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Does the field of animal personality provide any new insights for behavioral ecology?

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The field of animal personalities claims to fill a gap in our understanding of animal behavior, because it explicitly studies the adaptive significance of behavioral differences. This is a controversial claim given that the field of behavioral ecology firmly places the study of animal behavior in an evolutionary context. In fact, it is the evolutionary context that differentiates behavioral ecology from ethology and animal behavior, 2 fields that were already concerned with the study of behavior in nonhuman animals. So, if behavioral ecology already takes an evolutionary approach to variation in behavior, we ask what is personality research about exactly? This question is particularly pertinent now the focus of personality research shifts and the field moves away from being mainly descriptive to include quantitative frameworks. As a result, the field has come to borrow heavily from already established fields. In our view, this has resulted in "animal personality" studies becoming nothing more than a rebranding of existing fields of research—fields that are far more solidly grounded and hypothesis driven than the often vague and superficial focus on animal personalities.

Key words: **animal personality, behavioral ecology, behavioral syndromes.**

> "[…] and unless profitable variations do occur, natural selection can do nothing."
>
> Charles Darwin In *The Origin Of Species*,
> Chapter Natural Selection

INTRODUCTION

The last decade of animal behavior research has seen the rise of animal personality; a field of study defined as examining individual differences in behavior, or suites of correlated behaviors, that are consistent over time and context. Initially, the field was driven by the perceived need to study correlated behaviors not in isolation, as was allegedly done in behavioral ecology, but together (Sih et al. 2004a, 2004b). By incorporating variation among or within individuals into behavioral ecology, the field attempts to elucidate when and where individual plasticity or fixed behaviors might evolve (Dall et al. 2004). The field's initial goal quickly led to a divergence in the main approaches taken by researchers. On the one hand, a strong theoretical body of literature arose to examine how within- or among-individual differences might evolve (McElreath and Strimling 2006; Wolf et al. 2007, 2008, 2011; Wolf and McNamara 2012). Simultaneously, we saw a rapid increase of mainly descriptive papers pointing to correlations among behaviors and measuring behavioral repeatability (reviewed in Bell et al. 2009). Even though in the latter case claims were made that such studies provide novel insights into the existence of behavioral variation, little attempt was made to link observed behaviors to evolutionary theory. Unsurprisingly, this latter approach was met with bemusement among many in the field of behavioral ecology, a field that explicitly places animal behavior in an evolutionary context and, by doing so, deals directly with interindividual differences in the traits of interest. Moreover, there have always been fields directly concerned with understanding both the proximate and ultimate mechanisms underlying variation in behavior—for example, life-history theory, foraging theory, behavioral genetics, game theory, quantitative genetics, reaction norms and behavioral (neuro)endocrinology. The main difference appears to be that the field of personality stresses the importance of behavioral consistency, although the focus on consistency was later relaxed (see further).

An early verbal and often informal criticism of animal personality was that it was simply "putting old wine in new bottles," and that the field contributed nothing new except a media-friendly hype term (Crews 2013). We do not fully agree with this criticism, as the focus on animal personality has certainly led to advances in the tools available to behavioral ecologists to examine interindividual variation and repeatability of behavioral traits (Dingemanse,

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Dochtermann, et al. 2010; Mathot et al. 2012; Roche et al. 2016). In fact, the need to quantify consistent behavioral differences has led to a separate field that has been described as "behavioral ecology of variance components," which traces its origins to the statistical framework employed in quantitative genetics (Dingemanse and Dochtermann 2014; Araya-Ajoy et al. 2015; Westneat et al. 2015). Our criticism of the field of animal personality lies in its appropriation of existing methodological frameworks while maintaining that it constitutes an independent research field (Roche et al. 2016). If the field now relies heavily on existing frameworks, we question the additional value of continuing the use of "animal personality."

