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PERSPECTIVES IN ORNITHOLOGY

EVOLUTION OF PERSONALITY: DEVELOPMENTAL CONSTRAINTS ON BEHAVIORAL FLEXIBILITY

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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, Theiry 2007, McNamara and Houston 2009). A developmental perspective bridges this longstanding gap

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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

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, Chilverud 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

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.

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