Insights for Behavioral Ecology from Behavioral Syndromes

Andrew Sih[*] and Alison M. Bell[†]

[*]environmental science and policy, university of california, davis, davis, california 95616

[†]school of integrative biology, university of illinois, urbana-champaign, urbana, illinois 61801

I. Introduction

A few years ago, we coauthored two papers outlining the concept of behavioral syndromes, a research approach that focuses on correlations and carry-overs among behaviors that have historically been often studied separately (Sih *et al.*, 2004a,b). A behavioral syndrome involves behavioral consistency, both within and between individuals. Within-individual consistency occurs when individuals behave in a consistent way through time or across situations, that is individuals have a behavioral type. Between-individual consistency occurs when individuals differ in their behavioral type, which would be reflected statistically as a behavioral correlation among individuals. An example of a behavioral syndrome is the positive correlation between boldness and aggressiveness that has been documented in several species (Bell, 2005; Bell and Sih, 2007; Dingemanse *et al.*, 2007; Dochtermann and Jenkins, 2007; Duckworth and Badyaev, 2007; Huntingford, 1976a; Johnson and Sih, 2005; Kortet and Hedrick, 2007; Moretz *et al.*, 2007; Reaney and Backwell, 2007). Individual animals that are more bold (than others) in the face of predation risk also tend to be more aggressive toward conspecifics. Our earlier papers emphasized evolutionary and ecological implications of behavioral syndromes as well as the potential for behavioral syndromes to serve as a conceptual bridge integrating proximate mechanisms (genetics, development, and neuro-endocrine mechanisms) with the ecology and evolution of behavior.

In recent years, there has been an explosion of interest and research activity examining behavioral syndromes and the closely related concepts of animal personality, temperament, and coping styles (Dingemanse and

Réale, 2005; Gosling, 2001; Koolhaas *et al.*, 1999, 2006; Overli *et al.*, 2007; Reale *et al.*, 2007). Several symposia discussed these concepts at major behavior conferences, including one asking "Do behavioral syndromes represent a paradigm shift in behavioral ecology?" (International Society for Behavioural Ecology meeting in Tours, France, 2006). The *New York Times*' Magazine full-length, cover article on animal personalities (January 22, 2006) was a testament to the appeal of the topic to the general public. This burst of activity generated numerous exciting new ideas and insights as well as criticism, controversy, and, in our view, some misunderstandings.

Here, we present our suggested roadmap for the future study of behavioral syndromes. We first outline a brief history of the concept, and clarify some misunderstandings about the definition of a behavioral syndrome. While these points are not inherently forward thinking, we feel that they must be clarified before proceeding. Then, we describe exciting avenues of study that derive from the fact that in the last 5 years, enough studies have been done to show that for at least two main types of behavior—boldness and aggressiveness—we often see behavioral correlations, but sometimes we do not. Further, sometimes behavioral correlations are stable over time, but other times they are not. One major challenge for the next wave of studies should thus be to better understand the factors that influence when behaviors are clustered together as a behavioral syndrome, and when the behavioral correlations are decoupled. Here, we describe recent developments using both proximate and adaptive frameworks to explain patterns of variation in behavioral syndromes. We champion an approach that blends these two views. Finally, although boldness and aggressiveness (and associated coping styles) have received considerable attention, we note here several other, potentially important, behavioral syndromes that have not yet received much attention. These expand the scope of behavioral syndromes to cover a broader range of issues, including many that have rarely been addressed by behavioral ecologists. We close by summarizing some directions for future study.

II.   A BRIEF HISTORY OF THE IDEA

One criticism of the concept of behavioral syndromes has been that it is not new. We agree. Some behavioral ecologists have long emphasized the importance of individual variation in behavioral type. In addition, behavioral consistency is a major area of study in several other subfields of behavior (e.g., behavioral genetics, applied animal behavior, the study of personality in humans, and other animals). And, the importance of correlated traits has long been emphasized in evolutionary biology. Thus, the recent surge of interest in behavioral syndromes does not derive from it being a truly new

idea, but comes instead from the possibility that it represents an opportunity for new insights to emerge from the melding of ideas and methods from several, interrelated, but somewhat disparate fields.

Among behavioral ecologists, an effective tactic for studying the role of particular ecological circumstances in governing behavior has been to compare groups exposed to different treatments (e.g., with or without predation risk, high or low food) rather than focus on individuals. That is, a standard methodology is to use different individuals in different treatment groups, and to focus on mean-level differences. Although this approach is effective at determining whether a specific factor is driving behavioral differences, an important alternative view is to regard individual variation as more than mere noise. Several prominent behavioral ecologists brought attention to the importance of individual behavioral variation in the 1980s and 1990s (Arnqvist and Henriksson, 1997; Clark and Ehlinger, 1987; Huntingford, 1976b; Magurran, 1993; Riechert and Hedrick, 1993; Slater, 1981; Stamps, 1991; Wilson, 1998; Wilson et al., 1994). In addition, discrete, bimodal behavioral types, such as alternative strategies (producer/scrounger, hawk/dove, defect/cooperate) have long been a mainstream area of study in behavioral ecology. Other familiar types of discrete behavioral variation include dominant/subordinate, territory holder/floater, or for that matter, male/female. Indeed, much of game theory is concerned with interactions that can be between individuals with different behavioral types, a point we develop later in the chapter. However, despite this tradition and precedent, most studies in behavioral ecology have not analyzed or emphasized individual variation.

Similarly, until recently, most studies in behavioral ecology have focused on behavior within a given situation without looking to see if behavioral tendencies carry over to other situations. For example, while many have looked at alternative male strategies in mating contests, until recently, few have asked whether those strategies carry over to other contexts, such as aggressiveness toward females during courtship, to parental care behavior, to feeding voracity, or boldness in the presence of predators. Based on the reasoning that natural selection favors optimal behavior in every situation, most studies have focused on behavior in one situation.

In contrast, the study of individual variation in behavioral type and carryovers across situations has been a central issue for numerous studies of proximate mechanisms underlying behavior. A focal question has been: What role do genes and neuroendocrine mechanisms play in explaining why some individuals are more aggressive or more anxious than others as a general coping style expressed in many situations? Indeed, the tradition of studying proximate mechanisms governing different coping styles in laboratory rodents (Benus et al., 1987, 1991; Koolhaas et al., 1999; Meaney, 2001), primates (Capitanio et al., 1998; Suomi, 1987), and farm animals

(Hessing *et al.*, 1993) played a major role in guiding recent studies on animal personalities, in particular, in Europe (Drent *et al.*, 2003; Verbeek *et al.*, 1994, 1996). Along similar lines, individual variation in behavioral tendencies across multiple situations is, of course, at the heart of the study of human personalities (Plomin and Dunn, 1986), and analogous work on animal personalities as conducted by psychologists (Gosling, 2001). While these fields have a history of studying behavioral consistency and behavioral correlations, to our knowledge, until recently, these studies were not on the radar for most behavioral ecologists.

Another situation where individual variation has traditionally been quantified is where, perhaps due to logistical constraints, the standard methodology involves studying a relatively small number of individuals over a relatively long period. For example, primatologists have long noted that certain individuals have particular behavioral characteristics, being sociable or aggressive (Stevenson-Hinde *et al.*, 1980). We think that the extensive documentation of temperament in nonhuman primates does not mean that they have ''more personality'' than other animals. Instead, a more practical explanation for this bias is that the number of individuals available for study is generally more limited in primatology than in studies of other animals. Therefore, primatologists gathered a lot of data on the same individuals and were thus immediately confronted by the personalities of their subjects.

Behavioral correlations are potentially important for the same reason that correlations, in general (in any field of science, logic, etc.), can be important. Essentially, it means that to understand one behavior, we need to consider other correlated behaviors. The idea that traits might be correlated and that trait correlations might be important has long been understood and studied by evolutionary biologists. For example, life history theory has long emphasized that to understand fundamental traits like deferred reproduction or senescence, it is crucial to consider trade-offs generated by correlations across the life history (Roff, 1992). In addition, evolutionary biologists have a history of studying limited plasticity, an idea that is implied by within-individual consistency in behavior (Schlichting and Pigliucci, 1998). Finally, evolutionary biologists have been studying the evolution of correlated traits, mostly with respect to morphological traits, long before they were drawing the attention of behavioral ecologists (Armbruster and Schwaegerle, 1996; Brodie, 1992; Lande and Arnold, 1983).

A current area of excitement in evolutionary biology focuses on the interplay between selection and genetics in governing the evolution of integrated phenotypes, packages that could include morphological, physiological, life history, and behavioral traits (Pigliucci and Preston, 2004). In this context, studying behavioral syndromes is too narrow a view. When possible, we should further broaden our view to study how behavioral

syndromes are integrated with other aspects of the organisms' overall pheno-type. Overall, progress in understanding behavioral syndromes clearly has been and should continue to be enhanced by drawing from analogous, well-established fields of study.

III. Clarifying the Definition of a Behavioral Syndrome

In discussions at recent symposia, in recent papers, and in anonymous reviews of our papers and grant proposals, we have often encountered several main misconceptions about the definition of a behavioral syndrome. In our earlier paper (Sih *et al*., 2004a,b), we defined a behavioral syndrome as ''a suite of correlated behaviors across multiple (two or more) observa-tions.'' Others have only considered studies with more than two observa-tions per individual as addressing a behavioral syndrome; however, we did not do that in our original definition. Our conceptual focus is on the importance of behavioral correlations per se. Thus, we do not see a basis or value for excluding the minimal situation (two observations, one corre-lation) from the bailiwick of behavioral syndromes.

Because we define a behavioral syndrome as a correlation, the critical statistical test is whether a correlation between behaviors is significantly different from zero. Obviously, a stronger correlation (judged by the cor-relation coefficient, not by the p value) reflects a tighter and potentially more important relationship between two behaviors. However, even a relatively weak correlation ($r \sim 0.2$–0.3, which is the effect size observed in many studies), especially if it is a genetic correlation (Roff, 1995), can still have important ecological and evolutionary implications. For example, even a very low genetic correlation on the order of 0.1–0.2 can still produce biologically meaningful correlated response to selection on the unselected trait, depending on the intensity of selection and the heritabilities of the two traits (Falconer and Mackay, 1996).

