



On the Origins of Adaptive Behavioral Complexity: Developmental Channeling of Structural Trade-offs

Renée A. Duckworth¹, Ahva L. Potticary, Alexander V. Badyaev

University of Arizona, Tucson, AZ, United States

¹Corresponding author: e-mail address: rad3@email.arizona.edu

Contents

1. Developmental Perspective on the Evolution of Behavioral Strategies: Approach	1
2. Evidence of Ontogenetic Behavioral Linkages and Dependencies	3
2.1 Early Developmental Origins of Behavioral Variation	3
2.2 Trade-offs in Neural Processes and Personality	5
2.3 Maintenance of Variation in Behavioral Expression Along Trade-off Axes	8
3. Developmental Origins of Behavioral Variation	10
3.1 Design Principles of the Brain and Mechanisms Underlying Neural Trade-offs	10
3.2 Developmental Channeling: Mechanism for Separating Individuals Along Trade-off Axes	12
4. Applying the Concept of Developmental Channeling: Dispersal Strategies as an Example	17
4.1 Evolution of Dispersal Strategies	17
4.2 Maternally Induced Dispersal Behavior	21
5. Conclusion and Future Directions	25
Acknowledgments	27
References	27



1. DEVELOPMENTAL PERSPECTIVE ON THE EVOLUTION OF BEHAVIORAL STRATEGIES: APPROACH

Behavioral strategies are complex combinations of behaviors with strikingly different origins and determinations—from innate to learned, from stably expressed to emergent and contingent. Coexpression of a subset of behaviors at a certain time and place can be adaptive and the fitness

consequences of such coexpression is often hypothesized to be the driving force behind the evolution of complex and environmentally contingent behavioral strategies. Consequently, the frequency and precision of expression of a composite behavioral strategy is often thought to reflect the historical prevalence of ecological contexts in which behavioral coexpression was adaptive. The central, but implicit, assumption of this perspective is that components that comprise a behavioral strategy are ontogenetically independent of each other or, at least, have equal chances to form functional associations when selection favors them. We see two main problems with this view. First, many complex behaviors are an outcome of sequential, hierarchical, and nonrandom accumulation of components, where the coexpression of components at the preceding developmental stage restricts the range of subsequent behavioral associations, independently of their eventual fitness consequences. Second, consistent selection on coexpression of behavioral components should deplete genetic variance in the mechanisms that produce coexpression, and thus, should restrict their ability to form new associations when the environment changes, ultimately limiting the evolution of new behavioral strategies. These problems are overcome when the structure of behavioral associations generated in ontogeny facilitates their evolution, and here, we argue that behavioral configurations and patterns arising during development greatly reduce the number of evolutionary steps needed for the evolution of adaptive and complex behavioral strategies (Badyaev, 2011, 2013).

New behavioral strategies necessarily arise when existing components that occur at different times and places in ontogeny are rearranged into new combinations. These novel combinations can be produced by developmental processes independent of their fitness consequences or can arise under stabilizing selection (Cheverud, 1984; Lande, 1980). To distinguish between these two possibilities, a knowledge of the mechanistic bases of behavioral associations is needed, and we begin our review with addressing the origin of ontogenetic behavioral linkages and dependencies, specifically focusing on neuroendocrine processes. We suggest that the basic elements of many behavioral strategies may arise from neural trade-offs that are formed very early in development. Under this scenario, particular behavioral associations arise, not because selection favors the association per se, but instead because design principles of neuroendocrine networks underlie axes of behavioral coexpression. This developmental perspective assumes a different starting point for the evolution of behavioral strategies compared to traditional models. Instead of distinct behaviors evolving coexpression gradually

in response to consistent external selection pressures, a developmental perspective assumes that coordination of some behaviors comes from their shared dependence on the same neuroendocrine pathways that either cannot be dissociated or require extraordinarily effective natural selection to break them apart. Finally, we suggest that ontogenetic linkages between and shared determination of behavioral components are important for understanding adaptive evolution of complex behavioral strategies because they can channel behavioral coexpression along the lines of least resistance, making certain behavioral combinations more likely to evolve repeatedly. We illustrate these ideas with the evolution of dispersal strategies.



2. EVIDENCE OF ONTOGENETIC BEHAVIORAL LINKAGES AND DEPENDENCIES

2.1 Early Developmental Origins of Behavioral Variation

Behavior is the final outcome of integration between many underlying neurobiological processes and information about current context and internal organismal state. Sensory information is processed in the brain by cognitive, motivational, and emotion circuits that influence the decisions an individual makes. In turn, the outcome of decision-making processes is expressed through actions of the individual that require coordinated interaction between the brain, physiology, and muscular-skeletal system. Thus, behavior is the endpoint of integration among diverse components of a dynamic system. As such, the development and expression of behavior is entangled in so many other traits that, even though behaviors are often thought to be highly flexible in evolution and expression, in some ways, they should be the most constrained of traits. At the very least, based on structural considerations, we should not expect coexpression of behaviors to be easily modifiable.

Indeed, there is accumulating evidence for permanent effects of events during development on behavior at even the earliest ontogenetic stages (Meaney & Szyf, 2005). For example, in rats, housing fathers in a more complex environment before mating influenced both brain methylation patterns and behavior of offspring (Mychasiuk et al., 2012). Another study in mice found that conditioned fear responses were inherited over multiple generations, potentially through epigenetic changes in the sperm that subsequently modify structural elements of the brain of future offspring (e.g., an increase in the number of M71 neurons; Dias & Ressler, 2014).

In humans, effects of early embryonic events on behavior are common (Werner et al., 2007) and can have permanent effects on adult behavior across individuals of different genetic backgrounds (e.g., Brown, Susser, Lin, Neugebauer, & Gorman, 1995; Hock, Brown, & Susser, 1998; Neugebauer, Hoek, & Susser, 1999; Susser & Lin, 1992).

Early developmental processes affect structural variation in the brain, either through the aforementioned epigenetic effects on developmental components or through direct impacts on cellular differentiation and growth that are particularly susceptible to environmental influences and mutual coordination. Thus, similar to morphological traits, the finite duration of growth and tissue organization is a sensitive period for behavioral development when environmental information is incorporated on a large-scale, shaping neuroendocrine structures, and necessarily limiting the range of variation that is possible later in life (Fox, Levitt, & Nelson, 2010; Knudsen, 2004). Yet, the role of early development in shaping subsequent behavioral variation has been largely overlooked even though massive and profound changes in the neuroendocrine system that occur at early developmental stages are largely completed by the birth or hatching and cannot be changed later in life (Kolb, 1995; Morgane et al., 1993). In this sense, the basic structural variation that arises early in development limits the scope of subsequent behavioral variation throughout an organism's life.

Recent studies implicate early developmental influences on structural components of the neuroendocrine system as a basis for permanent differences among individuals in temperament or personality traits, and evidence accumulates that these components remain relatively unchanged, once formed, for the life of an individual (reviewed in Duckworth, 2010, 2015). Evidence for this comes from numerous recent studies that linked personality variation to brain structure in humans (see Kennis, Rademaker, & Geuze, 2013 for review): for example, neuroticism (similar to fear-avoidance and reactivity in other animals) negatively correlated with overall brain size, white matter microstructure, and frontotemporal surface area (Bjornebekk et al., 2013). Extraversion and sociability were positively correlated with amygdala volume (Bickart, Wright, Dautoff, Dickerson, & Barrett, 2011; Cremers et al., 2011) which is generally associated with emotional responses in humans (LeDoux, 2000). Further, individual differences in anxiety-related personality traits were associated with reduced size of brain structures related to emotional control and self-consciousness (Fuentes et al., 2012).

Similarly, animal studies suggest that correlations between brain structural variation and personality differences reflect a causal link between the

two. Artificial selection on natural variation in guppy (*Poecilia reticulata*) brain size produced a correlated response in personality traits across generations (Kotrschal et al., 2014). Another study used transgenic mice to understand the frequently observed correlation in humans between smaller hippocampal volume and anxiety-related personality disorders (Persson et al., 2014). By creating mice that expressed the *CYP2C19* gene, which codes a metabolic enzyme in the human brain, researchers found that mice with the gene developed a smaller hippocampus compared to mice without it, leading to impaired stress acclimation as adults. Because the gene is expressed only in the fetal brain, this study established that morphological changes in the brain precede the behavioral changes later observed in adults, suggesting that reduced hippocampal volume during ontogeny is causally linked to increased stress and anxiety in adulthood.

2.2 Trade-offs in Neural Processes and Personality

While there is clear evidence that structural variation in the brain is correlated with behavioral variation, it is less clear how and why this structural variation should impact the evolution of behavioral strategies. We suggest that structural variation in the brain influences how information is gathered, integrated, and processed via trade-offs in neural function and these trade-offs are particularly important for decision-making processes. Recent neurobiological studies suggest that decision-making processes are guided by several key trade-offs that derive from variation in investment in different brain structural components. In this section, we outline the neurobiological evidence for each of these trade-offs and its link to both brain structure and personality variation.

2.2.1 Speed–Accuracy Trade-off

In the speed–accuracy trade-off, decisions are made slowly with high accuracy or fast with high error rate (Chittka, Skorupski, & Raine, 2009). The neurobiological basis of this trade-off is well characterized. In both the prefrontal cortex and subcortical areas of the brain, neurons associated with different perceptual choices gradually increase their firing rate as they integrate inputs from sensory neurons (Gold & Shadlen, 2007). A decision is made when the firing rate of the neurons associated with a particular choice exceeds a critical threshold and individuals told to prioritize speed in a cognitive task showed heightened baseline activation of brain areas involved with decision-making allowing them to reach the decision threshold faster (Bogacz, Wagenmakers, Forstmann, & Nieuwenhuis, 2009). Yet, such

flexibility in decision-making processes varies across individuals. Studies have found distinct patterns of brain activity and connectivity among individuals that preferentially prioritize speed and among individuals that vary in their ability to flexibly adjust their level of caution (sometimes prioritizing speed, sometimes accuracy; Forstmann et al., 2010; Perri, Berchicci, Spinelli, & Di Russo, 2014). In particular, individuals who are better able to flexibly adjust their level of caution have stronger structural connections between the supplementary motor area of the brain and the striatum, a subcortical part of the forebrain and a critical component of the reward system (Forstmann et al., 2010). Moreover, individuals that naturally prioritize speed had higher baseline activation of supplementary motor areas and individuals that naturally prioritize accuracy had higher baseline activity of areas in the prefrontal cortex (Perri et al., 2014). Thus, individual variation in speed vs accuracy of decision-making appears to reflect a trade-off between a greater baseline activity of areas associated with cognitive control (that slow down decision-making processes but increase their accuracy) and greater baseline activity of motor and subcortical areas (that enhance the speed of an action at the expense of accuracy). Finally, variation in how individuals deal with this trade-off has been shown to relate to a variety of personality dimensions such as risk sensitivity (Nagengast, Braun, & Wolpert, 2011), agreeableness (Bresin, Hilmert, Wilkowski, & Robinson, 2012) and neuroticism (Socan & Bucik, 1998) in humans, and alternative proactive and reactive coping styles in other animals (Sih & Del Giudice, 2012).

2.2.2 Immediate vs Delayed Reward

Responses dominated by cognitive vs emotion circuits of the brain are another major trade-off that influences decision-making processes (LeDoux, 1989). An example of this trade-off is between executive functions (higher-level cognitive processes that enable individuals to rationally assess the benefits of a delayed reward) and emotion circuits of the limbic system (that are associated with making decisions that give immediate reward; McClure, Laibson, Loewenstein, & Cohen, 2004). Importantly, individual variation in both executive function and brain structure underlying this network correlates with human personality variation (Williams, Suchy, & Rau, 2009). For example, more impulsive individuals have lower cortical thickness in areas associated with executive function (Schilling et al., 2012). Many of these studies used functional magnetic resonance imaging (fMRI) that is difficult to perform in nonhuman animals because it requires active participation from the subjects in performing thought tasks while

remaining motionless in a scanner. However, studies of nonhuman animals that attempted these methods find analogous results of neural correlates of individual variation in executive function: e.g., individual differences in cognitive control in the domestic dog correlated with activity in the same region of the brain that is associated with cognitive control in humans (Cook, Spivak, & Berns, 2016).

