

BEHAVIORAL VARIATION, ADAPTATION, AND EVOLUTION

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Individual animals behave differently from each other for myriad interrelated intrinsic and extrinsic reasons, and this behavioral variation is the raw substrate for evolutionary change. Behavioral variation can both enhance and constrain long-term evolution (Foster, 2013), and it provides the basic materials on which natural and sexual selection can act. A rich body of historical experimental and conceptual foundations precedes many of the topics discussed. This classic literature is vast and important, and we encourage the reader to examine it in detail (e.g., Lehrman, 1953; Lorenz, 1971; Schnerla, 1966; Waddington, 1959) because we discuss more recent literature. For example, the study of the mechanisms that underlie behavioral variation has a divisive history, which involves carving out the relative contributions of genes and environment to a particular phenotype. Developmental systems and reaction-norm views challenged the issue of gene or environment by arguing that the interplay between genetic substrates and environmental inputs defined adaptive phenotypes across multiple contexts (Foster, 2013; Gottlieb, 1991a, 1991b; Jablonka & Lamb, 2014). Identifying the interactional relationship between components permits researchers to understand how behavior becomes organized (Gottlieb, 1991a, 1991b) and can reveal links between individual variation and population-level persistence, species diversification (or stasis), and community dynamics (reviewed in Dingemanse & Wolf, 2013).

Similarly, the study of individual differences has a rich history situated in the areas of behavioral genetics, sociobiology, behavioral ecology, developmental psychology, personality theory, and studies of learning and cognition. Each area has its own goals, associated techniques, and levels of explanation. The study of behavioral variation during early development, for instance, has been documented primarily by psychologists studying proximate mechanisms in laboratory animal models, whereas the study of different adult morphs using the adaptationist perspective has been dominated by behavioral ecologists examining natural populations (Foster, 1995). A more complete description of individual differences requires an integrative study of the mechanisms (e.g., developmental, physiological) that guide intra-individual flexibility and the associated adaptive fine tuning of behavioral types. It is through this integration that researchers can make predictions about the response of different individual phenotypes, groups, populations, and species to novel situations (e.g., captive and urban environments).

BACKGROUND

The study of individual behavioral variation can be better understood through examination of two axes: developmental plasticity versus behavioral flexibility and continuity versus stability (reviewed in A. B. Clark & Ehlinger, 1987). *Developmental plasticity* is

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defined as the potential of a single genotype to produce more than one distinct phenotype (e.g., alternative reproductive strategies), and *behavioral flexibility* refers to the capacity of an individual to modify its behavior in response to novel challenges (e.g., alter diet in response to food availability; Fagen, 1982). It is important to note that being developmentally plastic does not mean that individuals of the species are particularly flexible in their behavior; the behavior of morphs may be particularly constrained after the initial switch. The second axis draws a distinction between stability and continuity, which has a strong temporal component. *Continuity* describes a trait's persistent effect on the behavior of the animal throughout time, whereas *stability* suggests that traits occur in the present form at the same level of intensity. The challenge, however, lies in identifying and defining consistent phenotypes because they often change during the lifetime of the individual, across seasons, in different social contexts, and in novel environments. To better understand the continuity and stability of a behavioral characteristic, the relationship between overt behavior and underlying mechanisms during development and their evolutionary constraints and selection pressures should be examined using an integrative lens.

In recent decades, early attempts to use isolation experiments to separate genetic and environmental components of behavior have given way to more comprehensive views that emphasize the importance of interaction effects, epigenetics, and evolving developmental trajectories or reaction norms (Snell-Rood, 2013; Stamps, 2015; see also Chapters 18 and 22, this volume). Researchers have recognized that some behavior patterns remain highly malleable throughout an individual's lifetime, whereas others are rapidly canalized early in development. Sex and social roles can be important, as can genetic background and physical context. Recent studies have offered profound new insight into the scope and structure of behavioral variation, fundamentally changing the understanding of how evolutionary forces shape that variation over longer periods of time. These studies explain why some individuals behave consistently regardless of context, whereas others vary their behavior depending on age, social context, or season. Here, we summarize and

highlight some of these recent findings, emphasizing those that influence behavioral evolution.

VARIATION

Most individual animals produce a wide range of behavior over their lifetime. Below, we summarize some of the key forms of behavioral variation, highlighting recent findings that offer fresh insight into well-studied examples of developmental plasticity and behavioral flexibility, mechanistic underpinnings, and their responses to anthropogenic change. Some types of behavior change during development are influenced by experience, such that individuals undergo profound and permanent shifts as they age. Other types of behavior vary periodically as part of circadian, reproductive, or other seasonal cycles (see Chapter 29, this volume). Finally, some types of behavior are context dependent, and individuals may behave in radically different ways depending on the situation in which they are found. In a recent review, Stamps (2015) emphasized underlying mechanisms by offering a comprehensive framework that distinguishes between variation due to endogenous (e.g., age-dependent or seasonal) or exogenous (e.g., learning, context-dependent) factors. In contrast, Snell-Rood (2013) emphasized the importance of timing and thus distinguished between context-dependent (activational) and developmental effects. Because both lines of distinction are blurred, we combine the two in our summary of behavioral variation below.

As We Age

Behavioral development continues to be an important and exciting area of new research. Although experiences that induce long-term effects on behavior can occur at any age, cues experienced early in life have the potential to play especially large roles (see Chapter 21, this volume). Many behavior patterns vary with age and experience (Bateson & Gluckman, 2012), and recent research has found differences between infants and adults in even their most fundamental aspects, including personality (Stamps & Groothuis, 2010; see also Chapter 9, this volume), social status (Fernald, 2015), and sex (Frisch, 2004).

Critical periods and *sensitive periods* are broad terms that apply whenever the effects of experience

on behavior are unusually strong during a limited period in development. Windows that occur early in life are salient opportunities for environmental stimuli to shape individual phenotypes. For example, zebra finch (*Taeniopygia guttata*) nestlings fed stress hormones for 2 weeks during early development were less choosy about social partners as adults and so became more central members of their adult flocks in ways that are likely to have profound impacts on many aspects of their lifestyle (Boogert, Farine, & Spencer, 2014). In humans, the impact of early stress on adult disease is so strong that medical researchers have proposed early childhood adversity as a useful way of categorizing patients and focusing treatment (Shonkoff & Garner, 2012). Many of the initial forays into understanding critical and sensitive periods involved the study of filial imprinting (Lorenz, 1937): Soon after birth (or hatching), infants learn to recognize and bond with their parents (Hess, 1973). The mechanisms that underlie sensitive periods were initially studied at the behavioral level, but now more is known about the neural mechanisms by which sensitive periods act (reviewed in Hensch, 2004).

Temporal polytheisms in honeybees present a unique opportunity to understand the social, neurochemical, genetic, and environmental mechanisms that underlie constrained developmental shifts. Early social factors can influence the timing of developmental switches, as in honeybees (*Apis mellifera*), in which the transition to nursing or foraging behavior is driven by the number of other individuals performing these tasks in the hive (reviewed in Johnson, 2010). Physiological mechanisms often reinforce the transition or stasis of individuals in a particular caste through endocrinological cascades and changes in gene expression. Two mutually reinforcing processes facilitate development and maintenance of nurse bee behavior. When a worker feeds the brood, she is exposed to queen mandibular gland pheromone and brood pheromone (which co-occur in the brood nest). Brood pheromone stimulates the hypopharyngeal glands, which trigger pollen feeding, and other hormonal changes that partially suppress the normal age-based changes (reviewed in Johnson, 2010). The mechanisms that drive individuals to switch during different points

during development might be stage dependent. For example, nurse bees are proposed to be pushed to switch by the development of workers behind them, and middle-aged workers are steered from their caste via interactions with the caste ahead of them. The behavioral flexibility may be constrained in some castes and not others because the transition from cell cleaner stage to nurse is a continuous process, and the developmental sequence is compromised when the necessary cues (e.g., protein) are absent (Schulz, Huang, & Robinson, 1998).

Researchers have also learned that even small differences in early experience can have major and widespread impact on adult behavior and group-level characteristics. For example, sparse food stores lead younger bees to forage earlier in life and cause colonies to have radically different compositions (i.e., starved colonies have more foragers), which may have consequences for productivity (Schulz et al., 1998). Environmental factors can disrupt and induce temporal polytheisms, making it difficult to tease out cause and effect (reviewed in Johnson, 2010). For example, during the winter, when loss of workers is paramount, bees often become generalists.

One exciting area of recent research has emphasized the blurring of endogenous and exogenous mechanisms by highlighting the often profound role of pre- and postnatal maternal physiology on offspring behavior (see Chapters 19, 21, 35, and 36, this volume). Some effects occur even before birth. In mammals, maternal disease and immune activity during gestation can have an impact on offspring brain development and later behavior (e.g., Bauman et al., 2014). A mother's diet can have profound consequences on offspring fertility (Gardner, Ozanne, & Sinclair, 2009) and on their gastrointestinal microbiota and overall health (Thum et al., 2012). A growing body of literature across vertebrates in general has shown that mothers use stress hormones to translate environmental context into offspring phenotypes (Love, McGowan, & Sheriff, 2013). For example, in stickleback fish (*Gasterosteus aculeatus*), maternal stress leads to eggs that contain higher levels of stress hormones and juveniles that exhibit stronger antipredator behavior (tighter shoals; Giesing, Suski, Warner, & Bell, 2011; see also Chapter 40, this volume) and different gene

expression (Mommer & Bell, 2014; see also Chapter 18, this volume).