At this point, we do not see a compelling reason to draw precise bound-aries on the situations or contexts that are worth examining in a behavioral syndromes framework, although correlations across seemingly unrelated contexts and that are long-lasting might be particularly interesting. In fact, variation in diverse behavioral contexts (in addition to the well-studied shy-bold or aggression axes) such as mating behavior, parental behavior, learning styles, coping styles, cooperative behavior, and information proces-sing all are candidates for study from a behavioral syndromes perspective (see Section IV). In our original definition, we took a broad, inclusive view that a behavioral syndrome could involve: (1) different contexts at the same point in time (e.g., feeding vs mating activity in one set of conditions), (2) the

same context but at different points in time (e.g., feeding activity in the presence vs absence of predators, or feeding voracity as a juvenile vs as an adult), or (3) different contexts at different points in time (e.g., aggression toward conspecifics in the absence of predators vs feeding activity in the presence of predators). To emphasize, a behavioral syndrome could involve behavioral consistency through time in either the same basic context, for example, voracity in juveniles and adults (Johnson, 2003), or across contexts, for example aggression in a parental and competitive context (Ketterson and Nolan, 1999).

Below, we describe how, according to this very general definition of a behavioral syndrome, a behavioral syndrome does not have to: (1) be stable over a lifetime or even over a large proportion of a lifetime, (2) involve a genetic basis, (3) involve both multiple contexts and multiple situations, (4) be independent of social status or condition, (5) involve a dichotomy of behavioral types, and (6) be associated with suboptimal behavior. They certainly do not require animals to show little or no behavioral plasticity. While a behavioral syndrome might be more interesting or more important if it has a strong genetic basis, is stable over a lifetime, carries over across multiple contexts, and results in suboptimal behavior, these are not part of the definition of the concept.

According to our definition, behavioral syndromes need not involve stability of behavioral types over an individual's entire lifetime. Long-term stability is more likely to represent a developmental constraint than short-term stability if it means that an individual is "stuck" with a behavioral type throughout its entire lifetime. For example, behavioral correlations through ontogeny mean that selection on behavior at one age could have correlated effects later in life (Bell and Stamps, 2004). However, even short-term behavioral consistency can be very important. For example, a short-term carryover of aggressiveness into other contexts could make the difference between life and death if it means that a male that is pumped up on testosterone behaves inappropriately in the presence of a predator.

Overall, we see no valid way or compelling reason to draw absolute cutoffs to define how stable a behavioral correlation needs to be in order to be interesting. Instead, we suggest that it would be more useful to focus on determining the causes and consequences of different degrees of stability. It is here, especially, that we think we have a lot to learn from the human personality literature, which suggests that some personality dimensions are more stable than others, and different periods of development are characterized by more or less change (Caspi et al., 2005; Roberts et al., 2006). Therefore, an interesting question is the relative durability or stability of a behavioral syndrome—is it stable throughout an organism's entire lifetime, or more likely to change during particular developmental periods such

as adolescence, or only in the presence of a social group? Determining whether an individual's behavioral type is solidified only after critical period of time has elapsed, or following a major habitat shift, such as migration, is a promising task for future work.

Furthermore, a behavioral syndrome need not have a genetic basis [note that we differ here from some definitions of personality (e.g., van Oers *et al.*, 2005)]. We define a behavioral syndrome in a statistical sense—as a correlation between behaviors—without any underlying assumptions about its proximate cause or source. Although behavioral types appear to usually depend on genes [and on environmental experiences and a gene×environment interaction (Bell, 2005; Bell and Stamps, 2004; Carere *et al.*, 2001)], a genetic basis to an individual's behavioral types is not part of the definition of a behavioral syndrome. Even if variation in behavioral types is entirely determined by differences in early experience (or maternal effects), we still consider this to be a behavioral syndrome. Similarly, even if behavioral types are largely regulated by social status or differences in condition (i.e., even if behavioral type is labile if status or condition changes), if individuals exhibit behavioral consistency and differ from one another, this is a behavioral syndrome. Some view behavioral syndromes that are primarily due to social status (e.g., dominants are more aggressive than subordinates) as less interesting; however, in our view, this is not relevant to the definition per se. By adopting a broad, inclusive view that conceptualizes a behavioral syndrome as a reaction norm, where an individual's behavioral type is a product of genetic, environmental, and G×E sources, we can avoid the person-situation debate (i.e., is human personality more determined by the "person" or the "situation"?), which preoccupied psychologists several decades ago (Mischel, 2004; Penke *et al.*, 2007).

Behavioral syndromes do not have to be associated with suboptimal behavior; they can be adaptive. Although the term "syndrome" has negative connotations in the clinical literature (e.g., chronic fatigue syndrome), and although some examples of behavioral syndromes have emphasized suboptimal outcomes (Johnson and Sih, 2005; Sih *et al.*, 2003), our definition does not require either suboptimality or limited plasticity relative to the optimal. The term behavioral syndromes was coined because the term syndrome is used in other areas of evolutionary biology. For example, suites of covarying traits forming "pollination syndromes" (Johnson and Steiner, 2000), "migratory syndromes" (Dingle, 2001), or "life history syndromes" (Roff, 1992) are generally thought to be adaptive responses to selection which favors responses in multiple traits, not just one.

Along these lines, behavioral syndromes are not, by definition, incompatible with adaptive behavioral plasticity. Some have suggested that behavioral syndromes imply little or no behavioral plasticity and that

examples of adaptive behavioral plasticity are evidence against behavioral syndromes (Neff and Sherman, 2004). The definition of behavioral syndromes, however, is agnostic about the degree of behavioral plasticity. Even if all individuals are highly plastic (e.g., change their activity substantially in the presence versus absence of predators), if the rank-order differences between individuals is maintained (i.e., individuals that are more active than others in the absence of predators continue to be more active than others in the presence of predators), then we have a behavioral syndrome. If individuals show limited plasticity (less than optimal plasticity) associated with their behavioral type (Duckworth, 2006; Johnson and Sih, 2005; Sih *et al.*, 2003), this makes the behavioral syndrome particularly important in determining fitness; however, limited plasticity is not an inherent part of the definition of a behavioral syndrome.

Finally, although some discussions of behavioral syndromes or coping styles talk about a dichotomy of behavioral types (e.g., proactive vs reactive or shy vs bold), the concept of a behavioral syndrome does not imply any particular frequency distribution of behavioral types. Populations often have a continuous distribution (perhaps a normal distribution) of behavioral types. The exception might be that when behavioral types are associated with discrete morphotypes (e.g., males vs females, or alternative male mating morphotypes), then they might also show a discrete behavioral dichotomy. However, to emphasize, although the distribution of behavioral types is a characteristic of a behavioral syndrome, it is not the part of the definition.

The relationship between behavioral syndromes and the related concepts of temperament, personality, and coping style is described by Reale *et al.* (2007). We prefer the term behavioral syndrome for two primary reasons. First, the term is inclusive and general: unlike many definitions of temperament (Reale *et al.*, 2007), for example, a behavioral syndrome does not have to be genetically based or a characteristic of juveniles or to be stable across the life course. We prefer a broad definition because we see behavioral syndromes as an important conceptual bridge with wide-ranging implications for many topics in behavioral ecology. Second, because behavioral syndromes are defined as correlations, the study of behavioral syndromes fits squarely within the existing framework for studying suites of traits, covariation, syndromes, etc. in evolutionary ecology.

IV. UNDERSTANDING VARIATION IN BEHAVIORAL SYNDROMES

In recent years, dozens of studies have tested for behavioral correlations in numerous taxa. Many studies have found significant behavioral correlations, but others have not. Clearly, the question is thus not—do they exist

or not? Instead, a key issue now is to explain *variation* in behavioral syndromes. First, what are the patterns? For a set of behaviors over multiple contexts and situations, which behaviors are correlated and which are not? For behaviors that are sometimes correlated, how stable are the correlations over ontogeny, and over an evolutionary timescale? Or, conversely, when are behaviors decoupled? Second, what explains the observed patterns? Can they be best understood in terms of proximate constraints or adaptive (cost/benefit) considerations or a combination of the two? If proximate constraints are important, which types of constraints underlie which correlations? And, if adaptive approaches are useful, what role do ecological or social selection pressures play in shaping behavioral syndromes? At the most fundamental level, what conceptual framework should we use to explain and ideally predict patterns of variation in behavioral syndromes? These are very exciting, challenging questions that the field is just beginning to address.

Before proceeding, we first clarify the distinction between variation in behavioral type and variation in behavioral syndromes. Behavioral ecologists have a long history of thinking about and quantifying population variation in mean behavioral type. For example, conventional wisdom suggests that we expect, and indeed often see, that animals are more bold (with or without predators present) if they have evolved in situations with low predation risk [e.g., islands or ponds without important predators (Cox and Lima, 2006; Giles and Huntingford, 1984; Magurran, 1986; Reznick, 1983)]. Or, animals are more aggressive if they have evolved in situations where resources are defensible [e.g., fish hatcheries as compared to wild fish (e.g., Sundstrom *et al.*, 2004)]. These are statements about the mean value of boldness or aggressiveness for individuals in a population. The clear expectation is that cost/benefit considerations can often explain variations in behavioral type.

In contrast, we are only beginning to quantify and think about variation in behavioral syndromes. Why is it that in some species and under some circumstances, behaviors cluster together into a correlated package, but in other cases, individual behavior is not consistent through time or across situations? For example, although it is clear that higher risk often favors reduced boldness (i.e., due to a higher cost of being bold), it is not clear how we might expect predation risk to influence the correlation between boldness and aggressiveness. Intriguingly, recent studies show that there is a connection between predation risk and the correlation between boldness and aggressiveness in sticklebacks (Bell, 2005, 2007; Dingemanse *et al.*, 2004); however, we challenge the reader to decipher which way this relationship goes. Is a significant positive correlation between these behaviors found in populations with high risk or low risk? And, more importantly, why should it be that way? Indeed, what conceptual framework should we

use to understand this pattern—a framework based on cost/benefit consid-erations (selection on the correlation), or one that emphasizes proximate mechanisms, or both? In human terms, the question is—what framework should we use to understand the structure of personality? While in what follows, we emphasize questions about behavioral syndromes, the same broad framework should ideally help to also understand issues about varia-tion in behavioral types.

Before we can offer an interesting biological explanation for variation in a behavioral syndrome, it is first necessary to determine whether the failure to find a significant correlation in some circumstances is being caused by lack of statistical power, for example, due to low sample sizes or lack of variance. That is, for detecting covariances or correlations, a key possible problem is low variance in one or both variables. Without variance in both variables, it is difficult to detect covariance. Thus, one reason why a behav-ioral correlation might be detected at some ages but not others could be that individuals are generally less behaviorally variable at one age, there-fore, giving the impression that a link is no longer present. Alternatively, a correlation might appear to change simply due to a change in variance in one variable (Fig. 1). Changes in variance can prompt interesting biological questions about the cause of changes in covariance: one reason why indivi-duals are not predictable from one context to the next is because they are all doing the same thing in one of the contexts under consideration. Therefore, we suggest that simply examining changes in the distribution of behaviors is a useful first step along the way to understand the causes of variable correlations. Also, some studies might overemphasize the importance of behavioral syndromes by focusing on the extreme behavioral types (the most bold vs most shy). If the distribution of behav-ioral scores does not really follow a clean bimodal distribution, then such a classification ignores possibly important intermediates. This is especially important when individuals at the extreme are qualitatively different from the intermediates.