Here, we ask what the recent focus on animal personality has contributed that was not already being addressed more rigorously in other fields. We address this question by asking 1) if there was ever a justified need for animal personality research to describe correlations among behaviors, 2) whether the detour into this highly descriptive field has yielded any new insights into behavioral variation, or rather if it hindered progress, and 3) whether the term "animal personality" can be safely abandoned as the field itself incorporates more rigorous and established approaches toward studying individual variation in behavior.

ANIMAL PERSONALITIES—WHAT ARE THEY AND SHOULD WE CARE?

Individuals differ in their behavior. This is true for humans but also for nonhuman animals. When individuals differ consistently from one another, they are said to have a "personality" (Dingemanse and Wolf 2010; Carere and Maestripieri 2013). The term "animal personality" attempts to capture 2 concepts—the first is repeatability in a behavioral response across time and context. The second concept is the notion that the expression of certain behaviors may be correlated with the expression of other behaviors, constituting a "syndrome" (Sih et al. 2004a). Central to the growth of the field is that the concept of animal personality has clear appeal to a nonspecialist audience—the idea that animals are like humans in that they have a "personality," or that they may even come to have similar personalities to their owners in domesticated species (Gosling 2001). Obviously, there is nothing wrong with a field of research receiving media attention, but one does need to be mindful of the possibility that the field receives instant mass-media appeal regardless of the strength of the findings or the quality of the journals in which they appear (Dall et al. 2004; Pennisi 2005). In addition, many early personality studies were experimentally straightforward, requiring only behavioral observations and basic statistics (although these were most often incorrectly applied, see Biro and Stamps 2015), and were often entirely descriptive, further contributing to the ease of producing and publishing such studies. The choice of terminology was also attractive to the nonspecialist audience. "Boldness," for example, is a much more appealing and publicly understood concept than average velocity, distance from a certain point or structure, or total distance travelled, but it is the latter behaviors that can be measured. The use of a secondary term to describe what is actually measured is therefore a marketing exercise, especially if its use adds nothing to our understanding. Moreover, because "boldness" is used to refer to different behaviors, comparisons among studies are problematic or even impossible (David and Dall 2016). There may never be a universal definition of terms such as "bold," "shy," or "sociable," but even if there were, it is difficult to justify their ongoing use if the only apparent value they have is increased media accessibility.

A second question is whether individual variation has indeed largely been ignored in the past. While Charles Darwin in the Origin of Species did not explicitly mention the importance of individual variation, natural selection has nothing to act on when there is no variation, as the quote at the beginning of this paper makes clear. In our view, it is therefore surprising that ignorance of this variation was held as the central justification for the invention of the new field of animal personality (Carere and Maestripieri 2013). Understanding why and how behavior differs among individuals, how behavior develops over time, how selection acts on behavior, and the reasons behind the maintenance of behavioral differences are indeed all valid and important questions. Behavioral ecology as a field has never "ignored" individual variation in behavior, be it consistent across time or variable and correlated with other behaviors or not, but rather holds variation among individuals as a central component of understanding the evolution of behavior. While earlier models, aimed at understanding the origin and maintenance of individual variation, did not differentiate between among- and within-individual variation (reviewed in Dingemanse and Wolf 2010; Wolf and Weissing 2010), this does not mean understanding individual variation was not a primary and ongoing goal of the field of behavioral ecology.

DOES "PERSONALITY" PROVIDE ANY CONCEPTUAL ADVANCES?

There is no debate that questions about why and how behavior differs among individuals, how behavior develops over time, and how selection acts on behavior are useful and should be fundamental to understanding behavior. But we disagree with any claim that animal personality research is the only field to fully attempt to achieve this goal (Sih et al. 2004a). Rather, understanding variation in behavior has been the primary focus of numerous fields, such as behavioral genetics, life-history theory, alternative reproductive tactics, and foraging theory, over the past 100 years. When existing fields are relabeled, there is a danger that the rebranding creates a disconnect among the body of theory and developments that have gone before, thus giving the impression of the birth of a "new" field. In our view, such a disconnect is especially applicable to animal personality research; the field appears to have built an edifice without a foundation by largely ignoring the historical literature (see review by Crews 2013).

