BioOne COMPLETE

Evolution of Personality: Developmental Constraints on Behavioral Flexibility

Author: Duckworth, Renée A.

Source: The Auk, 127(4) : 752-758

Published By: American Ornithological Society

URL: https://doi.org/10.1525/auk.2010.127.4.752

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://complete.bioone.org/journals/The-Auk on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

The Auk 127(4):752–758, 2010
© The American Ornithologists' Union, 2010.
Printed in USA.

PERSPECTIVES IN ORNITHOLOGY

EVOLUTION OF PERSONALITY: DEVELOPMENTAL CONSTRAINTS ON BEHAVIORAL FLEXIBILITY

Renée A. Duckworth[1]

Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona 85721, USA

Recent studies suggest that personalities—in which the expression of behavior is highly consistent within individuals—are ubiquitous among animals; however, the evolution of personalities remains poorly understood (Dall et al. 2004, Bell 2007, Bergmüller and Taborsky 2010). Context-independent expression of behavior combined with fitness costs of behavioral inflexibility suggest that constraints on behavioral flexibility are important in shaping the evolution of personalities (Sih et al. 2004a, b; Duckworth 2006), yet we lack a framework for understanding the origin and occurrence of such constraints. Current models for the evolution of personality traits assume that inflexibility of behavior is a product of natural selection; however, intrinsic constraints on behavioral flexibility may explain the origin of behavioral inflexibility without the need to invoke natural selection. Here, I present a framework for investigating the evolution of personality traits that draws on concepts in the field of developmental evolution and explicitly considers constraints to behavioral flexibility. I argue that intrinsic limitations to behavioral flexibility due to time, energetic, or functional constraints can lead to individual specialization, which in turn results in natural selection for correlated suites of behaviors and life-history traits. Further, I suggest that studies of avian behavior are uniquely positioned to provide novel insights into the evolution and development of animal personalities.

Personality Variation: Rethinking Behavioral Adaptation

The study of nonhuman animal personalities is a recent addition to the field of behavioral ecology and is set against a background of several decades of research on the evolution of behavior from an optimality perspective (Sih et al. 2004a, Bell 2007, McNamara and Houston 2009), which assumes that animals strategically adjust their behavior to maximize their fitness given existing tradeoffs (Roff 1994). Behavioral ecologists have used this framework extensively to predict when and how individuals should reversibly adjust their behavior in different contexts (Krebs and Davies 1991). Thus, this view assumes that constraints to behavioral flexibility are weak or nonexistent and that behavior of individuals within a population will converge on a single optimal expression in a particular context. Yet the ubiquity of animal personalities challenges these basic assumptions because individuals commonly display limited flexibility of behavior, there are pronounced differences in behavior among individuals in the same context, and distinct behaviors are often closely integrated in expression, which indicates that their independent evolution may be limited (Dingemanse and Réale 2005, Bergmüller and Taborsky 2010). Explaining all these components of personality—within-individual consistency, between-individual differences, and correlations among behaviors—is necessary for a comprehensive understanding of the evolution of personality variation. Here, I focus on constraints to behavioral flexibility as an important causal factor in the origin of personality traits.

Several recent studies have advanced hypotheses for the evolution of personality, linking consistent differences among individuals in either state (e.g., body size or condition) or life-history strategy to consistent differences in behavior (e.g., Dall et al. 2004, Stamps 2007, Wolf et al. 2007, Careau et al. 2008). These models implicitly assume that there is unlimited potential for behavioral flexibility but that constancy in the expression of behavior evolves because selection favors its integration with other, less flexible traits or strategies. Other recent models have suggested that there are benefits to being predictable, which generates selection for within-individual consistency in behavior (McElreath and Strimling 2006, McNamara et al. 2009). What all these models have in common is an argument that consistency in behavior within individuals is largely or solely attributable to natural selection. Thus, the possibility that intrinsic constraints to behavioral flexibility play an important role in the evolution of personality traits, although noted in early discussions of behavioral syndromes (Sih et al. 2004a), has received less attention.

