



Evolution and Development of Individual Behavioral Variation

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LAST MODIFIED: 24 MARCH 2021

DOI: 10.1093/OBO/9780199941728-0135

Introduction

What makes individuals unique? The answer to this question lies in understanding why and how individuals respond to numerous internal and external factors that they experience over their lifetimes. This fundamental question lies at the heart of the study of human and animal behavior and is best addressed by integrating both proximate and ultimate perspectives. From a proximate perspective, we need to understand the molecular, hormonal, and physiological pathways involved in enacting behavioral changes within individuals. From an ultimate perspective, we need to understand when and why behavior changes in response to different internal and external factors and whether such changes are adaptive, a result of constraints, or pathological. Research on this topic draws links across several fields including developmental and abnormal psychology, personality in humans and animals, developmental plasticity, and parental effects. The development of individual behavioral variation encompasses many different processes because there are so many ways that behavior can vary within and across individuals. This article considers behavioral variation in both of these respects, that is, within-individual plasticity and among-individual differences. Within an individual, behavioral plasticity describes the way in which behavior can change across the lifespan as a result of changes in internal factors such as maturational state, or as a result of salient experiences. Among individuals, differences in average behavior can be a result of individual differences in internal factors, such as genetic variation, variation in their experiences, and variation in how they respond to the same experiences. Traditionally, students of behavioral variation in humans and animals focused on describing the mean levels of behavior expressed by groups of individuals as a function of changes in age or in response to specific experiences. More recently evolutionary and behavioral ecologists have become interested in patterns of within-individual plasticity and among-individual differences in behavior, and the factors that contribute to their development, which is the focus of this review here.

Journals

The evolution and development of behavioral variation is a broad topic and so many journals publish articles related to it. From a human perspective, major journals are the *Journal of Personality and Social Psychology*, *Psychological Science*, *Psychological Bulletin*, *Social Psychological and Personality Science*, and *Evolution and Human Behavior*. In nonhuman animals, journals such as *Behavioral Ecology*, *Animal Behaviour*, *Ethology*, and *Applied Animal Behaviour Science* all routinely publish research relating to the development and evolution of behavioral variation. The *Journal of Comparative Psychology* publishes papers on both humans and other species.

***Animal Behaviour*. 1953–.**

This broad journal publishes empirical and theoretical work on animal behavior including work from evolutionary, ethological, or more applied perspectives.

***Applied Animal Behaviour Science*. 1974–.**

This journal focuses on the behavior of domesticated or utilized animals with a focus on how this work can help inform animal management, husbandry, and/or welfare.

***Behavioral Ecology*. 1990–.**

This journal publishes both empirical and theoretical work dealing with the study of behavior from an eco-evolutionary perspective. This often includes research on animal personality and its development.

Ethology. 1937–.

This journal publishes research on behavior, generally in nonhuman animals, including its physiological mechanisms, function, and evolution.

Evolution and Human Behavior. 1979–.

This interdisciplinary journal focuses on linking the study of human behavior within an evolutionary context.

Journal of Comparative Psychology. 1921–.

This journal publishes empirical work focusing on the study of behavior and cognition across multiple species, including humans.

Journal of Personality and Social Psychology. 1965–.

This journal focuses on empirical work done on human personality and social psychology with special focus on the topics of social cognition, interpersonal relations, and individual differences in personality processes.

Psychological Bulletin. 1904–.

This journal specializes in publishing integrative research reviews and research syntheses to help summarize the current state and future directions of the field.

Psychological Science. 1990–.

This broad journal focuses on empirical work on any aspect of psychology, though routinely publishes work investigating the human personality and its development.

Social Psychological and Personality Science. 2010–.

This journal specializes on publishing short empirical articles of work considered to be major advancements to the field of social psychology and personality science.

Definitions

There are many terms that have been used to describe consistent differences in behavior among individuals that are maintained over time or across contexts. In humans, this is called “personality.” “Differential consistency” or “repeatability” refers to the extent to which among-individual differences in behavior are maintained over extended periods of time, whereas “structural consistency” describes the extent to which correlations across individuals between different types of behavior are stable over time. In nonhuman animals, some researchers use the term “animal personality”; others, such as in Sih, et al. 2004, use the term “behavioral type,” and Réale, et al. 2007 uses “temperament.” Koolhaas, et al. 1999 uses the term “coping style,” though this generally also includes differences in other traits related to stress coping responses. These terminologies reflect the simultaneous development of interest in this topic from several different perspectives, which has unfortunately led to a lack of clarity about exactly what each definition means and how they may differ from one another. It has been suggested that one way to rectify this is to apply the concept of reaction norms to behavior as a unifying principle. In evolutionary biology, a “reaction norm” describes the range of phenotypes a genotype can express as a function of different rearing environments (Schlichting and Pigliucci 1998). Nussey, et al. 2007 extends this concept to “individual reaction norms,” where the reaction norm is now a property of an individual rather than a genotype; the trait is the dependent variable and the independent variable can be time (repeated measures) or different contexts. Dingemans, et al. 2010 (cited under Statistical Methods) goes further to describe how an individual’s “personality” can be described by the elevation of the reaction norm thus characterizing its average behavior across time or contexts. The application of linear mixed modeling and the “animal model” to data sets that are hierarchically structured, that is, repeated measures nested within individuals, has enabled progress in this area (see Genetic and Genomic Methods). There are also many terms to describe changes within an individual’s behavior over its development, most commonly referred to as “behavioral plasticity.” Stamps and Groothuis 2010 provides clear definitions of the many terminologies that can be used to describe different patterns of within-individual change. For example, “contextual or activation plasticity” refers to the extent to which an individual’s behavior changes as an immediate response to a change in external stimuli. In contrast, “developmental plasticity” is usually used to refer to longer-lasting, and sometimes irreversible, changes in behavior as a result of experiences that occurred earlier in life. Roberts, et al. 2001 provides a useful overview of the terminologies used within

human personality research to describe patterns of behavioral change including "ipsative change" that indicates the extent to which behavioral correlations are stable over time within a single individual. From a statistical perspective, Dingemanse, et al. 2010 ties behavioral plasticity to the slope of an individual's behavioral reaction norm across the measured time or contexts.

Koolhaas, J. M., S. M. Korte, S. F. de Boer, et al. 1999. Coping styles in animals: Current status in behavior and stress-physiology. *Neuroscience & Biobehavioral Reviews* 23.7: 925–935.

This paper reviews and discusses how differences in individual stress responses (coping styles) may mediate behavioral differences among individuals. The focus is mainly on the physiological mechanisms underlying proactive versus reactive coping styles and the relationship between coping style and stress-related disease.

Nussey, D. H., A. J. Wilson, and J. E. Brommer. 2007. The evolutionary ecology of individual phenotypic plasticity in wild populations. *Journal of Evolutionary Biology* 20.3: 831–844.

Classic reaction norm approaches in quantitative genetics generally focus on differences among genotypes in reaction norms; here this paper applies this framework to individuals and discusses patterns of individual reaction norms and their ecological and evolutionary relevance.

Réale, D., S. M. Reader, D. Sol, P. T. McDougall, and N. J. Dingemanse. 2007. Integrating animal temperament within ecology and evolution. *Biological Reviews* 82.2: 291–318.

This paper proposes that temperament (consistent individual differences in behavioral responses) should be incorporated into an ecological and evolutionary framework. They outline terminology that can be used to describe and characterize different behaviors and hypothesize that there are five main axes of behavioral variation in animals: aggressiveness, avoidance of novelty, willingness to take risks, exploration, and sociality. This terminology is widely used within the study of individual behavioral variation in ecology and evolution.

Roberts, B. W., A. Caspi, and T. E. Moffitt. 2001. The kids are alright: Growth and stability in personality development from adolescence to adulthood. *Journal of Personality and Social Psychology* 81.4: 670–683.

Definitive empirical evidence for consistency of personality dimensions over the lifetime in humans. This paper also provides clear definitions of terminology used within human psychology to describe different patterns of behavioral change over time.

Schlichting, C. D., and M. Pigliucci. 1998. *Phenotypic evolution: A reaction norm perspective*. Sunderland, MA: Sinauer Associates.

Comprehensive book on the study of plasticity within a reaction norm framework.

Sih, A., A. Bell, and J. C. Johnson. 2004. Behavioral syndromes: An ecological and evolutionary overview. *Trends in Ecology & Evolution* 19.7: 372–378.

Landmark paper that established the study of consistent individual behavioral variation as important for ecological and evolutionary research.

Stamps, J. A., and T. G. G. Groothuis. 2010. Developmental perspectives on personality: Implications for ecological and evolutionary studies of individual differences. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365.1560: 4029–4041.

This paper reviews how personality can change across time and/or over contexts within a developmental context and provides clear definitions for the different terminologies used to describe different patterns of behavioral variation.

Overviews

There are many useful overviews related to the topic of the evolution and development of individual behavioral variation. Carere and Maestripieri 2013 provides a broad overview of the study of among-individual behavioral differences (personality) in animals from a behavioral ecological perspective. In addition to having an entire section on the development of personality, this book also covers a number of other topics including the taxonomic breadth of personality, the genetics of personality, and implications of personality research for conservation and animal welfare. Vonk, et al. 2017 is another edited

volume on the study of animal personality; this book also has chapters drawing links more explicitly between psychological and behavioral ecological perspectives on the study of individual behavioral variation. Bell, et al. 2009 is a meta-analysis that established that there is widespread evidence for the presence of among-individual differences in behavior in animals. Stamps and Groothuis 2010 and Trillmich, et al. 2015 both provide comprehensive reviews specifically on the development of animal personality. There are also several useful reviews on within-individual behavioral variation, that is, behavioral plasticity. Stamps 2016 and Snell-Rood 2013 are good places to start in this regard. Within ecology and evolution, Monaghan 2008 offers a review on the broader topic of phenotypic plasticity and its developmental underpinnings. West-Eberhard 2003 is an authoritative and comprehensive book exploring the causes and consequences of developmental plasticity for evolution generally. From a psychological perspective, Caspi, et al. 2005 is an extensive review on what is known about the patterns and consequences of personality development in humans. Bateson, et al. 2004 offers a review exploring developmental plasticity more broadly and its implications for human health.