2.2.3 Goal- vs Stimulus-Directed Attention

Competition between cognitive and emotion circuits is also reflected in the trade-off between goal- vs stimulus-directed attentional systems (Eysenck, Derakshan, Santos, & Calvo, 2007). In goal-directed behavior, executive functions that allow attentional control to a specific task can be disrupted by reactivity to stimuli that is irrelevant to the task. In humans, this trade-off has been linked to anxiety-related disorders with individuals that have poorer executive control showing more lapses in concentration and distraction from a task at hand (Bishop, 2009). However, individuals that are more easily distracted also more readily detect threat-related stimuli (Eysenck et al., 2007). In humans, such heightened awareness of stimuli in the environment that is irrelevant to a task at hand is often viewed negatively, as constant reactivity to irrelevant stimuli in a benign environment can have negative impacts on health and psychology (Bishop, 2009). However, in species that must constantly monitor the environment for threats from predators, individuals with an attentional system more oriented to environmental stimuli will likely have higher survival.

This trade-off is likely to be particularly important in understanding the evolution of variable foraging strategies and cognitive abilities among species because heightened attention to environmental stimuli can interfere with working memory (Braver, Cole, & Yarkoni, 2010) which is critical for both problem-solving and spatial memory tasks. Thus, evolution of a greater working memory capacity may require evolution of mechanisms that allow individuals to spend less of their brain capacity on constant scanning for threats. Species which require a higher spatial memory capacity, such as food-storing birds, have a larger hippocampus and a higher working memory capacity compared to birds that do not store food (Clayton, 1998; Sherry, Jacobs, & Gaulin, 1992). Interestingly, these are also highly social species that forage in family groups or in flocks. An intriguing possibility is that neural trade-offs between working memory and stimulus-directed attention have led to the evolution of higher sociality in these species as group foraging decreases the risk of predation and thus would lessen the need

for heightened vigilance from any one individual (Lima & Dill, 1990) allowing them to reserve working memory for foraging tasks. Thus, by taking neural trade-offs into account we can formulate novel hypotheses about the origin of behavioral strategies. In this case, a neural trade-off perspective reverses the direction of causality of the “social brain hypothesis” which proposes that large brain size evolved in response to the greater computational demands of living in social groups (Dunbar & Shultz, 2007). Instead, from a neural trade-off perspective, evolution of higher cognitive skills required for spatial memory tasks may have necessitated the evolution of social groups to release individuals from the requirements of constant threat monitoring, a brain function that would interfere with needed cognitive functions.

2.3 Maintenance of Variation in Behavioral Expression Along Trade-off Axes

Trade-offs between structural determinants of speed vs accuracy, executive vs emotion circuits, goal-directed vs stimulus-directed attention may be the basis for personality variation in animals (Duckworth, 2018; Sih & Del Giudice, 2012). These trade-offs may at least partially explain why different individuals within the same population make different decisions. This is contrary to the assumption of most models for the evolution of behavioral strategies that any two individuals in a population will converge on the same behavioral strategy if they are placed in the same environmental context (Gross, 1996). Instead, we suggest that different individuals are predisposed to make different decisions based on where they fall on spectrums of neural trade-offs and as such the structural trade-off axes outlined earlier can channel variation in behavioral strategies within a population along preexisting paths of least resistance. This raises the question of what determines where individuals are placed on a trade-off continuum in the first place.

Work on stress-induced phenotypes and coping styles in animals suggest that variation in personality traits may be affected by maternal stress during early development (Duckworth, 2015). For example, many long-term consequences of early developmental stress are caused by a resetting of fetal hypothalamic–pituitary–adrenal (HPA) axis sensitivity, which is a major cause of variation in many behavioral traits, including personality (Koolhaas et al., 1999; Meaney & Szyf, 2005; Seckl & Meaney, 2004). In the brain, activity in the interconnected amygdala, hippocampus, and hypothalamus activate and regulate the HPA axis (Charmandari, Tsigos, & Chrousos, 2005) which are the regions most immediately linked to the trade-offs outlined earlier. For example, the amygdala mediates value

judgments of external stimuli (Janak & Tye, 2015), the hypothalamus mediates reactions to stress and can impair performance in the prefrontal cortex (specifically in relation to executive functions; Phelps, Lempert, & Sokol-Hessner, 2014), whereas the hippocampus is part of a functional loop detecting novelty and transmitting behaviorally significant information into long-term memory (Lisman & Grace, 2005). Essentially, the HPA axis acts as a liaison between sensory systems, information acquisition, emotion systems, and higher cognitive processes. Importantly, these are the systems most affected by developmental stressors experienced in the prenatal environment (Charil, Laplante, Vaillancourt, & King, 2010).

Stress-induced behavioral phenotypes can be adaptive when they prepare individuals for a harsh future environment (Badyaev, 2005; Korte, Koolhaas, Wingfield, & McEwen, 2005; Wells, 2003). For example, in animals, aggression is linked to stress coping style, with more aggressive individuals being bolder, less exploratory, taking more risks in the face of potential dangers, and showing lower behavioral flexibility compared to less aggressive individuals (Korte et al., 2005). The aggressive strategy requires higher energy consumption and is thought to be at an advantage in predictable environments where food is abundant, whereas the nonaggressive, more behaviorally flexible type is thought to flourish in more stressful environments where resources are scarce (Korte et al., 2005). Such variation among individuals may be maintained by fluctuating selection exerted by variable food availability and, indeed, was a major determinant of survival of birds that differed in exploratory behavior (Dingemanse, Both, Drent, & Tinbergen, 2004). Most importantly, the way that these distinct personality types deal with environmental challenges and stress is different—proactive animals, because they rely on routines, are better at performing tasks despite minor distractions, but adapt slowly to changes in the environment, whereas reactive animals are easily distracted but adapt to novel conditions faster (Coppens, de Boer, & Koolhaas, 2010). Such variation in the response of proactive or reactive types to environmental changes is likely underlain by their placement on the trade-off continuums outlined earlier.

Taken together, these findings show that early developmental effects on personality traits have strong channeling effects on subsequent behavioral strategies. Because development is hierarchical, coexpression of behavioral components at preceding developmental stages necessarily limits and directs the opportunities for associations between behaviors at later stages. Integration among behaviors due to shared structures or developmental pathways

may be difficult to break apart, particularly if this integration occurs because of physical constraints. This is not to say that all coexpression of integrated behaviors is unbreakable or inevitable, but that in some cases developmental mechanisms make certain phenotypes more readily accessible than others (Maynard Smith et al., 1985).

Evolution of some behavioral strategies may be strongly influenced by the trade-offs outlined earlier, whereas for others, correlations among behaviors may be frequently broken and restructured. Thus, a greater understanding of the evolution of behavioral associations will be enabled by work that explicitly addresses how developmental processes may predispose some traits to coevolve and others to be easily decoupled. Studying such processes in a comparative context would be a particularly powerful approach. If physical constraints on the neuroendocrine system shape behavioral variation, then we expect that personality variation and its underlying developmental basis should be structured similarly across distant taxa. Indeed, consistent individual differences in boldness, exploration, activity, sociability, and aggressiveness have been repeatedly documented across a wide variety of species, across both vertebrates and invertebrates (Bell, Hankison, & Laskowski, 2009; Gosling & John, 1999; Mehta & Gosling, 2006; Réale, Reader, Sol, McDougall, & Dingemans, 2007). Whether these personality traits are underlain by the same neuroendocrine mechanisms across these taxa remains to be seen.

In the next section, we discuss how an understanding of design principles of neural wiring provides insight into general organization of the brain and can provide a mechanistic basis for the trade-offs outlined earlier. Specifically, patterns of integration of neuroendocrine components have strong downstream effects on the range of behavioral coexpression with important consequences for adaptive diversification of behaviors and the origin of novel behavioral associations.



3. DEVELOPMENTAL ORIGINS OF BEHAVIORAL VARIATION

3.1 Design Principles of the Brain and Mechanisms Underlying Neural Trade-offs

Early developmental effects that manifest themselves in structural variation in the brain may persist throughout an individual's life because of the costs and constraints of postontogenetic neural reorganization. The high energetic costs of developing and maintaining neural tissue are well established (Kety, 1957; Laughlin & Sejnowski, 2003), and, because the maintenance of

high flexibility of neural circuits is particularly expensive, such costs are a significant barrier to the evolution of behavioral flexibility (Niven & Laughlin, 2008) and thus may favor specialization among individuals along a particular axis of personality variation (Duckworth, 2010). Given this, how do such costs and constraints direct the range of behavioral variation available to selection?

Computer technology, systems theory, and engineering use neural architecture as a functionally and structurally analogous model (Bullmore & Sporns, 2012; Chermiak, Mokhtarzada, Rodriguez-Esteban, & Changizi, 2004; Hopfield, 1982). These studies highlight the design principles required to produce an efficient, information gathering, information storing, learning and problem-solving machine analogous to the brain and thus can provide insight into how energetic costs and physical constraints lead to structural variation in the brain. These studies show that the physical organization of the brain, such as distances between distinct components, influences structural connections among components (Raj & Chen, 2011). In the case of neural networks, greater distances incur high metabolic cost due to the formation and maintenance of axonal connections (referred to as “wiring costs”; Laughlin & Sejnowski, 2003), potentially explaining the juxtaposition of white and gray matter and the distance between functional components of the brain (Chermiak et al., 2004; Wen & Chklovskii, 2005).

White matter consists mainly of the axons and its main function is to connect different regions of the brain, whereas gray matter is comprised of the neuron bodies and is involved in the core functions of the brain. White matter is typically organized in the central part of the brain with gray matter on the periphery. There is a trade-off between connectivity and conduction speed such that increasing connectivity of different brain regions increases the volume of neurons in a particular region and also the distance between neurons, that in turn, requires longer wiring. This leads to slower conduction speed and fewer computational steps that can be performed (Wen & Chklovskii, 2005). The trade-off between connectivity and conductivity may provide a mechanistic explanation for the speed-accuracy trade-off and may also be a basis for observed variation in connectivity of brain regions that influence personality. Another trade-off that imposes wiring costs is between signal strength and the distance a signal needs to travel. Dendritic electrical signals decrease as a function of distance and therefore longer connections require thicker dendritic diameters to support the same conductive potential but increasing dendritic thickness is limited by space availability in the brain (Kanai & Rees, 2011). Thus, wiring costs make it clear that there is

an upper limit to connectivity among components that is enforced by both space limits in the brain and by the costs of enhanced connectivity.

These space and energy limitations may then profoundly impact investment in different brain regions providing an explanation for patterns of structural variation that underlie personality. An interspecific trade-off among the size of distinct brain regions is documented in carnivores; increases in the size of one brain region come at the expense of other brain regions (Swanson, Holekamp, Lundrigan, Arsznov, & Sakai, 2012). Moreover, changes in neocortex size generally scale with brain size across species, yet, there is a negative relationship between neocortex size and size of the limbic system across species (Finlay & Uchiyama, 2015). In particular, it is interesting to note, that the highest degree of evolutionary independence is between the cortex and the limbic system which are the areas that are most clearly involved in the neural trade-offs described earlier. These trade-offs between brain regions may underlie patterns of mosaic brain evolution in which the size of different brain regions evolve somewhat independently across species (Barton & Harvey, 2000). On a proximate level, these patterns of size variation among distinct brain regions may evolve by shifting the length of neurogenesis during development for different brain regions. For example, Finlay and Darlington (1995) found that the order of neurogenesis is largely conserved among mammals during development and that disproportionately large growth, such as occurs in the primate neocortex, occurs primarily for structures that are generated late in development and thus have a longer time to accumulate precursor cells.

These among-species patterns are reflected in similar patterns of variation within species. For example, in a quantitative genetic study of brain size variation in the three-spined stickleback (*Gasterosteus aculeatus*), one of the lowest genetic correlations was between the telencephalon (which includes the cortex and parts of the limbic system) and hypothalamus size (Noreikiene et al., 2015). Thus, the parts of the brain that are most clearly involved in the personality trade-offs outlined earlier are also the parts that are most likely to vary both among individuals and over evolutionary time, potentially accounting for observed variation in personality traits both among individuals and species.

