, Derryberry GE, Blum MJ, Luther D. 2020. Singing in a silent spring: Birds respond to a half-century soundscape reversion during the COVID-19 shutdown. *Science* 370:575–79

Dochtermann NA. 2011. Testing Cheverud's conjecture for behavioral correlations and behavioral syndromes. *Evolution* 65(6):1814–20

Dochtermann NA, Schwab T, Berdal MA, Dalos J, Royauté R. 2019. The heritability of behavior: a meta-analysis. *J. Heredity* 110:403–10

Ducatez S, Sol D, Sayol F, Lefebvre L. 2020. Behavioural plasticity is associated with reduced extinction risk in birds. *Nat. Ecol. Evol.* 4:788–93

Duckworth RA. 2009. The role of behavior in evolution: a search for mechanism. *Evol. Ecol.* 23:513–31

Duckworth RA, Potticary AL, Badyaev AV. 2018. On the origins of adaptative behavioral complexity developmental channeling of structural trade-offs. *Adv. Study Behav.* 50:1–36

Eberhard WG, Wcislo WT. 2011. Grade changes in brain-body allometry: morphological and behavioral correlates of brain size in miniature spiders, insects and other invertebrates. *Adv. Insect Physiol.* 40:155–213

Edgell TC, Lynch BR, Trussell GC, Palmer AR. 2009. Experimental evidence for the rapid evolution of behavioral canalization in natural populations. *Am. Nat.* 174(3):434–40

Emlen DJ, Nijhout HF. 2000. The development and evolution of exaggerated morphologies in insects. *Annu. Rev. Entomol.* 45:661–708

Ewer RF. 1960. Natural selection and neoteny. *Acta Biotheor.* 13:161–84

Foster SA. 2013. Evolution of behavioural phenotypes: influences of ancestry and expression. *Anim. Behav.* 85:1061–75

Freeman BJ, Tobias JA, Schluter D. 2019. Behavior influences range limits and patterns of coexistence across an elevational gradient in tropical bird diversity. *Ecography* 42:1832–40

Futuyma DJ. 2017. Evolutionary biology today and the call for an extended synthesis. *Interface Focus* 7:20160145

Gaspar P, Arif S, Sumner-Rooney L, Kittelmann M, Odey AJ, et al. 2020. Characterization of the genetic architecture underlying eye size variation within *Drosophila melanogaster* and *Drosophila simulans*. *Genes Genomes Genet*. 10(3):1005–18

Gause GF. 1942. The relation of adaptability to adaptation. *Q. Rev. Biol.* 17:99–114

Ghalambor CK, Angeloni L, Carroll SP. 2010. Behavior as phenotypic plasticity. In *Evolutionary Behavioral Ecology*, ed. C Fox, D Westneat, pp. 90–107. New York: Oxford Univ. Press

Godfray-Smith P. 2017. The subject as cause and effect in evolution. *Interface Focus* 7:20170022

Grosjean Y, Rytz R, Farine J-P, Abuin L, Cortot J, et al. 2011. An olfactory receptor for food-derived odours promotes male courtship in *Drosophila*. *Nature* 478:236–40

Hedrick BP, Dickson BV, Dumont ER, Pierce SE. 2020. The evolutionary diversity of locomotor innovation in rodents is not linked to proximal limb morphology. *Sci. Rep.* 10(1):717

Hendry AP, Farrugia TJ, Kinnison MT. 2008. Human influences on rates of phenotypic change in wild animal populations. *Mol. Ecol.* 17:20–29

Hernández-Hernández T, Wiens JJ. 2020. Why are there so many flowering plants? A multi-scale analysis of plant diversification. *Am. Nat.* 195:948–63

Hindle AG. 2020. Diving deep: understanding the genetic components of hypoxia tolerance in marine mammals. *J. Appl. Physiol.* 128:1439–46

Huey RB, Hertz PE, Sinervo B. 2003. Behavioral drive versus behavioral inertia in evolution: null model approach. *Am. Nat.* 161(3):357–66

Huxley JS. 1942. *Evolution. The Modern Synthesis*. London: Allen & Unwin

Ilardo MA, Moltke I, Korneliussen TS, Cheng J, Stern AJ, et al. 2018. Physiological and genetic adaptations to diving in sea nomads. *Cell* 173:569–80

Jezkova T, Wiens JJ. 2017. What explains patterns of diversification and richness among animal phyla? *Am. Nat.* 189:201–12

Jones BM, Robinson GE. 2018. Genetic accommodation and the role of ancestral plasticity in the evolution of insect eusociality. *J. Exp. Biol.* 21:jeb153163