A. PROXIMATE EXPLANATIONS FOR VARIATION IN BEHAVIORAL SYNDROMES

Above and beyond issues of statistical power per se, an approach for explaining why behavioral carryovers and consistency might exist (and potentially when they might break down) invokes proximate mechanisms (i.e., hormones, physiology, and genetics) that underlie multiple behaviors. At heart, the logic is that: (1) behavioral consistency might be explained by proximate mechanisms that are less plastic (more stable) over time than behavior per se and (2) that behavioral correlations across multiple
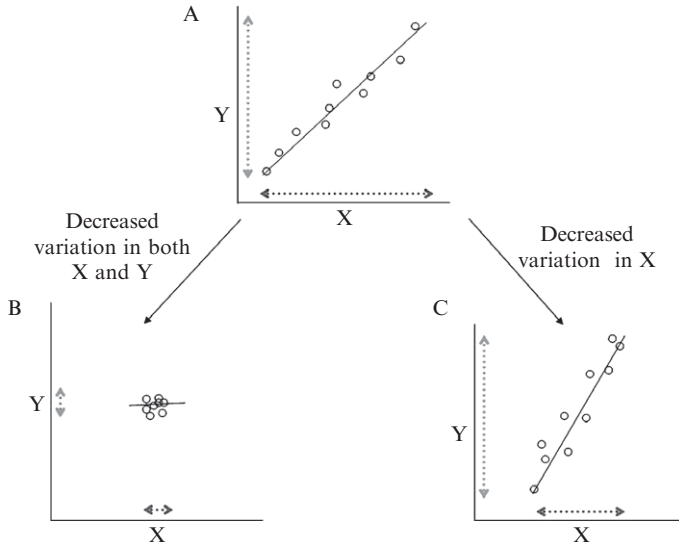
FIG. 1. Changes in behavioral correlations can be caused by changes in variance. Each data point represents a different individual. The range of values of *X* is in black, and that in *Y* is in gray. The best-fit regression line is shown. In (A), *X* and *Y* are positively correlated. In (B), variation in both *X* and *Y* has decreased, causing the correlation between *X* and *Y* to vanish. In (C), variation in *X* has decreased while that in *Y* is unchanged, causing the slope to increase.

contexts or situations might be due to proximate mechanisms that govern multiple behaviors (e.g., one hormone or one gene controls several behaviors).

An obvious place to start looking for the proximate source of behavioral correlations is genetics, if suites of behaviors are affected by the same genes or hormones (pleiotropy) (Mackay, 2004). Indeed, much of the literature on coping styles examines how genetic variation in the hypothalamic pituitary adrenal axis might underlie variation in behavioral type (Boyce and Ellis, 2005; Koolhaas *et al*., 1999).

However, it seems that the more we learn about genetic and neuroendo-crine mechanisms underlying suites of behaviors, the more it becomes clear that most systems are very complex, full of interactions and feedback, and that the behaviors of interest to behavioral ecologists are often many steps away from a simple genetic source (Henderson, 1990; Kendler and Greenspan, 2006). This complexity builds in flexibility and offers multiple opportunities for selection to act to uncouple deleterious combinations. For example, the effect of any given hormone, for example corticosteroids, can

depend on binding globulins, multiple receptors, receptor densities in different tissues, and interactions and feedbacks among multiple hormones (Sapolsky *et al.*, 2000). In some cases, higher levels of the same neurochemical can be associated with either higher or lower levels of risk seeking or aggressiveness (Bell *et al.*, 2007). Although it is tempting to offer casual causal statements such as high testosterone explains aggressiveness, other neurochemicals that have been suggested to relate to aggressiveness or boldness include vasopressin or AVT (e.g., Veenema *et al.*, 2006), corticosteroids (e.g., Carere *et al.*, 2003), and brain monoamines (e.g., Winberg and Nilsson, 1993). Indeed, the very fact that so many different neurochemicals can be associated with aggressiveness hints at the complexity of the overall behavioral system. We are only beginning to scratch the surface of the interactions (Veenema *et al.*, 2006), but we suggest that this complexity holds the key to help explain variation in behavioral syndromes.

For example, a candidate for explaining the correlation between boldness and aggressiveness might be a gene (e.g., monoamine oxidase) that regulates expression of other genes that control both pathways. Even if the genetic control of behavioral types is very complex (e.g., involves networks of many interacting genes), it remains plausible that variation in expression of some key genes could help explain the dynamics of the overall genetic network that underlies behavioral correlations. Modern genomic tools both empirical and theoretical (e.g., network theory) lend a sense of excitement to this developing field.

So what sorts of systems are likely to generate stable behavioral types which vary among individuals? We propose, generally, that aspects of systems that are less plastic (e.g., receptor density as opposed to circulating hormone levels) or that are the product of hormonally regulated, organizational processes early in development (e.g., structural differences in the brain) could underlie behavioral syndromes that are stable over ontogeny. In contrast, aspects of behavior that are regulated by more plastic aspects of the neuroendocrine system (e.g., circulating hormone levels) should be less likely to be part of a stable behavioral syndrome (Bell, 2007). Circulating hormone levels can change almost as rapidly as behavior per se, thus while they could potentially explain short-term carryovers, even across types of behavior (e.g., short-term spillovers from aggressiveness toward male conspecifics to aggressiveness toward females or toward a predator), they would not appear to be a good candidate for explaining long-term stability of behavioral types.

Morphological mechanisms (e.g., organ size or brain structures) that can only change slowly are especially good candidates for explaining stable behavioral types and a stable behavioral syndrome. Given that key morphological traits might develop relatively early in life, these represent developmental or ontogenetic constraints on behavioral syndromes. Life history

events that feature morphological restructuring (e.g., metamorphosis for insects or amphibians or onset of reproduction) might then be key cusps that cause changes in behavioral type and even behavioral syndromes. Furthermore, although relatively fixed, morphological mechanisms might result in stable behavioral types and syndromes within a lifetime, they need not constrain evolution of behavioral syndromes across generations. For example, the same proximate mechanisms that result in a positive correlation between boldness and aggressiveness among individuals within one population need not produce a positive correlation among populations (Bell, 2005).

One proximate source that could anchor a behavioral type involves physiological mechanisms associated with variation in growth rate (Biro and Stamps, 2008; Careau *et al.*, 2008; Stamps, 2007). Stamps (2007) proposed that animals might develop physiological mechanisms that favor a consistent, as opposed to a variable, growth rate. If there is a trade-off between growth rate and mortality, such that some individuals grow fast but risk predator-induced mortality while others play it safe by growing slowly [but both strategies have equal fitness (Mangel and Stamps, 2001)], then any behavior that contributes to the growth–mortality trade-off will be variable among individuals. This framework not only explains variation in behavioral types but also provides a mechanism for explaining behavioral correlations. Boldness and aggressiveness should be positively correlated because they are both components of an overall high risk, high gain life history type (Stamps, 2007). The two, however, would not be correlated if some key aspect of the behavior–life history relationship is violated; for example, if boldness or aggressiveness do not result in more resources, or if boldness does not result in higher mortality (e.g., if predation risk is low). We discuss this idea in more detail below.

A specific possibility is that variation in metabolic rates and associated physiological morphology underlies variation in feeding–growth strategies. High feeding and growth rates require high activity that, in turn, requires high metabolic rates. Most importantly, high-energy intake rates require large organs to process food (e.g., large intestines), take in oxygen (large lungs), and remove wastes (large liver or kidneys). The fact that organ size is relatively fixed then determines a physiological type that governs behavior and life history types (Biro and Stamps, 2008; Careau *et al.*, 2008).

B. Ultimate (Adaptive) Explanations for Variation in Behavioral Syndromes

An alternative, complementary approach uses adaptive (cost/benefit) considerations to explain variation in behavioral syndromes. Recent theoretical papers have proposed adaptive hypotheses based on three main

classes of mechanisms: (1) the benefits of specialization, (2) the benefits of consistency per se, what we call ''status quo'' selection, and (3) the social benefits of predictability. While these mechanisms have been discussed primarily in the context of explaining why individuals have consistent behavioral types, the hope is that these frameworks will also help understand the other issues about the structure of behavioral syndromes (see the list of issues at the beginning of Section III).

Before proceeding, note that here, we follow the evolutionary ecology tradition of referring to a trait as being ''adaptive'' if it yields high-current fitness. We are not addressing the alternative definition that an adaptation requires evolution of the trait for its current function (Gould and Vrba, 1982).

Perhaps the most general adaptive reason for an individual to maintain a particular behavioral type is that there are benefits to specializing on that type. Sih *et al.* (2004a,b) discussed how existing theory on the evolution of specialists versus generalists, and related theory on the evolution of fixed versus plastic traits, might offer insights on conditions favoring the evolution of consistent behavioral types. In essence, the issue is that in a variable environment, why should individuals evolve a relatively fixed strategy (a consistent behavioral type) rather than be highly plastic to track environmental change over space or time? According to earlier theory [that was couched in terms of developmental plasticity, and not behavior or behavioral syndromes; see Sih *et al.* (2004a,b)], two key factors are the cost of switching traits and the ability of individuals to accurately and adaptively match their traits to the current environment. Individuals should exhibit highly plastic behavior if the cost of switching behavioral strategies is low, and if individuals can accurately assess the current environment and behave accordingly. Conversely, individuals might maintain a consistent behavioral type if it is costly to switch behavioral types, or if they are ineffective at matching their behavior to the current environment.

One main reason why individuals might not be able to exhibit adaptive behavioral plasticity is if they lack precise information about the current environment. Consider, for example, the challenge of investing in the stock market. In order to buy and sell optimally, one needs useful information about different options and market conditions. Gathering that information takes time and energy (i.e., costly). Furthermore, even a well-informed individual still experiences considerable uncertainty about market conditions. Given these costs and uncertainties, it might often be better to choose a portfolio and stick with it (i.e., low plasticity), rather than attempt to play the market actively.