Bateson, P., D. Barker, T. Clutton-Brock, et al. 2004. Developmental plasticity and human health. *Nature* 430:419–421.

Far-reaching review that draws on plant and animal studies of developmental plasticity with a focus on insights these can provide into human development and disease susceptibility.

Bell, A. M., K. L. Laskowski, and S. Hankison. 2009. The repeatability of behaviour: A meta-analysis. *Animal Behaviour* 77.4: 771–783.

Meta-analysis of 759 published estimates of repeatability of diverse behavioral traits (foraging, aggression, parental behavior, mate preference, etc.) in ninety-eight species ranging from crustaceans to mammals. On average, the repeatability of behavioral traits was 0.37, providing strong evidence for consistent individual differences in animals.

Carere, C., and D. Maestriperi. 2013. *Animal personalities: Behavior, physiology, and evolution*. Chicago: Univ. of Chicago Press.

Edited volume covering broad topics related to the study of individual behavioral variation in animals from an ecological and evolutionary perspective. All chapters are written by well-established and active researchers in the field making this volume a good starting point for any new student to the study of animal personality.

Caspi, A., B. W. Roberts, and R. L. Shiner. 2005. Personality development: Stability and change. *Annual Review of Psychology* 56:453–484.

Extensive review on human personality development, with particular focus on changes in personality in childhood versus adulthood, evidence of genetic influences, and the role of personality in individual measures of success (social relationships, status, health).

Monaghan, P. 2008. Early growth conditions, phenotypic development and environmental change. *Philosophical Transactions of the Royal Society B: Biological Sciences* 363.1497: 1635–1645.

Review on how environmental effects can influence behavior either directly through personal experience, or indirectly through parental experience. Makes the important distinction between environmental effects that can constrain or limit optimal behavioral development, and those effects that may better prepare offspring for experiences later in life.

Snell-Rood, E. C. 2013. An overview of the evolutionary causes and consequences of behavioural plasticity. *Animal Behaviour* 85.5: 1004–1011.

Review on how plasticity will influence organisms' abilities to respond to environmental change. Compares and contrasts the relative importance and costs and benefits of two types of plasticity: developmental (irreversible) and activational (reversible).

Stamps, J. 2016. Individual differences in behavioural plasticities. *Biological Reviews* 91.2: 534–567.

This article describes different types of behavioral plasticities and reviews examples of each type. It discusses topics such as the effects of early experience on plasticity and how and why we might expect personality and plasticity to be related.

Stamps, J., and T. G. G. Groothuis. 2010. The development of animal personality: Relevance, concepts and perspectives. *Biological Reviews* 85.2: 301–325.

Extensive review that provides a framework for characterizing and testing hypotheses about how and why behavioral variation changes over development. Touches on a number of important topics including the use of developmental reaction norms, the potential importance of niche-picking and niche-

construction, and how the extensive literature on human personality can be applied to inform questions in animal behavior.

Trillmich, F., A. Günther, C. Müller, K. Reinhold, and N. Sachser. 2015. *New perspectives in behavioural development: Adaptive shaping of behaviour over a lifetime?*. *Frontiers in Zoology* 12:S1.

This paper reviews the current state of research on the development of individual differences in behavior, focusing on how the reaction norm concept has been used in both theoretical and empirical work. This is the opening paper in a special issue focused on individual behavioral development, and many other papers in this issue would be useful references for those interested in the topic.

Vonk, J., A. Weiss, and S. A. Kuczaj, eds. 2017. *Personality in nonhuman animals*. Cham, Switzerland: Springer International.

Edited volume covering the study of individual behavioral variation. This book also provides a useful historical perspective on the study of animal personality and makes more direct links between psychological and ecological and evolutionary perspectives.

West-Eberhard, M. J. 2003. *Developmental plasticity and evolution*. New York: Oxford Univ. Press.

Comprehensive book describing the role of developmental plasticity in evolution. Importantly West-Eberhard argues that plasticity can lead the way in evolution, rather than just responding to evolutionary processes.

Approaches

There are many approaches to measuring the evolution and development of behavioral variation due to the fact that there are many facets of behavioral variation (as described in Definitions) and many internal and external factors that can affect it. Which approach is most appropriate will largely depend on the major question of interest. Researchers can use and combine a variety of different experimental designs to help understand the potential influences of genetic, parental, and/or environmental effects on individual behavioral development. Some experimental designs are primarily used to describe how behavior changes within individuals as a function of age or life-stage, which is an important first step in any study of behavioral development. Other experimental designs are used to determine whether specific types of experiences earlier in life encourage the development of different types or levels of behavior, or whether individuals with different genetic makeup develop different behavior. Some experimental designs are able to address all of these topics, and quantify the extent to which behavioral variation is associated with differences in genotypes, parental effects, offspring experiences during ontogeny, and interactions between these factors.

Cross-Sectional Designs

Cross-sectional experimental designs are useful to answer questions about how mean levels of behavior differ as a function of age. Here, researchers take measurements on individuals that are different ages, that is, a cross-section of the population of interest. Advantages of these designs are that the data can be collected within a limited period of time and allow comparison of different groups of individuals at the same moment in time, potentially limiting variation that may be introduced due to immediate environmental effects. For example, Soto, et al. 2011 uses this experimental design to explore how personality traits in humans differ across different age classes from children to older adults. However, these designs generally are not able to capture patterns of within-individual behavioral plasticity, as the same individuals are not followed over time. There is also the possibility of variation among individuals of different ages in their experiences earlier in life (i.e., "cohort effects"), which can make it difficult to definitively attribute any differences among the sections to a given factor of interest.

Soto, C. J., O. P. John, S. D. Gosling, and J. Potter. 2011. *Age differences in personality traits from 10 to 65: Big Five domains and facets in a large cross-sectional sample*. *Journal of Personality and Social Psychology* 100.2: 330–348.

Large cross-sectional studies of personality traits in children, adolescents, and adults showing greater changes in trait during late childhood and eventual maturation of personality traits in adults.

Repeated Measures (Longitudinal) Designs

Longitudinal designs follow behavioral changes over ontogeny in the same set of individuals. Longitudinal designs can provide a fuller picture of behavioral development than cross-sectional designs, in which individuals of different ages are each measured once (see Cross-Sectional Designs) because they avoid potential cohort effects. However, it should be noted that this design is prone to bias if some individuals are easier to observe repeatedly. For

instance, Carter, et al. 2012 provides an example of how some individuals may be more or less likely to be captured in field studies. Such differences in “trappability” can bias data collection in favor of individuals that are more active, more conspicuous, or otherwise more likely to be included in the study. Despite potential drawbacks, longitudinal designs are especially powerful for addressing questions about how within-individual behavioral plasticity and/or among-individual behavioral differences develop over time. Such studies have also played major roles in the understanding of human personality development. Roberts, et al. 2006 provides an extensive meta-analysis of ninety-two longitudinal studies showing that personality traits continue to change well into adulthood, with individuals generally exhibiting greater conscientiousness and warmth as we grow older. Similar repeated measures studies have also been done on nonhuman animals. Brommer and Class 2015 provides a useful review of studies that have used such designs to investigate patterns of individual (or genotypic) differences in plasticity. Francis 1990 follows two cohorts of cichlid fish for eighteen months to understand how aggressiveness changes as a result of sexual maturity. Even longer-term studies exist on a handful of animal populations: Réale, et al. 2000 uses long-term data that has been collected on a population of bighorn sheep since 1971 to test for consistency in individual behavior. Hayward, et al. 2015 is an example of work done with a similar long-term data set on Soay Sheep. Modified longitudinal designs allow researchers to study the effects of different experiences on the development of behavior. In controlled, randomized designs, experimental subjects are randomly assigned to different groups, and then each group is assigned to a different experience. Stein, et al. 2016 and Monestier and Bell 2020 use such a design to measure how a formative life event during adulthood (becoming a parent and a mating opportunity, respectively) can change individual behavior. Such repeated measures designs not only allow researchers to determine the mean effects of the different treatments on the development of behavior, but also allow them to determine whether and when individuals differentially respond to the same treatments.

Brommer, J. E., and B. Class. 2015. The importance of genotype-by-age interactions for the development of repeatable behavior and correlated behaviors over lifetime. *Frontiers in Zoology* 12:S2.

This review and conceptual paper reviews empirical papers that use a reaction norm approach to outline how different patterns of age-related behavioral plasticity can arise as a result of individual and genotypic differences.

Carter, A. J., R. Heinsohn, A. W. Goldizen, and P. A. Biro. 2012. Boldness, trappability and sampling bias in wild lizards. *Animal Behaviour* 83.4: 1051–1058.

Shows that bolder lizards entered traps sooner and were caught more often, highlighting how difference in individual “trappability” may bias sampling in wild animals, which can create problems especially for longitudinal studies conducted in the field.

Francis, R. C. 1990. Temperament in a fish: A longitudinal study of the development of individual differences in aggression and social rank in the Midas cichlid. *Ethology* 86.4: 311–325.

Classic study on how aggression changes as a result of age and sexual maturity in cichlid fish.

Hayward, A. D., J. Moorad, C. E. Regan, et al. 2015. Asynchrony of senescence among phenotypic traits in a wild mammal population. *Experimental Gerontology* 71:56–68.

This study takes advantage of long-term data collected on an island population of Soay sheep to investigate patterns of among-individual age-related senescence in a number of different traits including behavior, but also measures such as reproductive performance and parasite loads.

Monestier, C., and A. M. Bell. 2020. Personality traits change after an opportunity to mate. *Proceedings of the Royal Society B: Biological Sciences* 287.1926: 20192936.

This study uses a controlled, randomized, and repeated measures experimental design to show that a key life event—mating for the first time—influences individual behavior development in sticklebacks.

Réale, D., B. Y. Gallant, M. Leblanc, and M. Festa-Bianchet. 2000. Consistency of temperament in bighorn ewes and correlates with behaviour and life history. *Animal Behaviour* 60.5: 589–597.

This study uses long-term data from a population of bighorn sheep to show that among-individual differences in response to trapping and handling (a measure of “docility”) are highly consistent over time. Additionally, this study takes an important next step to show that this behavior predicts aspects of an individual's reproductive success, suggesting important links between individual behavior and fitness.