Mothers can also influence their young by choosing to lay eggs, gestate, or give birth in particular physical and social contexts. Experience with siblings in a prenatal, maternal environment can also have important impacts (reviewed by Ryan & Vandenberg, 2002). For example, in European rabbits (*Oryctolagus cuniculus*), the presence of littermates can enhance motor development (Nicolás, Martínez-Gómez, Hudson, & Bautista, 2011) and contribute to differences in personality (Hudson, Bautista, Reyes-Meza, Montor, & Rödel, 2011). Female rabbits from intermediate-sized litters have higher lifetime reproductive success (i.e., produce more offspring that survive to maturity; Rödel, von Holst, & Kraus, 2009), whereas males from smaller litters are larger, more aggressive, and more successful in mating season battles (Rödel & von Holst, 2009). Early postnatal sensory experiences in particular physical contexts can also have profound effects on later behavior (e.g., as reviewed by Anderson & Anton, 2014; Galef & Laland, 2005). In ectotherms, for example, nest location can affect offspring size at hatching, antipredator behavior, and ultimately survival (Lorion, DeNardo, Gorelick, & Lourdais, 2012; Mitchell, Maciel, & Janzen, 2015). In rats (*Rattus norvegicus*), maternal stress may be communicated through offspring licking, the amount of which can influence the social and anxiety behavior of adult offspring (Meaney, 2001; see also Chapters 18 and 35, this volume).

Learning

Learning is a special form of behavioral plasticity that can in turn be affected by both previous experience and more fixed aspects of individual animals. In addition to the direct impacts of early experience on behavior, early experiences can influence an animal's future degree of behavioral plasticity. For example, zebra finches treated with stress hormones during early development improved their later learning of a foraging task (Crino, Driscoll, Ton, & Breuner, 2014), whereas those experiencing an immune challenge in early development were less able to learn (Grindstaff, Hunsaker, & Cox, 2012). Learning can happen in adults as well; for example,

in wild yellow-eyed penguins (*Megadyptes antipodes*), previous stressful experiences with humans compromised their habituation to casual human contact (Ellenberg, Mattern, & Seddon, 2009). Recent studies have also found that learning is influenced by individual personality type. For example, more exploratory Iberian wall lizards (*Podarcis hispanica*; Rodríguez-Prieto, Martín, & Fernández-Juricic, 2011) and humans (LaRowe, Patrick, Curtin, & Kline, 2006) habituate more quickly, and more innovative blue tits (*Cyanistes caeruleus*) have faster social learning (Aplin, Sheldon, & Morand-Ferron, 2013).

Animals that learn may also suffer unique evolutionary costs because of the need to sample their environments repeatedly (Murren et al., 2015). For example, female cabbage white butterflies (*Pieris rapae*) that quickly learn to use color to identify appropriate host plants for oviposition produce fewer eggs than do females that learn more slowly (Snell-Rood, Davidowitz, & Papaj, 2011). They moderate this cost by producing larger eggs (investing more to ensure the success of each offspring) and by varying their relative investments in learning versus reproduction depending on the requirements of their immediate habitat (Snell-Rood, Davidowitz, & Papaj, 2013).

From an evolutionary perspective, developmental and learned changes in behavior during the lifespan of an animal can be described as norms of reaction that themselves evolve and are subject to natural and sexual selection (Dingemans & Wolf, 2013; Kasumovic, 2013; Stamps, 2015). For example, learning can promote evolutionary change by increasing behavioral innovation and, perhaps, speciation rates (Dukas, 2013). Learning often has an exploratory phase when individuals show considerable interindividual and intraindividual variation as certain contingencies are strengthened, leading to the acquisition of novel responses. Sometimes, learning can lead to the acquisition of a novel food source, and subsequent genetic changes can permit the optimization of the new diet. In some cultures, dairy farmers promoted the consumption of milk-based products, which led to the evolution of lactase in human populations (Tishkoff et al., 2007). Lactase expression is a requisite for survival;

monophagic mammalian infants need lactase to process the simple sugars in milk. In most mammals, the activity of the enzyme is dramatically reduced after weaning, but it continues to persist postweaning and into adulthood among populations with domesticated livestock that produce milk for consumption. This physiological adaptation, lactose tolerance, is sustained by cultural shifts and subsequent changes in gene expression. Thus, social individuals also impose selective pressures on each other (Danchin, Giraldeau, Valone, & Wagner, 2004), shaping the evolutionary landscape through a process that has been termed *cultural niche construction* (Laland & O'Brien, 2011). When behavioral plasticity is the result of linked underlying mechanisms, such as overlapping patterns of lactase gene expression (Ingram, Mulcare, Itan, Thomas, & Swallow, 2009), plasticity can facilitate adaptive evolution by creating opportunities for large, pleiotropic change. Thus, behavioral plasticity can have an important impact on the ability of animals to respond to novel environments (Sih, 2013).

Cycles and Seasons

Individual behavior can vary in daily or seasonal cycles, and it is often influenced by endogenous factors that are calibrated by exogenous cues (see Chapter 29, this volume). Although laboratory rodents exhibit little evidence of seasonal or circannual cycles in behavior or response to experimental treatments (Ferguson & Maier, 2013), many animals show light-dependent or photoperiodic shifts in aggression, gonad expression, and reproductive behavior in the wild. The physiological, behavioral, and neurochemical bases of circadian rhythms are beginning to be etched out (Bell-Pedersen et al., 2005), and assessments have revealed a strong phylogenetic signal for much of the diversity observed in circadian rhythms (reviewed in Menaker, Moreira, & Tosini, 1997).

Integrating information about the molecular and neural mechanisms and phylogenetic tree permits several generalizations. First, there are three systems that are largely responsible for the regulation of overt rhythms: retinas, the pineal complex (pineal and parietal eye or organ), and the suprachiasmatic nucleus of the hypothalamus.

Their interconnections form a central circadian axis common to all vertebrates. Second, in many vertebrates (except mammals) the pineal gland is a photoreceptor and a circadian oscillator. Last, all nonmammalian vertebrates possess extraretinal (and extrapineal) circadian photoreceptors. Discontinuities between the circadian system and phylogenetic lines may represent transitions of the species through different photic niches because of other selection pressures (e.g., nocturnal bottleneck). It is reasoned that mammals became nocturnal to avoid reptilian predatory pressures, which caused a shift from multiple distributed circadian photoreceptors to a single site retina (reviewed in Menaker et al., 1997). Although it is methodologically prohibitive to test this hypothesis in extant mammals, nocturnal transitions in nonmammalian vertebrates have shown similar reductions in circadian photoreceptors.

Cycles that occur over longer temporal periods also have common evolutionary mechanisms. Comparative studies of seasonal flocking in estralid finches have revealed that neuroendocrine mechanisms underlie species differences in aggression (Goodson, Wilson, & Schrock, 2012). Labeling receptor densities in socially relevant brain regions in field sparrows (*Spizella pusilla*), which seasonally flock, and male song sparrows (*Melospiza melodia*), which are territorial year round, revealed extensive species differences. Binding sites for mesotocin and corticotropin-releasing hormone are more abundant in sparrows that form winter flocks than in species that show territorial aggression year round. Species differences in correlations between neurochemistry and aggression may reflect evolved mechanisms that differentiate the highly territorial song sparrow from the less aggressive field sparrow. Taken together, these studies suggest temporal variation at multiple levels may be the result of evolution targeting common mechanisms during different life histories.

Personality and Context

Sometimes individual animals exhibit the same behavior regardless of context, a phenomenon that has been described as personality or consistent individual differences (e.g., as reviewed by A. B. Clark & Ehlinger, 1987; Sih, Bell, Johnson, & Ziemba, 2004;

see also Chapter 9, this volume). This results in a population consisting of individuals that exhibit different personality types or morphs. In many species, morphological differences (e.g., colors) between individuals are associated with fundamental differences in their behavior. Color morphs are often secondary sexual characteristics expressed by species with strong sexual selection. Color variants are commonly associated with alternative reproductive tactics, which often involve variation in aggression. Two closely related populations of mesquite lizards (*Sceloporus grammicus*) have diverged in the associations between color and aggression (Bastiaans, Morinaga, Castañeda Gaytán, Marshall, & Sinervo, 2013). One population exhibits orange, yellow, and blue throat morphs in males, which is suggested to be a heritable polymorphism. The other population exhibits orange, yellow, and white color morphs in males, which are expected to be discrete variants with the exception of the rare white mutants. In both populations, male throat colors can be categorized by aggression level displayed during male agonistic interactions, but the specifics of which color is more aggressive depends on the population. The orange chinstrap is associated with decreased aggressions in populations with blue-colored males, whereas white-throated males have lower levels of aggression in populations in which they occur. The population differences in morph–aggression association are, perhaps, because of the balance between frequency-dependent and correlational selection (Lancaster, McAdam, Hipsley, & Sinervo, 2014). Correlational selection maintains favorable trait combinations within each morphotype, and negative frequency-dependent selection can lead females to disassortatively mate with rare male morphs to produce conditionally fit offspring. In other adult lizards, coloration is stable across years (e.g., wall lizard [*Podarcis muralis*]; Calsbeek, Hasselquist, & Clobert, 2010), and aggression levels using staged territorial intrusions can be reliably resampled by observers (López & Martín, 2001).

Some have suggested that consistency in color patterns are recognized by members of the population through learned associations. For example, males who have repeated agonistic interaction with the same partner show lower levels of aggression

with this opponent even if the outcome changes (López & Martín, 2001). The consistency of color patterns, individual recognition, and learning together may reduce the cost of aggressive encounters, thereby stabilizing population social structure. Thus, the maintenance of the genetic polymorphisms that influence multiple traits in the natural environment may be the result of stable, fluctuating, and at times conflicting selection pressures, which can be reinforced by social experience with life history traits.