McElreath and Strimling (2006) explored this conjecture with a formal model [based on Sih (1992)] exploring fixed versus plastic prey responses to variation in predation risk. Prey with complete information should hide

when predators are present, but forage actively when predators are absent. The problem is that prey might not know accurately if predators are currently present or not. McElreath and Strimling (2006) confirmed Sih's result (1992) that if prey are uncertain about whether predators are present or not, then fixed behavior can be favored over inaccurate tracking of risk. This does not, however, explain why some individuals are bold while others are shy. McElreath and Strimling (2006) added the exciting insight that differences between individuals in a state variable (e.g., size, vigor) that determines the relative ability to be bold (or shy) can explain why some are bold while others are shy. The key is that state variables (size, vigor, condition, energy reserves, life history stage, information state, skill level) change relatively slowly over time. Thus, although behavior can, in theory, change very rapidly, if the optimal behavior is connected to a slower, more stable state variable, then this connection can explain behavioral consistency, and differences in state can explain differences in behavioral type. Critical issues that McElreath and Strimling (2006) did not address are how might individual differences in state arise, and most importantly, why should these differences be maintained? If variation in state explains variation in behavior, then the key question is – what maintains within- and between-individual consistency in state?

Wolf et al. (2007a) examined a specific mechanism for generating variation in state. They posited that individuals might vary in their tendency to explore their environment early in life. Individuals that are more exploratory have more information (an asset) that they can use to gain resources (that can be converted into fitness) later in life. Conversely, individuals that have explored less have lower assets. Following the asset protection principle (Clark, 1994), animals that have more assets (more to protect) should play it safe (be less bold and less aggressive) relative to animals that have fewer assets. As noted above, as long as assets do not change appreciably, individuals should maintain a stable behavioral type. That is, as long as differences in assets are maintained, this model can explain three key things about behavioral syndromes: (1) why individuals maintain a consistent behavioral type, (2) why individuals differ in behavioral type, and (3) why boldness and aggressiveness might be positively correlated.

McElreath et al. (2007) noted, however, that the asset protection principle is inherently a negative feedback process that should not maintain differences in assets (or more generally, state). Individuals that have high assets should protect them by not taking risks (i.e., by being shy and unaggressive); however, assuming that being bold or aggressive is necessary to gain assets, over time, being shy and unaggressive should erode assets. In contrast, individuals with low assets should take risks to gain more assets. As long as they survive, their assets should increase. Thus, assets (state)

should converge over time, and if differences in state underlie differences in behavior, then behavior should converge over time. Thus, the Wolf *et al.* (2007a) mechanism can only explain long-term stability of behavioral syndromes if behavior has relatively little effect on state, for example, when individuals immediately (and in many cases, repeatedly) convert new assets into reproduction, rather than accumulate assets (Wolf *et al.*, 2007b).

The problem then is that in many, perhaps most, ecologically relevant situations, behavior should have important effects on state. In that case, to maintain stable differences in state (and thus in behavioral type), we need positive feedback between behavioral type and state. We (Sih, B. Luttbeg, and S. Fogarty) have explored a set of analytical and dynamic programming models to examine effects of positive feedback scenarios on behavioral syndromes. Here, we present a few main, intuitive reasonable points.

Positive feedback can occur if higher state increases the tendency to be bold (and/or aggressive) that maintains high state (and vice versa for lower state and shyness). Some general scenarios that could produce this positive feedback are diagrammed in Fig. 2. One simple mechanism occurs when higher state directly reduces the risk of being bold. For example, higher

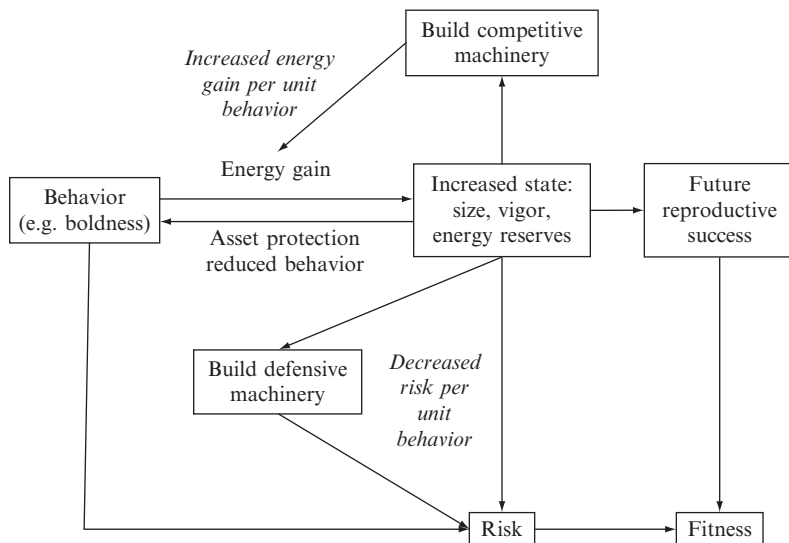FIG. 2. The interplay between negative feedback (via asset protection) that tends to break down consistent behavioral types and several positive feedback loops that tend to maintain consistent behavioral types. The positive feedback loops (in italics) come through higher state either increasing the benefit or decreasing the cost of further bold behavior. See the text for a more detailed description.

state could mean larger size, greater physical vigor, speed, or strength that result in higher escape success. Higher escape success translates into a lower probability of death (lower cost) while being bold. Alternatively, higher state could increase the benefit of being bold. For example, if larger, more vigorous individuals outcompete conspecifics for food, they stand to gain more resources per unit time spent being bold. In either case, the outcome is that high state individuals should continue to be bold, and to thus garner the resources required to maintain high state. To emphasize, this is in contrast to asset protection (Clark, 1994; Wolf *et al*., 2007a) where high state individuals should be less bold (to protect assets) and should thus decline in state over time.

The benefits of high state could either be direct (i.e., high state per se directly affects the benefits and costs of being bold) or be mediated through alterations in morphology (essentially a second state variable besides size, or energy reserves per se). For example, individuals with high-energy reserves could divert energy into building defensive morphologies (e.g., armor, spines), competitive morphologies (e.g., weapons for winning contests), or metabolic morphologies (e.g., larger liver) that increase the benefit or reduce the cost of being bold. Mechanisms that include induced morphological changes are important because they are slow, and often difficult to reverse, and might thus play a particularly strong role in locking an individual into a particular behavioral type.

In the above scenarios, low state individuals are shy or unaggressive as a ''best of a bad job'' strategy. There is much to be gained from being bold or aggressive to gain more resources; however, if the costs of being bold or aggressive while in low state are high enough (e.g., if predation risk or costs of fighting are very high), these individuals might be stuck with playing it safe. In essence, losers stay as losers. Note that, as is often the case in dynamic programming models, the time until a time horizon makes a difference. Early in the season, it may pay for a low state individual to take chances to increase state because there is plenty of time left to reap the benefits of high state. In contrast, with less time remaining, the benefits of being bold or aggressive to increase state are reduced.

In situations where the low state strategy (being shy and unaggressive) yields lower fitness, we might expect natural selection to weed out this strategy. Why should it persist? One simple possibility is that initial differences in state (which persist due to positive feedback mechanisms) are due largely to chance events early in life; that is, much of the observed variation in behavioral type might be environmentally induced rather than genetic. Behavioral types, however, are generally at least moderately heritable (Kendler and Greenspan, 2006; Penke *et al*., 2007; van Oers *et al*., 2005). Maintenance of genetic variation in personality types can be due to

frequency-dependence, or perhaps a mutation–selection balance (if behavioral types are influenced by many genes of small effect each of which can mutate; Penke *et al.*, 2007).

Positive feedback as outlined above can explain the existence and maintenance of two behavioral types—bold versus shy, or aggressive versus unaggressive. While some systems might indeed have a dichotomy of two behavioral types, many systems likely feature a continuous distribution of behavioral types. We suggest that a general mechanism to explain a continuous range of behavioral types is selection favoring behavioral consistency per se. We have termed this "individual status quo" selection (Sih *et al.*, in press)— where individuals do best if they continue to do what they have been doing. One well-known mechanism that can produce this effect is learning and increased skill with experience. In the context of behavioral syndromes, the notion is, for example, that bold individuals might learn, with experience, how to be effective at being bold, which should favor them continuing to be bold, which gives them more experience at being bold, and so on. Alternatively, shy individuals learn how to be shy, and intermediate shy–bold individuals learn how to be intermediate in their behavioral type, and so on.

Stamps (2007) emphasized a fascinating form of "status quo" selection that involves selection favoring individuals maintaining a consistent growth rate (see references in Stamps, 2007). Highly fluctuating growth rates can result in various physiological problems including low-quality tissues and disease (Arendt, 1997; Metcalfe and Monaghan, 2001; Stamps, 2007). In humans, in particular, low growth *in utero* followed by rapid compensatory growth afterward has been associated with subsequent heart disease, type-2 diabetes, and hypertension (Bateson *et al.*, 2004). Differences among individuals in preferred optimal growth rates (and thus in risks taken to achieve those growth rates) could then explain consistent differences in behavioral type.

The central issue addressed by most extant theory on evolution of behavioral syndromes has been the maintenance of within-individual and between-individual consistency in behavioral type. Another key challenge is to explain behavioral correlations across contexts. For example, why are boldness and aggressiveness positively correlated? Stamps (2007) and Wolf *et al.* (2007a) explained this positive correlation by noting that these two behavioral tendencies can represent alternative methods for gaining resources while taking risks. In that case, if selection favors one (e.g., boldness), it should favor the other (aggressiveness). In Stamps' (2007) framework, if an individual has a high growth rate life history, then it should be both bold and aggressive, and vice versa if it has a low growth rate life history. In a model of Wolf *et al.* (2007a), individuals that have high assets should be both shy and unaggressive, and others with low assets should be bold and aggressive. As Stamps (2007) emphasized, this logic holds only if both behavioral tendencies are indeed

associated with high growth rates. If, for example, aggressiveness is not associated with resource gain, then we do not expect aggressiveness and boldness to be positively correlated.

The positive feedback framework championed here provides an additional mechanism explaining why boldness and aggressiveness might be positively correlated. These two behavioral tendencies represent not just two alternative ways of gaining assets, they provide synergistic benefits. Being bold brings in resources that result in increased resource holding potential (RHP). Increased RHP enhances the benefit of being aggressive. In turn, being aggressive and winning contests brings in energy that increases escape success, and then allows individuals to be more bold.