Roberts, B. W., K. E. Walton, and W. Viechtbauer. 2006. Patterns of mean-level change in personality traits across the life course: A meta-analysis of longitudinal studies. *Psychological Bulletin* 132.1: 1–25.

Meta-analysis of several longitudinal studies on humans showing that people become more conscientious, warmer, and calmer after age thirty. These behavioral changes are generally associated with greater maturity.

Stein, L. R., R. M. Trapp, and A. M. Bell. 2016. Do reproduction and parenting influence personality traits? Insights from threespine stickleback. *Animal Behaviour* 112:247–254.

Longitudinal empirical study showing both behavioral and hormonal changes in fathers as a result of parenting in a nest-building fish.

Replicate Individual Designs

Replicate individual designs make use of genetically similar or identical individuals to allow researchers to follow and/or apply treatments to groups of individuals who are as comparable as possible at the beginning of the study. These designs are especially powerful for investigating questions about the importance of experiential factors on behavior while controlling for the effects of genetic variation, parental experiences, and early experiences on behavior. In humans, twin studies, where the behavior of mono- or dizygotic twins is followed over time, would be an example of such a “replicate individual” design. For example, Tellegen, et al. 1988 follows monozygotic twins that were either raised together in the same household or separately in different households, allowing them to begin to disentangle the influences of genetics from environment on personality development. Polderman, et al. 2015 provides a meta-analysis on such studies. In nonhuman animals, cross-fostering experiments are essentially dizygotic twin studies with the added level of experimental control whereby eggs or very young juveniles from a single clutch (or brood) are split between foster parents. This method can allow researchers to investigate how differences in parental care can affect the development of behavior in their offspring (see Experiences That Affect Behavioral Variation). Slagsvold, et al. 2002 is an example of this method in birds. There are a growing number of opportunities to use even more (genetically) similar individuals for such studies in the form of clonal organisms or isogenic or inbred lines to ensure that all animals have (nearly) identical genetic backgrounds. Bierbach, et al. 2017 investigates the development of among-individual behavioral differences in a naturally clonal fish; Freund, et al. 2013 and Ayroles, et al. 2015 report similar work using isogenic mice and fruit flies, respectively.

Ayroles, J. F., S. M. Buchanan, C. O’Leary, et al. 2015. Behavioral idiosyncrasy reveals genetic control of phenotypic variability. *Proceedings of the National Academy of Sciences of the United States of America* 112.21: 6706–6711.

This study demonstrated that not only does individual variation in behavior still emerge among genetically identical flies, but also that the level of variation differs among genotypes.

Bierbach, D., K. L. Laskowski, and M. Wolf. 2017. Behavioural individuality in clonal fish arises despite near-identical rearing conditions. *Nature Communications* 8:15361.

This study reared naturally clonal fish under highly standardized laboratory conditions and found that significant among-individual behavioral differences still emerged, suggesting epigenetic and/or microenvironmental variation must be important for behavioral development.

Freund, J., A. M. Brandmaier, L. Lewejohann, et al. 2013. Emergence of individuality in genetically identical mice. *Science* 340.6133: 756–759.

This study reared isogenic mice in enriched (spatially heterogenous) laboratory environments in social groups and found that individual differences in behavioral activity emerged over ontogeny.

Polderman, T. J. C., B. Benyamin, C. A. de Leeuw, et al. 2015. Meta-analysis of the heritability of human traits based on fifty years of twin studies. *Nature Genetics* 47:702–709.

Extensive meta-analysis of twin studies in humans showing that personality traits show an average heritability of 49 percent.

Slagsvold, T., B. T. Hansen, L. E. Johannessen, and J. T. Lifjeld. 2002. Mate choice and imprinting in birds studied by cross-fostering in the wild. *Proceedings of the Royal Society B: Biological Sciences* 269.1499: 1449–1455.

This study cross-fostered chicks of three different species to demonstrate how imprinting can affect these individual's later sexual preferences.

Tellegen, A., D. T. Lykken, T. J. Bouchard, K. J. Wilcox, N. L. Segal, and S. Rich. 1988. Personality similarity in twins reared apart and together. *Journal of Personality and Social Psychology* 54.6: 1031–1039.

Landmark study that showed that shared environmental effects contributed less to personality variation than non-shared environmental effects in twins.

Genetic and Genomic Methods

There are many genetic and genomic methods that can be used to investigate questions about the genetic and molecular basis of behavior. Quantitative genetic experiments can be used to understand the extent to which inherited factors influence behavioral development. Falconer and Mackay 1996 and Lynch and Walsh 1998 are authoritative books on how to design experiments and collect and analyze data for such questions; Boake 1994 applies these methods specifically to behavioral traits. Researchers have traditionally used sophisticated breeding designs to quantify the heritability of many traits. In animals, the two most common methods to estimate heritability are with parent-offspring regressions or pedigree family analysis. Dingemanse, et al. 2002 is an empirical example of how to estimate heritability of a personality trait in a wild population of birds. Kruuk 2004 and Wilson, et al. 2010 both provide very useful guides on how to apply the appropriate statistical models to such data (the “animal model”) to partition the influences of genetic and environmental factors on phenotypic traits. They focus particularly on data collected from wild populations. With the advancement of genetic and genomic tools, quantitative trait loci mapping (QTL), genome-wide association studies (GWAS), and other sequencing methods have become more common because they have the potential to reveal the actual genes and genetic variants that contribute to the resemblance among relatives, and conversely, the differences in trait values among nonrelatives. While QTL relies on deliberate crosses between divergent phenotypes, and then associating genetic markers with phenotypes, GWAS samples genetic information from a population exhibiting variation in the trait of interest and then tests for correlational patterns between the genetic and phenotypic variation. Cantor, et al. 2010 provides a useful review of the statistical methods required for these types of studies. However, finding the genetic variants that contribute to behavioral variation has been difficult, perhaps due to the highly polygenic nature of such traits; Manolio, et al. 2009 reviews the potential causes of this “missing heritability problem” (though the researchers’ focus is on complex diseases). Bell and Aubin-Horth 2010 reviews the ways in which studying how the genome responds to the environment via changes in gene expression can give insights into the causes of plasticity and variation. Bell and Dochtermann 2015 reviews pitfalls and promises of integrating studies of both the dynamic side of the genome, that is, gene expression and epigenetics, and the fixed side of the genome, that is, DNA sequence variation, to understand both among-individual behavioral differences and within-individual plasticity. Bengston, et al. 2018 provides an accessible overview of the application of genomic technologies to study individual behavioral variation.

Bell, A. M., and N. Aubin-Horth. 2010. What can whole genome expression data tell us about the ecology and evolution of personality? *Philosophical Transactions of the Royal Society B: Biological Sciences* 365.1560: 4001–4012.

This paper argues that because we are explicitly interested in both among-individual behavioral differences and within-individual behavioral plasticity, studying the dynamic side of the genome that responds to the environment via gene expression is likely to be highly insightful for animal personality studies.

Bell, A. M., and N. Dochtermann. 2015. Integrating molecular mechanisms into quantitative genetics in order to understand consistent individual differences in behavior. *Current Opinion in Behavioral Sciences* 6:111–114.

This paper suggests that animal personality prompts a new integration of quantitative genetics and molecular methods because it brings questions about the causes of variation and plasticity to the forefront.

Bengston, S. E., R. A. Dahan, Z. Donaldson, et al. 2018. Genomic tools for behavioural ecologists to understand repeatable individual differences in behaviour. *Nature Ecology and Evolution* 2:944–955.

This paper provides an accessible review of some of the most commonly used genetic and genomic techniques, including gene association methods, sequencing methods, and genetic manipulations, and how they can be applied specifically to the investigation of the genetic basis of behavioral traits.

Boake, C. R. B. 1994. *Quantitative genetic studies of behavioral evolution*. Chicago: Univ. of Chicago Press.

This edited volume summarizes the theory and methods of quantitative genetics. Includes case studies illustrating applications of these methods to behavioral traits.

Cantor, R. M., K. Lange, and J. S. Sinsheimer. 2010. Prioritizing GWAS results: A review of statistical methods and recommendations for their application. *American Journal of Human Genetics* 86.1: 6–22.

This paper reviews GWAS studies looking for genetic markers of human disease. Shows that these studies generally find few markers that only explain a very small portion of the variation in disease prevalence. They highlight how GWAS studies should only be considered a first step in the discovery of the genetic basis of any trait and outline further steps that need to be taken to improve gene discovery.

Dingemans, N. J., C. Both, P. J. Drent, K. van Oers, and A. J. van Noordwijk. 2002. Repeatability and heritability of exploratory behaviour in great tits from the wild. *Animal Behaviour* 64.6: 929–938.

One of the first studies to estimate heritability in a repeatedly measured personality trait (exploration) in wild birds. They found that great tits exhibit significant repeatability and heritability in this trait, suggesting it can respond to selection.

Falconer, D. S., and T. F. C. Mackay. 1996. *Introduction to quantitative genetics*. 4th ed. Harlow, UK: Longman.

Authoritative book on experimental and statistical methods to investigate quantitative genetic contributions to traits of interest.

Kruuk, L. E. B. 2004. Estimating genetic parameters in natural populations using the “animal model”. *Philosophical Transactions of the Royal Society B: Biological Sciences* 359.1446: 873–890.

The animal model is a powerful statistical approach that uses known pedigrees to partition variance in a trait of interest into its genetic and environmental components. This paper reviews studies that have applied the animal model to various phenotypic traits, including behavior.

Lynch, M., and B. Walsh. 1998. *Genetics and analysis of quantitative traits*. Sunderland, MA: Sinauer Associates.

Key book for both beginners and experts on quantitative genetics.

Manolio, T. A., F. S. Collins, N. J. Cox, et al. 2009. Finding the missing heritability of complex diseases. *Nature* 461:747–753.

This paper explains how even with the advent of whole genome sequencing, we have so far only been able to explain a small portion of the variance in human disease and traits due to genetic influences. This paper provides potential new avenues and techniques that can be explored to improve our ability to predict disease risk and the genetics of complex traits generally.