3.2 Developmental Channeling: Mechanism for Separating Individuals Along Trade-off Axes

One of the main functions of the brain is to integrate information to allow the organism to respond flexibly to challenges. Yet, the adult brain must also

preserve the circuitry and synaptic organization necessary to maintain continuity of behavior and long-term memories. Moreover, even though neural plasticity persists throughout the life span (Lledo, Alonso, & Grubb, 2006), it is severely limited in the adult brain compared to the developing brain (Kolb & Gibb, 2014). Large-scale reorganization of axons, dendrites, and myelination are constrained as these structures provide a stable scaffold underlying neural circuits and any changes in structure of the adult brain is local and often short term (Bavelier, Levi, Li, Dan, & Hensch, 2010). The costs of neural rewiring (Laughlin & Sejnowski, 2003) may lead to a significant behavioral inertia due to high costs of switching between behavioral patterns (Wood & Runger, 2016). Thus, even though learning and behavioral flexibility are core functions of the brain, a complete understanding of the origin and expression of behavioral strategies requires recognition that ontogenetic processes can channel and limit the flexibility that is expressed both within individuals and over evolutionary time.

There are numerous processes that can cause such channeling, including fundamental aspects of early brain development. Starting at the earliest stages of development, discrete domains form in the wall of the neural tube representing largely independent units of neural tissue, in which neural cells proliferate, migrate, and differentiate into neurons and glia (Redies & Puelles, 2001; Fig. 1). This embryonic patterning is achieved through the expression of variable cadherins, a family of adhesion molecules that are expressed on surface membranes of neurons and enable cells to preferentially associate with other cells expressing the same cadherin leading to the early organization of the neural tube into distinct tissue modules (Redies & Puelles, 2001). These embryonic modules lay the foundation for the functional modules that will later form the neural circuits in the brain (e.g., executive or emotion circuits), each with its own unique expression of cadherin. Interestingly, cadherins as a class were found to be differentially methylated and expressed in the brains of rats that were exposed to high and low maternal care (McGowan et al., 2011). Because low maternal care in rats produces a stress-induced behavioral phenotype (Weaver et al., 2004) these epigenetic effects on cadherin expression early in ontogeny link the experience of a stressful environment to a mechanism that modifies structural organization of the brain, potentially providing a way that stress on parents can directly impact brain structural organization in offspring.

Nutritional stress can have an even more direct impact on brain development (Antonow-Schlorke et al., 2011; Dobbing, 1964; Walhovd et al., 2012). Perhaps most importantly, the timing of neurogenesis differs across

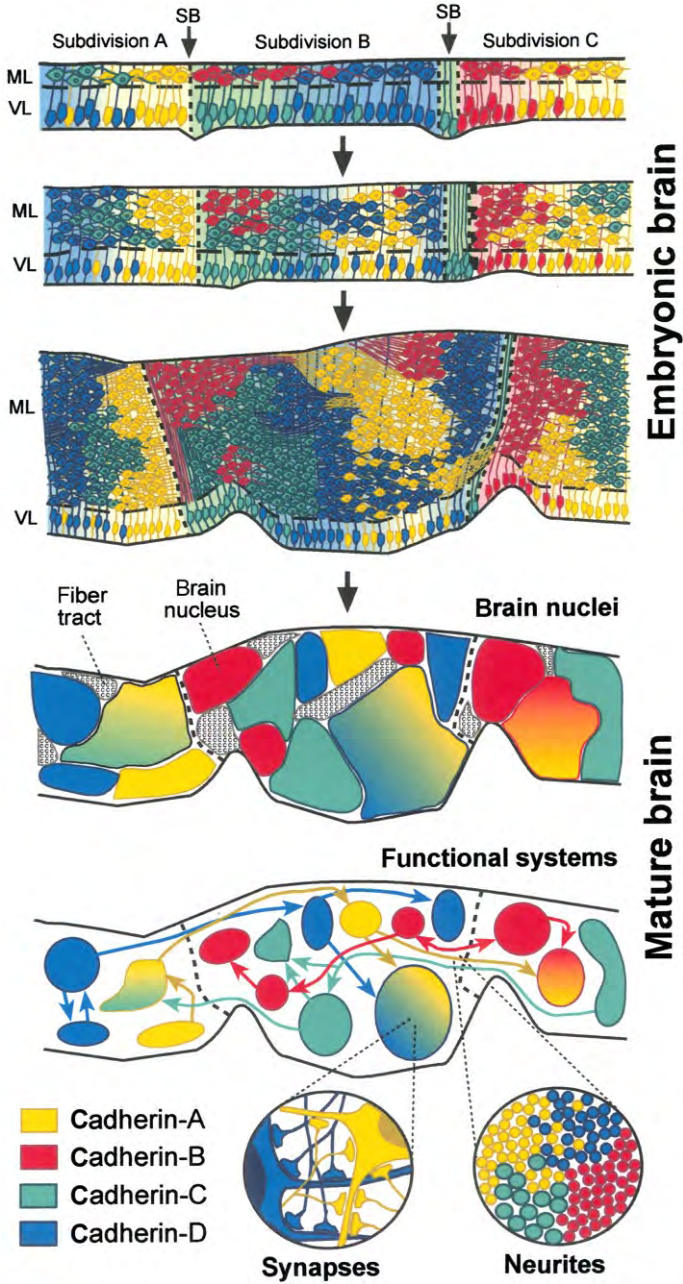


Fig. 1 See legend on opposite page.

brain regions meaning that the impact of nutritional stress crucially depends on its timing and duration relative to timing of key milestones of brain development (Andersen, 2003; Lupien, McEwen, Gunnar, & Heim, 2009; Fig. 2). Given this, even limited periods of nutritional or other stressors may differentially impact brain regions with changes in size or structure of earlier developing regions necessarily influencing the structure of later developing regions. Such differential impacts of stress may provide the proximate mechanism for the origin of individual variation in size and connectivity of brain structures that underlie personality.

Similar downstream effects should be evident in epigenetic programming as epigenetic marks that are present at the earliest stages of development can persist into adulthood (Meaney & Szyf, 2005) and, if tissue function requires coordinated patterns of gene expression, then it may be difficult (although not impossible, see Alvarado, Fernald, Storey, & Szyf, 2014) to reprogram cells within a tissue that vary in age without disrupting function. Structural constraints and epigenetic variation may interact to produce personality variation during development (Duckworth, 2015). In particular, structural constraints may play a primary role in the origin of behavioral stability with epigenetic programming evolving as a compensatory mechanism that further channels developmental variation, considering investment patterns in structural components at earlier stages (Badyaev, 2014).

The main consequence of these processes is that, from the earliest developmental stages there is variation among individuals that provides the foundation for the expression of behavioral strategies and should influence the decisions that individuals make. In the next section, we explore the insights

Fig. 1 Tissue modules patterned at the earliest stages of development retain their identity throughout development and into the mature brain where they form functional modules. Embryonic modules are mostly independent histogenetic fields, each of which is characterized by a particular mode of information processing. Embryonic patterning is achieved through expression of variable cadherins that promote early structural organization by allowing cells to preferentially associate with other cells expressing the same cadherin. These basic regions are connected through fiber tracts to other regions, providing the basis of functionally integrated systems, such as those that allow for the assimilation, processing, and interpretation of visual, olfactory, and auditory stimuli. These developmental associations provide a mechanism by which epigenetic influences on cadherin expression can influence early patterning of brain modules and subsequently channel structural variation in the brain that is retained in the mature brain. Adapted from Redies, C., Puelles, L. (2001). *Modularity in vertebrate brain development and evolution. BioEssays, 23, 1100–1111.*

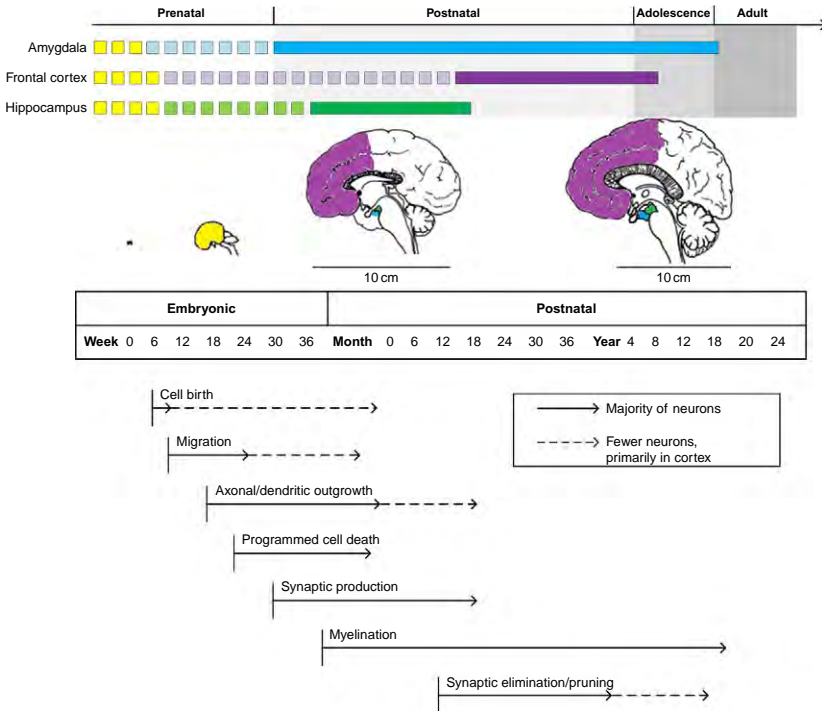


Fig. 2 Timing of sensitivity and development vary across neuroendocrine structures related to behavioral variation in humans. From conception onward, all developing brain areas are sensitive to environmental perturbations (*broken bars*); however, some areas are more sensitive than others later in development during the period of rapid growth which varies across major areas of the brain (*solid bars*). The hippocampus (*green*), amygdala (*blue*), and frontal cortex (*purple*) all derive from the same embryonic module, the telencephalon (*yellow*), and differentiation does not occur among structures until after 6 weeks. *Arrows* below the timeline show the windows of timing for specific events across human brain developmental period. While the majority of development occurs prior to birth, a large number of changes occur until early adulthood. *Adapted from Lupien, S. J., McEwen, B. S., Gunnar, M. R., Heim, C. (2009). Effects of stress throughout the lifespan on the brain, behaviour and cognition. Nature Reviews. Neuroscience, 10, 434–445; Andersen, S. L. (2003). Trajectories of brain development: Point of vulnerability or window of opportunity? Neuroscience and Biobehavioral Reviews, 27, 3–18.*

that can be gained into the origin of behavioral strategies by applying a developmental perspective to the evolution of alternative dispersal strategies. First, we discuss them as a general phenomenon and then, using the western bluebird (*Sialia mexicana*) system as an example, we show how maternally induced variation in personality traits can influence individual decision-making processes.



4. APPLYING THE CONCEPT OF DEVELOPMENTAL CHANNELING: DISPERSAL STRATEGIES AS AN EXAMPLE

4.1 Evolution of Dispersal Strategies

Distinct dispersal strategies are examples of behavioral strategies in which a behavior that is expressed early in life—the juvenile dispersal decision—is closely integrated with a suite of morphological, physiological, behavioral, and life-history traits (Roff & Fairbairn, 2001; Stevens et al., 2014). In animals, natal dispersal—when individuals decide to either stay in the natal population or to move to a new area to breed—is often viewed as a complex decision that is largely based on assessment of information from the current physical and social environments (Matthysen, 2012). While the influence of behaviors such as aggression and sociability have long been recognized in this process of decision-making, it has often been assumed that variation in these other behaviors are also a function of external factors, such as population density (Bekoff, 1977; Gaines & McClenagham, 1980). Thus, the behavioral components that comprise a dispersal strategy have frequently been viewed as ontogenetically independent with the dispersal decision itself occurring primarily in response to flexible changes in costs and benefits of dispersing or remaining philopatric (Bowler & Benton, 2005). Yet, at least in vertebrates, personality traits are often associated with dispersal (Cote, Clobert, Brodin, Fogarty, & Sih, 2010) and, as discussed earlier, expression of these traits is likely determined early in ontogeny well before the dispersal decision is made. Personality traits may influence both the information gathering process as well as the costs and benefits of dispersing, making some individuals predisposed to disperse regardless of cues about population density and resource availability that are typically associated with dispersal (Duckworth, 2012).