Jones PL, Agrawal AA. 2017. Learning in insect pollinators and herbivores. *Annu. Rev. Entomol.* 62:53–71

Joseph RM, Carlson JR. 2015. *Drosophila* chemoreceptors: a molecular interface between the chemical world and the brain. *Trends Genet*. 31:683–95

Kapheim KM. 2019. Synthesis of Tinbergen's four questions and the future of sociogenomics. *Behav. Ecol. Sociobiol.* 73:186. Correction. 2019. *Behav. Ecol. Sociobiol*. 73:28

Kapheim KM, Jones BM, Pan H, Cai L, Harpur BA, et al. 2020. Developmental plasticity shapes social traits and selection in a facultatively eusocial bee. *PNAS* 117(24):13615–25

Konner M. 2010. *The Evolution of Childhood*. Cambridge, MA: Harvard Univ. Press

LaFreniere P, MacDonald K. 2013. A post-genomic view of behavioral development and adaptation to the environment. *Dev. Rev.* 33(2):89–102

Langkilde T. 2009. Invasive fire ants alter behavior and morphology of native lizards. *Ecology* 90:208–17

Lapiedra O, Schoener TW, Leal M, Losos JB, Kolbe JJ. 2018. Predator-driven natural selection on risk-taking behavior in anole lizards. *Science* 360:1017–20

Lapiedra O, Sol D, Carranza S, Beaulieu JM. 2013. Behavioural changes and the adaptative diversification of pigeons and doves. *Proc. R. Soc. B* 280:20122893

Lefebvre L, Reader SM, Sol D. 2004. Brains, innovation and evolution in birds and primates. *Brain Behav. Evol.* 63:233–46

Levis NA, Pfennig DW. 2016. Evaluating 'plasticity-first' evolution in nature: key criteria and empirical approaches. *Trends Ecol. Evol.* 31(7):563–74

Levis NA, Pfennig DW. 2019. Plasticity-led evolution: a survey of developmental mechanisms and empirical tests. *Evol. Dev.* 22:71–87

Linneweber GA, Andriatsilavo M, Dutta S, Bengochea M, Hellbruegge L, et al. 2020. A neurodevelopmental origin of behavioral individuality in the *Drosophila* visual system. *Science* 367(6482):1112–19

Lister AM. 2014. Behavioural leads in evolution: evidence from the fossil record. *Biol. J. Linn. Soc.* 112(2):315–31

Lotka AJ. 1925. *Elements of Physical Biology*. Baltimore, MD: Williams & Wilkins Co.

Low BS, Wcislo WT. 1992. Foretibial plates and the mating behavior of *Crabro cribrellifer* (Hymenoptera: Sphecidae), with a review of expanded male forelegs in Apoidea. *Ann. Entomol. Soc. Am.* 85:219–23

Lu L, Fritsch PW, Matzke NJ, Wang H, Kron KA, et al. 2019. Why is fruit color so variable? Phylogenetic analyses reveal relationships between fruit-color evolution, biogeography, and diversification. *Glob. Ecol. Biogeo.* 28:891–913

Luque J, Feldman RM, Vernygora O, Schweitzer CE, Cameron CB, et al. 2019. Exceptional preservation of mid-Cretaceous marine arthropods and the evolution of novel forms via heterochrony. *Sci. Adv.* 5:eaav3875

Marciniak S, Perry G. 2017. Harnessing ancient genomes to study the history of human adaptation. *Nat. Rev. Genet.* 18:659–74

Mayr E. 1963. *Animal Species and Evolution*. Cambridge, MA: Harvard Univ. Press

Mayr E. 1988. *Toward a New Philosophy of Biology*. Cambridge, MA: Harvard Univ. Press

Müller J, Bickelmann C, Sobral G. 2018. The evolution and fossil history of sensory perception in amniote vertebrates. *Ann. Rev. Earth Planet. Sci.* 46:495–519

Mullins DE. 2015. Physiology of environmental adaptations and resource acquisition in cockroaches. *Annu. Rev. Entomol.* 60:473–92

Muñoz MM, Losos JB. 2018. Thermoregulatory behavior simultaneously promotes and forestalls evolution in a tropical lizard. *Am. Nat.* 191:E15–26

Nicolakakis N, Sol D, Lefebvre L. 2003. Behavioural flexibility predicts species richness in birds, but not extinction risk. *Anim. Behav.* 65:445–52