Wilson, A. J., D. Réale, M. N. Clements, et al. 2010. An ecologist’s guide to the animal model. *Journal of Animal Ecology* 79.1: 13–26.

Useful paper on the use and application of the animal model to data sets collected on wild animals. Includes extensive supplementary material with examples including code so researchers can apply these methods more easily to their own data.

Statistical Methods

The type of data necessary to study the development and evolution of individual behavioral variation can be complex because researchers often measure multiple different behaviors on the same individuals and/or because the same individuals are measured repeatedly in the same assay. If multiple behaviors are measured on the same individuals, researchers may need to employ multivariate techniques to analyze such data. Principal component analysis (PCA) and factor analysis (FA) are often used to find patterns of covariation among behavioral variables, and structural equation modeling (SEM) can be used to uncover direct and indirect influences of behavioral variables on each other. Fabrigar, et al. 1999 provides useful guidelines for factor analysis, and Crowley and Fan 1997 offers guidance on the use of SEM, both from a psychological perspective. Budaev 2010 provides some important caveats to the application of PCA to repeated measures of behavioral data, and Dingemans, et al. 2010 suggests alternative methods to PCAs that may be more robust. When multiple data points are made on a single individual, as in all repeated measures type data, this violates the assumption of independent data points of most classic parametric statistical methods, making analysis difficult. As such, researchers are now employing advanced mixed (or hierarchical or multilevel) models to such data. These types of models allow researchers to better partition behavioral variation at the appropriate levels (e.g., within-versus among-individual). The animal model (described in Genetic and Genomic Methods) is one such example of this type of model. Dingemans and Dochtermann 2013 provides a useful how-to guide on how to apply mixed models for behavioral data. Repeatability is often a statistic of major interest in these types of studies as it provides information about the proportion of variation that can be attributed to among-individual differences; Nakagawa and

Schielzeth 2010 provides the most comprehensive guide on how to estimate repeatability for different types of data. Westneat, et al. 2015 offers guidance on what statistical methods can be used to uncover patterns in variation at the within-individual level. Harrison, et al. 2018 provides a very useful guide on the application of mixed models more generally, all of which can be applied to behavioral data.

Budaev, S. V. 2010. Using principal components and factor analysis in animal behaviour research: Caveats and guidelines. *Ethology* 116.5: 472–480.

This paper is an excellent first start to understanding the use of PCA and FA in behavioral research. Provides brief background on both methods, and then uses simulated data to demonstrate common pitfalls and problems with interpretation, ultimately offering recommendations about best practices moving forward.

Crowley, S. L., and X. Fan. 1997. Structural equation modeling: Basic concepts and applications in personality assessment research. *Journal of Personality Assessment* 68.3: 508–531.

This paper explains structural equation modeling from a very accessible conceptual perspective. It is geared mostly toward (human) personality researchers, but it would be a good starting point for any researcher interested in a basic understanding of SEM methods.

Dingemans, N. J., and N. A. Dochtermann. 2013. Quantifying individual variation in behaviour: Mixed-effect modelling approaches. *Journal of Animal Ecology* 82.1: 39–54.

This methods paper explains the nature of the difficulty of dealing with repeated measures data and then provides guidance on how to apply linear mixed models to properly analyze such data. Extensive supplementary material with code in a number of common statistical programming languages.

Dingemans, N. J., N. A. Dochtermann, and J. Wright. 2010. A method for exploring the structure of behavioural syndromes to allow formal comparison within and between data sets. *Animal Behaviour* 79.2: 439–450.

This paper discusses the problems associated with analyzing multivariate behavioral data. Focuses on the comparison of behavioral syndrome (correlated among-individual behaviors) structure across data sets. Explains potential pitfalls associated with classic PCA and outlines a new method that more appropriately partitions the behavioral variance at the among- and within-individual levels.

Fabrigar, L. R., D. T. Wegener, R. C. MacCallum, and E. J. Strahan. 1999. Evaluating the use of exploratory factor analysis in psychological research. *Psychological Methods* 4.3: 272–299.

This review explores the use of factor analysis in human personality and psychological research. It offers useful recommendations in terms of how to first properly design experiments to collect the data and then how to use FA to appropriately explore it.

Harrison, X. A., L. Donaldson, M. E. Correa-Cano, et al. 2018. A brief introduction to mixed effects modelling and multi-model inference in ecology. *PeerJ* 6:e4794.

Very useful review of how to apply and interpret mixed models within ecology in general. Explains differences between fixed and random effects both from a statistical and conceptual perspective. Includes extensive code for running these types of models in R.

Nakagawa, S., and H. Schielzeth. 2010. Repeatability for Gaussian and non-Gaussian data: A practical guide for biologists. *Biological Reviews* 85.4: 935–956.

Landmark paper outlining the appropriate methods to use to estimate repeatability in a number of different types of data; their methods are largely considered the current “gold standard.”

Westneat, D. F., J. Wright, and N. J. Dingemans. 2015. The biology hidden inside residual within-individual phenotypic variation. *Biological Reviews* 90.3: 729–743.

This paper focuses on the hierarchical nature of modern behavioral data and explains how biological information can be gleaned from each level, with a particular focus on how within-individual variation can offer insight into patterns of behavioral plasticity.

Behavioral Maturation

Longitudinal and cross-sectional studies of humans and animals have shown that many types of behavior change as a function of age, life-stage, reproductive state, or other life-history landmarks. In animals, such changes occur even if the experimental subjects are maintained in the same social and physical environment throughout their lives, suggesting that changes in internal state over ontogeny contribute to these temporal changes in behavior. For instance, personality traits in animals may change in response to such important physiological and morphological transformations as metamorphosis. Wilson and Krause 2012 finds stability in personality traits in frogs before and after metamorphosis. This is not the case in beetles: Müller and Müller 2015 reports little consistency in behavioral traits before and after metamorphosis. We may also expect other major life-history divides, such as sexual maturation, to have large effects on behavior. In humans, Roberts, et al. 2006 shows that personality traits continue to change well into middle and older age in humans, contrary to previous theories that suggest that after adolescence personality is largely fixed. In animals, a number of different patterns of behavioral maturation have been found. In fish, Edenbrow and Croft 2011 finds that behavioral expression largely stabilized at sexual maturity. Bell and Stamps 2004 shows that correlations between behavioral traits remained largely stable, but the traits themselves were not stable over the life course in sticklebacks. Favati, et al. 2016 finds that jungle fowl continue to exhibit fairly low stability in personality traits throughout their entire lives. Experimental studies that manipulate and control particular life events (e.g., the age at first reproduction or the opportunity to reproduce) in animals have the potential to make important contributions in this area.

Bell, A. M., and J. A. Stamps. 2004. The development of behavioral differences between individuals and populations of threespined stickleback. *Animal Behaviour* 68:1339–1348.

One of the first empirical studies to demonstrate that behavioral correlations (i.e., syndromes) reliably differed among populations of animals, here sticklebacks. While individual expression of single traits (activity, aggression, and boldness) changed over development, the correlation between behaviors was stable across the lifetime, but only in one population and not the other.

Costa, P. T., R. R. McCrae, and C. E. Löckenhoff. 2019. Personality across the life span. *Annual Review of Psychology* 70:423–448.

Expansive review on personality change over the lifetime in humans. They highlight the main findings that traits are stable and generally show increasing maturation with age, but also point out how work is needed to develop more detailed hypotheses about specific changes in particular traits.

Edenbrow, M., and D. P. Croft. 2011. Behavioural types and life history strategies during ontogeny in the mangrove killifish, *Kryptolebias marmoratus*. *Animal Behaviour* 82.4: 731–741.

Empirical study that followed individual behavior and behavioral correlations changed over ontogeny in a self-fertilizing fish (i.e., replicate individuals). Showed that behavioral expression increased until maturity and then leveled off.

Favati, A., J. Zidar, H. Thorpe, P. Jensen, and H. Løvlie. 2016. The ontogeny of personality traits in the red junglefowl, *Gallus gallus*. *Behavioral Ecology* 27.2: 484–493.

This study followed the development of personality in jungle fowl, and contrary to work done on humans, found fairly low stability in personality traits over ontogeny and across sexual maturity.

Müller, T., and C. Müller. 2015. Behavioural phenotypes over the lifetime of a holometabolous insect. *Frontiers in Zoology* 12:S8.

This study followed the behavior of individual insects that experience complete metamorphosis. They found that behavior was consistent during adulthood but that there was little consistency from the larval to the adult period. This study suggests that major life-history divides can have large effects of behavior.

Roberts, B. W., K. E. Walton, and W. Viechtbauer. 2006. Patterns of mean-level change in personality traits across the life course: A meta-analysis of longitudinal studies. *Psychological Bulletin* 132.1: 1–25.

Large meta-analysis compiling evidence for how human personality changes over a lifetime. Showed that contrary to common belief, personality continues to change into adulthood, that is, humans are not perfectly “set in their ways” even as adults.

Wilson, A. D. M., and J. Krause. 2012. Personality and metamorphosis: Is behavioral variation consistent across ontogenetic niche shifts? *Behavioral Ecology* 23.6: 1316–1323.

This study examined the consistency of personality traits across a major life-history divide (metamorphosis) in frogs. In contrast to work done on beetles (Müller and Müller 2015), the authors here found there was some consistency in personality traits from larvae to adults.

Experiences That Affect Behavioral Variation

Understanding how external factors or experiences influence behavioral development across the lifetime provides insight both into developmental mechanisms and into how evolution has shaped these mechanisms. This research is often focused on the influence of some experience that occurs at a particular point in ontogeny, from conception through old age. In some cases, a given type of experience can only occur at a given age. Examples include parental effects that occur prior to birth or hatching (e.g., hormones in avian eggs) or in species with parental care, effects of parents on their offspring before the offspring become independent. However, other types of experiences (e.g., exposure to cues from predators) can occur at many different ages. In such cases, researchers may conduct experiments to determine whether the effects of a given type of experience on behavior are particularly strong if those experiences occur at a given age (i.e., “sensitive periods” or “sensitive windows”). Here we highlight examples of factors that influence behavioral development at major developmental milestones.