A Developmental Perspective on the Evolution of Behavior

Studies of the evolution of behavior have generally been slow to incorporate a developmental perspective (Stamps and Groothuis 2010) because, historically, behavioral research has focused on either proximate or ultimate questions, with little overlap between the two (Stamps 2003, Theirry 2007, McNamara and Houston 2009). A developmental perspective bridges this longstanding gap

[1]E-mail: rad3@email.arizona.edu

The Auk, Vol. 127, Number 4, pages 752–758. ISSN 0004-8038, electronic ISSN 1938-4254. © 2010 by The American Ornithologists' Union. All rights reserved. Please direct all requests for permission to photocopy or reproduce article content through the University of California Press's Rights and Permissions website, http://www.ucpressjournals.com/reprintInfo.asp. DOI: 10.1525/auk.2010.127.4.752

Downloaded From: https://complete.bioone.org/journals/The-Auk on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

because it requires knowledge of the origin of behavioral variation in order to understand the range of phenotypes available to selection (Arthur 2001, Young and Badyaev 2006). When intrinsic properties of developmental processes limit this range, the evolution of a phenotype is developmentally constrained (Atchley 1987, Arnold 1994). "Absolute constraints," which usually refer to limitations on organismal design due to physical laws, cannot be broken (Maynard Smith et al. 1985, Brakefield 2006), whereas most constraints are not absolute but instead bias the evolutionary pathway because some phenotypes are easier to produce than others (Arthur 2004).

Developmental constraints determine the starting point for evolutionary change, making a developmental perspective well suited to provide novel insights into the origin of personality traits. The main feature of personality traits that needs to be explained from an optimality perspective is constancy in the expression of behavior (Sih et al. 2004a, Bergmüller and Taborsky 2010). Why does an individual that behaves shyly one day not behave boldly the next day when experiencing a different context? From an optimality perspective, the answer to this question is that flexibility of behavior is itself the target of natural selection. However, a developmental perspective suggests that there may be intrinsic limits to flexibility of behavior and, thus, selection may play a minor or no role in the evolution of constancy in the expression of behavior. From this perspective, correlations between behaviors and other aspects of the phenotype occur secondarily and are not the primary cause of personality variation.

Potential Constraints to Behavioral Flexibility

Behavior is often assumed to be more plastic than other aspects of the phenotype, yet a rigorous evaluation of this assumption suggests that, although behaviors are more reversible in their expression, they are not necessarily more developmentally plastic than morphological or life-history traits (Gordon 1991, Pigliucci 2001, West-Eberhard 2003, Duckworth 2009). Behaviors are inherently reactive in their expression (e.g., an aggressive response to an intruder), but this needs to be distinguished from the level of expression of behavior (e.g., how aggressively an individual responds), which, when consistently different among individuals, constitutes personality (Duckworth 2009). Thus, the assumption of high plasticity of behavior is derived from the fact that, unlike morphological traits, there are no external structures to measure, and behaviors are only expressed in relation to an environmental cue. Yet all behavioral variation is underlain by a multitude of internal physical components, including variation in brain anatomy, neuronal connectivity, neurotransmitter synthesis and degradation, hormone secretion patterns, hormone receptor distribution, and endocrine gland function.

These components, to different extents, are limited in their flexibility through multiple potential constraints. First, the rate at which new tissue can be built is physically limited because it depends on how fast the processes of cell division, apoptosis, cell shape changes, cell migration, and cell differentiation can proceed (Jacobs and Wingfield 2000, Livnat and Pippenger 2006, Lessells 2008). Second, faster tissue growth is metabolically costly and can come at the expense of other organismal functions (Kety 1957, Livnat and Pippenger 2006). Finally, the necessity of maintaining functional integration between neural and endocrine systems may limit the rate at which these systems can change (Ketterson and Nolan 1999, Lessells 2008).

The time that it takes for the physical components that underlie behavior to change constitutes an absolute constraint to behavioral flexibility because it sets an upper limit to rates of behavioral change (Jacobs and Wingfield 2000). Many components of the neural and endocrine systems change very slowly, which suggests that rapid changes either are not possible or are costly. For example, in the adult brain, experience can stimulate the growth of new neurons and lead to new patterns of vascularization and connectivity among distinct modules (i.e., cortical rewiring) (Chklovskii et al. 2004); however, these changes are very slow, taking at least several weeks to many months or even years. Another example of a slow rate of change is seasonal changes in gonad size and function that occur annually in songbirds. It can take several weeks or even months for the gonads to fully mature prior to the onset of breeding (e.g., Hamner 1963, Hegner and Wingfield 1986). These are just two examples of neural and endocrine structures that change slowly; any behavioral changes that depend on such structural changes will also be slow.