Niepoth N, Bendesky A. 2020. How natural genetic variation shapes behavior. *Annu. Rev. Genom. Hum. Genet.* 21:437–63

Niklas KJ. 2004. Computer models of early land plant evolution. *Annu. Rev. Earth Planet. Sci.* 32:47–66

Odling-Smee FJ, Laland KN, Feldman MW. 2003. *Niche Construction: The Neglected Process in Evolution*. Princeton, NJ: Princeton Univ. Press

Opacheloemphan C, Yan H, Leibholz A, Desplan C, Reinberg D. 2018. Recent advances in behavioral (epi)genetics in eusocial insects. *Annu. Rev. Genet.* 52:489–510

Özer I, Carle T. 2020. Back to the light, coevolution between vision and olfaction in the "Dark-flies" (*Drosophila melanogaster*). *PLOS ONE* 15(2):e0228939

Papaj DR, Lewis AC, eds. 1993. *Insect Learning: Ecology and Evolutionary Perspectives*. London: Chapman and Hall

Pauw A, Kahnt B, Kuhlmann M, Michez D, Montgomery GA, et al. 2017. Long-legged bees make adaptive leaps: linking adaptation to coevolution in a plant-pollinator network. *Proc. R. Soc. B* 284(1862):20171707

Pegoraro M, Flavell LMM, Menegazzi P, Colombi P, Dao P, et al. 2020. The genetic basis of diurnal preference in *Drosophila melanogaster*. *BMC Genom.* 21:596

Policarová J, Cardinal S, Martins AC, Straka J. 2019. The role of floral oils in the evolution of apid bees (Hymenoptera: Apidae). *Biol. J. Linn. Soc.* 128:486–97

Porter CK, Akcali CK. 2020. Evolutionary implications of habitat choice. *eLS* 1. **https://doi.org/10.1002/9780470015902.a0029011**

Price TD. 2006. Phenotypic plasticity, sexual selection and the evolution of colour patterns. *J. Exp. Biol.* 209:2368–76

Price TD, Qvarnström A, Irwin DE. 2003. The role of phenotypic plasticity in driving genetic evolution. *Proc. R. Soc. B* 270:1433–40

Reader SM, Laland KN. 2002. Social intelligence, innovation, and enhanced brain size in primates. *PNAS* 99:4436–41

Rensch B. 1959. *Evolution Above the Species Level*. New York: Columbia Univ. Press

Renn SCP, Schumer ME. 2013. Genetic accommodation and behavioural evolution: insights from genomic studies. *Anim. Behav.* 85:1012–22

Renner SS, Schaefer H. 2010. The evolution and loss of oil-offering flowers: new insights from dated phylogenies for angiosperms and bees. *Phil. Trans. R. Soc. B* 635:423–35

Román-Palacios C, Scholl JP, Wiens JJ. 2019. Evolution of diet across the animal tree of life. *Evol. Lett.* 3:339–47

Roe A, Simpson GC (eds.). 1958. *Behavior and Evolution*. New Haven: Yale Univ. Press

Rubenstein DR, Agren JA, Carbone L, Elde NC, Hoekstra HE, et al. 2019. Coevolution of genome architecture and social behavior. *Trends Ecol. Evol.* 34(9):844–55

Rueffler C, van Dooren TJM, Metz JAJ. 2007. The interplay between behavior and morphology in the evolutionary dynamics of resources specialization. *Am. Nat.* 169(2):R34–52

Schlichting CD, Wund MA. 2014. Phenotypic plasticity and epigenetic marking: an assessment of evidence for genetic accommodation. *Evolution* 68(3):656–72

Schmalhausen II. 1949 (1986). *Factors of Evolution*. Chicago: Univ. Chicago Press

Scott-Phillips TC, Laland KN, Shuker DM, Dickins TE, West SA. 2014. The niche construction perspective: a critical appraisal. *Evolution* 68:1231–43

Seitz BM, Aktipis A, Buss DM, Alcock J, Bloom P, et al. 2020. The pandemic exposes human nature: 10 evolutionary insights. *PNAS* 117:27767–76

Simpson GC. 1953. The Baldwin effect. *Evolution* 7:110–17

Snell-Rood EC, Steck MK 2019. Behaviour shapes environmental variation and selection on learning and plasticity: review of mechanisms and implications. *Anim. Behav.* 147:147–56

Socolar JB, Epanchin PN, Beissinger SR, Tingley MW. 2017. Phenological shifts conserve thermal niches in North American birds and reshape expectations for climate-driven range shifts. *PNAS* 114(49):12976–81