Coping styles, behavioral types, behavioral syndromes, personality, and pace-of-life syndromes have all been proposed as novel explanations for variation in behavioral phenotypes and links among behaviors (Wilson et al. 1994; Gosling and John 1999; Sih et al. 2004b; Nettle and Penke 2010; Stamps and Groothuis 2010; David and Dall 2016). These terms have a greater or lesser link to existing fields but are placed under the umbrella of "animal personality" (David and Dall 2016; Roche et al. 2016). Such a wild growth in terminology is clearly not conducive to advancement of the field, a point made earlier by others (Dall and Griffith 2014; David and Dall 2016; Roche et al. 2016), but it is not the precise definitions that are of concern, but rather whether any new insight is gained from them at all. In our view, the main advance achieved by the field of animal personality is the increased use of rigorous quantitative methods to describe variance in measures of animal behavior. However, the development of a toolkit to allow a better understanding of the statistical properties of the data collected (Dingemanse and Wolf 2010) does not necessitate the use of new terminology, especially if that terminology is not used consistently across studies. While not as eye-catching as "boldness," reporting the reaction norm intercept of a velocity measurement would also allow direct comparisons among studies. It is disappointing that despite the fact similar arguments have been made before, it remains the case that "most studies are descriptive in nature" (Sih 2013) and the field focuses generally on descriptions of correlations among behavioral phenotypes and largely ignores mechanisms. The main point of progress has thus failed to translate to a shift in the actual methods employed by the bulk of the field.

While recently arguments have been made that claim that the field now does take a more hypothesis-driven approach (Roche et al. 2016), a shift in animal personality that moves beyond description of behavior actually causes it to cease being "personality" research. This is because the field will then be subsumed by the approaches it borrows from a range of existing disciplines to examine behavioral plasticity and variation (see below). Once variation, consistency, and correlations among behaviors are examined in the framework of their underlying genetics, life-history, and endocrine mechanisms, these studies necessarily become part of the established fields that existed long before the term "animal personality" emerged. This, then, raises the question what the benefit of using the term has been.

A remaining point is that, despite the initial focus on behavioral consistency, personality has now come to be used to describe cases in which behavior is flexible and is not consistent over long periods of time or context (see definition in Sih 2013). This makes any residual definition of personality so diffuse as to be meaningless and seems to undermine the definition entirely (e.g., Galhardo et al. 2012). We consider this confusion to be a symptom of the paucity of hypothesis-driven research in the field. For example, at what point does *consistent individual difference* become *behavioral plasticity*, or can all behavior, no matter the degree of consistency, be called personality? Is there a statistical threshold of correlation or repeatability, below which an animal can be said not to have a personality? While Sih and Bell (2008) attempted to answer this question, the ultimate answer put forward was that there is no workable definition, and any correlation at all must be considered a behavioral type. By definition, this means formal null hypotheses cannot exist, making it impossible to reject the prior assumption that animal personality actually exists, regardless of the data collected. "Animal personality" thus defined therefore relies purely on descriptive measures, lacks explanatory power, and does not fit within the framework of an hypothesis-driven scientific method.

WHY DO WE SEE SO MUCH VARIATION IN BEHAVIOR?