Embryonic Influences on Behavior

The environment can influence individuals' behavioral development even prior to birth or hatching. Mousseau and Fox 1998 provides a useful review on how mothers can influence the phenotypes of their offspring and how these effects may be adaptive for offspring fitness. A major goal of such studies is to uncover the proximate mechanisms through which these influences occur. Considerable research has focused on the impact of maternal stress prior to or during gestation on developing embryos. Prenatal maternal stress can have long-term effects on a wide range of offspring traits, including behavior. Mulder, et al. 2002 provides a review of evidence for this in humans. Hormonal mechanisms in both parents and offspring can play a key role in mediating these changes in behavior. Variation in exposure to testosterone prior to birth or hatching can have life-long consequences on later aggressive and sexual behavior, as Ryan and Vandenbergh 2002 reviews for mammals and Groothuis and Schwabl 2008 for birds. Embryonic effects also occur in poikilothermic vertebrates. Bull 1980 is the classic review of temperature-mediated sex determination in reptiles; Janzen and Morjan 2001 demonstrates how variation nest site selection in turtles is repeatable and therefore parents can strongly influence offspring phenotypes. Stein and Bell 2014 shows that fathering stickleback fish can influence the behavior of their offspring by the care they provide at the nest when their offspring are still eggs.

Bull, J. J. 1980. Sex determination in reptiles. *The Quarterly Review of Biology* 55.1: 3–21.

This is an extensive review on the mechanisms determining sex in reptiles showing how pre-hatching conditions have strong effects on offspring phenotype.

Groothuis, T. G. G., and H. Schwabl. 2008. Hormone-mediated maternal effects in birds: *Mechanisms matter but what do we know of them?* *Philosophical Transactions of the Royal Society B: Biological Sciences* 363.1497: 1647–1661.

Review on hormone-mediate maternal effects, with a focus on birds. They review what is known about specific mechanisms of how hormones are deposited, where they are deposited, and what effects they mediate in growing embryos.

Janzen, F. J., and C. L. Morjan. 2001. Repeatability of microenvironment-specific nesting behaviour in a turtle with environmental sex determination. *Animal Behaviour* 62.1: 73–82.

Here they showed that in turtles with temperature-dependent sex determination, females show repeatable differences in the thermal profiles of their nest site selection, providing natural variation for selection to act upon.

Mousseau, T. A., and C. W. Fox. 1998. The adaptive significance of maternal effects. *Trends in Ecology & Evolution* 13.10: 403–407.

Now-classic review paper that articulated the ways in which maternal effects can be adaptive; previously, maternal effects had been considered noise.

Mulder, E. J. H., P. G. Robles de Medina, A. C. Huizink, B. R. H. van den Bergh, J. K. Buitelaar, and G. H. A. Visser. 2002. Prenatal maternal stress: Effects on pregnancy and the (unborn) child. *Early Human Development* 70.1–2: 3–14.

This review covers the evidence for unfavorable offspring outcomes due to prenatal maternal stress. They find that mothers with high stress and anxiety during pregnancy have higher rates of spontaneous abortion and also their children are more likely to exhibit functional disorders.

Ryan, B. C., and J. G. Vandenbergh. 2002. Intrauterine position effects. *Neuroscience & Biobehavioral Reviews* 26.6: 665–678.

This paper reviews how proximity to male embryos (and the testosterone they produce) in utero can influence many phenotypic traits in mammals.

Stein, L. R., and A. M. Bell. 2014. Paternal programming in sticklebacks. *Animal Behaviour* 95:165–171.

Here the authors exposed fathers to predation threat while they were guarding their nests with eggs, resulting in changes in parenting behavior; these offspring then exhibited greater antipredator behavior themselves. This study provides a unique example of a parental effect mediated solely through paternal behavior.

Early Life Influences on Behavior

In species with altricial young, variation in parental care can be one major source of environmental variation after birth or hatching. Champagne, et al. 2003 is a now-classic example showing how the level of maternal grooming of young can have life-long consequences on offspring behavior. Champagne and Curley 2009 then later shows that these effects appear to be mediated via epigenetic changes. Rödel and Meyer 2011 demonstrates how litter size in rats can affect the development of personality in these animals likely through the offspring's interactions with each other. In many birds, interactions with conspecific males and their songs during the juvenile period affects the type of songs that they will sing or respond to after they mature. Classic empirical examples of this type of early life imprinting can be found in Payne 1981 and Baptista and Petrinovich 1984. Verzijden and ten Cate 2007 shows a different type of early life imprinting, sexual imprinting in fish; cichlids imprint on the type of fish that provide care to them during early life leading to a mate preference for that species later in life. Even in species with precocial young that do not require parental care, early life experiences can be formative. For example, Jonsson and Jonsson 2014 shows that juvenile salmon learn odors associated with their home stream and use these odor memories for homing as adults. Other examples in fish are Magurran 1990 that shows early life experience with a predator affects later antipredator behavior, and Laskowski, et al. 2016 that shows that early life social experience can influence later dominance behavior. Taborsky 2016 provides a useful review of more studies that have manipulated early life social experiences with effects on later adult behavior.

Baptista, L. F., and L. Petrinovich. 1984. Social interaction, sensitive phases and the song template hypothesis in the white-crowned sparrow. *Animal Behaviour* 32.1: 172–181.

Empirical study that investigates the timing and duration of sensitive periods for song learning in juvenile white-crowned sparrows. They also test how different types of sensory modalities (visual versus acoustic) impact song learning.

Champagne, F. A., and J. P. Curley. 2009. Epigenetic mechanisms mediating the long-term effects of maternal care on development. *Neuroscience & Biobehavioral Reviews* 33.4: 593–600.

This paper reviews potential epigenetic mechanisms that mediate the effects of maternal behavior on later offspring behavior.

Champagne, F. A., D. D. Francis, A. Mar, and M. J. Meaney. 2003. Variations in maternal care in the rat as a mediating influence for the effects of environment on development. *Physiology & Behavior* 79.3: 359–371.

This paper documents extensive consistent individual differences in maternal grooming behavior in rats. These behavioral differences have profound impacts on offspring behavior by influencing endocrine, emotional, and cognitive responses to stress.

Jonsson, B., and N. Jonsson. 2014. Early environment influences later performance in fishes. *Journal of Fish Biology* 85.2: 151–188.

This paper reviews what is known about how early life, and in some cases, maternal experiences can have long-lasting consequences on offspring growth rates, life-histories, and behavior in fishes.

Laskowski, K. L., M. Wolf, and D. Bierbach. 2016. The making of winners (and losers): How early dominance interactions determine adult social structure in a clonal fish. *Proceedings of the Royal Society B: Biological Sciences* 283.1830: 20160183.

This empirical paper was performed in a clonal fish allowing the authors to isolate the effects of early social experience on later adult behavior. They showed that early dominance interactions could predict dominance rank up to six months later, beyond sexual maturity.

Magurran, A. E. 1990. The inheritance and development of minnow anti-predator behaviour. *Animal Behaviour* 39.5: 834–842.

This empirical study explores how evolutionary history and personal experience with predation threat influences the development of antipredator behavior.

Payne, R. B. 1981. Song learning and social interaction in indigo buntings. *Animal Behaviour* 29.3: 688–697.

This paper tests how juvenile indigo buntings learn their songs showing early life effects of social experiences on later adult behavior (singing).

Rödel, H. G., and S. Meyer. 2011. Early development influences ontogeny of personality types in young laboratory rats. *Developmental Psychobiology* 53.6: 601–613.

This empirical paper tests how early life experience affects the development of personality traits in rats. The authors focus on how interactions with litter mates (i.e., litter size) affects behavior, showing that it is not just variation in parental care that can influence later offspring behavior.

Taborsky, B. 2016. Opening the black box of developmental experiments: Behavioural mechanisms underlying long-term effects of early social experience. *Ethology* 122.4: 267–283.

This is a review of studies that have manipulated early life social experience and measured later effects on adult behavior, highlighting how these behavioral differences later in life can suggest different mechanisms through which those effects were realized.

Verzijden, M. N., and C. ten Cate. 2007. Early learning influences species assortative mating preferences in Lake Victoria cichlid fish. *Biology Letters* 3.2: 134–136.

This empirical paper used a cross-fostering design to show that female cichlids sexually imprint on the phenotype of the mother that reared them.

Influences Later in Life

Although researchers studying behavioral development have traditionally focused on the effects of experiences early in life on the behavior expressed later in life, it is clear that experiences later in life can also contribute to variation in behavior. For example, work on humans in Fuhrmann, et al. 2015 suggests that adolescence (the period between the late juvenile period and early adulthood) may be a sensitive period for the effects of social and other environmental factors on behavioral development. Along the same lines, Dion, et al. 2019 reviews experimental studies of spiders and insects with incomplete (hemimetabolous) metamorphosis, showing that exposure to cues from conspecifics during the late juvenile stages can affect the reproductive behavior expressed by both males and females after maturity. In humans, studies of post-traumatic stress disorder (PTSD) indicate that particularly stressful events that occur after maturity can have long-lasting effects on physiology and behavior. Clinchy, et al. 2013 demonstrates that exposure to predator cues can have long-lasting effects on behavior and physiology in nonhuman animals, with Pittman, et al 2012 even suggesting that adult predator-exposure can be a useful model for PTSD. While much of the previous work has focused on mean-level changes in behavior over development, there is a growing body of work explicitly investigating how patterns of among- and within-individual behavioral variation changes over time. Relyea 2003 is a classic empirical example showing changes in behavioral plasticity in tadpoles; while behavioral plasticity was more flexible early in life, it did not completely disappear later in life. Stamps, et al. 2018 shows how patterns of within-individual (or rather, genotype) behavioral plasticity decreases with time in adult isogenic fruit flies. Biro, et al. 2010 and Nakayama, et al. 2016 both investigate changes in among- and within-individual behavioral variation across temperature gradients in adult ectothermic animals, an important environmental gradient in many ectothermic animals.

Biro, P. A., C. Beckmann, and J. A. Stamps. 2010. Small within-day increases in temperature affects boldness and alters personality in coral reef fish. *Proceedings of the Royal Society B: Biological Sciences* 277.1678: 71–77.