In Table 1, we summarize studies that investigated the correlation between dispersal and a set of behavioral traits that have been categorized as personality traits in various species. It is notable that the relationship between many of the studied traits and dispersal is remarkably consistent across diverse taxa. Dispersers are generally more active, bolder, and more explorative than philopatric or less dispersive individuals (see Cote et al., 2010 for a similar conclusion). These patterns bring up the question of whether the propensity to disperse exists independently of personality variation or whether dispersal is an emergent property of individual variation in

Table 1 Summary of Correlations Between Dispersal Behavior and Behavioral Traits Across Animal Taxa

Behavioral Trait	Relationship to Dispersal	Taxa	Citations
Activity	Positive (14)	Amphibians Birds Gastropods Insects Arachnids Mammals Reptiles	Utida (1972), Fairbairn (1978), O’Riain, Jarvis, and Faulkes (1996), Belthoff and Dufty (1998), Bonte, Lens, and Maelfait (2004), Krug and Zimmer (2004), Aragón, Meylan, and Clobert (2006), Jokela, Elovainio, Kivimäki, and Keltikangas-Järvinen (2008), Hoset et al. (2011), Kobler, Maes, Humblet, Volckaert, and Eens (2011), Maes, Van Damme, and Matthysen (2012), Saastamoinen, Brakefield, and Ovaskainen (2012), Edelsparre, Vesterberg, Lim, Anwari, and Fitzpatrick (2014), and Mueller et al. (2014)
Aggression	Positive (7)	Bony fishes Arthropoda Birds Mammals	Myers and Krebs (1971), Fairbairn (1978), Mehlman et al. (1995), Trefilov, Berard, Krawczak, and Schmidtke (2000), Duckworth and Kruuk (2009), Pintor, Sih, and Kerby (2009), and Groen et al. (2012)
	Negative (6)	Bony fishes Insects Mammals	Myers and Krebs (1971), Holekamp and Smale (1998), Holway, Suarez, and Case (1998), Schradin and Lamprecht (2002), Guerra and Pollack (2010), and McCauley (2010)
Boldness	Positive (15)	Bony fishes Amphibians Birds Gastropods Insects Mammals Reptiles	De Fraipont, Clobert, John, and Meylan (2000), Fraser, Gilliam, Daley, Le, and Skalski (2001), Dingemanse, Both, van Noordwijk, Rutten, and Drent (2003), Krackow (2003), Rehage and Sih (2004), Chapman et al. (2011), Atwell et al. (2012), Lopez, Jungman, and Rehage (2012), Maes et al. (2012), Zajitschek, Zajitschek, Clobert, and Moulis (2012), Knop, Rindlisbacher, Ryser, and Gruebler (2013), Brodin and Drotz (2014), Ducatez, Humeau, Congretel, Fréville, and Baguette (2014), Edelsparre et al. (2014), and Gonzalez-Bernal, Brown, and Shine (2014)

Exploration	Positive (19)	Bony fishes Amphibians Birds Gastropods Insects Mammals Reptiles	Clobert et al. (1994) , Dingemanse, Both, Drent, van Oers, and Van Noordwijk (2002) , Dingemanse et al. (2003) , Krackow (2003) , Quinn, Patrick, Bouwhuis, Wilkin, and Sheldon (2009) , Chapple, Simmonds, and Wong (2011) , Hoset et al. (2011) , Marentette et al. (2011) , Quinn, Cole, Patrick, and Sheldon (2011) , Atwell et al. (2012) , Liebl and Martin (2012) , Maes et al. (2012) , Rasmussen and Belk (2012) , Debeffe et al. (2013) , Knop et al. (2013) , Korsten, van Overveld, Adriaensen, and Matthysen (2013) , Brodin and Drotz (2014) , Ducatez et al. (2014) , and van Overveld, Careau, Adriaensen, and Matthysen (2014)
	Negative (1)	Mammals	Myers and Krebs (1971)
Sociability	Positive (2)	Mammals Reptiles	Cote and Clobert (2007) and Jokela et al. (2008)
	Negative (12)	Bony fishes Arachnids Insects Mammals Annelid worms Reptiles	Bekoff (1977) , Ims (1990) , Mehlman et al. (1995) , O’Riain et al. (1996) , Toonen and Pawlik (2001) , Aragón et al. (2006) , Cote and Clobert (2007) , Jokela et al. (2008) , Blumstein, Wey, and Tang (2009) , Schtickzelle, Fjerdingstad, Chaine, and Clobert (2009) , Corcobado, Rodríguez-Gironés, Moya-Laraño, and Avilés (2012) , and Aguillon and Duckworth (2015)

personality. After all, heightened activity levels can lead to longer distances traveled without any need to invoke active decision-making processes by the organism. For example, *Tetrahymena thermophile* is a protozoan that shows the same correlation between activity levels and dispersal as is seen across animals (Pennekamp, Mitchell, Chaine, & Schtickzelle, 2014), suggesting that higher order cognitive functions are not necessary to explain the link between activity and dispersal behavior. Yet, many of the other traits frequently correlated with dispersal, such as boldness and exploratory behavior, likely do involve decision-making processes.

Boldness in animals is generally defined as the willingness to take more risks in exchange for higher reward (e.g., greater access to mates or resources) and is thought to be a core facet of the human personality dimension of extraversion (Gosling & John, 1999). Variation among individuals in extraversion is linked to variation in areas of the prefrontal cortex that are associated with decision-making in response to the processing of reward information, self-evaluation, and emotional regulation (Adelstein et al., 2011; DeYoung et al., 2010). Similar associations between decision-making processes and areas of the brain involved in risk-taking and reward have been found in nonhuman primates (Roesch & Olson, 2004) and birds (Scarf et al., 2011). Thus, associations between dispersal propensity and boldness may reflect variation among individuals in risk/reward-based decision-making processes; however, it is expected that boldness will influence only very local scale decision-making processes, such as local foraging decisions under predation risk. Given this, it is still unclear whether variation in personality traits are linked to dispersal because of their influence on local scale movements that inevitably scale up to influence broader movement patterns, or whether they more directly influence the propensity of individuals to disperse by influencing their overall assessment of the risk of leaving the natal population.

Only aggression and sociability appear to be expressed relatively independently of dispersal propensity across taxa (Table 1), indicating that the correlation between these traits and dispersal might vary with environmental context or be particularly evolutionarily labile. Interestingly, activity, boldness, and exploration are traits that can be expressed outside the context of social interactions; however, aggression and sociability are only expressed in response to interactions with other individuals. Therefore, how these traits correlate with dispersal may be highly dependent on variation in social systems across species. For example, philopatric individuals possess traits that allow them to succeed in high-density populations. In some species, this

requires high competitive ability (Guerra & Pollack, 2010; Yamane, Okada, Nakayama, & Miyatake, 2010) whereas in others, it requires higher sociability and cooperation (Aguillon & Duckworth, 2015; Cote & Clobert, 2007; Sinervo & Clobert, 2003). Similarly, highly social individuals may disperse from a low density population to seek out more conspecifics but remain philopatric when in a high density population (Cote & Clobert, 2007). Finally, high aggression may enable individuals to have greater flexibility in dispersal behavior if it means that they can outcompete conspecifics across both high and low density populations.

These observations suggest that the influence of various personality traits on dispersal may be hierarchical. First, variation in activity, boldness, and exploration may determine the propensity of individuals to undertake longer movements from familiar territory. Then, aggression and social behavior may interact with environmental factors such as population density to influence the likelihood that individuals can successfully remain in or leave their natal population. Given this, information on the timing of expression of personality traits relative to the dispersal decision can provide insight into the causal mechanisms behind individual variation in dispersal propensity. Finally, the personality traits most clearly associated with dispersal—activity levels, boldness, and exploratory behavior—are related to proactive and reactive coping styles, which may be stress induced (Korte et al., 2005). Numerous studies that have shown that dispersal strategies are determined early in development and are influenced by maternal effects (Larios & Venable, 2015; Mackay & Lamb, 1979; Massot & Clobert, 1995; Meylan & Clobert, 2004; Mousseau & Dingle, 1991), suggesting that dispersal variation may frequently be an emergent outcome of stress-induced maternal programming. Thus, it will be highly informative in future studies of the link between personality traits and dispersal to determine the relative timing of expression of these traits in development and the role of parental effects in their expression.

4.2 Maternally Induced Dispersal Behavior

Maternal effects on offspring dispersal are common and particularly well studied in plants and insects (Donohue, 1999; Harrison, 1980; Larios & Venable, 2015; Mousseau & Dingle, 1991). In these taxa, maternal effects are often responsible for an association between dispersal and major changes in morphology (e.g., wings in insects and seed morphology in plants). Maternally induced dispersal phenotypes make sense in these species because

such large-scale reorganization of the phenotype is easier to accomplish if it occurs earlier rather than late in development (Badyaev, 2008; Uller, 2008). However, the often documented maternal effects on dispersal decisions in vertebrates (e.g., Duckworth, 2009; Massot & Clobert, 1995; Sinervo et al., 2006; Tschirren, Fitze, & Richner, 2007) have been puzzling because dispersal strategies are rarely associated with obvious morphological changes and thus it is unclear why maternal rather than direct induction of alternate dispersal strategies evolves. The finding that dispersal decisions of vertebrates are frequently influenced by personality traits (Table 1) sheds some light on this problem. In essence, if our structural view of personality variation is correct, then the developmental processes that underlie personality variation are analogous to the major morphological changes that are required to produce distinct dispersal morphs in plants and insects. This is because they often require significant organizational effects on the brain (Section 2.1). Thus, the study of the developmental processes that underlie personality variation in vertebrates can provide novel insight into the evolution of dispersal strategies in general, and into maternal induction of these strategies, in particular.

Maternally induced dispersal strategies of western bluebirds provide an example of how the links between dispersal and other traits might evolve in a species-specific way. Western bluebirds overlap with their sister species, mountain bluebirds (*Sialia currucoides*), across much of their range in the northwestern United States. The two species aggressively compete with each other and with other secondary cavity nesters for nest cavities in successional postfire habitat. Differences in competitive ability and dispersal propensity produce cycles of species replacement that result in predictable changes in breeding density and resource competition over time (Duckworth, 2012; Duckworth, Belloni, & Anderson, 2015).

The competitive environment experienced by mothers during oogenesis induces alternative dispersal strategies in western bluebirds (Duckworth et al., 2015). Females breeding on territories with low resource availability (few nest cavities) experience heightened aggressive interference for their primary nest cavity from heterospecific competitors whereas females on territories with high resource availability (many nest cavities) experience reduced aggression because heterospecific competitors simply breed in one of the extra cavities, keeping others of their own kind away from the bluebirds' territory. The peak of these aggressive interactions overlap with the peak period of oogenesis, making a mother's aggressive interactions with heterospecifics not only a reliable cue of nest cavity availability on the territory, but also a circumstance whose timing is uniquely suited to influence

early developmental processes. Indeed, experimental manipulation of nest cavity availability on bluebird territories, which in turn manipulates aggressive interactions with heterospecifics, influenced the amount of androgen allocated to eggs—females with extra nest cavities on their territories allocate more testosterone to the clutch than females with few or no extra nest cavities (Fig. 3; Duckworth et al., 2015). In turn, on high competition territories (few nest cavities, many aggressive interactions) aggressive sons were produced whereas, on low competition territories (numerous nest cavities, few aggressive interactions), nonaggressive sons were produced (Fig. 3; Aguillon & Duckworth, 2015; Duckworth, 2009). Exposure to different levels of androgens at the earliest stage of development determined lifetime expression of aggression (Duckworth & Sockman, 2012) presumably through organizational effects on the neuroendocrine system (Groothuis, Müller, von Engelhardt, Carere, & Eising, 2004).