Although there is potential for flexibility in all components of neural and endocrinological systems, some generalizations can be made about the relative speed of changes of these components. Flexibility of anatomical structures, such as the size or connectivity of different brain regions or changes in endocrine gland size, are more restricted than flexibility of physiological systems, such as circulating hormone levels. Thus, personality variation is unlikely to be caused by individual differences in current physiological states (Ball and Balthazart 2008, R. A. Duckworth and K. W. Sockman unpubl. data). However, certain changes in physiological systems may also be slow if they necessitate a system-wide reorganization, such as large-scale changes in coordination between hormone levels, receptor density and distribution, and binding proteins.

Another potential constraint to behavioral flexibility, though not absolute, is the energetic demands of reorganizing physiological and neurological pathways. The high energetic costs of developing and maintaining neural tissue are well established (Kety 1957, Laughlin and Sejnowski 2003), and, because maintaining high flexibility of neural circuits is particularly expensive, such costs have the potential to limit the evolution of behavioral flexibility (Niven and Laughlin 2008). There may also be energetic costs associated with the endocrine system's functioning. Although the direct costs of producing hormones and their receptors are generally thought to be low, they have never been quantified (Lessells 2008, Williams 2008). However, the functioning of the neuroendocrine system as a whole necessitates coordination of multiple components, and if changes in one of these parameters necessitate changes in another, the cumulative energetic costs could become substantial. Ultimately, high energetic costs of switching between behavioral phenotypes do not necessarily preclude evolution of behavioral flexibility but may produce a developmental bias toward consistency in behavioral expression even in the absence of selection for behavioral consistency per se.

"Functional constraints" are limitations on trait evolution due to functional interactions among suites of traits (Schwenk and Wagner 2001). Functional integration could limit behavioral

Downloaded From: https://complete.bioone.org/journals/The-Auk on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

flexibility at two levels. First, developmental interactions among components of the endocrine and nervous system might limit their flexibility if a change in one component impedes the functioning of the system as a whole (Schwenk and Wagner 2001, Merilä and Björklund 2004, Adkins-Regan 2008). Such selection that results from the need for internal components of an organism to work together properly is termed "internal selection" because it occurs irrespective of the external environment that an organism experiences (Whyte 1965). The strength of internal selection depends on the extent of coordination among distinct components of the system, and if internal selection is strong and external selection pressures for decoupling the components are weak, their independent evolution will be limited (Olson and Miller 1958, Whyte 1965, Badyaev 2004). Second, integration of personality traits and other aspects of the phenotype can limit flexibility if close coordination of behavioral components increases organismal performance and flexibility in one trait would weaken this interaction. This type of constraint due to functional integration is a potential mechanism underlying state- and life-history dependence in the evolution of personalities. Selection for functional integration among traits can lead to the evolution of genetic integration among these traits (Houle 1991, Atchley et al. 1994, Cheverud 1996, Badyaev 2010), and this further limits independent evolution of behavioral traits. However, such genetic constraints are most important in the short term, and long-term selection for independent expression of traits can break this constraint (Roff 1997, Beldade et al. 2002, Schwenk and Wagner 2004). In sum, functional integration of behaviors due to external selection is likely to pose minimal constraints under strong selection for behavioral flexibility, whereas functional integration due to internal selection, depending on the extent of coordination among underlying developmental pathways and whether there are intrinsic limits to the flexibility of any of these pathways, may strongly constrain behavioral flexibility.

Questions and Predictions That Arise from A Developmental Perspective

The aforementioned constraints to flexibility in behavioral development can reduce the benefits of behavioral plasticity and favor individual specialization (Padilla and Adolph 1996, DeWitt et al. 1998, Dall et al. 2004, Gabriel et al. 2005), which in turn can lead to correlated expression of a suite of traits that enable individuals to maximize their performance in a particular context (Futuyma and Moreno 1988, Wilson 1998, Badyaev 2004). Thus, from a developmental perspective, consistency in the expression of personality traits is not necessarily due to natural selection for behavioral inflexibility, but instead can emerge as a result of limits to flexibility in the developmental pathways of behavioral components. In other words, inflexibility of personality traits could be the default state, whereas functional integration of personality traits with life-history traits and other behaviors may occur secondarily under natural selection. Proximate studies of the development of personality variation in combination with ultimate studies of the fitness consequences of behavioral flexibility will be necessary to determine the relative importance of constraints and selection in the evolution of personality traits.

A developmental perspective also predicts that correlations between personality traits and other traits (e.g., specific axes of life history, behavior, or state-dependent variation) may differ across species and even across populations, depending on the specific natural history of the population. This is in contrast to models that predict consistent links between life history and state-dependent variation and behavior. The developmental perspective is supported by studies of Three-spined Sticklebacks (*Gasterosteus aculeatus*), in which correlations between behaviors vary across ontogeny and among populations (Bell 2005, Bell and Sih 2007).