From the perspective of behavioral ecology, it is not clear why the above question is so frequently asked in personality research (Muller and Chittka 2008; Dingemanse, Kazem, et al. 2010). Natural selection requires variation and behavior is subject to natural selection. Hence, the question of interest is what factors maintain variation within populations. Wolf and Weissing (2010) make the distinction between "stable and labile" states to understand why some behaviors are more variable than others. Stable states are states that are very costly, time-consuming, or even impossible to change. Behavior affected by stable states will therefore be consistent and can lead to variation at the population level but not at the individual level. Obvious stable states are those that have a strong genetic or developmental component. Students of social insects are very familiar with such states. In fact, the effect of genetics on individual behavior has been an active field of research in the social insect community for decades. In many social insects, colonies are comprised of individuals with different fathers (polyandry) or different mothers (polygyny) or sometimes both. Given the importance of high relatedness for the evolution of sociality (Hamilton 1964a, 1964b; Hughes et al. 2008), such "dilution" of relatedness requires an adaptive explanation. Many studies have shown that colonies comprised of individuals that differ in their propensity to perform certain tasks do better (reviewed in Oldroyd and Fewell 2007). None of these studies use the term "personality." And if they would, the added terminology would not provide any insights into the origin of the differences. By linking the maternity and paternity of workers to the tasks they are most likely to perform, behavioral genetics, does provide us insights into the cause of the behavioral differences. Similarly, whether or not a female honeybee is raised as a queen or a worker is determined by epigenetic modification triggered by differential feeding (Kucharski et al. 2008). Saying that queens and workers differ in their personality because they display behavioral differences that are consistent over time and between contexts, would be fairly considered absurd. Instead their behavioral repertoire is constrained by development, a difference of degree, but not kind, to established "personality" comparisons. The same argument could be made for any of the numerous examples of alternative reproductive tactics or phenotypes, each of which has a highly consistent suite of behaviors that would fulfill even the most strict definition of "animal personality." When "personality" is applied to social insects, the studies revert to a simple description of consistent collective behavior with no predictive power (e.g., Wray et al. 2011).

In contrast to stable states, labile states can lead to behavioral variability at the individual level. Examples of labile states are gene expression levels, differences in hormone levels or energy reserves. Because in order to qualify as a "personality," behavior needs to be consistent (but over what period is not defined [Sih 2013]), it seems that labile states pose a problem. Labile states thus require an explanation so that their presence does not undermine the concept of "personality." Hormone and energy levels in particular can fluctuate wildly over relatively short time spans, so how can they result in consistent behavior? Wolf and Weissing (2010) argue that labile states can become nonlabile via positive feedback mechanisms. If a hungry individual continues to be successful in obtaining food, its energy levels will remain high. When energy levels affect foraging behavior, for instance how likely an organism is to take risks while foraging, then the argument goes that positive feedback results in behavioral consistency. Similar arguments have been made in the past and are known collectively as optimal foraging theory (Charnov 1976; Kacelnik and Bateson 1996; Perry and Pianka 1997). More generally, state-dependent behavior is a concept that was developed in the 1980s to understand behavioral variation and how selection acts on such variation (Houston and Davies 1985; Houston and McNamara 1988). State-dependent behavior can be subject to frequency dependence when a particular behavioral repertoire affects that of an alternative behavioral repertoire (Wolf and Weissing 2010), an insight that has been around since Maynard-Smith's pivotal work on game theory and evolutionary stable strategies (Maynard Smith 1982).

Dingemanse, Kazem, et al. (2010) in fact argue that it is an organism's behavioral response over an environmental gradient ("context") that is the trait of interest. They therefore use the term behavioral reaction norm to describe the set of behavioral phenotypes that a single individual produces in a given set of environments. When an individual behaves differently in different environments, in other words its reaction norm is nonhorizontal, it shows phenotypic plasticity. The authors themselves directly link behavioral reaction norms to phenotypic plasticity, an important driving force in adaptive evolution. If this is taken as a novel insight, it is worth comparing it to the origin of the concept of phenotypic plasticity. In 1896, Baldwin argued for a "new factor in evolution." This "new" factor referred to traits acquired during the ontogeny of the organism. Baldwin called this new factor "the organic selection" factor. Nowadays, we would refer to such factor as phenotypic plasticity, and there is a great deal of research on and understanding about behavioral plasticity, for example in the context of niche specialization (Bolnick et al. 2003). Even though the inclusion of reaction norms into personality research has encouraged a stronger statistical basis, the introduction of a new term itself—behavioral reaction norm—has not added new insight into the evolution of behavioral variation.