One way that this maternal influence on offspring aggression translates into variation in dispersal is through downstream effects on the opportunities available to offspring to pursue distinct dispersal strategies (Fig. 3). Nonaggressive sons, because they are poor competitors, are able to gain territories by breeding near family members. Parents often tolerate sons

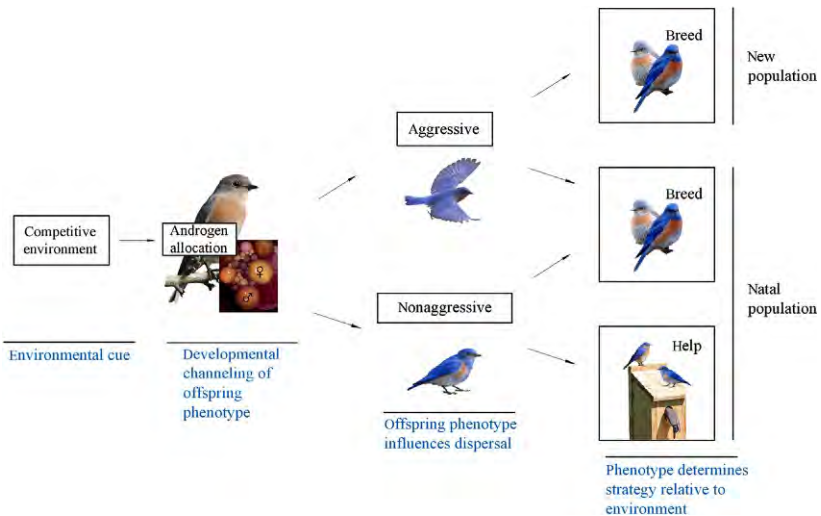


Fig. 3 Early developmental channeling of offspring phenotype limits the range of breeding and dispersal strategies pursued by male western bluebird. The competitive environment induces females to allocate either high or low amounts of androgen to a clutch, producing organizational effects on offspring aggression. This has downstream effects on formation of breeding and dispersal strategies (see text for details).

breeding in a nest cavity that is quite close to their own nest cavity, but only if this son is nonaggressive (Aguillon & Duckworth, 2015). Moreover, territory boundaries between family members are either not defended (Aguillon & Duckworth, 2015) or are cooperatively defended (Dickinson, Euaparadorn, Greenwald, Mitra, & Shizuka, 2009; R.A.D., pers. obs). Nonaggressive males have high lifetime fitness compared to aggressive males (Duckworth, 2008); however, the cost of having a low aggression phenotype is that nonaggressive sons are poor competitors (Duckworth, 2006). In fact, when stochastic events produce a mismatch between offspring behavioral phenotype and resource availability on the parental territory, nonaggressive sons only choice is to forego independent breeding to help at a relative's nest (Potticary & Duckworth, 2017).

At the other end of the behavioral spectrum, aggressive males are good competitors and, unlike nonaggressive males, they have the option to either disperse or stay in their natal population. However, parents rarely allow them to breed nearby and aggressive sons that choose to stay in their natal population typically either have no relatives in the population (e.g., because their parents did not survive the winter) or they are breeding at a territory that is far away from family members (Aguillon & Duckworth, 2015). Aggressive sons have a wider array of dispersal opportunities available to them than nonaggressive sons; however, they are restricted in their opportunities to cooperate with relatives and the cooperative breeding strategy is only observed in the least aggressive males of the population (Potticary & Duckworth, 2017). Thus, the early organizational effects of androgens on a son's aggression restricts the range of breeding and dispersal strategies available, in the case of nonaggressive sons, by limiting their ability to compete for territories on their own and, in the case of aggressive sons, by limiting their ability to breed near their parents (Fig. 3). In turn, this early developmental channeling then impacts the later decisions that aggressive and nonaggressive males will make, ultimately influencing the expression of breeding and dispersal strategies.

Findings in the western bluebird system indicate a causal role of development in delineating pathways that affect the expression of dispersal strategies. Early inducement of personality and its effects on subsequent decision processes shows that the costs and benefits of pursuing a particular behavioral strategy depend on an individual's personality type and emphasizes that the behavioral components that comprise a dispersal strategy are not ontogenetically independent. Moreover, a developmental perspective in this system also answers the question of why western bluebirds' dispersal strategies

are induced by cues in the maternal environment rather than through direct environmental induction in the offspring generation. The realization that a personality trait, which may require significant organizational effects in the brain, lays the foundation for the expression of alternative dispersal strategies in this species provides an explanation for the maternally induced inheritance of these complex and seemingly contingent behavioral strategies. Learning the neurological basis of these organizational effects on the brain is the next step in this system and will provide further insight into how dispersal strategies are influenced by the neural trade-offs outlined earlier (Section 3.1).



5. CONCLUSION AND FUTURE DIRECTIONS

The empirical findings outlined earlier raise several questions. How do species differences in behavioral strategies arise? Do they result primarily from regulatory changes in upstream developmental pathways or the reshuffling of downstream elements? On what timescales do correlations between behavioral elements change?

Returning to dispersal strategies as an example, many insect and plant species do not display dispersal polymorphisms, or in the case of vertebrates, distinct dispersal strategies. As a case in point, mountain bluebirds are much more dispersive than western bluebirds as a species because they lack the philopatric strategy completely—offspring rarely remain in their natal population to breed (Power & Lombardo, 1996). Moreover, mountain bluebirds are less competitive than western bluebirds because they lack the highly aggressive phenotype that is present in western bluebirds (Duckworth & Badyaev, 2007; Duckworth & Semenov, 2017). Finally, among the three bluebird species of the genus *Sialia*, the western bluebird is the only one that displays cooperative behavior. Thus, across the species of this clade, western bluebirds appear to have evolved three new behavioral strategies—nonaggressive philopatry, aggressive dispersers, and cooperative breeding—by expanding the range of their dispersal distances, aggressiveness, and sociability and by linking the expanded variation of these traits in novel ways.

Given the novel patterns of trait expression, how then does it evolve into such complex, finely tuned, and often maternally induced adaptive strategies? One possibility is that alternative strategies emerged out of preexisting personality variation, such that the underlying developmental pathways that lead to alternate strategies are relatively conserved across taxa. In this

scenario, what has to evolve are the links between the strategy and the cues. Thus, understanding how axes of personality variation that are seemingly ubiquitous across species become integrated with dispersal behavior (or mating behavior or foraging behavior, etc.) may be key to understanding the evolution of alternative strategies. Do alternative strategies within a species always emerge through an expansion of variation along predefined personality axes? Or do novel strategies require recombining distinct axes of personality variation in different ways? These questions assume that personality variation is correlated with variation in behavioral strategies. This assumption seems justified based on the fact that most studies of behavioral strategies measure traits like aggression, sociability, activity levels (e.g., foraging rates, mate searching effort, parental effort), and boldness (e.g., risk-taking behavior) which have been shown to be personality traits in at least some species. However, explicit connections between personality traits and behavioral strategies are needed across a wide variety of species to determine whether this assumption holds across taxa.

Further, there is accumulating evidence that early organizational effects on the brain that underlie personality variation are stress induced such that what likely evolves are the links between preexisting structural variation shaped by neural trade-offs, a species-specific strategy, and the environmental cue that indicates species-specific stressors. If this is the case, then whether and how personality variation is integrated with dispersal, mating, parental, or foraging behavior will depend on the life history and ecology of the species. Thus, this framework predicts that brain structure should show the same trade-offs across a wide variety of taxa which should map similarly onto personality variation across taxa. However, depending on their ecology, species should vary in the range of personality variation they express and in how and whether different extremes of this variation is linked to particular behavioral strategies.

The perspective we present here helps resolve one of the longest-standing questions in the evolution of behavior: how can complex, adaptive behavioral strategies evolve gradually over long evolutionary time when the strategy is only expressed and functional when all components are present? The insights gained from a developmental perspective are crucial to answering this question and more studies are needed to test the conceptual framework outlined earlier. In particular, are the findings from the human personality literature outlined in [Section 2.2](#), that personality variation is underlain by structural variation in the brain, corroborated by studies of nonhuman animals? Because of recent advances in MRI and fMRI

technology, there has been an explosion of studies on the neurobiology of individual differences in behavior of humans. These studies are well poised to guide research on the neurobiology of nonhuman animals, but is often difficult to generalize their findings because we lack a way of standardizing and linking measurements of human personality to measurements of personality in animals. Such standardization is also crucial to the goal of carrying out comparative studies on the patterns and neurobiological basis of personality variation from diverse taxa. Ultimately, comparative studies of the neurobiology of personality may help to resolve this issue as we gain a deeper understanding of underlying neural trade-offs.

In nonhuman animals, personality traits are often defined based on repeatability of behavior among individuals over time and across different contexts (Duckworth, 2015). However, this definition is only an imprecise approximation of what we truly mean by personality because behaviors are the very end result of a complex mental process that involves cognition, sensory input, and motivational state. Our perspective is that personality is the underlying stable structure that influences all of these processes, making the expression of particular behaviors more or less likely in a particular individual, but never predetermining the behavior an organism displays. Thus, we hope that by delving deeper into the underlying neural mechanisms that govern the way different individuals gather, evaluate, and think about information in their environment, we will not only gain a better understanding of what personality is, but also, how it evolves and how it influences the evolution of the behaviors we observe.

ACKNOWLEDGMENTS

We thank Dan Blumstein and one anonymous reviewer for insightful comments which improved this paper.

REFERENCES

- Adelstein, J. S., Shehzad, Z., Mennes, M., Deyoung, C. G., Zuo, X. N., Kelly, C., et al. (2011). Personality is reflected in the brain's intrinsic functional architecture. *PLoS One*, *6*, e27633.
- Aguillon, S. M., & Duckworth, R. A. (2015). Kin aggression and resource availability influence phenotype-dependent dispersal in a passerine bird. *Behavioral Ecology and Sociobiology*, *69*, 625–633.
- Alvarado, S., Fernald, R. D., Storey, K. B., & Szyf, M. (2014). The dynamic nature of DNA methylation: A role in response to social and seasonal variation. *Integrative and Comparative Biology*, *54*, 68–76.
- Andersen, S. L. (2003). Trajectories of brain development: Point of vulnerability or window of opportunity? *Neuroscience and Biobehavioral Reviews*, *27*, 3–18.