Given potential constraints to flexibility in the underlying physical components of behavior, it is not surprising that animals are often consistent in their behavior over time. Thus, from a developmental perspective, the main question is not why there is a lack of flexibility in behavior, but why there is a lack of flexibility in the particular behaviors that form different axes of personality variation. Variation in the same axes of behavior—boldness, exploration, activity, sociability, and aggressiveness—has been repeatedly documented across a wide variety of species (Gosling and John 1999, Mehta and Gosling 2006, Réale et al. 2007), which suggests that there may be similar constraints on the flexibility of these particular behaviors. Why do limits to flexibility exist for these behaviors in particular, and what are the mechanisms that underlie these limits? To answer these questions, we need a better understanding of the developmental processes that underlie these axes of personality variation.

If common constraints to flexibility underlie personality variation, we would expect similar developmental mechanisms across disparate taxa. There is some evidence of this. In humans and other mammals, brain structure and neurotransmitter systems have repeatedly been linked to individual differences in behavior (e.g., Aston-Jones et al. 1999, Most et al. 2006, Hariri 2009, Lebreton et al. 2009), and there is strong evidence of evolutionary conservation of many of these pathways (Koolhaas et al. 1999, Popova 2006, Øverli et al. 2007). One particularly well-studied axis of personality variation—aggressiveness—is linked to variation in the serotonergic system across a wide variety of species, from crayfish to foxes to humans (Popova 2006). However, not enough is known about the developmental basis of individual differences in behavior across species to draw conclusions about the universality of the links between particular pathways and behaviors.

Lack of knowledge about the proximate mechanisms of individual differences is due in large part to a focus on population means in both behavioral and physiological research (Williams 2008). This is changing rapidly as the importance of individual variation for understanding the evolution of life-history strategies, ecological niche breadth, and animal personalities becomes increasingly recognized.

Future Directions: The Promise of Avian Studies in Behavioral Development

Studies of birds are uniquely positioned to lead the way in advancing our understanding of the role of behavioral development in the evolution of personalities. First, more than any other

Downloaded From: https://complete.bioone.org/journals/The-Auk on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

vertebrate taxa, birds have been the focus of behavioral research for decades (Owens 2006). Most birds are diurnal and easy to observe, and, importantly for personality research, it is possible to observe the behavior of marked individuals across different contexts and stages of their life cycle. Moreover, because it is possible to follow individuals and family groups of many species throughout their lives, avian systems provide a unique opportunity to investigate the genetics and development of behaviors. Most importantly, studies of birds have been at the forefront of behavioral neuroendocrinology for decades and are uniquely positioned for research of the proximate basis of individual differences in behavior (Wingfield 2005b).

Perhaps the most well-studied proximate mechanism underlying avian behavioral variation is the link between hormones and behavior, particularly for aggression and the neuroendocrinology of song behavior (Ball et al. 2002, Wingfield 2005a). Collection of hormone samples in the field in conjunction with the use of hormone implants to experimentally investigate the links between hormones and behavior has become routine in avian studies. Because hormones respond to environmental stimuli very rapidly, they are excellent integrators of flexible phenotypes (Ketterson and Nolan 1999, Dufty et al. 2002, Badyaev and Duckworth 2005, McGlothlin and Ketterson 2008) and, as such, it seems unlikely that the activational effects of hormones are the main proximate cause of personality variation (Ball and Balthazart 2008); however, this idea has rarely been tested (R. A. Duckworth and K. W. Sockman unpubl. data). This is not to suggest that circulating hormone levels are completely decoupled from personality differences; quite to the contrary, stress-hormone profiles differ between reactive versus proactive coping styles (Koolhaas et al. 1999, Øverli et al. 2007), and androgen elevation often covaries with variation in aggression (Wingfield 2005a). However, these hormonal differences are likely to be a consequence of personality variation rather than a cause, and distinguishing the causal links between neuroendocrine function and behavior remains a challenge for future studies.