LIFE-HISTORY EVOLUTION, TRADE-OFFS, AND PACE OF LIFE

Much of the emphasis for animal personality studies comes from a purported increase in our ability to understand how selection acts on suites of behaviors. Because the behavioral phenotype itself is not carried across generations—only the mechanism that generates that behavior, be it genetic, epigenetic, or even cultural—understanding selection on correlated phenotypes without insight into a mechanism that may respond to selection is a cursory approach. A central claim made by personality researchers is that they take a more integrative approach to understanding why animals behave the way they do (Réale et al. 2010), and that "animal personality" was the first field to assess the role of hormones, physiology, and metabolism in shaping an organism's behavior (Réale et al. 2010). Yet, Wolf and Weissing (2010) in the same issue explicitly mention that behavioral correlations can often be understood in terms of the genetic, physiological, neurobiological and cognitive systems that underlie behavior, and proceed to mention many examples from the literature. In fact, life-history evolution had already incorporated behavior, genetics, physiology, neurobiology, and cognition (Roff 1992; Stearns 1992). The whole point of life-history theory is to understand how natural selection acts on physiology, anatomy, and behavior to affect behavior and life span. This is true regardless of whether the behaviors studied are correlated with others or the time scale over which they vary. Moreover, a crucial aspect of life-history theory is that of trade-offs—the notion that behaviors may be selected for strongly in one domain to the detriment of performance in another. The idea of trade-offs has permeated the personality literature to explain why a particular behavior or suite of behaviors may be adaptive in one context but not the other (Sih et al. 2004a; Dingemanse, Kazem, et al. 2010), but this cannot be considered an insight generated by personality research, but rather as another example of conceptual appropriation and relabeling by animal personality researchers.

Definitions of behavioral syndromes, such as an overall "bold" phenotype, are based on measuring correlations among a suite of behaviors, frequently using measurements like emergence time, exploration, time out from cover, distance from a novel object, and speed of movement. That these behaviors are correlated within individuals is often taken as a meaningful signature of selection or a common underlying mechanism, but a necessary null hypothesis that they are in fact different interpretations of the same measurement must surely be considered. For example, individual speed functions as an explanatory factor for numerous aspects of social interactions and movement that might otherwise be considered as separate social behaviors (Katz et al. 2011; Tunstrøm et al. 2013). Therefore, a "behavioral syndrome" may actually be composed of the same behavior measured and interpreted in different ways, and therefore based firmly in life-history theory and biophysics rather than animal personality. This is generally captured in Morgan's Canon that "In no case is an animal activity to be interpreted in terms of higher psychological processes if it can be fairly interpreted in terms of processes which stand lower in the scale of psychological evolution and development" (Morgan 1903). Approaches such as those employed in computational ethology and unsupervised machine learning (Kabra et al. 2013; Anderson and Perona 2014) further remove the need for a priori labels and, with their increased usage, will render arbitrary divisions among behaviors or groups of behaviors irrelevant.

One physiological trait that likely affects activity levels, growth, and fecundity is an animal's resting metabolic rate (Hulbert et al. 2007). Thus, animals with high resting metabolic rates can be classified as "bold" individuals (Biro and Stamps 2010), simply because resting metabolic rate influences a suite of behaviors. More generally, we can see energy metabolism as a general physiological explanation for individual differences simply because levels of energy affect almost anything an organism does or can do (Biro and Stamps 2010). An animal with a higher metabolism moves faster and therefore explores greater areas and is more likely to enter new environments (Réale et al. 2010). It therefore offers no insight to conclude that ectotherms become more "bold" as temperature increases due to an increase in their activity levels (Forsatkar et al. 2016). Likewise, individuals with higher levels of testosterone are more aggressive, potentially allowing them to compete successfully with conspecifics over access to both food or mates, although carrying costs in the form of reduced immune function or increased predation risk. And indeed, Réale et al. (2010) argue that the correlation between metabolism and "personality" (and hormones and "personality") is an example of a "pace-of-life" syndrome, which, in turn, really refers to a trade-off between longevity and metabolic rate (Hulbert et al. 2007).