- Antonow-Schlorke, I., Schwab, M., Cox, L. A., Li, C., Stuchlik, K., Witte, O. W., et al. (2011). Vulnerability of the fetal primate brain to moderate reduction in maternal global nutrient availability. *Proceedings of the National Academy of Sciences of the United States of America*, *108*, 3011–3016.
- Aragón, P., Meylan, S., & Clobert, J. (2006). Dispersal status-dependent response to the social environment in the Common Lizard, *Lacerta vivipara*. *Functional Ecology*, *20*, 900–907.
- 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.
- Badyaev, A. V. (2005). Stress-induced variation in evolution: From behavioral plasticity to genetic assimilation. *Proceedings of the Royal Society of London B*, *272*, 877–886.
- Badyaev, A. V. (2008). Maternal effects as generators of evolutionary change: A reassessment. *Annals of the New York Academy of Sciences*, *1133*, 151–161.
- Badyaev, A. V. (2011). How do precise adaptive features arise in development? Examples with evolution of context-specific sex ratios and perfect beaks. *The Auk*, *128*, 467–474. <https://doi.org/10.1525/auk.2011.11103>.
- Badyaev, A. V. (2013). “Homeostatic hitchhiking”: A mechanism for the evolutionary retention of complex adaptations. *Integrative and Comparative Biology*, *53*, 913–922.
- Badyaev, A. V. (2014). Epigenetic resolution of the “curse of complexity” in adaptive evolution of complex traits. *The Journal of Physiology*, *592*, 2251–2260.
- Barton, R. A., & Harvey, P. H. (2000). Mosaic evolution of brain structure in mammals. *Nature*, *405*, 1055–1058.
- Bavelier, D., Levi, D. M., Li, R. W., Dan, Y., & Hensch, T. K. (2010). Removing brakes on adult brain plasticity: From molecular to behavioral interventions. *The Journal of Neuroscience*, *30*, 14964–14971.
- Bekoff, M. (1977). Mammalian dispersal and ontogeny of individual behavioral phenotypes. *American Naturalist*, *111*, 715–732.
- Bell, A. M., Hankison, S. J., & Laskowski, K. L. (2009). The repeatability of behaviour: A meta-analysis. *Animal Behaviour*, *77*, 771–783.
- Belthoff, J. R., & Dufty, A. M. (1998). Corticosterone, body condition and locomotor activity: A model for dispersal in screech-owls. *Animal Behaviour*, *55*, 405–415.
- Bickart, K. C., Wright, C. I., Dautoff, R. J., Dickerson, B. C., & Barrett, L. F. (2011). Amygdala volume and social network size in humans. *Nature Neuroscience*, *14*, 163–164.
- Bishop, S. J. (2009). Trait anxiety and impoverished prefrontal control of attention. *Nature Neuroscience*, *12*, 92–98.
- Bjornebekk, A., Fjell, A. M., Walhovd, K. B., Grydeland, H., Torgersen, S., & Westlye, L. T. (2013). Neuronal correlates of the five factor model (FFM) of human personality: Multimodal imaging in a large healthy sample. *NeuroImage*, *65*, 194–208.
- Blumstein, D. T., Wey, T. W., & Tang, K. (2009). A test of the social cohesion hypothesis: Interactive female marmots remain at home. *Proceedings of the Royal Society of London B*, *276*, 3007–3012.
- Bogacz, R., Wagenmakers, E.-J., Forstmann, B. U., & Nieuwenhuis, S. (2009). The neural basis of the speed-accuracy tradeoff. *Trends in Neurosciences*, *33*, 10–16.
- Bonte, D., Lens, L., & Maelfait, J.-P. (2004). Lack of homeward orientation and increased mobility result in high emigration rates from low-quality fragments in a dune wolf spider. *Journal of Animal Ecology*, *73*, 643–650.
- Bowler, D. E., & Benton, T. G. (2005). Causes and consequences of animal dispersal strategies: Relating individual behaviour to spatial dynamics. *Biological Reviews*, *80*, 205–225.
- Braver, T. S., Cole, M. W., & Yarkoni, T. (2010). Vive les differences! Individual variation in neural mechanisms of executive control. *Current Opinion in Neurobiology*, *20*, 242–250.

- Bresin, K., Hilmert, C. J., Wilkowski, B. M., & Robinson, M. D. (2012). Response speed as an individual difference: Its role in moderating the agreeableness–anger relationship. *Journal of Research in Personality, 46*, 79–86.
- Brodin, T., & Drotz, M. K. (2014). Individual variation in dispersal associated behavioral traits of the invasive Chinese mitten crab (*Eriocheir sinensis*, H. Milne Edwards, 1854) during initial invasion of Lake Vänern, Sweden. *Current Zoology, 60*, 410–416.
- Brown, A., Susser, E., Lin, S., Neugebauer, R., & Gorman, J. (1995). Increased risk of affective disorders in males after second trimester prenatal exposure to the Dutch hunger winter of 1944–45. *British Journal of Psychiatry, 166*, 601–606.
- Bullmore, E., & Sporns, O. (2012). The economy of brain network organization. *Nature Reviews. Neuroscience, 13*, 336–349.
- Chapman, B. B., Hulthén, K., Blomqvist, D. R., Hansson, L.-Å., Nilsson, J.-Å., Brodersen, J., et al. (2011). To boldly go: Individual difference in boldness influence migratory tendency. *Ecology Letters, 14*, 871–876.
- Chapple, D. G., Simmonds, S. M., & Wong, B. B. M. (2011). Know when to run, know when to hide: Can behavioral differences explain the divergent invasion success of two sympatric lizards? *Ecology and Evolution, 1*, 278–289.
- Charil, A., Laplante, D. P., Vaillancourt, C., & King, S. (2010). Prenatal stress and brain development. *Brain Research Reviews, 65*, 56–79.
- Charmandari, E., Tsigos, C., & Chrousos, G. (2005). Endocrinology of the stress response. *Annual Review of Physiology, 67*, 259–284.
- Cherniak, C., Mokhtarzada, Z., Rodriguez-Esteban, R., & Changizi, K. (2004). Global optimization of cerebral cortex layout. *Proceedings of the National Academy of Sciences of the United States of America, 101*, 1081–1086.
- Cheverud, J. M. (1984). Quantitative genetic and developmental constraints on evolution by selection. *Journal of Theoretical Biology, 110*, 155–171.
- Chittka, L., Skorupski, P., & Raine, N. E. (2009). Speed-accuracy tradeoffs in animal decision making. *Trends in Ecology & Evolution, 24*, 400–407.
- Clayton, N. S. (1998). Memory and the hippocampus in food-storing birds: A comparative approach. *Neuropharmacology, 37*, 441–452.
- Clobert, J., Massot, M., Lecomte, J., Sorci, G., De Fraipont, M., & Barbault, R. (1994). Determinants of dispersal behavior: The common lizard as a case study. In L. J. Vitt & E. R. Pianka (Eds.), *Lizard Ecology: Historical and Experimental Perspectives*, 206. Princeton University Press.
- Cook, P. F., Spivak, M., & Berns, G. (2016). Neurobehavioral evidence for individual differences in canine cognitive control: An awake fMRI study. *Animal Cognition, 19*, 867–878.
- Coppens, C. M., de Boer, S. F., & Koolhaas, J. M. (2010). Coping styles and behavioural flexibility: Towards underlying mechanisms. *Philosophical Transactions of the Royal Society B, 365*, 4021–4028.
- Corcobado, G., Rodríguez-Gironés, M. A., Moya-Laraño, J., & Avilés, L. (2012). Sociality level correlates with dispersal ability in spiders. *Functional Ecology, 26*, 794–803.
- Cote, J., & Clobert, J. (2007). Social personalities influence natal dispersal in a lizard. *Proceedings of the Royal Society of London B, 274*, 383–390.
- Cote, J., Clobert, J., Brodin, T., Fogarty, S., & Sih, A. (2010). Personality-dependent dispersal: Characterization, ontogeny and consequences for spatially structured populations. *Philosophical Transactions of the Royal Society B, 365*, 4065–4076.
- Cremers, H., van Tol, M. J., Roelofs, K., Aleman, A., Zitman, F. G., van Buchem, M. A., et al. (2011). Extraversion is linked to volume of the orbitofrontal cortex and amygdala. *PLoS One, 6*, e28421.
- De Fraipont, M., Clobert, J., John, H., & Meylan, S. (2000). Increased pre-natal maternal corticosterone promotes philopatry of offspring in common lizards *Lacerta vivipara*. *Journal of Animal Ecology, 69*, 404–413.

- Debeffe, L., Morellet, N., Cargnelutti, B., Lourtet, B., Coulon, A., Gaillard, J. M., et al. (2013). Exploration as a key component of natal dispersal: Dispersers explore more than philopatric individuals in roe deer. *Animal Behaviour*, *86*, 143–151.
- DeYoung, C. G., Hirsh, J. B., Shane, M. S., Papademetris, X., Rajeevan, N., & Gray, J. R. (2010). Testing predictions from personality neuroscience. Brain structure and the big five. *Psychological Science*, *21*, 820–828.
- Dias, B. G., & Ressler, K. J. (2014). Parental olfactory experience influences behavior and neural structure in subsequent generations. *Nature Neuroscience*, *17*, 89–96.
- Dickinson, J. L., Euaparadorn, M., Greenwald, K., Mitra, C., & Shizuka, D. (2009). Cooperation and competition: Nepotistic tolerance and intrasexual aggression in western bluebird winter groups. *Animal Behaviour*, *77*, 867–872.
- Dingemans, N. J., Both, C., Drent, P. J., & Tinbergen, J. M. (2004). Fitness consequences of avian personalities in a fluctuating environment. *Proceedings of the Royal Society of London B*, *271*, 847–852.
- Dingemans, N. J., Both, C., Drent, P. J., van Oers, K., & Van Noordwijk, A. J. (2002). Repeatability and heritability of exploratory behaviour in great tits from the wild. *Animal Behaviour*, *64*, 929–938.
- Dingemans, N. J., Both, C., van Noordwijk, A. J., Rutten, A. L., & Drent, P. J. (2003). Natal dispersal and personalities in great tits (*Parus major*). *Proceedings of the Royal Society of London B*, *270*, 741–747.
- Dobbing, J. (1964). The influence of early nutrition on the development and myelination of the brain. *Proceedings of the Royal Society of London B*, *159*, 503–509.
- Donohue, K. (1999). Seed dispersal as a maternally influenced character: Mechanistic basis of maternal effects and selection on maternal characters in an annual plant. *American Naturalist*, *154*, 674–689.
- Ducatez, S., Humeau, A., Congretel, M., Fréville, H., & Baguette, M. (2014). Butterfly species differing in mobility show different structures of dispersal-related syndromes in the same fragmented landscape. *Ecography*, *37*, 378–389.
- Duckworth, R. A. (2006). Aggressive behaviour affects selection on morphology by influencing settlement patterns in a passerine bird. *Proceedings of the Royal Society of London B*, *273*, 1789–1795.
- Duckworth, R. A. (2008). Adaptive dispersal strategies and the dynamics of a range expansion. *American Naturalist*, *172*, S4–S17.
- Duckworth, R. A. (2009). Maternal effects and range expansion: A key factor in a dynamic process? *Philosophical Transactions of the Royal Society B*, *364*, 1075–1086.
- Duckworth, R. A. (2010). Evolution of personality: Developmental constraints on behavioral flexibility. *The Auk: Ornithological Advances*, *127*, 752–758.
- Duckworth, R. A. (2012). Evolution of genetically integrated dispersal strategies. In J. Clobert, M. Baguette, T. G. Benton, & J. M. Bullock (Eds.), *Dispersal ecology and evolution* (pp. 83–94). Oxford: Oxford University Press.
- Duckworth, R. A. (2015). Neuroendocrine mechanisms underlying behavioral stability: Implications for the evolutionary origin of personality. *Annals of the New York Academy of Sciences*, *1360*, 54–74.
- Duckworth, R. (2018). Reconciling the tension between behavioral change and stability. In D. S. Wilson & S. C. Hayes (Eds.), *Evolution science and contextual behavioral science: A reintegration* (chapter 17). Oakland, CA: New Harbinger Publications. in press.
- Duckworth, R. A., & Badyaev, A. V. (2007). Coupling of dispersal and aggression facilitates the rapid range expansion of a passerine bird. *Proceedings of the National Academy of Sciences of the United States of America*, *104*, 15017–15022.
- Duckworth, R. A., Belloni, V., & Anderson, S. R. (2015). Cycles of species replacement emerge from locally induced maternal effects on offspring behavior in a passerine bird. *Science*, *374*, 875–877.