Boldness and aggressiveness are, however, not always significantly correlated. In particular, a few empirical studies suggest that boldness and aggressiveness appear to be positively correlated only in populations experiencing high predation risk (Bell, 2005; Bell and Sih, 2007; Dingemanse *et al.*, 2007). How can theory explain this pattern? Extant theories hinge on some variation of a growth/mortality trade-off. Bold, aggressive individuals collect more resources (and grow faster) but suffer higher risks. If predation risk is indeed high, the synergy between boldness and aggressiveness favors a positive correlation between the two. If, however, risk is low, then the trade-off is no longer important. All individuals should be bold when predators are absent, and if no one has built a defensive morphology, then when predators are present (e.g., in the experiment to evaluate boldness), all individuals should be apparently shy. In that case, there should be little variance among individuals in boldness and thus little opportunity for significant covariance of boldness with aggressiveness. While this theory predicts the observed relationship between risk and the correlation between boldness and aggressiveness, it does not explain the maintenance of variation in boldness in populations with low risk (e.g., Bell, 2005; Bell and Sih, 2007; Dingemanse *et al.*, 2007). To us, this highlights the need for further theoretical work to better explain observed patterns.

Note that many of the positive feedback and individual status quo scenarios discussed above involve a coupling of behavioral type with a physiological mechanism. Individuals exhibit a consistent behavioral type, and different individuals have different behavioral types because their behavioral type is anchored to a less plastic state variable. These less plastic state variables could be aspects of physiology or morphology that we discussed in the section on proximate mechanisms underlying variations in behavioral syndromes. For example, variation in boldness and aggressiveness (and other personality traits associated with resource acquisition under risk) might be connected to variation in metabolic rates that are ultimately

anchored by organ size (e.g., liver, kidney, heart, or lung size) and other relatively stable aspects of metabolic machinery (Biro and Stamps, 2008; Careau *et al.*, 2008). Or, individual differences in sensitivity, choosiness, or learning styles might be associated with variation in relatively stable aspects of brain morphology/physiology or sensory machinery (see Section IV).

Some general integrative insights are as follows: (1) to explain stable differences in behavioral type, we should look for associated proximate mechanisms (e.g., metabolic or sensory machinery) that are less plastic than behavior; (2) these proximate mechanisms should not, however, be viewed simply as fixed constraints that determine behavioral type. Instead, they are part of a feedback loop with behavior where the optimal behavior depends on the proximate mechanism and adaptive plasticity in the proximate mechanism depends on behavior; finally, (3) positive or status quo feedback loops can enhance small, initial differences in individual traits (e.g., in metabolic machinery and associated boldness and aggressiveness) to produce long-term, stable differences in behavioral type. This is a simple, adaptive explanation for why early experiences (early developmental time windows) might be particularly important in shaping both behavioral types and associated proximate mechanisms.

To emphasize, the positive feedback and status quo mechanisms discussed above do not obviate the negative feedback inherent in the asset protection principle. Our view is thus that the maintenance of stable behavioral types emerges from an interplay between asset protection (negative feedback) tending to breakdown both within-individual and between-individual consistency, opposed by positive feedback and status quo mechanisms tending to maintain behavioral syndromes. The next wave of models on adaptive behavioral syndromes should aim to incorporate biologically specific mechanisms including both negative and positive feedbacks.

A final class of explanations for behavioral consistency emphasizes the social benefits of being predictable (Dall *et al.*, 2004; McNamara *et al.*, 2008). In a social context, the problem with being consistent is that predictable individuals run the risk of being exploited. Individuals that are reliably cooperative can be easily cheated, and individuals that are predictably unaggressive doves can lose out to individuals that would otherwise also play dove. When is it beneficial to be predictable? Dall *et al.* (2004) suggest that it can be beneficial to be consistent if consistency allows one to manipulate the behavior of others via credible threats or promises. A threat to be highly aggressive can cause an opponent to back off rather than engage in a highly costly fight. However, this threat should only be taken seriously if it is actually credible, that is, if the individual is indeed reliable. Similarly, a promise to cooperate can induce a partner to trade favors, but only if the promise is reliable.

McNamara *et al*. (2008) modeled the joint evolution of trustworthiness (being reliably cooperative) and social sensitivity about the trustworthiness of others. Socially sensitive individuals gain the benefits of recognizing cooperators from cheaters but accept sampling costs (i.e., the time and energy required to evaluate and remember who is a cooperator and who is a cheater) to gain that social information. Insensitive individuals save on sampling costs, but know less about the trustworthiness of their social partners. In the absence of variation in trustworthiness, there is no need to be socially sensitive. If, however, the population includes both cooperators and cheaters, then this favors the maintenance of variation in social sensitivity. Given that a population has some socially sensitive individuals, this favors the persistence of both cheaters and reliable, trustworthy cooperators. Cheaters exploit insensitive cooperators while reliable cooperators gain the trust of sensitive reciprocators.

Interestingly, the models by Dall *et al*. (2004) and McNamara *et al*. (2008) predict that behavioral consistency should be more common or more developed in species with more social interaction. That is, if the social benefits of predictability are a major factor explaining the evolution of behavioral syndromes, then social species should clearly exhibit ''more personality'' than asocial congeners. In addition, if aggressive, competitive contests play an important role in driving the evolution of behavioral consistency, then again, species where aggressive interactions are more common or important should exhibit more clear-cut behavioral syndromes. This hypothesis can be tested by comparing closely related species or populations that differ in sociality, ideally within a phylogenetic framework.

To date, attempts to explain behavioral syndromes have focused primarily on why individuals exhibit behavioral consistency (why they have a behavioral type) and why different individuals have different behavioral types. Only a few have explicitly addressed why particular behaviors (e.g., boldness and aggressiveness) should be correlated, and even fewer have looked at how either proximate or adaptive factors might explain variation in these behavioral correlations. To us, this final issue is the most exciting one. Why should the correlation between boldness and aggressiveness be stronger under higher predation risk? What explains variation among systems in the stability of behavioral correlations over ontogeny and over evolutionary time? Can we predict *a priori* how males and females should differ in behavioral syndromes in species with different mating systems? Can we predict *a priori* how species with different ecologies or different population genetic structures should differ in their behavioral syndromes? Our hope is that the next decade will see the development of a unified theory of behavioral syndromes that will enhance our understanding on all of these exciting issues.

V.   BEYOND THE USUAL BEHAVIORAL SYNDROMES

To date, much of the ecologically based work on behavioral syndromes has focused on variation in boldness, aggressiveness, or activity per se. These three are often interrelated (Bell, 2005; Huntingford, 1976a; Johnson and Sih, 2005; Riechert and Hedrick, 1993). Boldness is also associated with an individual's exploratory tendency, another frequently invoked personality trait. Relative to low explorers, high explorers are bolder in novel situations, and perhaps generally bolder with risk and more aggressive. The proactive/reactive axis also embodies elements of boldness, aggressiveness, and activity, where proactive individuals tend to be more bold, active, and aggressive than reactive ones (Koolhaas *et al.*, 1999). As noted by Stamps (2007), an ecologically important connection between these behavioral tendencies is that higher values for all of these often results in both higher resource intake and higher mortality risk. That is, they can be viewed as alternative ways of taking risks to gain rewards.

While the above behavioral tendencies reflect major fields of study in behavioral ecology (e.g., predator–prey behavior, competition), other important areas of behavioral ecology (e.g., cooperation, mate choice, parental care, learning) focus on other aspects of behavior that have not yet received much attention from a behavioral syndrome view. We suggest that behavioral consistency likely appears and plays an important role in these other aspects of behavior. Thus, we next discuss several underexamined, potential behavioral syndromes that should benefit from more study. In particular, we focus on syndromes associated with: (1) environmental and social sensitivity, (2) learning, (3) choosiness, (4) mating, (5) parental styles, (6) cooperativeness, and (7) dispersal. En route, we note that many focal issues in behavioral ecology might involve the interplay of multiple behavioral syndromes. For example, mating success might be influenced by behavioral tendencies relative to aggressiveness, boldness, social sensitivity, choosiness, cooperativeness, and parental style.

A.   ENVIRONMENTAL AND SOCIAL SENSITIVITY

The behavioral ecology approach implicitly assumes that animals respond to environmental variation, make adaptive choices (prefer high-quality options over others), and often modify their behavior based on previous experiences. That is, individuals exhibit environmental sensitivity, adaptive choosiness, and learning. Here, we suggest that further study of individual variation in these three traits should prove highly insightful. By environmental sensitivity, we mean the tendency to alter behavior in response to environmental variation. The term "environmental responsiveness" might be more evocative; however,

an existing literature (Boyce and Ellis, 2005; Koolhaas *et al*., 1999) uses the term ''sensitivity.'' In our terminology, sensitivity does not necessarily imply choosiness, learning, or the ability to make intelligent (adaptive) decisions. Learning involves alteration of future behavior following experiences. Thus, learning implies sensitivity to earlier experiences; however, sensitivity does not necessarily result in learning. Choosiness is the tendency to prefer some options over others. It requires sensitivity but could involve innate preferences that need not be learned. We next outline and discuss frameworks for thinking about syndromes of sensitivity, learning, and choosiness.

To organize our thinking about sensitivity, we distinguish three sequential stages in ecologically important tasks, each of which could involve individual variation in sensitivity: (1) first, individuals choose a time and place for a given task; (2) they next choose (or avoid) particular ''partners'' (e.g., social partners or predators or prey); and (3) finally, they respond, often flexibly, to those ''partners.'' For example, predators evaluate (and choose) places to search for prey [optimal patch use (Stephens and Krebs, 1986); here, prey are ''partners''], evaluate different prey items (Sih and Christensen, 2001), and adjust their attack strategy to overcome prey escape and defense tactics (Curio, 1976). Prey do the opposite in each stage. In a mating context, males and females evaluate (and choose) places to search for mating partners, evaluate the quality of different potential mates, and then adjust courtship behavior in response to signals from a particular potential mate. In a cooperative situation, theory assumes that individuals can distinguish between cooperators and defectors and behave accordingly (McNamara *et al*., 2008). In a contest situation or a dominance hierarchy, individuals are assumed to evaluate relative RHP and/or dominance of different contestants (Maynard Smith, 1982), and to adjust their behavior as a contest unfolds (Riechert and Hammerstein, 1983). In each of these tasks and stages, individuals likely differ in their sensitivity.