BEHAVIORAL GENETICS AND BEHAVIORAL NEUROENDOCRINOLOGY: UNDERSTANDING BEHAVIORAL VARIATION

Consider a population of white-throated sparrows, *Zonotrichia albicollis*. Male and female sparrows come in 2 morphs: tan or white, based on the color of the median crown stripe. White males are more aggressive, frequently intrude into neighboring territories, spend less time guarding their mates, occasionally attempt polygyny, and provide less parental care than tan males (Tuttle 2003). It is clear that a male cannot simultaneously pursue additional matings and provide high levels of paternal care to his young. Thus, white and tan morph males practice different reproductive strategies based on the trade-off between securing additional matings and parental effort. In order to be successful in obtaining extrapair copulations, white males behave aggressively and frequently intrude into another male's territory to gain access to mates. We could thus argue that white males are bold, whereas tan males are shy. But does that reveal the underlying cause of the behavioral differences between white and tan males? It does not. What we know is that white and tan males differ in a suite of behaviors.

We cannot understand the white-throated sparrow males' behavior if we ignore the behavior of the females. White-throated sparrows mate disassortatively so that most white males pair up with tan females and vice versa. When a tan female's mate reduces his parental effort because he is pursuing extrapair copulations, the tan female will compensate by increasing her parental effort. This basically "allows" the white males to increase his reproductive output via extrapair copulations as his earlier brood's future is secured thanks to the female's parental effort. Tan males are not afforded such luxury, as their white mates will not compensate for a reduction in parental effort, thus forcing tan males to remain faithful. Hence, both reproductive strategies are maintained in the population because both color morphs have equal reproductive success (Tuttle 2003). Genetically polymorphism is maintained because of "supergenes", linked clusters of coevolved genes that give rise to divergent fitness-related traits that are variable within species (Schwander et al. 2014; Tuttle et al. 2016). Hence, while personality researchers would have been satisfied with identifying behavioral differences (e.g., Malange et al. 2016; Michelangeli et al. 2016; Yuen et al. 2016), the fields of life-history evolution and behavioral genetics allows us to understand why individuals differ in their behavior. This is just one of many examples of studies that have identified the genetic mechanisms underlying animal behavior. Whether or not a worker honeybee becomes reproductively active is determined by a single gene, called *anarchy* (Ronai, Oldroyd, et al. 2016; Ronai, Vergoz, et al., 2016) and the social structure of several species of ants is determined by a "social chromosome" (Purcell et al. 2014). Similarly, the kind of burrow dug by deer mice is under the influence of a set of well-characterized genes (Hu and Hoekstra 2017). Identifying the genetic basis of behavior is obviously much more labor intensive, not to mention expensive, than simply describing differences in "personality," but actually provides us insights into the underlying mechanisms.

Another well-understood mechanism mediating suites of behavior can be found in the African cichlid *Astatotilapia burtoni*. Males of this species display distinct behavioral phenotypes, depending on their social context (cf. Bergmüller and Taborsky 2010) and condition. Males form social hierarchies in which a small number of males are highly aggressive, territorial, brightly colored, swim rapidly, have large ranges, and are reproductively active. The other males in these groups are submissive, have reduced coloration, swim slowly, and have a restricted range (Maruska 2015). These differences in behavior and physiology are based on the relative social position and relationships to other individuals in the social network. Males can rapidly transition among these states based on social context, leading to massive changes in individual behaviors, as well as the correlations among these behaviors. These social phenotypes are plastic and reversible, meaning that individual males may frequently switch between dominant and subordinate social status.