Seasonal changes in the avian song nuclei provide a particularly rich model for understanding the actions of hormones on neural plasticity and for studying developmental changes in the brain, particularly in relation to hormonal influences on this process (Ball et al. 2002). These studies have shown that neuroplasticity can be induced by steroids acting on multiple brain sites to activate complex, often sexually dimorphic, behavior (Arnold 1990, Ball et al. 2002). Such studies of the neuroendocrine control of the development of sexual differences in behavior have paved the way for studies on the development of individual differences in behavior. Moreover, early developmental exposure to yolk steroids has been shown to influence behavior in adulthood (Schwabl 1993, Forstmeier et al. 2004, Strasser and Schwabl 2004, Vercken et al. 2006), and an integration of studies of neuroplasticity with studies investigating the link between yolk hormones and variation in behavior may shed important light on the organizational effects of hormones on personality differences.

Finally, the development of avian behavior has been most comprehensively studied in the field of imprinting. Imprinting is a process of phase-sensitive learning, and the approaches that have been used to understand imprinting may also be useful in understanding personality development. Sensitive periods during development, such as occur during imprinting, are widespread and can trigger a wide range of phenotypes, but once the phenotype is committed to a particular developmental pathway, it cannot switch to the alternative (Bateson 2005). Recent studies suggest that conditions during early development can have profound effects on how individuals respond to different situations later in life (Spear 2000, Nelson et al. 2009). Thus, sensitive stages in development might help explain both within-individual consistency in behavior and between-individual differences.

Conclusions

Understanding the origin and evolution of personality traits necessitates acquiring knowledge of the proximate developmental mechanisms that underlie behavioral variation. Intrinsic constraints to behavioral flexibility due to time, energetic, or functional constraints may explain the origin of personality traits without the need to invoke natural selection for inflexibility of behavior. These intrinsic constraints on behavioral flexibility, in turn, may reduce the benefits of behavioral plasticity and favor individual specialization, which ultimately can lead to correlated expression of a suite of traits that enable individuals to maximize their performance in a particular context. Thus, a developmental perspective makes distinct predictions from other recent models of the evolution of personality traits, in that correlations between personality and other traits occur as a secondary consequence of constraints to behavioral flexibility.

Determining whether constraints are important requires empirical data on the proximate mechanisms that underlie behavioral development as well as studies of personality variation across a wide range of taxa. The rich history of research on avian neuroendocrine and endocrine mechanisms of behavioral variation in the laboratory and in the wild makes studies of birds well suited to lead the way in an integration of ultimate and proximate perspectives on the evolution of animal personalities. Such integration would not only enable a better understanding of the evolution of personality traits, but would bridge the gap between proximate and ultimate mechanisms in behavioral research once and for all.

Acknowledgments

I thank A. Badyaev and laboratory members for comments and discussion that improved the manuscript. I am grateful to A. Bell and an anonymous reviewer for insightful comments. This work was supported by funding from National Science Foundation grant 0918095.

Literature Cited

Adkins-Regan, E. 2008. Do hormonal control systems produce evolutionary inertia? Philosophical Transactions of the Royal Society of London, Series B 363:1599–1609.

Arnold, A. P. 1990. The passerine bird song system as a model in neuroendocrine research. Journal of Experimental Zoology 4 (Supplement):22–30.

Arnold, S. J. 1994. Constraints on phenotypic evolution. Pages 258–278 *in* Behavioral Mechanisms in Evolutionary Biology (L. A. Real, Ed.). University of Chicago Press, Chicago, Illinois.

Downloaded From: https://complete.bioone.org/journals/The-Auk on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Arthur, W. 2001. Developmental drive: An important determinant of the direction of phenotypic evolution. Evolution & Development 3:271–278.

Arthur, W. 2004. The effect of development on the direction of evolution: Toward a twenty-first century consensus. Evolution & Development 6:282–288.

Aston-Jones, G., J. Rajkowski, and J. Cohen. 1999. Role of locus coeruleus in attention and behavioral flexibility. Biological Psychiatry 46:1309–1320.

Atchley, W. R. 1987. Developmental quantitative genetics and the evolution of ontogenies. Evolution 41:316–330.

Atchley, W. R., S. Xu, and C. Vogl. 1994. Developmental quantitative genetic models of evolutionary change. Developmental Genetics 15:92–103.

Badyaev, A. V. 2004. Developmental perspective on the evolution of sexual ornaments. Evolutionary Ecology Research 6:1–17.

Badyaev, A. V. 2010. The beak of the other finch: Coevolution of genetic covariance structure and developmental modularity during adaptive evolution. Philosophical Transactions of the Royal Society of London, Series B 365:1111–1126.

Badyaev, A. V., and R. A. Duckworth. 2005. Evolution of plasticity in hormonally-integrated parental tactics. Pages 375–386 *in* Functional Avian Endocrinology (A. Dawson and P. J. Sharp, Eds.). Narosa Publishing House, New Delhi, India.