- Duckworth, R. A., & Kruuk, L. E. B. (2009). Evolution of genetic integration between dispersal and colonization ability in a bird. *Evolution*, *63*, 968–977.
- Duckworth, R. A., & Semenov, G. A. (2017). Hybridization associated with cycles of ecological succession in a passerine bird. *The American Naturalist*, *190*, E94–E105. <https://doi.org/10.1086/693160>.
- Duckworth, R. A., & Sockman, K. W. (2012). Proximate mechanisms of behavioural inflexibility: Implications for the evolution of personality traits. *Functional Ecology*, *26*, 559–566.
- Dunbar, R. I., & Shultz, S. (2007). Understanding primate brain evolution. *Philosophical Transactions of the Royal Society B*, *362*, 649–658.
- Edelspanner, A. H., Vesterberg, A., Lim, J. H., Anwari, M., & Fitzpatrick, M. J. (2014). Alleles underlying larval foraging behaviour influence adult dispersal in nature. *Ecology Letters*, *17*, 333–339.
- Eysenck, M. W., Derakshan, N., Santos, R., & Calvo, M. G. (2007). Anxiety and cognitive performance: Attentional control theory. *Emotion*, *7*, 336–353.
- Fairbairn, D. J. (1978). Dispersal of deer mice, *Peromyscus maniculatus*: Proximal causes and effects on fitness. *Oecologia*, *32*, 171–193.
- Finlay, B. L., & Darlington, R. B. (1995). Linked regularities in the development and evolution of mammalian brains. *Science*, *268*, 1578–1585.
- Finlay, B. L., & Uchiyama, R. (2015). Developmental mechanisms channeling cortical evolution. *Trends in Neurosciences*, *38*, 69–76.
- Forstmann, B. U., Anwander, A., Schafer, A., Neumann, J., Brown, S., Wagenmakers, E.-J., et al. (2010). Cortico-striatal connections predict control over speed and accuracy in perceptual decision making. *Proceedings of the National Academy of Sciences of the United States of America*, *107*, 15916–15920.
- Fox, S. E., Levitt, P., & Nelson, C. E. I. (2010). How the timing and quality of early experiences influence the development of brain architecture. *Child Development*, *81*, 28–40.
- Fraser, D. F., Gilliam, J. F., Daley, M. J., Le, A. N., & Skalski, G. T. (2001). Explaining leptokurtic movement distributions: Intrapopulation variation in boldness and exploration. *The American Naturalist*, *158*, 124–135.
- Fuentes, P., Barros-Loscertales, A., Bustamante, J. C., Rosell, P., Costumero, V., & Avila, C. (2012). Individual differences in the behavioral inhibition system are associated with orbitofrontal cortex and precuneus gray matter volume. *Cognitive, Affective, & Behavioral Neuroscience*, *12*, 491–498.
- Gaines, M. S., & McClenagh, L. R. (1980). Dispersal in small mammals. *Annual Review of Ecology and Systematics*, *11*, 163–196.
- Gold, J. I., & Shadlen, M. N. (2007). The neural basis of decision making. *Annual Review of Neuroscience*, *30*, 535–574.
- Gonzalez-Bernal, E., Brown, G. P., & Shine, R. (2014). Invasive cane toads: Social facilitation depends upon an individual's personality. *PLoS One*, *9*, e102880.
- Gosling, S. D., & John, O. P. (1999). Personality dimensions in nonhuman animals: A cross-species review. *Current Directions in Psychological Science*, *8*, 69–75.
- Groen, M., Sopinka, N. M., Marentette, J. R., Reddon, A. R., Brownscombe, J. W., Fox, M. G., et al. (2012). Is there a role for aggression in round goby invasion fronts? *Behaviour*, *149*, 685–703.
- Groothuis, T. G. G., Müller, W., von Engelhardt, N., Carere, C., & Eising, C. (2004). Maternal hormones as a tool to adjust offspring phenotype in avian species. *Neuroscience and Biobehavioural Reviews*, *29*, 329–352.
- Gross, M. R. (1996). Alternative reproductive strategies and tactics: Diversity within sexes. *Trends in Ecology & Evolution*, *11*(2), 92–98.
- Guerra, P. A., & Pollack, G. S. (2010). Colonists and desperadoes: Different fighting strategies in wing-dimorphic male Texas field crickets. *Animal Behaviour*, *79*, 1087–1093.

- Harrison, R. G. (1980). Dispersal polymorphisms in insects. *Annual Review of Ecology and Systematics*, *11*, 95–118.
- Hock, H., Brown, A., & Susser, E. (1998). The Dutch famine and schizophrenia spectrum disorders. *Social Psychiatry and Psychiatric Epidemiology*, *33*, 373–379.
- Holekamp, K. E., & Smale, L. (1998). Dispersal status influences hormones and behavior in the male spotted hyena. *Hormones and Behavior*, *33*, 205–206.
- Holway, D. A., Suarez, A. V., & Case, T. J. (1998). Loss of intraspecific aggression in the success of a widespread invasive social insect. *Science*, *282*, 949–952.
- Hopfield, J. J. (1982). Neural networks and physical systems with emergent collective computational abilities. *Proceedings of the National Academy of Sciences of the United States of America*, *79*, 2554–2558.
- Hoset, K. S., Ferchaud, A. L., Dufour, F., Mersch, D., Cote, J., & Le Galliard, J. F. (2011). Natal dispersal correlates with behavioral traits that are not consistent across early life stages. *Behavioral Ecology*, *22*, 176–183.
- Ims, R. A. (1990). Determinants of natal dispersal and space use in grey-sided voles, *Clethrionomys rufocanus*: A combined field and laboratory experiment. *Oikos*, 106–113.
- Janak, P. H., & Tye, K. M. (2015). From circuits to behaviour in the amygdala. *Nature*, *517*, 284–292.
- Jokela, M., Elovainio, M., Kivimäki, M., & Keltikangas-Järvinen, L. (2008). Temperament and migration patterns in Finland. *Psychological Science*, *19*, 831–837.
- Kanai, R., & Rees, G. (2011). The structural basis of inter-individual differences in human behaviour and cognition. *Nature Reviews. Neuroscience*, *12*, 231–242.
- Kennis, M., Rademaker, A. R., & Geuze, E. (2013). Neural correlates of personality: An integrative review. *Neuroscience and Biobehavioral Reviews*, *37*, 73–95.
- Kety, S. S. (1957). *Metabolism of the nervous system*. London: Pergamon.
- Knop, E., Rindlisbacher, N., Ryser, S., & Grüebler, M. U. (2013). Locomotor activity of two sympatric slugs: Implications for the invasion success of terrestrial invertebrates. *Ecosphere*, *4*, art92.
- Knudsen, E. (2004). Sensitive periods in the development of the brain and behavior. *Journal of Cognitive Neuroscience*, *16*, 1412–1425.
- Kobler, A., Maes, G. E., Humblet, Y., Volckaert, F. A. M., & Eens, M. (2011). Temperament traits and microhabitat use in bullhead, *Cottus perifretum*: Fish associated with complex habitats are less aggressive. *Behaviour*, *148*, 603–625.
- Kolb, B. (1995). *Brain plasticity and behavior*. New Jersey: Lawrence Erlbaum Associates Mahwah.
- Kolb, B., & Gibb, R. (2014). Searching for the principles of brain plasticity and behavior. *Cortex: A Journal Devoted to the Study of the Nervous System and Behavior*, *58*, 251–260.
- Koolhaas, J. M., Korte, S. M., De Boer, S. F., Van Der Vegt, B. J., Van Reenen, C. G., Hopster, H., et al. (1999). Coping styles in animals: Current status in behavior and stress-physiology. *Neuroscience and Biobehavioral Reviews*, *23*, 925–935.
- Korsten, P., van Overveld, T., Adriaensen, F., & Matthysen, E. (2013). Genetic integration of local dispersal and exploratory behaviour in a wild bird. *Nature Communications*, *4*, 2362.
- Korte, S. M., Koolhaas, J. M., Wingfield, J. C., & McEwen, B. S. (2005). The Darwinian concept of stress: Benefits of allostasis and costs of allostatic load and the trade-offs in health and disease. *Neuroscience and Biobehavioral Reviews*, *29*, 3–38.
- Kotrschal, A., Lievens, E. J., Dahlblom, J., Bundsen, A., Semenova, S., Sundvik, M., et al. (2014). Artificial selection on relative brain size reveals a positive genetic correlation between brain size and proactive personality in the guppy. *Evolution*, *68*, 1139–1149.
- Krackow, S. (2003). Motivational and heritable determinants of dispersal latency in wild male house mice (*Mus musculus musculus*). *Ethology*, *109*, 671–689.

- Krug, P. J., & Zimmer, R. K. (2004). Developmental dimorphism: Consequences for larval behavior and dispersal potential in a marine gastropod. *The Biological Bulletin*, 207, 233–246.
- Lande, R. (1980). The genetic covariance between characters maintained by pleiotropic mutations. *Genetics*, 94, 203–214.
- Larios, E., & Venable, D. L. (2015). Maternal adjustment of offspring provisioning and the consequences for dispersal. *Ecology*, 96, 2771–2780.
- Laughlin, S. B., & Sejnowski, T. J. (2003). Communication in neuronal networks. *Science*, 301, 1870–1874.
- LeDoux, J. E. (1989). Cognitive-emotional interactions in the brain. *Cognition & Emotion*, 3, 267–289.
- LeDoux, J. E. (2000). Emotions circuits in the brain. *Annual Review of Neuroscience*, 23, 155–184.
- Liebl, A. L., & Martin, L. B. (2012). Exploratory behaviour and stressor hyper-responsiveness facilitate range expansion of an introduced songbird. *Proceedings of the Royal Society of London B*, 279, 4375–4381.
- Lima, S. L., & Dill, L. M. (1990). Behavioral decisions made under the risk of predation: A review and prospectus. *Canadian Journal of Zoology*, 68, 619–640.
- Lisman, J. E., & Grace, A. A. (2005). The hippocampal-VTA loop: Controlling the entry of information into long-term memory. *Neuron*, 46, 703–713.
- Lledo, P. M., Alonso, M., & Grubb, M. S. (2006). Adult neurogenesis and functional plasticity in neuronal circuits. *Nature Reviews. Neuroscience*, 7, 179–193.
- Lopez, D. P., Jungman, A. A., & Rehage, J. S. (2012). Nonnative African jewelfish are more fit but not bolder at the invasion front: A trait comparison across an Everglades range expansion. *Biological Invasions*, 14, 2159–2174.
- Lupien, S. J., McEwen, B. S., Gunnar, M. R., & Heim, C. (2009). Effects of stress throughout the lifespan on the brain, behaviour and cognition. *Nature Reviews Neuroscience*, 10, 434–445.
- Mackay, P. A., & Lamb, R. J. (1979). Migratory tendency in aging populations of the pea aphid, *Acyrtosiphon-pisum* Oecologia, 39, 301–308.
- Maes, J., Van Damme, R., & Matthysen, E. (2012). Individual and among-population variation in dispersal-related traits in Natterjack toads. *Behavioral Ecology*, 24, 521–531.
- Marentette, J. R., Wang, G., Tong, S., Sopinka, N. M., Taves, M. D., Koops, M. A., et al. (2011). Laboratory and field evidence of sex-biased movement in the invasive round goby. *Behavioral Ecology and Sociobiology*, 65, 2239–2249.
- Massot, M., & Clobert, J. (1995). Influence of maternal food availability on offspring dispersal. *Behavioral Ecology and Sociobiology*, 37, 413–418.
- Matthysen, E. (2012). Multicausality of dispersal: A review. In J. Clobert, M. Baguette, T. G. Benton, & J. M. Bullock (Eds.), *Dispersal ecology and evolution*, Oxford University Press.
- Maynard Smith, J., Burian, R., Kauffman, S., Alberch, P., Campbell, J., Goodwin, B., et al. (1985). Developmental constraints and evolution: A perspective from the Mountain Lake Conference on development and evolution. *The Quarterly Review of Biology*, 60, 265–287.
- McCauley, S. J. (2010). Body size and social dominance influence breeding dispersal in male *Pachydiplax longipennis* (Odonata). *Ecological Entomology*, 35, 377–385.
- McClure, S. M., Laibson, D. I., Loewenstein, G., & Cohen, J. D. (2004). Separate neural systems value immediate and delayed monetary rewards. *Science*, 306, 503–507.
- McGowan, P. O., Suderman, M., Sasaki, A., Huang, T. C., Hallett, M., Meaney, M. J., et al. (2011). Broad epigenetic signature of maternal care in the brain of adult rats. *PLoS One*, 6, e14739.
- Meaney, M. J., & Szyf, M. (2005). Environmental programming of stress responses through DNA methylation: Life at the interface between a dynamic environment and a fixed genome. *Dialogues in Clinical Neuroscience*, 7, 103–123.