In other situations, individual behavior depends on context, in a sort of norm of reaction (Dingemans, Kazem, Réale, & Wright, 2010; Stamps, 2015; Stamps & Groothuis, 2010) or activational plasticity (Snell-Rood, 2013). As described previously for learning, recent studies have emphasized that the degree to which each individual can respond to its environment is itself a trait that can evolve (e.g., Murren et al., 2015). The degree of behavioral plasticity with respect to context can be influenced by underlying mechanisms, which can include endogenous or exogenous factors and often a complex interaction between the two (reviewed in Kasumovic, 2013). Color is often investigated as a trait that is stable throughout the life spans of individuals (e.g., color morphs in lizards), but many animals exhibit sequential color changes or reversible color plasticity during their lifetimes. Color changes can parallel ontogenetic and seasonal patterns, which are associated with developmental transitions or immediate adaptations to the environment. The buckeye butterfly (*Precis coenia*) exhibits a polyphenism in response to seasonal shifts in temperature and photoperiod (Rountree & Nijhout, 1995). Long days and higher temperatures during the summer induce earlier onset of ecdysteroid production, permitting the pale beige linea form to develop. If ecdysteroids are not present during a critical period in the early pupal stage, then the dark reddish-brown rosa morph develops (Rountree & Nijhout, 1995). Still, some populations of *Precis* differ in the ease with which the rosa form can be induced. This is reflected in the development of rosa or intermediate phenotypes by a small percentage of the population even when pupa are reared under optimal linea-inducing temperatures and

photoperiods, suggesting that other mechanisms are at work.

Some classic experimental designs can serve as powerful tools to examine the interdependencies of genes, the environment, and their products (e.g., cross-fostering [Meaney, 2001], transplant [Marchinko, 2003; Pruitt & Goodnight, 2014], split-population [Théry, 2007]). Reciprocal transplant and cross-fostering experiments involve removing young (or adults) from genotype-specific rearing environments and rearing them in a surrogate environment for populations involved, yielding a full-factorial design. For example, reciprocal wing transplant studies between genetic *rosa* and wild-type strains have shown that the *rosa* gene alters the physiological response mechanism that follows the ecdysteroid-sensitive period for linea morph induction.

Another experimental design used to understand how environmental factors influence plasticity is the split-population design. The split-population design involves placing a representative sample of the same population in all tested environmental conditions, which also produces a full-factorial design. By using a split-population design in the lab, the accuracy with which crab spiders (*Misumena vatia*) change color to match the white and yellow flowers on which they are found was shown to depend on the light reflected by the background and recent diet (Théry, 2007). The crab spider can reversibly change its color from white to yellow to match the color of the flower on which they are found. Prey consumed and light reflected by the background are important external factors in determining color change in crab spiders: Individuals exposed to a yellow background and fed red-eyed flies are better camouflaged than individuals exposed to a yellow background and provisioned with other prey morphs (Théry, 2007). The links among these factors are often forged through whole-organism performance traits, such as activity level or endurance (e.g., Miles, Sinervo, Hazard, Svensson, & Costa, 2007). Plasticity of this sort is then subject to natural and sexual selection (Dingemanse & Wolf, 2013) and can be studied effectively in comparisons of ancestral and derived forms (Foster, 2013).

Extrinsic Factors

Physical and social environments can contribute to individual variation. Intraspecific differences arising from organism–context interactions are influenced by developmental and activational plasticity, and here we emphasize entirely extrinsic factors. We parse out the organism–context interactions into social and physical contexts because it is a traditional distinction that remains effective in understanding individual variation, adaptation, and evolution.

Social environment is a particularly important context in which behavior can be plastic. Recent studies have highlighted the importance of noninteracting social partners in determining behavior. Animals modulate their behavior depending on the presence, and sometimes the identity, of bystanders in a phenomenon known as the *audience effect*. Wolf spiders (*Schizocosa ocreata*), for example, pay attention to the courtship signals produced by nearby rivals and then match those signals in producing their own (D. L. Clark, Roberts, & Uetz, 2012). It seems plausible that bystanders can exert significant selection pressure on individual behavior and the dynamics of cooperation, courtship, and conflict interactions (reviewed in Earley, 2010). For example, female crayfish (*Procambarus clarkii*) determine suitable mates by integrating information gathered from male–male aggressive encounters and individual recognition (Aquiloni & Gherardi, 2010). Eavesdropping female crayfish were positioned so that they had access to visual and chemical information of competing males, then had to choose between dominant and subordinate males that were either familiar (female observed them fight) or unfamiliar (female did not witness them fight). Females only preferred dominant males when they observed the particular male in a fight. This sophisticated form of mate selection may drive male crayfish to initiate more agonistic interactions or fight more vigorously in the presence of the female. Through these more intense displays, the signaling male might obtain benefits, such as securing the observing mate or deterring a current opponent, and enhance its future access to mates and minimize the occurrence or intensity of future agonistic interactions. Audience effects will thus exert positive selection pressure on

signalers to exhibit more risky behavior (reviewed in Earley, 2010).

Individuals may also differ in behavior because of differences in their roles within a social group. For example, keystone individuals, individuals with an inordinately large effect on group behavior, often behave quite differently than do other animals in the group (reviewed in Modlmeier, Keiser, Watters, Sih, & Pruitt, 2014). They may choose the direction of group travel, control access to a resource, or speed the transmission of diseases. In some cases, these individuals are larger, more dominant, or otherwise phenotypically distinct from other group members. Evolution can shape the degree to which groups contain individuals with different social roles, how easily individuals move in and out of those roles (e.g., Vital & Martins, 2011), and the relative proportion of individuals in each role in the larger group (e.g., Pruitt & Riechert, 2011).

Group composition can influence collective success. For example, aggregates of water striders (*Aquarius remigis*) differing in behavioral type (i.e., activity and aggression) showed differences in mating success (Sih & Watters, 2005). Groups with either active hyperaggressive or docile inactive males had a lower a frequency of matings than did groups with intermediate compositions. This is likely due to hyperaggressive males chasing off females and inactive males not exploring for mates. Thus, group composition may have a strong selective pressure on biobehavioral outcomes, and groups should regulate their compositions to achieve optimal success. Indeed, a socially polymorphic spider (*Anelosimus studiosus*) exhibits a behavioral polymorphism in which females exhibit either a docile or an aggressive behavioral phenotype, and colonies adjust their composition via locally adapted mechanisms (Pruitt & Goodnight, 2014). Experimentally created colonies of known composition were placed at sites that differed in resource abundance. Many colonies perished, but those that survived adjusted their composition to match naturally occurring mixtures at each site. The mechanism posited to underlie local adaptation of these colonies is behavioral plasticity in response to social context. For example, members may have selectively evicted colony members or ceased to produce these

behavioral types that were higher in abundance than optimal. Developmental plasticity, however, cannot be ruled out because some spiders might have transitioned to different phenotypes guided by similar mechanisms as described earlier with caste polytheism in another social insect, honeybees.

Environmental structure can have profound effects on relatively stable and transient behavioral traits. Recent studies have highlighted the influence of spatial organization on relatively stable traits such as size polymorphisms (e.g., Couvillon & Dornhaus, 2009) and division of labor (e.g., Jandt & Dornhaus, 2009). The spatial location of bumblebee (*Bombus impatiens*) larvae is spatially fixed in the nest, and centrally located pupae are larger than pupae on the periphery (Couvillon & Dornhaus, 2009). Later in life, the larvae tend to assume different social roles, with larger workers serving as foragers and smaller ones caring for the brood (Jandt & Dornhaus, 2009).

Other studies have shown that simple physical mechanisms can underlie transient behavior, such as group cohesion (available space; Shelton, Price, Ocasio, & Martins, 2015) and aggression (enclosure shape; Bazazi et al., 2008). These spatial characteristics are especially important in captive environments in which space is often at a premium and individuals are crammed into standardized enclosures (Mason et al., 2013). Physical environments can be powerful selective forces that alter life history traits. For example, barnacles (*Balanus glandularis*) exposed to greater water velocities produce shorter feeding appendages, but when transplanted to lower water velocity zones, appendages grow dramatically (i.e., growth change is greater than 100%; Marchinko, 2003). Plastic responses to the physical environment occur in juvenile and adult barnacles, which is a dramatic example of age-independent phenotypic plasticity.

Plastic responses to stochastic events have the potential to alter the selective environments experienced by individuals, thereby facilitating evolutionary change (e.g., Sih, 2013; West-Eberhard, 2003). An elegant example involves the predator-induced shift in Caribbean *Anolis* lizards. The introduction of a terrestrial predator led to differences in habitat use (e.g., arboreality) and, ultimately, population-level shifts in morphology because of altered selection in

the new environment (Losos, Schoener, & Spiller, 2004). Other unpredictable events, such as climatic changes, that parallel shifts in resource availability can influence evolution. Recent evidence has suggested that asynchrony in climatic conditions (e.g., precipitation) can drive evolutionary divergence because individuals locally adjust their reproductive behavior to current resource availability (e.g., water), which is changing rapidly with the onslaught of anthropogenic change (Quintero, González-Caro, Zalamea, & Cadena, 2014).

Although these findings may be particularly useful in predicting response to anthropogenic disturbance and climate change, much more research is needed before general conclusions can be drawn. For example, although sometimes animals make very rapid shifts in behavior, such as songbirds that sing at higher pitches to stand out above urban noise (Slabbekoorn, 2013), other differences may require genetic changes that accumulate over longer periods of time (e.g., Robison & Rowland, 2005).

Inheritance

Behavioral variation is shaped by a large variety of mechanisms, all of which can influence how differences in behavior are passed from ancestors to descendants. Inheritance can be classified into two categories: (a) genetic, or the transmission of DNA variation from parents to offspring, and (b) exogenous, or non-DNA sequence-based inheritance. Inheritance theory has been dominated by the first category of inheritance, or analytically tractable models of Mendelian segregation of DNA sequence. Some have suggested that the inheritance debate was conclusively settled by the overwhelming number of tightly coupled empirical and computational studies with evidence in exclusive support of the Mendelian genetic model and the impossible inheritance of traits that lacked a DNA sequence, exogenous inheritance (Mayr & Provine, 1980). Although largely ignored, evidence for exogenous inheritance continues to accumulate (Gottlieb, 1991a, 1991b; Jablonka & Lamb, 2014; West & King, 1987).