This paper shows how small fluctuations in daily temperature affected the expression of individual behavior: rank-order in behavior changed but correlations among behaviors did not.

Clinchy, M., M. J. Sheriff, and L. Y. Zanette. 2013. Predator-induced stress and the ecology of fear. *Functional Ecology* 27.1: 56–65.

This review highlights the importance of studying the chronic, long-lasting effects of predator-induced stress. They highlight how animal models might be useful for understanding chronic stress in humans (PTSD).

Dion, E., A. Monteiro, and C. M. Nieberding. 2019. The role of learning on insect and spider sexual behaviors, sexual trait evolution, and speciation. *Frontiers in Ecology and Evolution* 6:225.

This review highlights how previous social experience in insects and spiders can influence later adult reproductive behavioral decisions, with potential impacts on the evolution of sexual traits and speciation.

Fuhrmann, D., L. J. Knoll, and S. J. Blakemore. 2015. Adolescence as a sensitive period of brain development. *Trends in Cognitive Sciences* 19.10: 558–566.

Reviews the mechanisms by which the adolescent brain is sensitive to environmental input.

Nakayama, S., K. L. Laskowski, T. Klefoth, and R. Arlinghaus. 2016. Between- and within-individual variation in activity increases with water temperature in wild perch. *Behavioral Ecology* 27.6: 1676–1683.

This study investigates what environmental factors influence patterns of behavioral variation in a group of wild perch tagged with acoustic transmitters. They found that both among- and within-individual behavioral variation increased with increasing temperature.

Pittman, R. K., A. M. Rasmusson, K. C. Koenen, et al. 2012. Biological studies of post-traumatic stress disorder. *Nature Reviews Neuroscience* 13:769–787.

Extensive review on what is known about the mechanisms generating long-term behavioral, cognitive, and emotional effects of traumatic environmental effects.

Relyea, R. A. 2003. Predators come and predators go: The reversibility of predator-induced traits. *Ecology* 84.7: 1840–1848.

This empirical study exposes tadpoles to cues from predators at several time points and found that while behavioral (and other trait) plasticity decreased, even older tadpoles retained some flexibility.

Stamps, J. A., P. A. Biro, D. J. Mitchell, and J. B. Saltz. 2018. Bayesian updating during development predicts genotypic differences in plasticity. *Evolution* 72.10: 2167–2180.

This empirical study shows that variation among genotypes in adult fruit flies in their initial behavior was related to the subsequent plasticity of those genotypes in response to exposure to the same experience.

Niche-Picking and Niche Construction

While different external factors and experiences influence individual behavior, it is important to recognize that individuals are not passive recipients of experiences, but are often able to choose (“niche-picking”) or modify (“niche construction”) the conditions in which they will live and develop. These processes will influence the environment an individual experiences and hence the expression and development of its behavior. Laland, et al. 2000 outlines how niche construction can influence the selective pressures on an individual, resulting in changes to evolution. Edelaar, et al. 2008 describes how habitat choices by dispersing individuals can generate nonrandom gene flow affecting patterns of evolution in populations. Among-individual differences in niche-picking or niche-construction can occur as a result of genetic differences, early experiences, and combinations of these and other factors. However, disentangling the contribution of genetic and environmental influences can be especially tricky if individuals with different genotypes prefer different environments, or they inherit particular environments from their parents. Such genotype-environment correlations are well recognized; Plomin, et al. 1977 highlights this potential confound in reference to human twin studies and Price and Jaffee 2008 offers methods to disentangle genetic and environmental effects in the face of such correlations. Narusyte, et al. 2008 provides an interesting empirical study demonstrating how human children play an active role in evoking particular environments from their parents. Offspring may also inherit the environment of their parents, be it a physical environment in the form of a nest site, for example, or a social environment, as is the cases in hyenas where daughters inherit a social rank from their mothers. Bonduriansky and Day 2009 is a broad review on different modes of nongenetic inheritance, including environmental and behavioral mechanisms such as described here. An individual's own experiences, especially early in life, can also influence the environments it chooses or modifies later in life. Davis and Stamps 2004 offers a review on one example of this, natal habitat preference induction, whereby individuals' preferences for habitats later in life are influenced, either positively or negatively, by their experience with their natal habitat earlier in life. Karpestam, et al. 2012 is a useful empirical example of active habitat preferences in grasshoppers.

Bonduriansky, R., and T. Day. 2009. Nongenetic inheritance and its evolutionary implications. *Annual Review of Ecology, Evolution, and Systematics* 40:103–125.

Expansive review on modes of nongenetic inheritance including epigenetic, cytoplasmic, nutritional, environmental, and behavioral mechanisms. Reviews the current literature and outlines a framework for conceptualizing the potential evolutionary implications of decoupling the genotype and phenotype.

Davis, J. M., and J. A. Stamps. 2004. The effect of natal experience on habitat preferences. *Trends in Ecology & Evolution* 19.8: 411–416.

Review on natal habitat preference induction, a process whereby individual habitat preferences are shaped by their earlier experience in a particular habitat. The authors show the wide taxonomic breadth of this phenomenon and discuss the potential adaptive significance of it.

Edelaar, P., A. M. Siepielski, and J. Clobert. 2008. Matching habitat choice causes directed gene flow: A neglected dimension in evolution and ecology. *Evolution* 62.10: 2462–2472.

This review and conceptual paper discusses the idea of directed gene flow, whereby dispersing individuals non-randomly chose habitats to match their phenotypes. The authors argue that contrary to random gene flow, this process can actually promote population differentiation and local adaptation.

Karpestam, E., L. Wennersten, and A. Forsman. 2012. Matching habitat choice by experimentally mismatched phenotypes. *Evolutionary Ecology* 26:893–907.

This empirical study tests the matching habitat choice hypothesis and shows that individual grasshoppers distribute themselves across habitats differently based on their (experimentally manipulated) color, showing that habitat choice is a plastic behavioral decision in this species.

Laland, K. N., J. Odling-Smee, and M. W. Feldman. 2000. Niche construction, biological evolution, and cultural change. *Behavioral and Brain Sciences* 23.1: 131–146.

Extensive review paper that seeks to integrate habitat choice and niche construction within a larger evolutionary framework. The authors argue that niche construction allows individuals to play a much more active role in evolution by modifying the selection pressures they experience.

Narusyte, J., J. M. Neiderhiser, B. M. d'Onofrio, et al. 2008. Testing different types of genotype-environment correlation: An extended children-of-twins model. *Developmental Psychology* 44.6: 1591–1603.

This paper examines how well different models of genotype by environment interactions describe interactions between parent and child behavior in humans. They find best support for a model of evocative genotype-environment correlation, meaning children take an active role in eliciting particular behaviors from their parents.

Plomin, R., J. C. deFries, and J. C. Loehlin. 1977. Genotype-environment interaction and correlation in the analysis of human behavior. *Psychological Bulletin* 84.2: 309–322.

This empirical paper shows the genotype-environment correlations may bias estimates of genetic and environmental influences on personality in human twin studies, but likely does not affect adoption studies where genotype and environmental correlations are disrupted.

Price, T. S., and S. R. Jaffee. 2008. Effects of the family environment: Gene-environment interaction and passive gene-environment correlation. *Developmental Psychology* 44.2: 305–315.

In this paper the authors outline a method that human personality researchers can use to disentangle the effects of passive genotype-environment correlations on behavior in humans.

Theory on the Evolution and Development of Adaptive Variation in Behavior

Many theoreticians have considered the factors that might be responsible for consistent individual differences in behavior in animals and humans from evolutionary and developmental perspectives. From an evolutionary perspective, mechanisms such as balancing selection, assortative mating and

spatiotemporal variation in selection pressures can all act to maintain variation within populations. From a developmental perspective, some types of positive feedbacks are often evoked to explain the generation and maintenance of among-individual behavioral variation over ontogeny. A major class of models has explored how differences in individual behavior might occur because they are coupled to some relatively slowly changing internal (or external) "state" variables, for example, differences in physiological states or life-history tactics (see Pace-of-Life Syndrome Hypothesis). Other models have explored how state dependent feedbacks (State-Dependent Feedbacks), and particularly those involving social interactions (Social Interactions) can lead to the stable expression of individual behavior.

Pace-of-Life Syndrome Hypothesis

The pace-of-life syndrome (POLS) hypothesis is currently a popular hypothesis to explain the presence of among-individual differences in behavior. Réale, et al. 2010 is the landmark paper that conceptualized this hypothesis building on ideas about the metabolic costs of behavior (Careau, et al. 2008) and classic life-history theory such as *r/K* selection (Reznick, et al. 2002). This hypothesis predicts that some individuals will exhibit faster paces-of-life where they prioritize reproduction, generally with a higher probability of mortality and also exhibit more active, bolder, and/or aggressive behaviors. On the other hand, individuals can exhibit slower paces of life where they prioritize survival, having delayed reproduction, being less active, shyer, and/or less aggressive. This variation is maintained on an evolutionary timescale as both strategies are expected to achieve equal fitness in the long run. This hypothesis has also been applied to human personality; Stearns and Rodrigues 2020 offers a critical review and guidance on next steps for theory and empirical work within human psychology. While the POLS hypothesis has inspired considerable empirical work, so far the evidence supporting the main predictions of the hypothesis are quite mixed. Royauté, et al. 2018 presents a meta-analysis and finds little support for strong correlations among behavioral, physiological, and life-history traits. Similarly, the meta-analysis Moiron, et al. 2020 finds that individuals that exhibit consistently riskier behavior are not more likely to suffer greater mortality, which runs counter to a key assumption for this hypothesis. Montiglio, et al. 2018 revisits the pace-of-life syndrome hypothesis and provides guidance for next steps that can be taken to update and improve this hypothesis.

Careau, V., D. Thomas, M. M. Humphries, and D. Réale. 2008. Energy metabolism and animal personality. *Oikos* 117.5: 641–653.

This review and conceptual paper presents the idea that among-individual differences in behavior and resting metabolic rates may be linked with variation in personality affecting an individual's response to stress and hence metabolic rate.

Moiron, M., K. L. Laskowski, and P. T. Niemelä. 2020. Individual differences in behaviour explain variation in survival: A meta-analysis. *Ecology Letters* 23.2: 399–408.