Ball, G. F., and J. Balthazart. 2008. Individual variation and the endocrine regulation of behaviour and physiology in birds: A cellular/molecular perspective. Philosophical Transactions of the Royal Society of London, Series B 363:1699–1710.

Ball, G. F., L. V. Riters, and J. Balthazart. 2002. Neuroendocrinology of song behavior and avian brain plasticity: Multiple sites of action of sex steroid hormones. Frontiers in Neuroendocrinology 23:137–178.

Bateson, P. 2005. The return of the whole organism. Journal of Bioscience 30:31–39.

Beldade, P., K. Koops, and P. M. Brakefield. 2002. Modularity, individuality, and evo-devo in butterfly wings. Proceedings of the National Academy of Sciences USA 99:14262–14267.

Bell, A. M. 2005. Behavioural differences between individuals and two populations of stickleback (*Gasterosteus aculeatus*). Journal of Evolutionary Biology 18:464–473.

Bell, A. M. 2007. Future directions in behavioural syndromes research. Proceedings of the Royal Society of London, Series B 274:755–761.

Bell, A. M., and A. Sih. 2007. Exposure to predation generates personality in threespined sticklebacks (*Gasterosteus aculeatus*). Ecology Letters 10:828–834.

Bergmüller, R., and M. Taborsky. 2010. Animal personality due to social niche specialisation. Trends in Ecology and Evolution 25: in press.

Brakefield, P. M. 2006. Evo-devo and constraints on selection. Trends in Ecology and Evolution 21:362–368.

Careau, V., D. Thomas, M. M. Humphries, and D. Réale. 2008. Energy metabolism and animal personality. Oikos 117:641–653.

Cheverud, J. M. 1996. Developmental integration and the evolution of pleiotropy. American Zoologist 36:44–50.

Chklovskii, D. B., B. W. Mel, and K. Svoboda. 2004. Cortical rewiring and information storage. Nature 431:782–788.

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 7:734–739.

DeWitt, T. J., A. Sih, and D. S. Wilson. 1998. Costs and limits of phenotypic plasticity. Trends in Ecology and Evolution 13:77–81.

Dingemanse, N. J., and D. Réale. 2005. Natural selection and animal personality. Behaviour 142:1159–1184.

Duckworth, R. A. 2006. Behavioral correlations across breeding contexts provide a mechanism for a cost of aggression. Behavioral Ecology 17:1011–1019.

Duckworth, R. A. 2009. The role of behavior in evolution: A search for mechanism. Evolutionary Ecology 23:513–531.

Dufty, A. M., J. Clobert, and A. P. Møller. 2002. Hormones, developmental plasticity and adaptation. Trends in Ecology and Evolution 17:190–196.

Forstmeier, W., D. W. Coltman, and T. R. Birkhead. 2004. Maternal effects influence the sexual behavior of sons and daughters in the Zebra Finch. Evolution 58:2574–2583.

Futuyma, D. J., and G. Moreno. 1988. The evolution of ecological specialization. Annual Review of Ecology and Systematics 19:207–233.

Gabriel, W., B. Luttbeg, A. Sih, and R. Tollrian. 2005. Environmental tolerance, heterogeneity, and the evolution of reversible plastic responses. American Naturalist 166:339–353.

Gordon, D. M. 1991. Variation and change in behavioral ecology. Ecology 72:1196–1203.

Gosling, S. D., and O. P. John. 1999. Personality dimensions in nonhuman animals: A cross-species review. Current Directions in Psychological Science 8:69–75.

Hamner, W. M. 1963. Diurnal rhythm and photoperiodism in testicular recrudescence of the House Finch. Science 142:1294–1295.

Hariri, A. R. 2009. The neurobiology of individual differences in complex behavioral traits. Annual Review of Neuroscience 32:225–247.

Hegner, R. E., and J. C. Wingfield. 1986. Gonadal development during autumn and winter in House Sparrows. Condor 88:269–278.

Houle, D. 1991. Genetic covariance of fitness correlates: What genetic correlations are made of and why it matters. Evolution 45:630–648.

Jacobs, J. D., and J. C. Wingfield. 2000. Endocrine control of life-cycle stages: A constraint on response to the environment? Condor 102:35–51.

Ketterson, E. D., and V. Nolan, Jr. 1999. Adaptation, exaptation, and constraint: A hormonal perspective. American Naturalist 154:S4–S25.