In addition to DNA, parents transmit many things to their offspring, such as siblings, traditions, territories, dominance rank, microbiota, and the machinery that can transmit these nongenetic

traits (e.g., epigenetic mechanisms), whose quality and quantity can influence offspring phenotype and success (Alberts, 2008; Meaney, 2001; Mousseau & Fox, 1998; Rödel et al., 2009; Thum et al., 2012; West & King, 1987). A well-studied example of exogenous inheritance comes from studies of maternal care in rats (see Chapter 35, this volume). Rat mothers differ in levels of pup-directed licking, grooming, and arch-back nursing (Meaney, 2007). Offspring show profound maternal care-dependent differences in cognition, neurochemistry, sexual behavior, and emotionality (Cameron et al., 2005; Meaney, 2007). Cross-fostering studies have revealed that female rats adopt maternal care patterns experienced in infancy, which suggests that exogenous mechanisms can lead to long-term changes in behavior. These changes have molecular signatures, such as changes in patterns of DNA methylation and histone modification (see Chapters 18 and 22, this volume). Although more research is needed, recent studies have linked molecular and experiential mechanisms to characterize the cascade of changes responsible for the normal process of development (Cameron et al., 2005; Kundakovic, Lim, Gudsnuk, & Champagne, 2013; see also Chapter 22, this volume).

ADAPTATION

Phenotypic diversity is thought to reflect extensive genetic variation, even among populations of the same species, through genetic adaptation. Neurochemical pathways, genetic markers, and morphological structures, however, are broadly conserved (e.g., Bell-Pedersen et al., 2005; Goodson et al., 2012; Menaker et al., 1997), leading some to suggest that the mechanisms for the origin and evolution of diversity invoke modifications of existing genetic networks rather than the evolution of novel genes or genetic pathways, leading to ontogenetic adaptation (reviewed in West-Eberhard, 2003). In genetic and ontogenetic adaptation perspectives, similar forces are sometimes described in guiding the match of the organism to the environment, but the scale and timing at which these selective forces act differ. In the genetic adaptation view, selective forces are described as operating at the level of gene frequencies in adults, who pass on those genes. The

ontogenetic adaptation perspective pushes one to view the specialized responses of the organism to specific environmental stimuli. The concept of ontogenetic adaptation suggests that each developmental stage is complete, not an immature form of the adult goal (reviewed in Alberts, 2008). The idea that selection can operate on each developmental time point is an evolutionary tenet introduced by the ontogenetic adaptation perspective.

Several conceptual frameworks were put forth to explain how different inputs can be modulated to suit a variety of developmental roles and contexts. One hypothesis for the link between genetic mechanisms and developmental states suggests that evolutionary change is facilitated by sensitivity to environmental cues and by modifications of organismal development that produce selectable phenotypic variation (e.g., Gottlieb, 1991b; Jablonka & Lamb, 2014; West & King, 1987). Through this process, previously neutral genetic variation may gain function under novel or stressful conditions, either through expression of genotypic variation or through the action of expressed gene products. The induction and recruitment of this newly revealed variation may facilitate the generation of new and favored phenotypes through developmental changes activated by novel gene expression. This complex of interactions was posited to evolve through heterochronic shifts. Moreover, heterochronic shifts were predicted to buffer development under fluctuating environments while maintaining epigenetic sensitivity for species-typical development and local adaptation. Historically, one of the hindrances to the ontogenetic view was the absence of experimental evidence demonstrating how existing genetic networks can be modulated to suit a variety of developmental roles and contexts.

Recent advances in understanding how gene expression influences behavioral plasticity help to link causes of individual development with the causes of individual differences, permitting a more comprehensive understanding of the mechanisms of evolutionary change (e.g., Fernald, 2015; Meaney, 2001). Although hormones and neurotransmitters are clearly involved in producing behavioral variation, it now appears that the primary mechanism associated with differences between individuals

and how individuals behave in different contexts is the abundance and distribution of hormone and neurotransmitter receptors. The abundance and distribution of oxytocin receptors seem to be particularly important in determining variation in social behavior. For example, differences in prairie vole (*Microtus ochrogaster*) social behavior are associated with variation in the sequence and expression of a vasopressin receptor gene, and the degree of monogamy of young male prairie voles can be manipulated by blocking the production of new vasopressin receptors in the brain (Barrett et al., 2013). In other organisms, receptors for nonapeptides (Goodson et al., 2012) and androgens (Rosvall et al., 2012) are clearly also important.

Pleiotropy also contributes to behavioral plasticity, often through the action of regulatory switches, which again coordinate the expression of gene networks underlying complex phenotypes. In several vertebrates, for example, individuals that are darker in color also tend to be more aggressive (Ducrest, Keller, & Roulin, 2008), more sexually active, and more able to evade predators (Kim & Velando, 2015; van den Brink, Dolivo, Falourd, Dreiss, & Roulin, 2012). All of these phenomena can be explained, in part, by the pleiotropic effects of melanocortin receptors, which are involved in both color production and several hormonal (Ducrest et al., 2008) and immune (Männiste & Hörak, 2014) pathways. A gene's susceptibility to mediate covariation in behavioral traits, via pleiotropic effects, lies in the promiscuous properties of its biochemical products and their ability to bind to a number of receptors with widespread distribution. For example, coloration by melanin is regulated by the melanocortin system. The melanocortin system involves post-translational products of the proopiomelanocortin locus or melacortins, which bind to five melacortin receptors located in a number of tissues (reviewed in Ducrest et al., 2008). Key melacortin receptors and products of the proopiomelanocortin gene are involved in various endocrinological pathways, which are important for behavioral responses.

Another important contributor to behavioral variation is epistasis, which describes the non-independent effects of genetic polymorphisms that influence the same behavioral phenotype.

Epistatic effects are implicated in transcripts that underlie nervous system function (Chesler et al., 2005), dominance and reproduction (Renn, Aubin-Horth, & Hofmann, 2008), odor-guided behavior (Anholt et al., 2003), and other behavioral phenotypes (reviewed in Mackay, 2014). Evolution by sexual selection can promote the formation of such pleiotropic links as condition-dependent signals for communication and mate choice (Hill, 2011). From this perspective, it is not surprising that aggression in *Drosophila* is influenced more by pleiotropic and epistatic effects than by the simple effects of homozygous genes (Zwarts et al., 2011). Similarly, pleiotropic and epistatic genetic effects dominate nervous system function (Chesler et al., 2005), dominance and reproduction (Renn et al., 2008), odor-guided behavior (Anholt et al., 2003), and other behavioral phenotypes (see also review by Mackay, 2014). Mapping these complex genetic interactions and their relationship with behavioral traits poses a strong experimental and empirical challenge (Mackay, 2014). The development of statistical tools, complex experimental designs, and model organisms will provide the methodological muscle to allow future advances to be made.

HUMAN IMPACTS

Epigenetics, epistasis, pleiotropy, and cultural evolution all contribute to producing behavioral variation in wild animal populations, the raw substrate on which evolution acts. Humans also play an important role in shaping future evolution. Human-induced rapid environmental change is becoming recognized as an increasingly important factor underlying behavioral variation (e.g., Sih, 2013; Wong & Candolin, 2015). Although meta-analyses have confirmed that the number of individuals entering a new area (propagule pressure) is the most important factor determining the ability of animal species to successfully exploit new environments (Jeschke & Strayer, 2006), behavioral flexibility can also influence that success. Animal species that are plastic and can respond appropriately to a wide range of contexts are easier to domesticate and may do better in urban contexts (e.g., Mason et al., 2013; see also Chapter 16, this volume). This plasticity,

however, may also slow the pace of adaptive evolution, making it more difficult for them to withstand more major shifts resulting from climate change and pollution. In this section, we consider this opposition of forces in detail, making some specific predictions about the impact of anthropogenic effects.

Profound Change Through Shifts in Fundamental Physiology

In many cases, human-induced rapid environmental change has an impact on behavior through its wide-ranging direct and indirect effects on physiology. For example, shifts in temperatures affect ectotherm locomotion (Johnston & Temple, 2002), but temperature fluctuations can also have profound indirect effects on other aspects of behavior (see Chapter 45, this volume). For example, in coral reef fishes, increased temperature leads to higher CO₂ levels, which impair sensory ability (Munday, McCormick, & Nilsson, 2012). Goldfish (*Carassius auratus*) that have recently acclimated to warmer temperatures can also be hyperexcitable and engage in excessive antipredator behavior (Szabo, Brookings, Preuss, & Faber, 2008). Some individuals become bolder in increasing temperature, whereas others do not, such that small temperature fluctuations can lead to profound changes in social context (Biro, Beckmann, & Stamps, 2009). This change in phenotype might have consequences for mate choice and competition, especially if these newly bold individuals fare better in aggressive interactions, which allows them to gain greater access to mates and other resources.

Temperature fluctuations can also affect different species differently, for example significantly altering the interactions between predators and prey (Gri-galtchik, Ward, & Seebacher, 2012). Other environmental factors can also be important. Temperature often interacts with light (Swaddle et al., 2015), which can have unexpectedly far-reaching physiological effects. For example, exposure to artificial lights at night can lead to obesity and changes in foraging behavior (Fonken & Nelson, 2014). Changes in an inherited phenotype can open the gates to evolution (Swaddle et al., 2015), whether via genetic or cultural mechanisms (as with bird song, e.g., Slab-bekoorn, 2013; see also Chapter 15, this volume and Volume 2, Chapter 20, this handbook).