The literature on proactive/reactive coping styles emphasizes individual variation in environmental sensitivity (Benus *et al*., 1987, 1990; Koolhaas *et al*., 1999). Reactive individuals are highly sensitive to changes in their environment. In contrast, proactive individuals follow set behavioral routines and are relatively insensitive to environmental changes. These differences in coping style are associated with genetically based differences in neuroendocrine profiles (Koolhaas *et al*., 1999) and have ecological and evolutionary implications. Notably, the differences in sensitivity are also related to differences in response to environmental challenges. Sensitive, reactive individuals tend to be more fearful, whereas proactive individuals tend to be more bold and aggressive. Proactive individuals thus tend to dominate in stable environments; however, because proactive individuals are insensitive to environmental change, they do poorly in fluctuating

environments (Benus *et al*., 1987, 1991; Dingemanse *et al*., 2004). Coping styles have been studied in some detail in a range of animals including laboratory rodents (Benus *et al*., 1987, 1991; Koolhaas *et al*., 1999), farm animals (Hessing *et al*., 1993), great tits (Drent *et al*., 2003; Verbeek *et al*., 1994, 1996), rainbow trout (Overli *et al*., 2007), and primates (Capitanio *et al*., 1998; Suomi, 1987).

A parallel literature in humans (Aron, 1996; Boyce and Ellis, 2005; Jawer, 2005) notes that variation in sensitivity might be associated with variation in habitat and job choice (highly sensitive people avoid highly stimulating situations), in fine-scale behavior (e.g., preferred volume level while listening to music), in other aspects of personality (e.g., creativity), and in mental and physical well-being (e.g., extreme sensitivity might be associated with depression, migraine headaches, and suppressed immune systems).

Although the recent growth of interest in animal personality has brought the literature on coping styles to the attention of behavioral ecologists, to date, with the exception of the work on great tits, few studies in behavioral ecology have quantified either individual variation in environmental or social sensitivity, or its effect on behavior or performance. One notable exception is the work by Patricelli *et al.* (2002, 2006) on bowerbirds. Male bowerbirds display for females in front of elaborate bowers. Patricelli *et al.* (2002, 2006) used a robot female that they could control to evaluate the relative ability of different males to adjust their courtship intensity to signals from the female. They found that males that displayed very intensely regardless of signals of interest (or not) from females tended to scare females away. Most notably, their quantitative analysis revealed that a large proportion of the variance in male mating success could be explained by the male's sensitivity (and adjustment) to female signals (Patricelli *et al*., 2002, 2006); that is, social sensitivity could play a large role in sexual selection.

A second example, again associated with mating success, involves hyper-aggressive males in water striders (Sih and Watters, 2005). Males show individual variation in their response to females, males, and male–female pairs. Ideally, males should attempt to mate with females, but should not attempt to mate with males, and have almost no success at separating pairs in order to take over a female. Most males are sensitive to the nature of other water striders; that is, they attempt to mate with females, but not with males or pairs; however, some are hyperaggressive—they expend a great deal of effort toward trying to mate forcibly with not just females, but also males or pairs. Quantitative analyses showed that hyperaggressiveness in water striders has important negative effects on mating success. Does it exist in other species? Our view is that in numerous seminars over the years,

we have heard anecdotes and often seen photographs of males attempting to mate (and in some cases, mating) with inappropriate partners (e.g., with males, females of other species, dead females, inanimate objects that, in some sense, resemble conspecific females). Our suggestion is that it would be useful to quantify individual variation in this aspect of social sensitivity in more systems.

In both of the above examples, social sensitivity was associated with what can be termed ''social skill,'' the ability to adjust behavior adaptively to environmental variation. In the context of sexual selection, following the three-stage view outlined earlier, mating success might depend on individual variation in skill in: choosing the right places and times to search for mates, efficient mate choice (e.g., Sih and Watters, 2005), and courtship and response to potential mates (e.g., Patricelli *et al*., 2002, 2006). Most studies of sexual selection focus on relatively static traits (e.g., male size, color, ornaments). Here, we hypothesize that unexplained variation in mating success might be due to individual variation in behavioral tendencies that underlie variation in multiple aspects of social skill.

In each of the above mating examples, the emphasis was on one aspect of social sensitivity. In the syndrome context, an interesting issue is whether social sensitivity carries over across different tasks and contexts. For example: (1) within one stage of the mating context, for example, the mate choice stage, is ability to distinguish the correct species correlated to ability to distinguish the correct gender, and/or the ability to evaluate variation in mate quality within the correct gender? (2) across stages, though still all within the mating context, is sensitivity within the mate choice stage correlated to environmental sensitivity in choosing the time or place to search for mates, for example, sensitivity in choosing among social situations that might differ in density, sex ratio, and/or the mix of behavioral types present? Or, (3) is sensitivity in the mate choice stage correlated to sensitivity to subtle signals in the male–female interplay that results in successful mating? (4) Going beyond mating, is sensitivity in the mating context correlated to social sensitivity in other contexts, for example,, in partner choice and adjustments to social situations or partners in the context of cooperation or competition? And, (5) going beyond social situations, is social sensitivity in one or more social situations correlated to sensitivity relative to other fitness-related options, for example, habitat choice or diet choice? Finally, is sensitivity correlated to other aspects of personality? The coping style literature and the work on water striders suggest that sensitivity is negatively related to boldness and aggressiveness, but is this a general feature of nature?

Should we expect to generally see positive or negative correlations between aspects of sensitivity? If individuals vary along a general sensitivity index, then sensitivity should be positively correlated across different tasks

or situations. Alternatively, if sensitivity draws on a finite pool of attention (Dukas, 1998), then we might expect negative correlations between sensitivity in different tasks; for example, sensitivity toward potential mates might draw attention away from, and thus reduce sensitivity toward food or predators.

In addition, although our general syndrome-based expectation might be that individuals that are more sensitive than others to the presence of conspecifics per se should also be relatively sensitive to differences among conspecifics in mate quality, this does not appear to hold for hyperaggressive individuals. They are highly sensitive to the presence of conspecifics but insensitive to variations in mate quality; they quickly orient toward, approach and attempt to mate with all conspecifics—male or female. Thus, variation in hyperaggressiveness can generate a negative correlation between sensitivity in different stages of the mating sequence.

How might a sensitivity syndrome influence correlations between other behavioral axes? Because the response of a sensitive individual can either be fearful or aggressive, variation in sensitivity can generate either a positive or a negative correlation between boldness and aggressiveness. The proactive-reactive literature on coping styles suggests that sensitive individuals are generally fearful; that is, they are shy and unaggressive. Variation in sensitivity then contributes to a positive correlation between boldness and aggressiveness. If, however, sensitive individuals respond by being aggressive (as opposed to insensitive individuals ignoring conspecifics), then the result should be a negative correlation between boldness and aggressiveness. Insensitive individuals ignore conspecifics (i.e., they are unaggressive) and predators (i.e., they are bold). Bell and Sih (2007) found that in stickleback fish, these bold, unaggressive animals tend to suffer high predation.

In the above examples involving mating behavior, as well as in the literature on coping styles, there is ample evidence that individual variation in sensitivity influences components of fitness. A generality might be that extremes in sensitivity (extremely sensitive people, hyperaggressive water strider males) are selected against (but see Boyce and Ellis, 2005), but that for an intermediate range, selection on sensitivity depends on environmental conditions and environmental stability, generating stabilizing selection on sensitivity. In addition, social sensitivity might be under frequency-dependent selection. Finally, a key to understanding selection on sensitivity should be understanding how it relates to an overall, potentially broad behavioral syndrome.

Our overall view is that enough examples exist (particularly in the coping styles literature) to suggest that individual variation in environmental and social sensitivity is common, potentially quite important and worthy of

further study. In particular, from the behavioral syndrome view, we suggest the need for more study on correlations among different aspects of sensitivity and between sensitivity and other aspects of behavioral type (e.g., boldness, aggressiveness, and cooperativeness).

B. LEARNING

A major field in animal behavior that is related to sensitivity and has also not been well explored from a behavioral syndromes view involves individual differences in learning. For example, if individuals that are good at learning about one type of task are also good at learning about others, then there could be an important carryover across learning tasks. On the other hand, if there are trade-offs between performance on different learning tasks, then what is gained by learning to solve one problem could come at the expense of learning something else. Another question is whether individual learning styles form part of an individual's overall behavioral type: particularly exploratory individuals might have more opportunities to experience stimuli and to learn from them. Both of these questions are discussed below.

If individual differences in learning and memory are correlated across contexts, then individuals that are good at learning about how to avoid predators, for example, might also be good at remembering where they stored food last year, or what are the reliable cues indicating a suitable nest site. On the other hand, if there are costs of learning, then what an individual has learned about one thing might come at the expense of something else.

There are several different ways in which correlated individual differences in learning could be manifested. For example, if general process theory is correct (Shettleworth, 1998), then individual differences in the mechanisms underlying associative learning will generate consistent individual differences in performance on associative learning. Alternatively, there might be correlated individual differences in types of learning (operant and classical conditioning, habituation, sensitization, imprinting, and song learning), all of which involve different ecological contexts, cognitive, and perceptual systems. On the other hand, there might be correlated individual differences in learning that involve the same perceptual systems; for example, individuals that are good at learning how to associate a visual signal with food are also good at associating visual signals with predators, or mates. Finally, there might be correlated individual differences in learning about specific ecological tasks, for example, individuals that are good at associating a chemical cue with the presence of a predator also have good spatial memory about the location of particularly dangerous areas of habitat.

Despite the rich literature on the mechanisms of learning, we know relatively little about correlated learning tasks in ecologically relevant contexts. A relevant body of literature is concerned with whether there is such a thing as general cognitive ability, which improves individual performance on a variety of learning tasks. If such a general learning syndrome exists, then individual differences in learning are really reflecting differences in "intelligence," rather than differences in motivation or exploration. For example, studies on mice have shown that up to 38% of the variation in performance on a battery of learning tests assessing a variety of different cognitive tasks can be attributed to general cognitive ability, even when differences in exploration are accounted for (Galsworthy et al., 2002; Matzel et al., 2003, 2006).

From a behavioral ecological point of view, the key question is whether there are carryovers or trade-offs between abilities on different ecological tasks, not necessarily whether that reflects something about general cognitive ability. Despite the obvious ecological importance of such carryovers, correlated differences in learning have rarely been tackled from an ecological or evolutionary point of view. The most intuitive, adaptive expectation is that natural selection should favor general intelligence, but the growing literature on cognitive ecology is showing that animals are especially clever about the most ecologically pertinent challenges (Healy and Braithwaite, 2000; Real, 1993; Shettleworth, 1998). Measuring individual differences in learning in several different contexts across a wide range of ecologically relevant challenges is an obvious priority for future work.