Sol D, Price TD. 2008. Brain size and the diversification of body size in birds. *Am. Nat.* 172(2):170–77

Sol D, Stirling DG, Lefebvre L. 2005. Behavioral drive or behavioral inhibition in evolution: subspecific diversification in Holarctic passerines. *Evolution* 59(12):2669–77

Stewart AJ, Persons TL, Plotkin JB. 2016. Evolutionary consequences of behavioral diversity. *PNAS* 113(45):e7003–9

Storz JF, Scott GR, Cheviron ZA. 2010. Phenotypic plasticity and genetic adaptation to high-altitude hypoxia in vertebrates. *J. Exp. Biol.* 213:4125–36

Streelman JT, Danley PD. 2003. The stages of vertebrate evolutionary radiation. *Trends Ecol. Evol.* 18:126–31

Tan S, Amos W, Laughlin SB. 2005. Captivity selects for smaller eyes. *Curr. Biol.* 15(14):R540–42

Tierney SM, Friedrich M, Humphreys WF, Jones TM, Warrant EJ, Wcislo WT. 2017. Consequences of evolutionary transitions in changing photic environments. *Aust. Entomol.* 56(1):23–46

Tierney SM, Sanjur O, Grajales GG, Santos LM, Bermingham E, Wcislo WT. 2012. Photic niche invasions: phylogenetic history of the dim-light foraging augochlorine bees (Halictidae). *Proc. R. Soc. B* 279:794–803

Toju H. 2009. Natural selection drives the fine-scale divergence of a coevolutionary arms race involving a long-mouthed weevil and its obligate host plant. *BMC Evol. Biol.* 9:273

Trewavas T. 2014. *Plant Behaviour and Intelligence*. Oxford, UK: Oxford Univ. Press

Uy JAC, Irwin DE, Webster MS. 2018. Behavioral isolation and incipient speciation in birds. *Annu. Rev. Ecol. Evol. Syst.* 49:1–24

Vermeij GJ. 2013. On escalation. *Annu. Rev. Earth Planet. Sci.* 41:1–19

Vermeij GJ. 2017. How the land became the locus of major evolutionary innovations. *Curr. Biol.* 27:3178–82.e1

Wada-Katsumata A, Silverman J, Schal C. 2013. Changes in taste neurons support the emergence of an adaptative behavior in cockroaches. *Science* 340:972–75

Waddington CH. 1975. *The Evolution of an Evolutionist*. Ithaca, NY: Cornell Univ. Press

Wcislo WT. 1989. Behavioral environments and evolutionary change. *Ann. Rev. Ecol. Syst.* 20:137–69

Wcislo WT, Fewell JH. 2017. Sociality in bees. In *Comparative Social Evolution*, ed. DR Rubenstein, P Abbot, pp. 50–83. Cambridge, UK: Cambridge Univ. Press

Wcislo WT, Tierney S. 2009. Behavioral environments and niche construction: the evolution of dim-light foraging in bees. *Biol. Rev. Camb. Philos. Soc.* 84:19–37

West-Eberhard MJ. 2003. *Developmental Plasticity and Evolution*. Oxford, UK: Oxford Univ. Press

West-Eberhard MJ. 2019. Modularity as a universal emergent property of biological traits. *J. Exp. Zool. (Mol. Dev. Evol.)* 332(8):356–64

Whishaw Q, Sarnas JR, Pellis SM. 1998. Evidence for rodent-common and species-typical limb and digit use in eating, derived from a comparative analysis of ten rodent species. *Behav. Brain Res.* 96:79–91

Wiens JJ, Tuschhoff E. 2020. Songs versus colours versus horns: what explains the diversity of sexually selected traits? *Biol. Rev.* 95:847–64

Wilson DS, Hayes SC, Biglan A, Embry DD. 2014. Evolving the future: toward a science of international change. *Behav. Brain Sci.* 37(4):395–416

Wittwer B, Hefetz A, Simon T, Murphy LEK, Elgar MA, et al. 2017. Solitary bees reduce investment in communication compared with their social relatives. *PNAS* 114(25):6569–74

Wright S. 1931. Evolution in Mendelian populations. *Genetics* 16:97–159

Yohe LR, Brand P. 2018. Evolutionary ecology of chemosensation and its role in sensory drive. *Curr. Zool.* 64(4):525–33

York RA. 2018. Assessing the genetic landscape of animal behavior. *Genetics* 209:223–32

Zuk M, Bastiaans E, Langkilde T, Swanger E. 2014. The role of behaviour in the establishment of novel traits. *Anim. Behav.* 92:333–44