Plasticity Has a Sweet Spot

Although behavioral plasticity can be an important way that animals cope with rapid environmental change, sometimes the plasticity is insufficient to counter the effects of anthropogenic change and increases a species' vulnerability to extinction (e.g., Sinervo et al., 2010). There are many examples of the benefits of plasticity to species survival. Animals that are able to make use of novel food sources may be more successful in a new context. Omnivorous freshwater fish are more likely to be successful invaders, making use of novel food items more readily than do specialist feeders (Ruesink, 2005). Animals with bigger brains are more successful in novel environments (Maklakov, Immler, Gonzalez-Voyer, Rönn, & Kolm, 2011; Sol, Bacher, Reader, & Lefebvre, 2008). However, this investment in a larger brain may constrain other plastic responses. For example, guppies (*Poecilia reticulata*) artificially selected for either large or small relative brain size evolved rapidly in response to divergent selection. Small-brained fish performed poorer in learning tasks than large-brained fish, which developed smaller guts and produced fewer offspring. Thus, large brains can lead to trade-offs with growth and reproduction (e.g., Kotschal et al., 2013).

However, too much flexibility can be a hindrance to the long-term success of a species in a new context. Some flexible species moving into a new area may rely heavily on low-quality resources rather than expend energy searching for higher quality food or shelter (an evolutionary trap; Robertson, Rehage, & Sih, 2013). Similarly, migratory birds tend to be less successful in establishing themselves in new areas (Blackburn, Cassey, & Lockwood, 2009). These costly effects of migration may result from migrants moving from a heterogeneous environment to an environment in which they are not favored by selection. Adrenocortical stress response is one plastic hormonal response used to cope effectively with environmental perturbations. However, prolonged or repeated incidences of stress can result in dysregulation of many endocrine processes and long-term damage. Thus, the most resilient individuals may be those that do not respond flexibly to the environment (Wingfield, 2013). There appears to be an optimal amount of behavioral flexibility that

allows animals to be successful in new or changing environments.

Many of the stressors experienced by animals in captivity (reviewed by Morgan & Tromborg, 2007) parallel those experienced by animals in urban environments (reviewed by Sol, Lapiedra, & González-Lagos, 2013). Thus, individuals that are successful (or not) in captivity may be similarly successful (or not) in urban environments (Mason et al., 2013). Traits that help animals thrive in close proximity to humans often also predict invasiveness in the wild (Jeschke & Strayer, 2006). For example, boldness may be one reason that zoo life and urban environments are less stressful for some wild species than others (Atwell et al., 2012). In contrast, species with expansive home ranges, such as carnivores, are less suited for both zoo and urban contexts (Clubb & Mason, 2003, 2007). Captive animals that have also undergone domestication may be different in that their responses to the human-altered environment often have a genetic basis (e.g., Robison & Rowland, 2005; see also Chapter 16, this volume), adding another layer of complexity. Thus, although the amount of behavioral variation can have immense predictive power in identifying a behavioral variant's ability to cope with rapid environmental change, the optimal level of plasticity also varies with context, thus complicating predictions.

CONCLUSION

In summary, behavioral phenotypes are shaped by a host of interactions occurring at multiple levels in a particular context. In the examples we presented, many of the experiential mechanisms influenced similar traits. The redundant pathways serve as buffers against perturbation and assurances that the organism will continue down the normal path of development. The multitude of interaction channels demonstrates the malleability of behavioral phenotypes, and their sensitivity to variation makes them a prime target for selection. Experience can also reduce behavioral variation, which can make it resistant to selection and potentially an agent of evolutionary change. Defining the mechanisms that cause individual variation is a crucial step in understanding the link between developmental mechanisms,

population processes, and macroevolutionary patterns. Understanding the mechanisms that underlie individual behavioral variation will help us better predict how individuals, groups, populations, and species will respond to human-induced rapid environmental change.

References

- Alberts, J. R. (2008). The nature of nurturant niches in ontogeny. *Philosophical Psychology*, *21*, 295–303. <http://dx.doi.org/10.1080/09515080802169814>
- Anderson, P., & Anton, S. (2014). Experience-based modulation of behavioural responses to plant volatiles and other sensory cues in insect herbivores. *Plant, Cell & Environment*, *37*, 1826–1835. <http://dx.doi.org/10.1111/pce.12342>
- Anholt, R. R. H., Dilda, C. L., Chang, S., Fanara, J.-J., Kulkarni, N. H., Ganguly, I., . . . Mackay, T. F. C. (2003). The genetic architecture of odor-guided behavior in *Drosophila*: Epistasis and the transcriptome. *Nature Genetics*, *35*, 180–184. <http://dx.doi.org/10.1038/ng1240>
- Aplin, L. M., Sheldon, B. C., & Morand-Ferron, J. (2013). Milk bottles revisited: Social learning and individual variation in the blue tit, *Cyanistes caeruleus*. *Animal Behaviour*, *85*, 1225–1232. <http://dx.doi.org/10.1016/j.anbehav.2013.03.009>
- Aquiloni, L., & Gherardi, F. (2010). Crayfish females eavesdrop on fighting males and use smell and sight to recognize the identity of the winner. *Animal Behaviour*, *79*, 265–269. <http://dx.doi.org/10.1016/j.anbehav.2009.09.024>
- Atwell, J. W., Cardoso, G. C., Whittaker, D. J., Campbell-Nelson, S., Robertson, K. W., & Ketterson, E. D. (2012). Boldness behavior and stress physiology in a novel urban environment suggest rapid correlated evolutionary adaptation. *Behavioral Ecology*, *23*, 960–969. <http://dx.doi.org/10.1093/beheco/ars059>
- Barrett, C. E., Keebaugh, A. C., Ahern, T. H., Bass, C. E., Terwilliger, E. F., & Young, L. J. (2013). Variation in vasopressin receptor (Avpr1a) expression creates diversity in behaviors related to monogamy in prairie voles. *Hormones and Behavior*, *63*, 518–526. <http://dx.doi.org/10.1016/j.yhbeh.2013.01.005>
- Bastiaans, E., Morinaga, G., Castañeda Gaytán, J. G., Marshall, J. C., & Sinervo, B. (2013). Male aggression varies with throat color in 2 distinct populations of the mesquite lizard. *Behavioral Ecology*, *24*, 968–981. <http://dx.doi.org/10.1093/beheco/art010>
- Bateson, P., & Gluckman, P. (2012). Plasticity and robustness in development and evolution. *International Journal of Epidemiology*, *41*, 219–223. <http://dx.doi.org/10.1093/ije/dyr240>
- Bauman, M. D., Iosif, A.-M., Smith, S. E. P., Bregere, C., Amaral, D. G., & Patterson, P. H. (2014). Activation of the maternal immune system during pregnancy alters behavioral development of rhesus monkey offspring. *Biological Psychiatry*, *75*, 332–341. <http://dx.doi.org/10.1016/j.biopsych.2013.06.025>
- Bazazi, S., Buhl, J., Hale, J. J., Anstey, M. L., Sword, G. A., Simpson, S. J., & Couzin, I. D. (2008). Collective motion and cannibalism in locust migratory bands. *Current Biology*, *18*, 735–739. <http://dx.doi.org/10.1016/j.cub.2008.04.035>
- Bell-Pedersen, D., Cassone, V. M., Earnest, D. J., Golden, S. S., Hardin, P. E., Thomas, T. L., & Zoran, M. J. (2005). Circadian rhythms from multiple oscillators: Lessons from diverse organisms. *Nature Reviews Genetics*, *6*, 544–556. <http://dx.doi.org/10.1038/nrg1633>
- Biro, P. A., Beckmann, C., & Stamps, J. A. (2009). Small within-day increases in temperature affects boldness and alters personality in coral reef fish. *Proceedings of the Royal Society: Series B, Biological Sciences*, *277*, 71–77.
- Blackburn, T. M., Cassey, P., & Lockwood, J. L. (2009). The role of species traits in the establishment success of exotic birds. *Global Change Biology*, *15*, 2852–2860. <http://dx.doi.org/10.1111/j.1365-2486.2008.01841.x>
- Boogert, N. J., Farine, D. R., & Spencer, K. A. (2014). Developmental stress predicts social network position. *Biology Letters*, *10*, 20140561.
- Calsbeek, B., Hasselquist, D., & Clobert, J. (2010). Multivariate phenotypes and the potential for alternative phenotypic optima in wall lizard (*Podarcis muralis*) ventral colour morphs. *Journal of Evolutionary Biology*, *23*, 1138–1147. <http://dx.doi.org/10.1111/j.1420-9101.2010.01978.x>
- Cameron, N. M., Champagne, F. A., Parent, C., Fish, E. W., Ozaki-Kuroda, K., & Meaney, M. J. (2005). The programming of individual differences in defensive responses and reproductive strategies in the rat through variations in maternal care. *Neuroscience and Biobehavioral Reviews*, *29*, 843–865. <http://dx.doi.org/10.1016/j.neubiorev.2005.03.022>
- Chesler, E. J., Lu, L., Shou, S., Qu, Y., Gu, J., Wang, J., . . . Williams, R. W. (2005). Complex trait analysis of gene expression uncovers polygenic and pleiotropic networks that modulate nervous system function. *Nature Genetics*, *37*, 233–242. <http://dx.doi.org/10.1038/ng1518>
- Clark, A. B., & Ehlinger, T. J. (1987). Pattern and adaptation in individual behavioral differences In P. P. G. Bateson & P. H. Klopfer (Eds.), *Perspectives in ethology* (pp. 1–47). http://dx.doi.org/10.1007/978-1-4613-1815-6_1
- Clark, D. L., Roberts, J. A., & Uetz, G. W. (2012). Eavesdropping and signal matching in visual courtship displays of spiders. *Biology Letters*, *8*, 375–378.