This meta-analysis finds that among-individual behavior and survival were linked, but the direction of this effect is not as predicted: individuals that exhibit riskier behaviors do not appear to suffer any mortality costs.

Montiglio, P.-O., M. Dammhahn, G. Dubuc Messier, and D. Réale. 2018. The pace-of-life syndrome revisited: The role of ecological conditions and natural history on the slow-fast continuum. *Behavioral Ecology and Sociobiology* 72:116.

This article reviews the pace-of-life hypothesis, notes that empirical support for it is mixed, and suggests how relaxing some of its assumptions might suggest alternate relationships among behavior, physiology, and life-history.

Réale, D., D. Garant, M. M. Humphries, P. Bergeron, V. Careau, and P.-O. Montiglio. 2010. Personality and the emergence of the pace-of-life syndrome concept at the population level. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365.1560: 4051–4063.

This article suggests extending the pace-of-life hypothesis originally formulated to predict correlations across populations between metabolic, hormonal, and immunity traits and particular life-history traits to apply to within-population variation, and to include behavioral traits as well as physiological and life-history traits.

Reznick, D., M. J. Bryant, and F. Bashey. 2002. *r*- and *K*-selection revisited: The role of population regulation in life-history evolution. *Ecology* 83.6: 1509–1520.

This paper first provides a good historical overview of the development and subsequent problems with *r/K* selection theory. They then argue that these ideas should not be discarded completely but could offer good insight into patterns of life-history differences among populations using guppies as a case study.

Royauté, R., M. A. Berdal, C. R. Garrison, and N. A. Dochtermann. 2018. Painless life? A meta-analysis of the pace-of-life syndrome hypothesis. *Behavioral Ecology and Sociobiology* 72:64.

This meta-analysis of forty-two independent studies finds no consistent evidence for correlations among a number of behavioral, physiological, or life-history traits suggesting that predictions about trait integration may need to be reevaluated.

Stearns, S. C., and A. M. M. Rodrigues. 2020. On the use of “life history theory” in evolutionary psychology. *Evolution and Human Behavior* 41.6: 474–485.

This paper reviews the use of “life-history theory” within human evolutionary psychology and importantly points out areas where greater theoretical and empirical precision is needed.

State-Dependent Feedbacks

From a developmental perspective, one major class of hypotheses predicts that state-dependency in behaviors can be a major driver of stable individual behavioral differences within an animal's lifetime. Initial models such as that in Wolf and Weissing 2010 focused on explaining the maintenance of individual differences in behavior over the lifespan. Theory suggested that when an individual's behavioral expression is coupled to some relatively slowly changing internal (or external) “state” variable, simple positive feedback mechanisms can encourage the maintenance of individual differences in behavior, which is nicely reviewed in Dingemanse and Wolf 2010. For instance, Biro and Stamps 2010 predicts that if an individual's metabolic rate is linked to its behavior, then individual differences in both would be expected to be maintained over time. State-dependent safety is another example of a positive feedback mechanism; a model in Luttbeg and Sih 2010 explores how increases in an individual's body size reduces its vulnerability to predation leading to increasing variation among individuals in body size and behavior. Brown and Laland 2003 presents an example of a different “state” variable: previous experience can also generate positive feedback through learning or increasing skill. Griffin, et al. 2015 highlights potential links between cognition and behavior; suggesting cognitive abilities might be considered an important state variable. Many of these models also show or imply that if individual differences in behavior do not already exist at birth or hatching, positive feedbacks will encourage the emergence of individual differences later in life (a “fanning-out” pattern). Stamps and Biro 2016 provides a review on how we may expect patterns like this to emerge over ontogeny from a conceptual perspective, whereas Sih, et al. 2015 offers guidance for empiricists on how to test patterns of state-dependence in individual behavior. It is important to note that currently, support for this hypothesis has been mixed. The meta-analysis Holtmann, et al. 2017 suggests that metabolic rates exhibit significant repeatability making them a likely state variable, though a different meta-analysis, Niemelä and Dingemanse 2018, finds that variation in state variables, such as metabolic rates, actually explained very little variation in individual behavior.

Biro, P. A., and J. A. Stamps. 2010. Do consistent individual differences in metabolic rate promote consistent individual differences in behavior? *Trends in Ecology & Evolution* 25.11: 653–659.

This article suggests that individual differences in energy metabolism encourage the maintenance of consistent individual differences in behavior patterns that either provide net energy (e.g., foraging activity) and/or consume energy (e.g., courtship activity).

Brown, C., and K. N. Laland. 2003. Social learning in fishes: A review. *Fish and Fisheries* 4.3: 280–288.

The authors review how fishes can learn from observing conspecifics (i.e., social learning) and demonstrates that learning is a widespread phenomenon in fishes with strong effects on their behavior in a number of contexts (e.g., antipredator, mating, foraging behavior).

Dingemanse, N. J., and M. Wolf. 2010. Recent models for adaptive personality differences: A review. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365.1560: 3947–3958.

This paper reviews and dissects theoretical models used to explain the adaptive evolution of personality differences. Focuses mostly on models that have assumptions of feedbacks between states and behavior. They also highlight areas where more formal modeling is needed to explore other patterns of behavioral variation.

Griffin, A. S., L. M. Guillette, and S. D. Healy. 2015. Cognition and personality: An analysis of an emerging field. *Trends in Ecology & Evolution* 30.4: 207–214.

This paper reviews and critiques work done on linking cognition and personality traits in animals and provides suggestions for improvements and future directions.

Holtmann, B., M. Lagisz, and S. Nakagawa. 2017. Metabolic rates, and not hormone levels, are a likely mediator of between-individual differences in behaviour: A meta-analysis. *Functional Ecology* 31.3: 685–696.

Meta-analysis that compared published repeatability estimates of several potential state variables, including hormone levels and metabolic rates. They found that metabolic rates showed higher repeatability than hormone levels, suggesting they may be a better predictor of personality differences.

Luttbeg, B., and A. Sih. 2010. Risk, resources and state-dependent adaptive behavioural syndromes. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365.1560: 3977–3990.

Theoretical model that uses the concept of “state-dependent safety” to explore how feedbacks between an individual’s state and its vulnerability to predation can generate positive feedbacks leading to consistent individual differences in behavior.

Niemelä, P. T., and N. J. Dingemans. 2018. Meta-analysis reveals weak associations between intrinsic state and personality. *Proceedings of the Royal Society B: Biological Sciences* 285.1873: 20172823.

Meta-analysis that compiled estimates of the relationship between behavior and several state variables. They found that while behavior and states (metabolic rates, hormone levels, body size) were significantly related, the strength of that relationship was relatively small (variation in state variables explained 5 percent of the variation in behavior).

Sih, A., K. J. Mathot, M. Moirón, P.-O. Montiglio, M. Wolf, and N. J. Dingemans. 2015. Animal personality and state–behaviour feedbacks: A review and guide for empiricists. *Trends in Ecology & Evolution* 30.1: 50–60.

Reviews models that are based on the assumptions of either positive or negative feedback between different state variables and behavior. Most importantly, suggests and outlines directions for future experimental research.

Stamps, J. A., and P. A. Biro. 2016. Personality and individual differences in plasticity. *Current Opinion in Behavioral Sciences* 12:18–23.

Conceptual paper that reviews what is currently known about changes over time in patterns of individual behavioral variation. Discusses different hypotheses, and how to test them, about what factors would cause among-individual variation to be maintained, increase, or decrease over ontogeny.

Wolf, M., and F. J. Weissing. 2010. An explanatory framework for adaptive personality differences. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365.1560: 3959–3968.

Verbal model that seeks to explain why individuals exhibit different behavior from each other and why they do so consistently over time. They use state-dependent behavior coupled with selective pressures such as frequency-dependent and spatially variable selection as the main mechanism to explain such patterns of behavioral variation.

Social Interactions

Other models have explored how social interactions can generate and/or maintain among-individual differences in behavior. Models, such as those developed in Dall, et al. 2004; McNamara, et al. 2009; and Wolf, et al. 2011 predict that repeated social interactions with the same group of individuals increase the benefits of predictable behavior within individuals and encourage the maintenance of behavioral differentiation among individuals. This is because such consistent individual behavioral differences can help reduce competition and align interests if groups have a mutual goal. Bergmüller and Taborsky 2010 and Montiglio, et al. 2013 build on this to suggest such processes can generate positive feedbacks leading to the exaggeration of among-individual differences in behavior within a group over time. This type of feedback has been termed competitive displacement or social niche specialization. Support for such social niches has been mixed: Laskowski and Bell 2013 demonstrates that groups of sticklebacks exhibit competitive displacement resulting in consistent individual differences in foraging behavior, a key prediction of the hypothesis; however, the hypothesis also predicts that these individual differences in behavior should become stronger with increasing familiarity within a group, which was not supported by the follow-up study Laskowski and Bell 2014. Favati, et al. 2014 is another example of an empirical test of the social niche specialization hypothesis, this time looking at dominance roles in domestic fowl. Interestingly, the model in Wolf, et al. 2008 predicts that such interactions are predicted to favor individuals that are highly responsive to other individuals in their group, as well as individuals that are less responsive, providing an explanation for maintenance of individual differences in behavioral plasticity as well.

Bergmüller, R., and M. Taborsky. 2010. Animal personality due to social niche specialisation. *Trends in Ecology & Evolution* 25.9: 504–511.

Conceptual paper that proposes that repeated social interactions may generate individual social roles or niches, thereby promoting consistent individual differences in behavior (personality).

Dall, S. R. X., A. I. Houston, and J. M. McNamara. 2004. The behavioural ecology of personality: Consistent individual differences from an adaptive perspective. *Ecology Letters* 7.8: 734–739.

One of the earlier papers to outline a verbal model to explain the presence of consistent individual differences in behavior. They use a game theoretic approach to propose that personalities can be selected if fitness payoffs are frequency dependent and there is positive feedback in maintaining a similar behavioral strategy.

Favati, A., O. Leimar, T. Radesäter, and H. Løvlie. 2014. Social status and personality: Stability in social state can promote consistency of behavioural responses. *Proceedings of the Royal Society B: Biological Sciences* 281.1774: 20132531.