Probably because the physiological mechanisms underlying the transition between the above described behavioral states, and the links among behaviors are well characterized, there has been no need or benefit to describe them as personality differences. When the social environment changes such that males either ascend (subordinate to dominant) or descend (dominant to subordinate) in rank, there are rapid changes in behavior, circulating hormones, and levels of gene expression in the brain that reflect the direction of transition (Maruska 2014). Socially ascendant and dominant males have increased activation of brain nuclei in the social behavior network, and higher levels of sex steroids in the plasma, which affect numerous behaviors. Ascending males also show rapid changes in levels of neuropeptide and steroid receptors in the brain, as well as in the pituitary and testes (reviewed in Maruska 2014). Although these dominance changes result in massive and correlated behavioral changes, which are consistent within individuals and over time, the deeper understanding of the mechanisms underlying this switch seem to preclude the need to refer to these behavioral states as "personality." This example again emphasizes how little is gained from labels such as "bold" and "shy" in the face of rigorous inquiry into the causes and consequences of fixed and labile behaviors.

FINAL WORDS

There is nothing inherently wrong with constructing a new research field around animal behavior that leans heavily on existing fields, particularly if the claimed aim is to integrate separate research areas. After all the field of behavioral ecology has its origin in the integration of ethology, evolutionary biology, game theory, and economic decision-making. While ethology traditionally described how animals behave, behavioral ecology started to ask *why* they behave in a particular way and not another way. The incorporation of economic thinking and game theory into the study of animal behavior increased the biologist's mathematical tool kit, allowing researchers to construct models that predict how organisms should behave under particular conditions. Combined with the realization that selection acts at the level of genes and not groups or individuals (with some exceptions) has allowed behavioral ecology to achieve what ethology cannot: understand how selection shapes the behavior of animals in different contexts.

Behavioral ecology can explain why individuals sometimes appear to behave against their own interest. Why abandon your young so that they are bound to die? One answer is that if a parent is forced to look after young alone because the other parent has left first, it may be in the remaining parent's best interest to secure resources for the next breeding season instead of attempting to raise young alone. Some parents may be in sufficient condition to be able to successfully raise their young alone, particularly when environmental conditions too are favorable, whereas a parent in poor condition is forced to call it quits. Thus, both differences in physiology and environmental conditions can cause behavioral differences among individuals faced with the same choice. In the field of animal personality, one might claim that the 2 individuals have different personalities, even as a function of their life-history, but what does that tell us we did not know already without reference to personality? Herein lies the crux of the matter. For a research field to be of value, it needs to be hypothesis driven and have predictive power. Simply coining individual differences "personalities" has no predictive power. To be convinced that animal personality research should be taken seriously, we need clear hypotheses and predictions. In the absence of both, we equate "animal personality" with "ethology"; a well-established field that describes behavior. Indeed, animals behave and they do not all behave in the same way. But in order to advance the field, we need to understand why animals differ in the way they behave. The expanding use of quantitative methods to study behavioral variation is an advance but has diverged from and should no longer be considered part of personality research, instead becoming a conduit between the existing fields of behavioral ecology and quantitative genetics.

A general and pervasive problem in animal personality research is that the problems and questions it claims to address were, and continue to be addressed more rigorously in existing fields. In our view the detour into, and then out of, personality obfuscates the history and development of our scientific understanding of behavioral variation and plasticity. This can present a serious barrier to understanding for new students interested in this field, because they may be left with the impression that variation in behavior can be understood using simple correlational approaches to behavioral phenotypes that typify the bulk of the field. We therefore hope that our piece will initiate an honest debate regarding the validity of animal personality research, while highlighting the more valuable offshoots that diverged in the early days of the field. If indeed the use of "animal personality" does not add anything new to behavioral ecology, as we argue, then let us please resume discussion of variation and consistency of behavior in the context of behavioral ecology, and abandon the concept and terminology of animal personality entirely.

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