- Clubb, R., & Mason, G. J. (2003). Animal welfare: Captivity effects on wide-ranging carnivores. *Nature*, 425, 473–474. <http://dx.doi.org/10.1038/425473a>
- Clubb, R., & Mason, G. J. (2007). Natural behavioural biology as a risk factor in carnivore welfare: How analysing species differences could help zoos improve enclosures. *Applied Animal Behaviour Science*, 102, 303–328. <http://dx.doi.org/10.1016/j.applanim.2006.05.033>
- Couvillon, M. J., & Dornhaus, A. (2009). Location, location, location: Larvae position inside the nest is correlated with adult body size in worker bumblebees (*Bombus impatiens*). *Proceedings of the Royal Society: Series B, Biological Sciences*, 276, 2411–2418. <http://dx.doi.org/10.1098/rspb.2009.0172>
- Crino, O. L., Driscoll, S. C., Ton, R., & Breuner, C. W. (2014). Corticosterone exposure during development improves performance on a novel foraging task in zebra finches. *Animal Behaviour*, 91, 27–32. <http://dx.doi.org/10.1016/j.anbehav.2014.02.017>
- Danchin, E., Giraldeau, L.-A., Valone, T. J., & Wagner, R. H. (2004). Public information: From nosy neighbors to cultural evolution. *Science*, 305, 487–491. <http://dx.doi.org/10.1126/science.1098254>
- Dingemanse, N. J., Kazem, A. J. N., Réale, D., & Wright, J. (2010). Behavioural reaction norms: Animal personality meets individual plasticity. *Trends in Ecology & Evolution*, 25, 81–89. <http://dx.doi.org/10.1016/j.tree.2009.07.013>
- Dingemanse, N. J., & Wolf, M. (2013). Between-individual differences in behavioural plasticity within populations: Causes and consequences. *Animal Behaviour*, 85, 1031–1039. <http://dx.doi.org/10.1016/j.anbehav.2012.12.032>
- Ducrest, A.-L., Keller, L., & Roulin, A. (2008). Pleiotropy in the melanocortin system, coloration and behavioural syndromes. *Trends in Ecology & Evolution*, 23, 502–510. <http://dx.doi.org/10.1016/j.tree.2008.06.001>
- Dukas, R. (2013). Effects of learning on evolution: Robustness, innovation and speciation. *Animal Behaviour*, 85, 1023–1030. <http://dx.doi.org/10.1016/j.anbehav.2012.12.030>
- Earley, R. L. (2010). Social eavesdropping and the evolution of conditional cooperation and cheating strategies. *Philosophical Transactions of the Royal Society: Series B, Biological Sciences*, 365, 2675–2686. <http://dx.doi.org/10.1098/rstb.2010.0147>
- Ellenberg, U., Mattern, T., & Seddon, P. J. (2009). Habituation potential of yellow-eyed penguins depends on sex, character and previous experience with humans. *Animal Behaviour*, 77, 289–296. <http://dx.doi.org/10.1016/j.anbehav.2008.09.021>
- Fagen, R. (1982). Evolutionary issues in development of behavioral flexibility. In P. P. G. Bateson & P. H. Klopfer (Eds.), *Ontogeny* (pp. 365–383). http://dx.doi.org/10.1007/978-1-4615-7578-8_8
- Ferguson, S. A., & Maier, K. L. (2013). A review of seasonal/circannual effects of laboratory rodent behavior. *Physiology & Behavior*, 119, 130–136. <http://dx.doi.org/10.1016/j.physbeh.2013.06.007>
- Fernald, R. D. (2015). Social behaviour: Can it change the brain? *Animal Behaviour*, 103, 259–265. <http://dx.doi.org/10.1016/j.anbehav.2015.01.019>
- Fonken, L. K., & Nelson, R. J. (2014). The effects of light at night on circadian clocks and metabolism. *Endocrine Reviews*, 35, 648–670. <http://dx.doi.org/10.1210/er.2013-1051>
- Foster, S. A. (1995). Constraint, adaptation, and opportunism in the design of behavioral phenotypes. *Perspectives in Ethology*, 11, 61–81.
- Foster, S. A. (2013). Evolution of behavioural phenotypes: Influences of ancestry and expression. *Animal Behaviour*, 85, 1061–1075. <http://dx.doi.org/10.1016/j.anbehav.2013.02.008>
- Frisch, A. (2004). Sex-change and gonadal steroids in sequentially-hermaphroditic teleost fish. *Reviews in Fish Biology and Fisheries*, 14, 481–499. <http://dx.doi.org/10.1007/s11160-005-3586-8>
- Galef, B. G., & Laland, K. N. (2005). Social learning in animals: Empirical studies and theoretical models. *Bioscience*, 55, 489–499. [http://dx.doi.org/10.1641/0006-3568\(2005\)055\[0489:SLIAES\]2.0.CO;2](http://dx.doi.org/10.1641/0006-3568(2005)055[0489:SLIAES]2.0.CO;2)
- Gardner, D. S., Ozanne, S. E., & Sinclair, K. D. (2009). Effect of the early-life nutritional environment on fecundity and fertility of mammals. *Philosophical Transactions of the Royal Society: Series B, Biological Sciences*, 364, 3419–3427. <http://dx.doi.org/10.1098/rstb.2009.0121>
- Giesing, E. R., Suski, C. D., Warner, R. E., & Bell, A. M. (2011). Female sticklebacks transfer information via eggs: Effects of maternal experience with predators on offspring. *Proceedings of the Royal Society: Series B, Biological Sciences*, 278, 1753–1759.
- Goodson, J. L., Wilson, L. C., & Schrock, S. E. (2012). To flock or fight: Neurochemical signatures of divergent life histories in sparrows. *Proceedings of the National Academy of Sciences, USA*, 109(Suppl. 1), 10685–10692. <http://dx.doi.org/10.1073/pnas.1203394109>
- Gottlieb, G. (1991a). Experiential canalization of behavioral development: Results. *Developmental Psychology*, 27, 35–39. <http://dx.doi.org/10.1037/0012-1649.27.1.35>
- Gottlieb, G. (1991b). Experiential canalization of behavioral development: Theory. *Developmental Psychology*, 27, 35–39. <http://dx.doi.org/10.1037/0012-1649.27.1.35>

- Psychology*, 27, 4–13. <http://dx.doi.org/10.1037/0012-1649.27.1.4>
- Grigaltchik, V. S., Ward, A. J. W., & Seebacher, F. (2012). Thermal acclimation of interactions: Differential responses to temperature change alter predator–prey relationship. *Proceedings of the Royal Society: Series B, Biological Sciences*, 279, 4058–4064.
- Grindstaff, J. L., Hunsaker, V. R., & Cox, S. N. (2012). Maternal and developmental immune challenges alter behavior and learning ability of offspring. *Hormones and Behavior*, 62, 337–344. <http://dx.doi.org/10.1016/j.yhbeh.2012.04.005>
- Hensch, T. K. (2004). Critical period regulation. *Annual Review of Neuroscience*, 27, 549–579. <http://dx.doi.org/10.1146/annurev.neuro.27.070203.144327>
- Hess, E. H. (1973). *Imprinting: Early experience and the developmental psychobiology of attachment*. New York, NY: Van Nostrand Reinhold.
- Hill, G. E. (2011). Condition-dependent traits as signals of the functionality of vital cellular processes. *Ecology Letters*, 14, 625–634. <http://dx.doi.org/10.1111/j.1461-0248.2011.01622.x>
- Hudson, R., Bautista, A., Reyes-Meza, V., Montor, J. M., & Rödel, H. G. (2011). The effect of siblings on early development: A potential contributor to personality differences in mammals. *Developmental Psychobiology*, 53, 564–574. <http://dx.doi.org/10.1002/dev.20535>
- Ingram, C. J. E., Mulcare, C. A., Itan, Y., Thomas, M. G., & Swallow, D. M. (2009). Lactose digestion and the evolutionary genetics of lactase persistence. *Human Genetics*, 124, 579–591. <http://dx.doi.org/10.1007/s00439-008-0593-6>
- Jablonka, E., & Lamb, M. J. (2014). *Evolution in four dimensions, revised edition: Genetic, epigenetic, behavioral, and symbolic variation in the history of life*. Cambridge, MA: MIT Press.
- Jandt, J. M., & Dornhaus, A. (2009). Spatial organization and division of labour in the bumblebee *Bombus impatiens*. *Animal Behaviour*, 77, 641–651. <http://dx.doi.org/10.1016/j.anbehav.2008.11.019>
- Jeschke, J. M., & Strayer, D. L. (2006). Determinants of vertebrate invasion success in Europe and North America. *Global Change Biology*, 12, 1608–1619. <http://dx.doi.org/10.1111/j.1365-2486.2006.01213.x>
- Johnson, B. R. (2010). Division of labor in honeybees: Form, function, and proximate mechanisms. *Behavioral Ecology and Sociobiology*, 64, 305–316. <http://dx.doi.org/10.1007/s00265-009-0874-7>
- Johnston, I. A., & Temple, G. K. (2002). Thermal plasticity of skeletal muscle phenotype in ectothermic vertebrates and its significance for locomotory behaviour. *Journal of Experimental Biology*, 205, 2305–2322.
- Kasumovic, M. M. (2013). The multidimensional consequences of the juvenile environment: Towards an integrative view of the adult phenotype. *Animal Behaviour*, 85, 1049–1059. <http://dx.doi.org/10.1016/j.anbehav.2013.02.009>
- Kim, S.-Y., & Velando, A. (2015). Phenotypic integration between antipredator behavior and camouflage pattern in juvenile sticklebacks. *Evolution: International Journal of Organic Evolution*, 69, 830–838. <http://dx.doi.org/10.1111/evo.12600>
- Kotrschal, A., Rogell, B., Bundsen, A., Svensson, B., Zajitschek, S., Brännström, I., . . . Kolm, N. (2013). Artificial selection on relative brain size in the guppy reveals costs and benefits of evolving a larger brain. *Current Biology*, 23, 168–171. <http://dx.doi.org/10.1016/j.cub.2012.11.058>
- Kundakovic, M., Lim, S., Gudsnuk, K., & Champagne, F. A. (2013). Sex-specific and strain-dependent effects of early life adversity on behavioral and epigenetic outcomes. *Frontiers in Psychiatry*, 4, 78. <http://dx.doi.org/10.3389/fpsy.2013.00078>
- Laland, K., & O'Brien, M. (2011). Cultural niche construction: An introduction. *Biological Theory*, 6, 191–202. <http://dx.doi.org/10.1007/s13752-012-0026-6>
- Lancaster, L. T., McAdam, A. G., Hipsley, C. A., & Sinervo, B. R. (2014). Frequency-dependent and correlational selection pressures have conflicting consequences for assortative mating in a color-polymorphic lizard, *Uta stansburiana*. *American Naturalist*, 184, 188–197. <http://dx.doi.org/10.1086/676645>
- LaRowe, S. D., Patrick, C. J., Curtin, J. J., & Kline, J. P. (2006). Personality correlates of startle habituation. *Biological Psychology*, 72, 257–264. <http://dx.doi.org/10.1016/j.biopsycho.2005.11.008>
- Lehrman, D. S. (1953). A critique of Konrad Lorenz's theory of instinctive behavior. *Quarterly Review of Biology*, 28, 337–363. <http://dx.doi.org/10.1086/399858>
- López, P., & Martín, J. (2001). Fighting rules and rival recognition reduce costs of aggression in male lizards, *Podarcis hispanica*. *Behavioral Ecology and Sociobiology*, 49, 111–116. <http://dx.doi.org/10.1007/s002650000288>
- Lorenz, K. (1937). Imprinting. *Auk*, 54, 245–273. <http://dx.doi.org/10.2307/4078077>
- Lorenz, K. (1971). *Studies in animal and human behaviour: Vol. II* (R. Martin, Trans.). <http://dx.doi.org/10.4159/harvard.9780674430426>
- Lorrioux, S., DeNardo, D. F., Gorelick, R., & Lourdis, O. (2012). Maternal influences on early development: Preferred temperature prior to oviposition hastens embryogenesis and enhances offspring traits in the Children's python, *Antaresia childreni*. *Journal of*