This paper provided an empirical test of the hypothesis that stability in social roles promotes individual behavioral differences. They found that behavioral expression in domestic fowl was dependent on their social status (dominance rank), but that some aspects of behavior (boldness) were independent of social status.

Laskowski, K. L., and A. M. Bell. 2013. Competition avoidance drives individual differences in response to a changing food resource in sticklebacks. *Ecology Letters* 16.6: 746–753.

This empirical paper tested the idea of competitive displacement and was one of the first tests of theory on the adaptive evolution of personality differences. It shows that sticklebacks exhibit stronger among-individual behavioral variation when it helps them limit competition in a foraging context.

Laskowski, K. L., and A. M. Bell. 2014. Strong personalities, not social niches, drive individual differences in social behaviours in sticklebacks. *Animal Behaviour* 90:287–295.

This empirical paper showed that among-individual differences in behavior did not become more pronounced with increasing familiarity within stickleback groups, suggesting that social roles may be less important in species with fluid group membership.

McNamara, J. M., P. A. Stephens, S. R. X. Dall, and A. I. Houston. 2009. Evolution of trust and trustworthiness: Social awareness favours personality differences. *Proceedings of the Royal Society B: Biological Sciences* 276.1657: 605–613.

A model of trust and cooperation that shows how allowing individuals to monitor each other's cooperative tendencies can select for consistent individual differences in trustworthiness, which in turn favors "social awareness" in some individuals. The model shows how these sorts of feedbacks can encourage the maintenance of individual differences in social behavior.

Montiglio, P.-O., C. Ferrari, and D. Réale. 2013. Social niche specialization under constraints: Personality, social interactions and environmental heterogeneity. *Philosophical Transactions of the Royal Society B: Biological Sciences* 368.1618: 20120343.

This paper further explores the social niche specialization hypothesis and focuses on how different ecological factors and social mechanisms can promote the generation and maintenance of social niches and thus individual differences in behavior.

Wolf, M., G. S. van Doorn, and F. J. Weissing. 2008. Evolutionary emergence of responsive and unresponsive personalities. *Proceedings of the National Academy of Sciences of the United States of America* 105.41: 15825–15830.

This modeling paper explores how interactions among individuals will affect behavior. They show that variation in responsiveness can select for consistent behavior, and then in turn, consistent behavior selects for variation in responsiveness. This increases payoffs to individuals by decreasing competition.

Wolf, M., G. S. van Doorn, and F. J. Weissing. 2011. On the coevolution of social responsiveness and behavioural consistency. *Proceedings of the Royal Society B: Biological Sciences* 278.1704: 440–448.

This paper builds on their 2008 paper further expanding on the feedbacks between responsiveness and behavioral consistency. The presence of one selects for the other, creating a feedback promoting individual differences in behavior.

Predictive Adaptive Responses versus Adaptive Responses to Different Phenotypes

Theory suggests at least two adaptive explanations for why an individual's behavior later in life can be affected by its parent's experiences and/or its own experiences earlier in life, which are nicely outlined in Nettle and Bateson 2015. First, environmental conditions in the parental generation may provide an offspring with information about the conditions they are likely to encounter. Bateson, et al. 2014 terms this the "predictive adaptive response" (PAR) hypothesis, and it has been incorporated in several formal models such as McNamara, et al. 2016. Based on this idea, theoreticians have investigated the factors, including patterns of spatial or temporal variation in environmental conditions, and the reliability of the cues available to parents and to their offspring, that would favor the evolution of parental effects, ontogenetic plasticity, or both. Kuzawa, et al. 2010 suggests this hypothesis can explain some aspects of reproductive behavior in humans, though Wells 2012 provides a thoughtful critique of the PAR hypothesis with a special focus on human health and disease. Second, environmental conditions early in life (or in the parental generation) may have direct, lasting effects on offspring phenotypes, and different behaviors may be optimal for offspring with different phenotypes. For instance, Smallegange 2011 provides an empirical example where a poor diet early in life leads to a reduced body size after maturity in mites. In these smaller males, "scrambler" behavior appears to be the optimal response, whereas fighting behavior might be optimal for adult males with larger body sizes.

Bateson, P., P. Gluckman, and M. Hanson. 2014. The biology of developmental plasticity and the Predictive Adaptive Response hypothesis: Developmental plasticity and the PAR response. *The Journal of Physiology* 592.11: 2357–2368.

A review of the predictive adaptive response (PAR) hypothesis, which posits that experiences early in life provide information about the conditions an individual is likely to encounter later in life.

Kuzawa, C. W., T. W. McDade, L. S. Adair, and N. Lee. 2010. Rapid weight gain after birth predicts life history and reproductive strategy in Filipino males. *Proceedings of the National Academy of Sciences of the United States of America* 107.39: 16800–16805.

This empirical paper found that weight and weight gain in early life in humans predicted adult male reproductive behavior, suggesting that the prenatal environment adaptively alters the offspring behavior for their predicted later adult environment.

McNamara, J. M., S. R. X. Dall, P. Hammerstein, and O. Leimar. 2016. Detection vs. selection: Integration of genetic, epigenetic and environmental cues in fluctuating environments. *Ecology Letters* 19.10: 1267–1276.

One of several theoretical models that assume that experiences early in life provide individuals with information about the conditions that they are likely to encounter later in life. This model assumes that information about the external environment can also come from other sources (including genes, maternal experiences, and maternal phenotypes).

Nettle, D., and M. Bateson. 2015. Adaptive developmental plasticity: What is it, how can we recognize it and when can it evolve? *Proceedings of the Royal Society B: Biological Sciences* 282.1812: 20151005.

A review that distinguishes between early experiences that have adaptive effects on behavioral development because they provide information and experiences that have adaptive effects on behavioral development because they have lasting effects on the somatic state. The authors outline the steps required to demonstrate that either of these processes can explain a given empirical example of the developmental plasticity of behavior.

Smallegange, I. M. 2011. Complex environmental effects on the expression of alternative reproductive phenotypes in the bulb mite. *Evolutionary Ecology* 25:857–873.

An empirical study that shows that the level of nutrition provided to juvenile mites affects their body size as adults, and that body size at adulthood determines a male's reproductive behavior, whether he will be a fighter (able to kill other mites) or a benign scrambler.

Wells, J. C. 2012. A critical appraisal of the predictive adaptive response hypothesis. *International Journal of Epidemiology* 41.1: 229–235.

This opinion piece critiques the predictive adaptive response hypothesis, focusing on whether or not many of the assumptions of the PAR (stability of the environment, predictability of cues) are reasonable in biological systems, with a particular focus on humans.

Individual and Genotypic Differences in Developmental Trajectories

In contrast to classical theory on behavioral plasticity, which predicts the optimal behavior at a single age or life-stage, recent models consider changes in behavior that can occur over the course of a lifetime. If measured at the genotypic level, this can be conceptualized as classic “G x E” reaction norms. Nussey, et al. 2007 highlights how individual differences in plasticity can be conceptualized as “I x E” reaction norms. Models based on Bayesian approaches assume that behavior is affected by estimates of conditions in the external environment, that information about these conditions can be provided by many sources (including genes, parental experiences, and offspring experiences), and that an individual’s estimate of these conditions can be updated throughout its lifetime based on its experiences. Stamps and Frankenhuis 2016 provides a conceptual review on use of Bayesian processes to describe behavioral development and plasticity, and Frankenhuis and Walasek 2020 applies these processes explicitly to understanding how sensitive windows may emerge over development. Class and Brommer 2016 is an empirical example of the measurement of individual trajectories over time in a wild population of birds. In contrast to many of the state-dependent models, which explain why individual differences in mean trait values might increase over ontogeny (a “fanning out” pattern), Stamps and Frankenhuis 2016 describes how Bayesian models can be used to explain situations in which individual differences in behavior are already present early in life, and then converge over development (a “fanning in” pattern). Lendvai, et al. 2015 and Class, et al. 2019 are two empirical examples of such “fanning in” patterns in animals.

Class, B., and J. E. Brommer. 2016. Senescence of personality in a wild bird. *Behavioral Ecology and Sociobiology* 70:733–744.

An empirical study that uses longitudinal data from a field study of a bird to examine age-related changes in individual differences in a behavioral assay (handling aggression), and which demonstrates that individual differences in this behavior decline with age.

Class, B., J. E. Brommer, and K. van Oers. 2019. Exploratory behavior undergoes genotype–age interactions in a wild bird. *Ecology and Evolution* 9.16: 8987–8994.

This field study investigates age-related changes in the mean and in the additive genetic variance of exploratory behavior in wild birds. They find that variation attributable to genetic differences declined with age, and that the genetic correlation between the behavior expressed by juveniles versus adults was relatively low.

Frankenhuis, W. E., and N. Walasek. 2020. Modeling the evolution of sensitive periods. *Developmental Cognitive Neuroscience* 41:100715.

A review of recent Bayesian models of the evolution of sensitive periods, which outlines the tenets, insights, and predictions of these models; describes insights for empiricists provided by them; and suggests new avenues of research on this topic.

Lendvai, Á. Z., M. Giraudeau, V. Bókony, F. Angelier, and O. Chastel. 2015. Within-individual plasticity explains age-related decrease in stress response in a short-lived bird. *Biology Letters* 11.7: 20150272.

An empirical study in which the stress responses of the same birds were recorded in successive years, finding that the stress responses of different individuals tended to converge as they aged.

Nussey, D. H., A. J. Wilson, and J. E. Brommer. 2007. The evolutionary ecology of individual phenotypic plasticity in wild populations. *Journal of Evolutionary Biology* 20.3: 831–844.

This paper outlines an analytical framework that can be used to describe and analyze patterns of change within individuals over time by applying a reaction norm approach.

Stamps, J. A., and W. E. Frankenhuis. 2016. Bayesian models of development. *Trends in Ecology & Evolution* 31.4: 260–268.

A review of Bayesian models of development, which shows how individual differences in developmental trajectories across the lifetime can arise when the behavior expressed at a given age is jointly affected by information about the external environment provided by different sources (e.g., genes, maternal effects, personal experiences).

[back to top](#)