Implicit in the argument against general intelligence is that there are costs of learning (Stephens, 1991) that could impose trade-offs between different forms of learning. For example, learning a new association of color with food caused bumblebees to perform errors in a previously learned task (interference) (Worden et al., 2005). Similarly, flies that had been selected for learning ability showed a trade-off between short- and long-term memory (Mery et al., 2007), a cost of long-term memory in terms of stress resistance (Mery and Kawecki, 2005), productivity (egg laying rate) when subjected to nutritional stress (Mery and Kawecki, 2004), and larval competitive ability (Mery and Kawecki, 2003).

Familiar behavioral axes such as shy–bold or aggressive–nonaggressive might also be correlated with differences in learning. For example, although proactive individuals perform consistently better than reactive individuals in a standard task, when faced with a change in the environment, reactive mice and great tits are more likely to change their search patterns and to adaptively modulate their behavior than proactive individuals (Benus et al., 1987; Verbeek et al., 1994). Such behavioral flexibility is not due to an intrinsic difference in learning ability between the two types of individuals because both types of individuals are equally capable of learning the task (Benus

et al., 1987, 1990). Instead, the difference reflects a difference in the amount of exploration between the two groups; the reactive individuals acquire information about the environment that they use in subsequent behavior.

Surprisingly few other studies have asked whether individual differences in learning reflect a personality "type." Individual variation in innovation, or adopting a new behavior pattern when the environment changes, has been documented in several different species (Boogert *et al.*, 2006; Godin *et al.*, 2005; Pfeffer *et al.*, 2002; Reader, 2003), but we know little about whether variation in innovation reflects general learning ability, sociality, boldness, or state dependence [reviewed in Laland and Reader (1999b)]. Some studies have suggested that innovators are likely to be those at the outskirts of social groups (Kummer and Goodall, 1985) and experimental work on guppies has shown that while state-dependent factors such as sex and hunger level are partly responsible for foraging innovations, some individuals are consistently more likely to innovate than others (Laland and Reader, 1999a,b).

Finally, in systems with social learning, there appear to be individual differences in tendency to rely on individual-based learning (using personal, private information) as opposed to social learning (using public information (Galef and Giraldeau, 2001; Marchetti and Drent, 2000; Valone, 2007). Some of the variation in tendency to learn from others is associated with age; for example in mate copying, younger, inexperienced females tend to copy the mate preferences of older females rather than rely on their own assessments of mate quality (Amlacher and Dugatkin, 2005; Dugatkin and Godin, 1993). However, public versus private learning might also be related to behavioral type. An obvious hypothesis that, to our knowledge, has not been tested is whether individual variation in sociability or affiliativeness is positively correlated to tendency to rely on social learning. Presumably, more sociable individuals will, on average, be exposed to more opportunities for social learning. The question here is, even with equal opportunities for social learning, do more sociable individuals tend to rely more (than less sociable individuals) on public information, as opposed to personal experiences? Alternatively, the producer–scrounger literature suggests that more aggressive, dominant individuals might rely relatively more on public information (generated by subordinates) about resources (Liker and Barta, 2002).

A strong reliance on public information (e.g., copying) can generate rapid swings in group preferences ("fads") that can strongly favor particular types (Gladwell, 2000). This can have important effects on evolutionary dynamics (Kirkpatrick and Dugatkin, 1994). In addition, the relative use of public versus private information can have major impacts on the dynamics of how social groups respond to changing environments (Valone, 2007), a key issue in a heavily human-altered modern world. If social learning style is correlated to personality, then selection on behavioral type influences social learning

and vice versa. Thus, an important additional insight that can come from the behavioral syndrome view involves the dynamics of the joint evolution and ontogenetic development of social learning and personality.

C. Choosiness

Choosiness is the strength of preference for some options over others. If individuals set a threshold criterion where options are only accepted if they are above the threshold in quality, then choosy individuals have a higher threshold. If options are evaluated sequentially, being choosy often involves evaluating more options before making a choice. Choice has been studied in many isolated contexts, for example, diet choice (Sih and Christensen, 2001), mate choice (Andersson and Simmons, 2006), or habitat choice (Stamps et al., 2005). Although studies of mate choice often assume that a given individual has fixed preferences, in other contexts (e.g., diet choice), the usual notion is that individuals alter their choosiness depending on the magnitude of differences in quality between different options, and on the availability of high-quality options (Crowley et al., 1991; Stephens and Krebs, 1986). For example, in a simple scenario with only two types of options, A and B, where A is better than B, individuals should be more choosy if A is much better than B, and if A is highly abundant. In contrast, if A is only a bit better than B, or if A is scarce, then the same individuals should not be as choosy, they should accept either A or B.

It is important to note the distinction between variation in choosiness and variation in preference (Jennions and Petrie, 1997). For the latter, females are known to vary, for example, in what sorts of male traits they prefer (Brooks and Endler, 2001; Cummings and Mollaghan, 2006; Forstmeier and Birkhead, 2004; Jang and Greenfield, 2000; Morris et al., 2003). Less is known about variation among females in choosiness per se, that is, in the *strength* of their preference (but see Reinhold et al., 2002).

A choosiness syndrome can then be evaluated either within a given context or across contexts. In the diet choice context, for example, if the individual foragers that are most choosy when food is abundant are also the most choosy when food is scarce, then the result is a choosiness syndrome. In the diet choice literature, although hundreds of studies have documented average preferences and how mean choosiness varies with the abundance of different prey types (reviewed in Sih and Christensen, 2001), we know of no studies that explicitly tested for consistency in choosiness. In humans, we have the sense that some people are consistently choosier than others in what they are willing to eat, but we know of no data on this issue.

In a mating context, a classic method for evaluating female choice involves offering the focal female an opportunity to interact with two males (e.g., on opposite sides of a partitioned aquarium). The usual goal

is to test whether, on average, females prefer particular male phenotypes (e.g., larger males or more colorful males). Our impression is that a typical result might be to find that 16 of 20 females prefer the larger male, so the conclusion is that females prefer larger males. However, in many cases, the investigator might ''toss out'' females that showed no significant preference, and among the 20 that showed a preference, they varied substantially in the strength of their preference. Some strongly preferred the larger male, whereas others exhibited only a weak preference for the larger male. The point here is that substantial variation might exist in female choosiness; however, to date, the field generally has not focused on this variation. In the syndrome context, we are interested in whether females are repeatable in their choosiness across trials in the same basic situation, and whether they are consistent in their mate choosiness across different situations (e.g., different types of focal male traits or different male abundances).

Across contexts, the issue is whether the same individuals that are choosier than others about their diets are also relatively choosy about their mates (and about other social partners, about aspects of habitat use etc). In humans, we know people who are particularly choosy about their diets and about their wines, or about their music, movies, or TV shows, or about their brands of clothing or electronic equipment, or about their mating partners. The question is: ''Is choosiness correlated across these different situations?'' Optimality theory identifies an optimal degree of choosiness in any given situation. Just as behavioral correlations in the shy–bold or aggressive–unaggressive syndromes can spillover to be associated with suboptimal behavior, a choosiness syndrome can result in suboptimal behavior. A behavioral syndrome hypothesis is that, if a choosiness syndrome exists, an individual that is generally very choosy across many situations will likely be too choosy in some situations.

D. MATING BEHAVIOR

Perhaps the most often studied subject in behavioral ecology is mating behavior and sexual selection. Despite the fact that behavioral tendencies such as aggressiveness and social sensitivity clearly influence mating tactics and mating success, to date, few studies have integrated the behavioral syndrome approach into studies of mating and sexual selection. That is, relatively few studies have quantified whether individual variation in mating tactics is correlated with behavior in other contexts.

In many systems, males clearly exhibit individual variation in mating tactics. In some cases, males have alternative mating morphs, often involving large territorial males versus smaller, sneaky males (Emlen, 1997; Shuster, 1989; Sinervo and Lively, 1996; Watters, 2005). Although it

seems obvious that males with very different morphologies (e.g., size, ornamentation) will also likely differ in their overall behavioral type (as expressed in various nonmating contexts—foraging, antipredator, dispersal etc), few have actually quantified how these alternative male types differ in behavior outside of the mating context. In other cases, males within a given population differ in mating tactics, but without major, obvious differences in morphology. For example, in the search phase, males can either be territorial (or simply, site-faithful) or actively explore a large area across many territories. When females are encountered, males can either display to them, be sneaky, or attempt to coerce females to mate (Magellan and Magurran, 2007; Reichard *et al*., 2007). In socially monogamous systems, males can either be faithful to a female (and often, provide parental care) or be a philanderer who devotes considerable effort toward gaining extrapair copulations (Westneat and Sargent, 1996).

In turn, other studies have documented individual variation among females in their preferences (Brooks and Endler, 2001; Cummings and Mollaghan, 2006; Forstmeier and Birkhead, 2004; Jang and Greenfield, 2000; Morris *et al*., 2003). For example, some females like symmetrical males while others like asymmetrical ones (Morris *et al*., 2006). Some females copy the preferences of other females while others rely on their own assessment of males. The obvious syndrome question is whether there is something else distinctive about females with different preferences, apart from obvious attributes such as size (Morris *et al*., 2006) or age. In the particular situation where females engage in sexual cannibalism, individual females differ in their tendency to attack males versus mate with them (Johnson and Sih, 2005).

In the syndrome context, the question is: Do individual differences in mating tactics reflect differences in overall behavioral type? Are mating tactics part of a behavioral syndrome? If so, then this potentially introduces another form of interaction or even conflict between natural selection and sexual selection. For ornaments, observed traits are thought to be shaped by a trade-off between sexual selection favoring exaggeration of the ornament versus natural selection preventing further elaboration (Endler, 1995; Kokko *et al*., 2006). For behavior, a similar trade-off might often exist where sexual selection favors more highly active, aggressive, or bold behavioral types than is favored by natural selection in other contexts (e.g., in a parental care context or when predators are present). That is, selection favoring high aggressiveness in male–male competition for access to females might spillover to cause apparently inappropriate parental care behavior (Wingfield *et al*., 1990), or inappropriately bold responses to predation risk. Of course, conversely, it is also possible that selection favoring high aggressiveness in nonmating contexts could spillover to

cause inappropriately aggressive behavior toward mates. An example of the latter involves sexual cannibalism in fishing spiders where selection favoring high voracity in a nonmating context (in a food-limited environment) appears to have spilled over to contribute to excess sexual cannibalism (Johnson and Sih, 2005). Overall, a full understanding of selection on mating tactics (male and female) might require knowing how these tactics are part of a broader behavioral syndrome.

If mating tactics are part of a broader behavioral syndrome, then this suggests the possibility of adaptive female choice based on the male's behavioral type. Theory predicts that females should prefer male traits that are indicators that the male can provide either direct benefits or good genes. In humans, mate choice is often based not just on resources or good looks, but on personality. The notion that the same idea might apply in other animals has rarely been studied explicitly. Our suggestion here is that there are several ways that a male's behavioral type (e.g., as revealed by his mating tactics or displays) might provide useful indicators for guiding female choice.