- Experimental Biology*, 215, 1346–1353. <http://dx.doi.org/10.1242/jeb.059113>
- Losos, J. B., Schoener, T. W., & Spiller, D. A. (2004). Predator-induced behaviour shifts and natural selection in field-experimental lizard populations. *Nature*, 432, 505–508. <http://dx.doi.org/10.1038/nature03039>
- Love, O. P., McGowan, P. O., & Sheriff, M. J. (2013). Maternal adversity and ecological stressors in natural populations: The role of stress axis programming in individuals, with implications for populations and communities. *Functional Ecology*, 27, 81–92. <http://dx.doi.org/10.1111/j.1365-2435.2012.02040.x>
- Mackay, T. F. C. (2014). Epistasis and quantitative traits: Using model organisms to study gene–gene interactions. *Nature Reviews Genetics*, 15, 22–33. <http://dx.doi.org/10.1038/nrg3627>
- Maklakov, A. A., Immler, S., Gonzalez-Voyer, A., Rönn, J., & Kolm, N. (2011). Brains and the city: Big-brained passerine birds succeed in urban environments. *Biology Letters*, 7, 730–732. <http://dx.doi.org/10.1098/rsbl.2011.0341>
- Männiste, M., & Hörak, P. (2014). Emerging infectious disease selects for darker plumage coloration in greenfinches. *Frontiers in Ecology and Evolution*, 2, 4. <http://dx.doi.org/10.3389/fevo.2014.00004>
- Marchinko, K. B. (2003). Dramatic phenotypic plasticity in barnacle legs (*Balanus glandula* Darwin): Magnitude, age dependence, and speed of response. *Evolution: International Journal of Organic Evolution*, 57, 1281–1290. <http://dx.doi.org/10.1111/j.0014-3820.2003.tb00336.x>
- Mason, G. J., Burn, C. C., Dallaire, J. A., Kroshko, J., McDonald Kinkaid, H., & Jeschke, J. M. (2013). Plastic animals in cages: Behavioural flexibility and responses to captivity. *Animal Behaviour*, 85, 1113–1126. <http://dx.doi.org/10.1016/j.anbehav.2013.02.002>
- Mayr, E., & Provine, W. B. (Eds.). (1980). *The evolutionary synthesis: Perspectives on the unification of biology*. <http://dx.doi.org/10.4159/harvard.9780674865389>
- Meaney, M. J. (2001). Maternal care, gene expression, and the transmission of individual differences in stress reactivity across generations. *Annual Review of Neuroscience*, 24, 1161–1192. <http://dx.doi.org/10.1146/annurev.neuro.24.1.1161>
- Meaney, M. J. (2007). Environmental programming of phenotypic diversity in female reproductive strategies. *Advances in Genetics*, 59, 173–215. [http://dx.doi.org/10.1016/S0065-2660\(07\)59007-3](http://dx.doi.org/10.1016/S0065-2660(07)59007-3)
- Menaker, M., Moreira, L. F., & Tosini, G. (1997). Evolution of circadian organization in vertebrates. *Brazilian Journal of Medical and Biological Research*, 30, 305–313. <http://dx.doi.org/10.1590/S0100-879X1997000300003>
- Miles, D. B., Sinervo, B., Hazard, L. C., Svensson, E. I., & Costa, D. (2007). Relating endocrinology, physiology and behaviour using species with alternative mating strategies. *Functional Ecology*, 21, 653–665. <http://dx.doi.org/10.1111/j.1365-2435.2007.01304.x>
- Mitchell, T. S., Maciel, J. A., & Janzen, F. J. (2015). Maternal effects influence phenotypes and survival during early life stages in an aquatic turtle. *Functional Ecology*, 29, 268–276. <http://dx.doi.org/10.1111/1365-2435.12315>
- Modlmeier, A. P., Keiser, C. N., Watters, J. V., Sih, A., & Pruitt, J. N. (2014). The keystone individual concept: An ecological and evolutionary overview. *Animal Behaviour*, 89, 53–62. <http://dx.doi.org/10.1016/j.anbehav.2013.12.020>
- Mommer, B. C., & Bell, A. M. (2014). Maternal experience with predation risk influences genome-wide embryonic gene expression in threespined sticklebacks (*Gasterosteus aculeatus*). *PLoS ONE*, 9, e98564. <http://dx.doi.org/10.1371/journal.pone.0098564>
- Morgan, K. N., & Tromborg, C. T. (2007). Sources of stress in captivity. *Applied Animal Behaviour Science*, 102, 262–302. <http://dx.doi.org/10.1016/j.applanim.2006.05.032>
- Mousseau, T. A., & Fox, C. W. (1998). The adaptive significance of maternal effects. *Trends in Ecology and Evolution*, 13, 403–407. [http://dx.doi.org/10.1016/S0169-5347\(98\)01472-4](http://dx.doi.org/10.1016/S0169-5347(98)01472-4)
- Munday, P. L., McCormick, M. I., & Nilsson, G. E. (2012). Impact of global warming and rising CO₂ levels on coral reef fishes: What hope for the future? *Journal of Experimental Biology*, 215, 3865–3873. <http://dx.doi.org/10.1242/jeb.074765>
- Murren, C. J., Auld, J. R., Callahan, H., Ghalambor, C. K., Handelsman, C. A., Heskell, M. A., . . . Schlichting, C. D. (2015). Constraints on the evolution of phenotypic plasticity: Limits and costs of phenotype and plasticity. *Heredity*, 115, 293–301.
- Nicolás, L., Martínez-Gómez, M., Hudson, R., & Bautista, A. (2011). Littermate presence enhances motor development, weight gain and competitive ability in newborn and juvenile domestic rabbits. *Developmental Psychobiology*, 53, 37–46. <http://dx.doi.org/10.1002/dev.20485>
- Pruitt, J. N., & Goodnight, C. J. (2014). Site-specific group selection drives locally adapted group compositions. *Nature*, 514, 359–362. <http://dx.doi.org/10.1038/nature13811>
- Pruitt, J. N., & Riechert, S. E. (2011). Within-group behavioral variation promotes biased task