Kety, S. S. 1957. The general metabolism of the brain in vivo. Pages 221–237 *in* Metabolism of the Nervous System (D. Richter, Ed.). Pergamon Press, London.

Koolhaas, J. M., S. M. Korte, S. F. De Boer, B. J. Van Der Vegt, C. G. Van Reenen, H. Hopster, I. C. De Jong, M. A. W. Ruis, and H. J. Blokhuis. 1999. Coping styles in animals: Current status in behavior and stress-physiology. Neuroscience and Biobehavioral Reviews 23:925–935.

Krebs, J. R., and N. B. Davies, Eds. 1991. Behavioral Ecology: An Evolutionary Approach, 3rd ed. Blackwell Scientific Publications, Oxford, United Kingdom.

Downloaded From: https://complete.bioone.org/journals/The-Auk on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Laughlin, S. B., and T. J. Sejnowski. 2003. Communication in neuronal networks. Science 301:1870–1874.

Lebreton, M., A. Barnes, J. Miettunen, L. Peltonen, K. Ridler, J. Veijola, P. Tanskanen, J. Suckling, M.-R. Jarvelin, P. B. Jones, and others. 2009. The brain structural disposition to social interaction. European Journal of Neuroscience 29:2247–2252.

Lessells, C. M. 2008. Neuroendocrine control of life histories: What do we need to know to understand the evolution of phenotypic plasticity? Philosophical Transactions of the Royal Society of London, Series B 363:1589–1598.

Livnat, A., and N. Pippenger. 2006. An optimal brain can be composed of conflicting agents. Proceedings of the National Academy of Sciences USA 103:3198–3202.

Maynard Smith, J., R. Burian, S. Kauffman, P. Alberch, J. Campbell, B. Goodwin, R. Lande, D. Raup, and L. Wolpert. 1985. Developmental constraints and evolution: A perspective from the Mountain Lake Conference on Development and Evolution. Quarterly Review of Biology 60:265–287.

McElreath, R., and P. Strimling. 2006. How noisy information and individual asymmetries can make 'personality' an adaptation: A simple model. Animal Behaviour 72:1135–1139.

McGlothlin, J. W., and E. D. Ketterson. 2008. Hormone-mediated suites as adaptations and evolutionary constraints. Philosophical Transactions of the Royal Society of London, Series B 363:1611–1620.

McNamara, J. M., and A. I. Houston. 2009. Integrating function and mechanism. Trends in Ecology and Evolution 24:670–675.

McNamara, J. M., P. 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 of London, Series B 276:605–613.

Mehta, P. H., and S. D. Gosling. 2006. How can animal studies contribute to research on the biological bases of personality? Pages 427–448 *in* Biology of Personality and Individual Differences (T. Canli, Ed.). Guilford Press, New York.

Merilä, J., and M. Björklund. 2004. Phenotypic integration as a constraint and adaptation. Pages 107–129 *in* Phenotypic Integration: Studying the Ecology and Evolution of Complex Phenotypes (M. Pigliucci and K. Preston, Eds.). Oxford University Press, New York.

Most, S. B., M. M. Chun, M. R. Johnson, and K. A. Kiehl. 2006. Attentional modulation of the amygdala varies with personality. NeuroImage 31:934–944.

Nelson, E. E., K. N. Herman, C. E. Barrett, P. L. Noble, K. Wojteczko, K. Chisholm, D. Delaney, M. Ernst, N. A. Fox, S. J. Suomi, and others. 2009. Adverse rearing experiences enhance responding to both aversive and rewarding stimuli in juvenile rhesus monkeys. Biological Psychiatry 66:702–704.

Niven, J. E., and S. B. Laughlin. 2008. Energy limitation as a selective pressure on the evolution of sensory systems. Journal of Experimental Biology 211:1792–1804.

Olson, E. C., and R. L. Miller. 1958. Morphological Integration. University of Chicago Press, Chicago, Illinois.

Øverli, Ø., C. Sørensen, K. G. T. Pulman, T. G. Pottinger, W. Korzan, C. H. Summers, and G. E. Nilsson. 2007. Evolutionary background for stress-coping styles: Relationships between physiological, behavioral, and cognitive traits in non-mammalian vertebrates. Neuroscience & Biobehavioral Reviews 31:396–412.

Owens, I. P. F. 2006. Where is behavioural ecology going? Trends in Ecology and Evolution 21:356–361.