- Mehlman, P. T., Higley, J. D., Faucher, I., Lilly, A. A., Taub, D. M., Vickers, J., et al. (1995). Correlation of CSF 5-HIAA concentration with sociality and the timing of emigration in free-ranging primates. *American Journal of Psychiatry*, *152*, 907–913.
- Mehta, P. H., & Gosling, S. D. (2006). How can animal studies contribute to research on the biological bases of personality? In T. Canli (Ed.), *Biology of personality and individual differences* (pp. 427–448). Guilford Press.
- Meylan, S., & Clobert, J. (2004). Maternal effects on offspring locomotion: Influence of density and Corticosterone elevation in the Lizard *Lacerta vivipara*. *Physiological and Biochemical Zoology*, *77*, 450–458.
- Morgane, P. J., Austin-LaFrance, R., Bronzino, J., Tonkiss, J., Diaz-Cintra, S., Cintra, L., et al. (1993). Prenatal malnutrition and development of the brain. *Neuroscience and Bio-behavioral Reviews*, *17*, 91–128.
- Mousseau, T. A., & Dingle, H. (1991). Maternal effects in insect life histories. *Annual Review of Entomology*, *36*, 511–534.
- Mueller, J. C., Edelaar, P., Carrete, M., Serrano, D., Potti, J., Blas, J., et al. (2014). Behaviour-related DRD4 polymorphisms in invasive bird populations. *Molecular Ecology*, *23*, 2876–2885.
- Mychasiuk, R., Zahir, S., Schmold, N., Ilnytsky, S., Kovalchuk, O., & Gibb, R. (2012). Parental enrichment and offspring development: Modifications to brain, behavior and the epigenome. *Behavioural Brain Research*, *228*, 294–298.
- Myers, J. H., & Krebs, C. J. (1971). Genetic, behavioral, and reproductive attributes of dispersing field voles *Microtus pennsylvanicus* and *Microtus ochrogaster*. *Ecological Monographs*, *41*, 53–78.
- Nagengast, A. J., Braun, D. A., & Wolpert, D. M. (2011). Risk sensitivity in a motor task with speed–accuracy trade-off. *Journal of Neurophysiology*, *105*, 2668–2674.
- Neugebauer, R., Hoek, H., & Susser, E. (1999). Prenatal exposure to wartime famine and development of antisocial personality disorder in early adulthood. *Journal of the American Medical Association*, *282*, 455–462.
- Niven, J. E., & Laughlin, S. B. (2008). Energy limitation as a selective pressure on the evolution of sensory systems. *The Journal of Experimental Biology*, *211*, 1792–1804.
- Noreikiene, K., Herczeg, G., Gonda, A., Balázs, G., Husby, A., & Merilä, J. (2015). Quantitative genetic analysis of brain size variation in sticklebacks: Support for the mosaic model of brain evolution. *Proceedings of the Royal Society of London B*, *282*(1810), pii: 20151008.
- O’Riain, M. J., Jarvis, J. U. M., & Faulkes, C. G. (1996). A dispersive morph in the naked mole-rat. *Nature*, *380*, 619–621.
- Pennekamp, F., Mitchell, K. A., Chaine, A., & Schtickzelle, N. (2014). Dispersal propensity in *Tetrahymena thermophila ciliates*—A reaction norm perspective. *Evolution*, *68*, 2319–2330.
- Perri, R. L., Berchicci, M., Spinelli, D., & Di Russo, F. (2014). Individual differences in response speed and accuracy are associated to specific brain activities of two interacting systems. *Frontiers in Behavioral Neuroscience*, *8*, 251.
- Persson, A., Sim, S. C., Viriding, S., Onishchenko, N., Schulte, G., & Ingelman-Sundberg, M. (2014). Decreased hippocampal volume and increased anxiety in a transgenic mouse model expressing the human CYP2C19 gene. *Molecular Psychiatry*, *19*, 733–741.
- Phelps, E. A., Lempert, K. M., & Sokol-Hessner, P. (2014). Emotion and decision making: Multiple modulatory neural circuits. *Annual Review of Neuroscience*, *37*, 263–287.
- Pintor, L. M., Sih, A., & Kerby, J. L. (2009). Behavioral correlations provide a mechanism for explaining high invader densities and increased impacts on native prey. *Ecology*, *90*, 581–587.
- Potticary, A. L., & Duckworth, R. A. (2017). When are maternal effects maternal strategies? An example of environmental mismatch in a passerine bird. *Evolutionary Ecology*, in review.

- Power, H. W., & Lombardo, M. P. (1996). Mountain bluebird. In A. Poole & F. Gill (Eds.), *The birds of North America* (pp. 1–21). Philadelphia, PA: Birds of North America, Inc.
- Quinn, J. L., Cole, E. F., Patrick, S. C., & Sheldon, B. C. (2011). Scale and state dependence of the relationship between personality and dispersal in a great tit population. *Journal of Animal Ecology*, *80*, 918–928.
- Quinn, J. L., Patrick, S. C., Bouwhuis, S., Wilkin, T. A., & Sheldon, B. C. (2009). Heterogeneous selection on a heritable temperament trait in a variable environment. *The Journal of Animal Ecology*, *78*, 1203–1215.
- Raj, A., & Chen, Y. (2011). The wiring economy principle: Connectivity determines anatomy in the human brain. *PLoS One*, *6*, e14832.
- Rasmussen, J. E., & Belk, M. C. (2012). Dispersal behavior correlates with personality of a North American fish. *Current Zoology*, *58*, 260–270.
- Réale, D., Reader, S. M., Sol, D., McDougall, P. T., & Dingemanse, N. J. (2007). Integrating animal temperament within ecology and evolution. *Biological Reviews*, *82*, 291–318.
- Redies, C., & Puelles, L. (2001). Modularity in vertebrate brain development and evolution. *BioEssays*, *23*, 1100–1111.
- Rehage, J. S., & Sih, A. (2004). Dispersal behavior, boldness, and the link to invasiveness: A comparison of four *Gambusia* species. *Biological Invasions*, *6*, 379–391.
- Roesch, M. R., & Olson, C. R. (2004). Neuronal activity related to reward value and motivation in primate frontal cortex. *Science*, *304*, 307–310.
- Roff, D. A., & Fairbairn, D. J. (2001). The genetic basis of dispersal and migration and its consequences for the evolution of correlated traits. In J. Clobert, E. Danchin, A. A. Dhondt, & J. D. Nichols (Eds.), *Dispersal* (pp. 191–202). New York: Oxford University Press.
- Saastamoinen, M., Brakefield, P. M., & Ovaskainen, O. (2012). Environmentally induced dispersal-related life-history syndrome in the tropical butterfly, *Bicyclus anyana*. *Journal of Evolutionary Biology*, *25*, 2264–2275.
- Scarf, D., Miles, K., Sloan, A., Goulter, N., Hegan, M., Seid-Fatemi, A., et al. (2011). Brain cells in the avian ‘prefrontal cortex’ code for features of slot-machine-like gambling. *PLoS One*, *6*, e14589.
- Schilling, C., Kuhn, S., Romanowski, A., Schubert, F., Kathmann, N., & Gallinat, J. (2012). Cortical thickness correlates with impulsiveness in healthy adults. *NeuroImage*, *59*, 824–830.
- Schradin, C., & Lamprecht, J. (2002). Causes of female emigration in the group-living cichlid fish *Neolamprologus multifasciatus*. *Ethology*, *108*, 237–248.
- Schtickzelle, N., Fjerdingstad, E. J., Chaine, A., & Clobert, J. (2009). Cooperative social clusters are not destroyed by dispersal in a ciliate. *BMC Evolutionary Biology*, *9*, 251.
- Seckl, J. R., & Meaney, M. J. (2004). Glucocorticoid programming. *Annals of the New York Academy of Sciences*, *1032*, 63–84.
- Sherry, D. F., Jacobs, L. F., & Gaulin, J. C. (1992). Spatial memory and adaptive specialization of the hippocampus. *Trends in Neurosciences*, *15*, 298–303.
- Sih, A., & Del Giudice, M. (2012). Linking behavioural syndromes and cognition: A behavioural ecology perspective. *Philosophical Transactions of the Royal Society B*, *367*, 2762–2772.
- Sinervo, B., Calsbeek, R., Comendant, T., Both, C., Adamopoulou, C., & Clobert, J. (2006). Genetic and maternal determinants of effective dispersal: The effect of sire genotype and size at birth in side-blotched lizards. *The American Naturalist*, *168*, 88–99.
- Sinervo, B., & Clobert, J. (2003). Morphs, dispersal behavior, genetic similarity, and the evolution of cooperation. *Science*, *300*, 1949–1951.
- Socan, G., & Bucik, V. (1998). Relationship between speed of information-processing and two major personality dimensions—Extraversion and neuroticism. *Personality and Individual Differences*, *25*, 35–48.

- Stevens, V. M., Whitmee, S., Le Galliard, J. F., Clobert, J., Bohning-Gaese, K., Bonte, D., et al. (2014). A comparative analysis of dispersal syndromes in terrestrial and semi-terrestrial animals. *Ecology Letters*, *17*, 1039–1052.
- Susser, E., & Lin, S. (1992). Schizophrenia after prenatal exposure to the Dutch hunger winter of 1944–1945. *Archives of General Psychiatry*, *49*, 983–988.
- Swanson, E. M., Holekamp, K. E., Lundrigan, B. L., Arsznov, B. M., & Sakai, S. T. (2012). Multiple determinants of whole and regional brain volume among terrestrial carnivorans. *PLoS One*, *7*, e38447.
- Toonen, R. J., & Pawlik, J. R. (2001). Foundations of gregariousness: A dispersal polymorphism among the planktonic larvae of a marine invertebrate. *Evolution*, *55*, 2439–2454.
- Trefilov, A., Berard, J., Krawczak, M., & Schmidtke, J. (2000). Natal dispersal in rhesus macaques is related to serotonin transporter gene promoter variation. *Behavior Genetics*, *30*, 295–301.
- Tschirren, B., Fitze, P. S., & Richner, H. (2007). Maternal modulation of natal dispersal in a passerine bird: An adaptive strategy to copy with parasitism? *The American Naturalist*, *169*, 87–93.
- Uller, T. (2008). Developmental plasticity and the evolution of parental effects. *Trends in Ecology & Evolution*, *23*, 432–438.
- Utida, S. (1972). Density dependent polymorphism in the adult of *Callosobruchus maculatus* (Coleoptera, Bruchidae). *Journal of Stored Products Research*, *8*, 111–125.
- van Overveld, T., Careau, V., Adriaensen, F., & Matthysen, E. (2014). Seasonal- and sex-specific correlations between dispersal and exploratory behaviour in the great tit. *Oecologia*, *174*, 109–120.
- Walhovd, K. B., Fjell, A. M., Brown, T. T., Kuperman, J. M., Chung, Y., Hagler, D. J., Jr., et al. (2012). Long-term influence of normal variation in neonatal characteristics on human brain development. *Proceedings of the National Academy of Sciences of the United States of America*, *109*, 20089–20094.
- Weaver, I. C., Cervoni, N., Champagne, F. A., D'Alessio, A. C., Sharma, S., Seckl, J. R., et al. (2004). Epigenetic programming by maternal behavior. *Nature Neuroscience*, *7*, 847–854.
- Wells, J. C. K. (2003). The thrifty phenotype hypothesis: Thrifty offspring or thrifty mother? *Journal of Theoretical Biology*, *221*, 143–161.
- Wen, Q., & Chklovskii, D. B. (2005). Segregation of the brain into gray and white matter: A design minimizing conduction delays. *PLoS Computational Biology*, *1*, e78.
- Werner, E. A., Myers, M. M., Fifer, W. P., Cheng, B., Fang, Y., Allen, R., et al. (2007). Prenatal predictors of infant temperament. *Developmental Psychobiology*, *49*, 474–484.
- Williams, P. G., Suchy, Y., & Rau, H. K. (2009). Individual differences in executive functioning: Implications for stress regulation. *Annals of Behavioral Medicine*, *37*, 126–140.
- Wood, W., & Runger, D. (2016). Psychology of habit. *Annual Review of Psychology*, *67*, 289–314.
- Yamane, T., Okada, K., Nakayama, S., & Miyatake, T. (2010). Dispersal and ejaculatory strategies associated with exaggeration of weapon in an armed beetle. *Proceedings of the Royal Society of London B*, *277*, 1705–1710.
- Zajitschek, S. R., Zajitschek, F., Clobert, J., & Moulis, F. (2012). The importance of habitat resistance for movement decisions in the common lizard, *Lacerta vivipara*. *BMC Ecology*, *12*, 13.