- performance and the emergence of a defensive caste in a social spider. *Behavioral Ecology and Sociobiology*, 65, 1055–1060. <http://dx.doi.org/10.1007/s00265-010-1112-z>
- Quintero, I., González-Caro, S., Zalamea, P. C., & Cadena, C. D. (2014). Asynchrony of seasons: Genetic differentiation associated with geographic variation in climatic seasonality and reproductive phenology. *American Naturalist*, 184, 352–363. <http://dx.doi.org/10.1086/677261>
- Renn, S. C. P., Aubin-Horth, N., & Hofmann, H. A. (2008). Fish and chips: Functional genomics of social plasticity in an African cichlid fish. *Journal of Experimental Biology*, 211, 3041–3056. <http://dx.doi.org/10.1242/jeb.018242>
- Robertson, B. A., Rehage, J. S., & Sih, A. (2013). Ecological novelty and the emergence of evolutionary traps. *Trends in Ecology and Evolution*, 28, 552–560. <http://dx.doi.org/10.1016/j.tree.2013.04.004>
- Robison, B. D., & Rowland, W. (2005). A potential model system for studying the genetics of domestication: Behavioral variation among wild and domesticated strains of zebra Danio (*Danio rerio*). *Canadian Journal of Fisheries and Aquatic Sciences*, 62, 2046–2054. <http://dx.doi.org/10.1139/f05-118>
- Rödel, H. G., & von Holst, D. (2009). Features of the early juvenile development predict competitive performance in male European rabbits. *Physiology and Behavior*, 97, 495–502. <http://dx.doi.org/10.1016/j.physbeh.2009.04.005>
- Rödel, H. G., von Holst, D., & Kraus, C. (2009). Family legacies: Short- and long-term fitness consequences of early-life conditions in female European rabbits. *Journal of Animal Ecology*, 78, 789–797. <http://dx.doi.org/10.1111/j.1365-2656.2009.01537.x>
- Rodríguez-Prieto, I., Martín, J., & Fernández-Juricic, E. (2011). Individual variation in behavioural plasticity: Direct and indirect effects of boldness, exploration and sociability on habituation to predators in lizards. *Proceedings of the Royal Society: Series B, Biological Sciences*, 278, 266–273.
- Rosvall, K. A., Bergeon Burns, C. M., Barske, J., Goodson, J. L., Schlinger, B. A., Sengelau, D. R., & Ketterson, E. D. (2012). Neural sensitivity to sex steroids predicts individual differences in aggression: Implications for behavioural evolution. *Proceedings of the Royal Society: Series B, Biological Sciences*, 279, 3547–3555. <http://dx.doi.org/10.1098/rspb.2012.0442>
- Rountree, D. B., & Nijhout, H. F. (1995). Genetic control of a seasonal morph in *Precis coenia* (Lepidoptera: Nymphalidae). *Journal of Insect Physiology*, 41, 1141–1145. [http://dx.doi.org/10.1016/0022-1910\(95\)00051-U](http://dx.doi.org/10.1016/0022-1910(95)00051-U)
- Ruesink, J. L. (2005). Global analysis of factors affecting the outcome of freshwater fish introductions. *Conservation Biology*, 19, 1883–1893. <http://dx.doi.org/10.1111/j.1523-1739.2005.00267.x>
- Ryan, B. C., & Vandenbergh, J. G. (2002). Intrauterine position effects. *Neuroscience and Biobehavioral Reviews*, 26, 665–678. [http://dx.doi.org/10.1016/S0149-7634\(02\)00038-6](http://dx.doi.org/10.1016/S0149-7634(02)00038-6)
- Schneirla, T. C. (1966). Behavioral development and comparative psychology. *Quarterly Review of Biology*, 41, 283–302. <http://dx.doi.org/10.1086/405056>
- Schulz, D. J., Huang, Z.-Y., & Robinson, G. E. (1998). Effects of colony food shortage on behavioral development in honey bees. *Behavioral Ecology and Sociobiology*, 42, 295–303. <http://dx.doi.org/10.1007/s002650050442>
- Shelton, D. S., Price, B. C., Ocasio, K. M., & Martins, E. P. (2015). Density and group size influence shoal cohesion, but not coordination in zebrafish (*Danio rerio*). *Journal of Comparative Psychology*, 129, 72–77. <http://dx.doi.org/10.1037/a0038382>
- Shonkoff, J. P., Garner, A. S.; Committee on Psychosocial Aspects of Child and Family Health, Committee on Early Childhood, Adoption, and Dependent Care, & Section on Developmental and Behavioral Pediatrics. (2012). The lifelong effects of early childhood adversity and toxic stress. *Pediatrics*, 129, e232–e246. <http://dx.doi.org/10.1542/peds.2011-2663>
- Sih, A. (2013). Understanding variation in behavioural responses to human-induced rapid environmental change: A conceptual overview. *Animal Behaviour*, 85, 1077–1088. <http://dx.doi.org/10.1016/j.anbehav.2013.02.017>
- Sih, A., Bell, A. M., Johnson, J. C., & Ziemba, R. E. (2004). Behavioral syndromes: An integrative overview. *Quarterly Review of Biology*, 79, 241–277. <http://dx.doi.org/10.1086/422893>
- Sih, A., & Watters, J. V. (2005). The mix matters: Behavioural types and group dynamics in water striders. *Behaviour*, 142, 1417–1431. <http://dx.doi.org/10.1163/156853905774539454>
- Sinervo, B., Méndez-de-la-Cruz, F., Miles, D. B., Heulin, B., Bastiaans, E., Villagrán-Santa Cruz, M., . . . Sites, J. W., Jr. (2010). Erosion of lizard diversity by climate change and altered thermal niches. *Science*, 328, 894–899. <http://dx.doi.org/10.1126/science.1184695>
- Slabbekoorn, H. (2013). Songs of the city: Noise-dependent spectral plasticity in the acoustic phenotype of urban birds. *Animal Behaviour*, 85, 1089–1099. <http://dx.doi.org/10.1016/j.anbehav.2013.01.021>
- Snell-Rood, E. C. (2013). An overview of the evolutionary causes and consequences of behavioural plasticity. *Animal Behaviour*, 85, 1004–1011. <http://dx.doi.org/10.1016/j.anbehav.2012.12.031>

- Snell-Rood, E. C., Davidowitz, G., & Papaj, D. R. (2011). Reproductive tradeoffs of learning in a butterfly. *Behavioral Ecology*, *22*, 291–302. <http://dx.doi.org/10.1093/beheco/arq169>
- Snell-Rood, E. C., Davidowitz, G., & Papaj, D. R. (2013). Plasticity in learning causes immediate and trans-generational changes in allocation of resources. *Integrative and Comparative Biology*, *53*, 329–339. <http://dx.doi.org/10.1093/icb/ict030>
- Sol, D., Bacher, S., Reader, S. M., & Lefebvre, L. (2008). Brain size predicts the success of mammal species introduced into novel environments. *American Naturalist*, *172*(Suppl. 1), S63–S71. <http://dx.doi.org/10.1086/588304>
- Sol, D., Lapiedra, O., & González-Lagos, C. (2013). Behavioural adjustments for a life in the city. *Animal Behaviour*, *85*, 1101–1112. <http://dx.doi.org/10.1016/j.anbehav.2013.01.023>
- Stamps, J., & Groothuis, T. G. G. (2010). The development of animal personality: Relevance, concepts and perspectives. *Biological Reviews of the Cambridge Philosophical Society*, *85*, 301–325. <http://dx.doi.org/10.1111/j.1469-185X.2009.00103.x>
- Stamps, J. A. (2016). Individual differences in behavioural plasticities. *Biological Reviews of the Cambridge Philosophical Society*, *91*, 534–567. <http://dx.doi.org/10.1111/brv.12186>
- Swaddle, J. P., Francis, C. D., Barber, J. R., Cooper, C. B., Kyba, C. C. M., Dominoni, D. M., . . . Longcore, T. (2015). A framework to assess evolutionary responses to anthropogenic light and sound. *Trends in Ecology and Evolution*, *30*, 550–560. <http://dx.doi.org/10.1016/j.tree.2015.06.009>
- Szabo, T. M., Brookings, T., Preuss, T., & Faber, D. S. (2008). Effects of temperature acclimation on a central neural circuit and its behavioral output. *Journal of Neurophysiology*, *100*, 2997–3008. <http://dx.doi.org/10.1152/jn.91033.2008>
- Théry, M. (2007). Colours of background reflected light and of the prey's eye affect adaptive coloration in female crab spiders. *Animal Behaviour*, *73*, 797–804. <http://dx.doi.org/10.1016/j.anbehav.2006.06.015>
- Thum, C., Cookson, A. L., Otter, D. E., McNabb, W. C., Hodgkinson, A. J., Dyer, J., & Roy, N. C. (2012). Can nutritional modulation of maternal intestinal microbiota influence the development of the infant gastrointestinal tract? *Journal of Nutrition*, *142*, 1921–1928. <http://dx.doi.org/10.3945/jn.112.166231>
- Tishkoff, S. A., Reed, F. A., Ranciaro, A., Voight, B. F., Babbitt, C. C., Silverman, J. S., . . . Deloukas, P. (2007). Convergent adaptation of human lactase persistence in Africa and Europe. *Nature Genetics*, *39*, 31–40. <http://dx.doi.org/10.1038/ng1946>
- van den Brink, V., Dolivo, V., Falourd, X., Dreiss, A. N., & Roulin, A. (2012). Melanic color-dependent antipredator behavior strategies in barn owl nestlings. *Behavioral Ecology*, *23*, 473–480. <http://dx.doi.org/10.1093/beheco/arr213>
- Vital, C., & Martins, E. P. (2011). Strain differences in zebrafish (*Danio rerio*) social roles and their impact on group task performance. *Journal of Comparative Psychology*, *125*, 278–285. <http://dx.doi.org/10.1037/a0023906>
- Waddington, C. H. (1959). Canalization of development and genetic assimilation of acquired characters. *Nature*, *183*, 1654–1655. <http://dx.doi.org/10.1038/1831654a0>
- West, M. J., & King, A. P. (1987). Settling nature and nurture into an ontogenetic niche. *Developmental Psychobiology*, *20*, 549–562. <http://dx.doi.org/10.1002/dev.420200508>
- West-Eberhard, M. J. (2003). *Developmental plasticity and evolution*. Oxford, England: Oxford University Press.
- Wingfield, J. C. (2013). The comparative biology of environmental stress: Behavioural endocrinology and variation in ability to cope with novel, changing environments. *Animal Behaviour*, *85*, 1127–1133. <http://dx.doi.org/10.1016/j.anbehav.2013.02.018>
- Wong, B. B. M., & Candolin, U. (2015). Behavioral responses to changing environments. *Behavioral Ecology*, *26*, 665–673. <http://dx.doi.org/10.1093/beheco/aru183>
- Zwarts, L., Magwire, M. M., Carbone, M. A., Versteven, M., Herteleer, L., & Anholt, R. R. H., . . . Mackay, T. F. C. (2011). Complex genetic architecture of *Drosophila* aggressive behavior. *Proceedings of the National Academy of Sciences, USA*, *108*, 17070–17075. <http://dx.doi.org/10.1073/pnas.1113877108>