Padilla, D. K., and S. C. Adolph. 1996. Plastic inducible morphologies are not always adaptive: The importance of time delays in a stochastic environment. Evolutionary Ecology 10:105–117.

Pigliucci, M. 2001. Phenotypic Plasticity: Beyond Nature and Nurture. Johns Hopkins University Press, Baltimore.

Popova, N. K. 2006. From genes to aggressive behavior: The role of serotonergic system. BioEssays 28:495–503.

Réale, D., S. M. Reader, D. Sol, P. T. McDougall, and N. J. Dingemanse. 2007. Integrating animal temperament within ecology and evolution. Biological Reviews 82:291–318.

Roff, D. A. 1994. Optimality modeling and quantitative genetics: A comparison of the two approaches. Pages 49–66 *in* Quantitative Genetic Studies of Behavioral Evolution (C. Boake, Ed.). University of Chicago Press, Chicago, Illinois.

Roff, D. A. 1997. Evolutionary Quantitative Genetics. Chapman & Hall, New York.

Schwabl, H. 1993. Yolk is a source of maternal testosterone for developing birds. Proceedings of the National Academy of Sciences USA 90:11446–11450.

Schwenk, K., and G. P. Wagner. 2001. Function and the evolution of phenotypic stability: Connecting pattern to process. American Zoologist 41:552–563.

Schwenk, K., and G. P. Wagner. 2004. The relativism of constraints on phenotypic evolution. Pages 390–408 *in* Phenotypic Integration: Studying the Ecology and Evolution of Complex Phenotypes (M. Pigliucci and K. Preston, Eds.). Oxford University Press, New York.

Sih, A., A. Bell, and J. C. Johnson. 2004a. Behavioral syndromes: An ecological and evolutionary overview. Trends in Ecology and Evolution 19:372–378.

Sih, A., A. M. Bell, J. C. Johnson, and R. E. Ziemba. 2004b. Behavioral syndromes: An integrative overview. Quarterly Review of Biology 79:241–277.

Spear, L. P. 2000. The adolescent brain and age-related behavioral manifestations. Neuroscience and Biobehavioral Reviews 24: 417–463.

Stamps, J. [A.] 2003. Behavioural processes affecting development: Tinbergen's fourth question comes of age. Animal Behaviour 66: 1–13.

Stamps, J. A. 2007. Growth-mortality tradeoffs and 'personality traits' in animals. Ecology Letters 10:355–363.

Stamps, J. [A.], and T. G. G. Groothuis. 2010. The development of animal personality: Relevance, concepts and perspectives. Biological Reviews 85:301–325.

Strasser, R., and H. Schwabl. 2004. Yolk testosterone organizes behavior and male plumage coloration in House Sparrows (*Passer domesticus*). Behavioral Ecology and Sociobiology 56:491–497.

Theirry, B. 2007. Behaviorology divided: Shall we continue? Behaviour 144:861–878.

Vercken, E., M. de Fraipont, A. M. Dufty, Jr., and J. Clobert. 2006. Mother's timing and duration of corticosterone exposure modulate offspring size and natal dispersal in the common lizard (*Lacerta vivipara*). Hormones and Behavior 51:379–386.

Downloaded From: https://complete.bioone.org/journals/The-Auk on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

West-Eberhard, M. J. 2003. Developmental Plasticity and Evolution. Oxford University Press, New York.

Whyte, L. L. 1965. Internal Factors in Evolution. George Braziller, New York.

Williams, T. D. 2008. Individual variation in endocrine systems: Moving beyond the 'tyranny of the Golden Mean.' Philosophical Transactions of the Royal Society of London, Series B 363:1687–1698.

Wilson, D. S. 1998. Adaptive individual differences within single populations. Philosophical Transactions of the Royal Society of London, Series B 353:199–205.

Wingfield, J. C. 2005a. A continuing saga: The role of testosterone in aggression. Hormones and Behavior 48:253–255.

Wingfield, J. C. 2005b. Historical contributions of research on birds to behavioral neuroendocrinology. Hormones and Behavior 48:395–402.

Wolf, M., G. S. van Doorn, O. Leimar, and F. J. Weissing. 2007. Life-history trade-offs favour the evolution of animal personalities. Nature 447:581–585.

Young, R. L., and A. V. Badyaev. 2006. Evolutionary persistence of phenotypic integration: Influence of developmental and functional relationships on complex trait evolution. Evolution 60:1291–1299.

Received 29 August 2010, accepted 12 September 2010.

Downloaded From: https://complete.bioone.org/journals/The-Auk on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use