One possibility is female choice for good genes, where the male's behavioral type [which is typically heritable (Penke et al., 2007; Reale et al., 2007; van Oers et al., 2005)] provides an ecological or social mechanism for why some male genotypes might enhance offspring fitness. By definition, a male's behavioral type provides information on how he copes with various environmental pressures. His boldness and aggressiveness influence his style and ability to cope with food limitation, competition, and predation risk. Boldness might also be associated with dispersal tendencies (Dingemanse et al., 2003; Fraser et al., 2001). Social sensitivity in mating displays might be correlated to social sensitivity in other contexts. If conditions are likely to be stable across generations, a female can prefer males that have a behavioral type that worked well in the present generation. If she can determine offspring environments [e.g., via maternally controlled habitat selection that might be followed by a tendency for offspring to prefer that habitat throughout their lives (Davis and Stamps, 2004)], then she can use her mate choice to provide her offspring with a suitable, adaptive behavioral type. Similarly, if offspring are likely to disperse on their own into new, different conditions, in principle, a female could choose a male with a behavioral type that fits the anticipated new conditions. Finally, if her offspring are likely to face unpredictable conditions, she could choose an environmentally sensitive male who can cope well with changing environments. Or, if success in social interactions inherently requires social sensitivity, then females might generally prefer males whose displays indicate high social sensitivity (e.g., Patricelli et al., 2002, 2006). This could, in part, explain the human female preference for males that are funny (Bressler and Balshine, 2006).

Alternatively, female choice might be for direct benefits. The benefit of preferring highly aggressive males that have won male–male contests can either derive from immediate resources provided by those males, or from future benefits associated with males that can provide a superior territory. In some cases, females prefer less aggressive males, perhaps because they are less likely to engage in costly sexual coercion that either wastes the female's time and energy, or can even injure females (Ophir *et al.*, 2005). Most interestingly, females might use the male's contest behavior or courtship displays to evaluate his future parental care or cooperation (variation in parental care is discussed below). This makes sense if his premating behavior is an honest indicator of his postmating behavior. An issue of general importance is: when a male ''promises'' to provide future benefits, why should he keep that promise? If males promise to provide good parental care, but then often renege on that promise, females should not trust the promise, and males should then not even bother to make the promise; that is, without honest signals, the system breaks down. The usual idea is that honesty is enforced by high signal costs (Zahavi, 1975). If the signal is costly (a handicap), then male production of the signal should be proportional to their ability to handle the cost. An alternative possibility is that the signal is an index—if there is a strong correlation between the male's signal and either his direct (possibly, deferred) benefits, or his genes (LeBas *et al.*, 2003; McGlothlin *et al.*, 2005). A tight behavioral syndrome possibly provides that correlation. If there is a negative correlation between a male's aggressiveness and paternal care (Wingfield *et al.*, 1990), then a male's aggressiveness during male–male competition or courtship displays might be a useful indicator of his future cooperation in parental care.

E. PARENTAL STYLES

How parents behave toward their offspring can strongly affect the fitness of their offspring. Still, within a given species, it is often reported that individuals differ in how they parent. Such individual variation might reflect state-dependent differences in sex, age, condition, or in the trade-off between current versus future reproduction. However, some individual birds consistently provide more parental care than others, that is, individual differences are repeatable (Schwagmeyer and Mock, 2003). A relatively unexplored area is whether such individual differences in parental behavior reflect part of an overall behavioral type.

For example, Budaev *et al.* (1999) found that parental convict cichlids differed in how they behaved toward their offspring, and those differences were correlated with behavior in other contexts. Individuals that provided more parental care (food provisioning) were also more exploratory and less

aggressive (Budaev *et al.*, 1999). Other studies have also reported evidence of a trade-off between parental behavior and aggression. One of the best examples of an aggressive spillover, in fact, is the image of a male pumped up on testosterone who does not behave as a good dad (Ketterson *et al.*, 1992; Nunes *et al.*, 2000; Ros *et al.*, 2004; Van Duyse *et al.*, 2000; Veiga *et al.*, 2002).

Another well-studied trade-off is between parental care and mate attraction: males that spend more time attracting mates or seeking EPCs provide less parental care (Bjelvenmark and Forsgren, 2003; Clark and Galef, 1999; De Ridder *et al.*, 2000; Duckworth *et al.*, 2003; Kokko, 1998; Magrath and Elgar, 1997; Magrath and Komdeur, 2003; Mitchell *et al.*, 2007; Peters, 2002; Qvarnstrom, 1997; Smith, 1995). There are at least two possible mechanisms that could produce this negative relationship. More ornamented males might provide less parental care because they can achieve relatively greater reproductive success from seeking EPCs [trade-off (Magrath and Komdeur, 2003)]. Or, females paired with attractive males provide more parental care in order to prevent the desertion of their attractive mates [differential allocation (Kokko, 1998)], and this, in turn, allows attractive males to provide less parental care.

An alternative view, however, is that a positive relationship between ornament size and parental behavior could be adaptive if females use a male's ornament as an indicator of his future behavior as a parent ("the good parent" hypothesis) (Pampoulie *et al.*, 2004). Female mate choice for ornamented males could really therefore reflect choice of a package of male traits that includes parental care (Schwagmeyer and Mock, 2003). This hypothesis has been formalized as the "sealed bid model," where individuals behave as if they have committed to a certain level of parental care at the outset and do not modify their care in response to the partner's effort (Schwagmeyer and Mock, 2003). This model is in contrast to the negotiation model, where individuals adjust their parental care facultatively in response to the efforts of their mate (McNamara *et al.*, 1999). The sealed bid model is broadly consistent with a behavioral syndrome: males vary in the amount of paternal care they provide, males are consistent across broods or seasons, and a male's parental type is indicated by an ornamental trait. However, the negotiation model also raises interesting syndrome questions related to individual variation in cooperation and social sensitivity, as discussed above.

And what about females? Do females differ in the quality of parental care they provide to their offspring? Several studies have shown that male birds are more consistent in their parental behavior relative to females. For example, in several birds, male feeding rate is repeatable and heritable, whereas females are not repeatable (Freeman-Gallant and Rothstein, 1999; MacColl and Hatchwell, 2003; Nakagawa *et al.*, 2007; Schwagmeyer and Mock, 2003). This finding has been interpreted as reflecting greater responsiveness on the part of the female to the needs of her offspring and the

behavior of her partner. On the other hand, female mice that had been artificially selected to be aggressive (low attack latency) actually engaged in more maternal behaviors such as nursing, licking, and grooming of her pups (Benus and Rondigs, 1996).

So do individual differences in parental style really matter? A fascinating recent line of research on the mechanisms of parental effects in rats offers a resounding "yes" to this question. Like the mice mentioned above, mothering rats differ in the amount of arched back nursing and licking and grooming behavior they perform. Pups that receive more licking and grooming are less fearful and less stress responsive than pups from less attentive mothers (Storey et al., 2006). Differences in the offspring of high licking and grooming versus low licking and grooming mothers emerged early in life and were long term (but reversible) (Weaver et al., 2004). In fact, the offspring of high licking and grooming mothers ended up becoming high licking and grooming mothers themselves (Champagne and Meaney, 2006). Using cross fostering, Meaney et al. have convincingly demonstrated that the inheritance of parental styles is epigenetic and occurs via DNA methylation of the glucocorticoid receptor.

There is converging evidence that something similar occurs in rhesus monkeys: some female monkeys are more "abusive" than others, as judged by differences in rates of maternal rejection and grooming. Variation among mothers influences their offspring's anxiety and fearfulness, eventually influencing the way these offspring behave as parents (Maestripieri et al., 2006). Cross fostering experiments have shown that these effects are also nongenetic, probably mediated by serotonergic transmission (Maestripieri et al., 2007).

Our understanding of the mechanisms linking the effects of mothers on their offspring has far outpaced our understanding of the evolutionary forces that could maintain variation among female rats and monkeys in maternal behaviors. One hypothesis is that it is adaptive: perhaps stressed, that is, low licking and grooming mothers "program" their kids to respond to adversity (Diorio and Meaney, 2007). Therefore, low licking and grooming mothers are favored in stressful environments. Alternatively, or in addition, perhaps a female's maternal style is part of her overall behavioral type; perhaps mothers that engage in more abusive behavior as parents are also distinctive in other respects, which outweigh the costs of impaired maternal performance (Bennett et al., 2002; Champoux et al., 2002).

F. COOPERATIVENESS

Cooperation is the subject of a great deal of behavioral study in both behavioral ecology and human psychology. Here, we consider the possible role of behavioral syndromes in the study of cooperation. Simple theory on

cooperation examines individuals that are either cooperators or defectors (or perhaps, follow a tit-for-tat, TFT, strategy). Few studies, however, have actually quantified individual variation in cooperativeness (Bergmuller *et al.*, 2007; Wright, 2007). In the syndrome context, a key question is: do individual differences in tendency to cooperate carry over across multiple contexts? Are the same individuals cooperative or even altruistic in social foraging, group vigilance, resource sharing, and cooperative breeding or shared parental care? In some situations, our general view is that individuals cooperate due to kin selection (Hamilton, 1964), whereas in others, the notion is that cooperation reflects reciprocal altruism (Trivers, 1971). Does frequent cooperation with kin spillover to result in excess cooperation with nonkin or vice versa?

Of course, theory does not assume that individuals should be unconditionally cooperative. Instead, if an individual is highly cooperative, then others should exploit that tendency by engaging in subtle cheating. This, in turn, favors the evolution of social sensitivity [to evaluate the trustworthiness of potential social partners (McNamara *et al.*, 2008)]. Put another way, analyses of cooperation are usually best thought of as an interplay between cooperation and conflict or deception (Dugatkin and Reeve, 1998).

This interplay suggests that behavior in cooperative scenarios might often reflect the intersection of several behavioral tendencies. Consider, for example, predator inspection. In several species of schooling fish (e.g., guppies, sticklebacks), individuals leave the school and approach predators apparently to gain information about the risk posed by the predator (Pitcher, 1992). Most interestingly, individuals often inspect in pairs. Several studies have examined whether these pairs might be reciprocal altruists where the lead individual (the one that is closer to the predator) at any given time is being altruistic—taking greater risks while generating benefits (information) for both members of the pair (Dugatkin and Alfieri, 1991; Milinski, 1987). The altruistic act is reciprocated repeatedly in one predator inspection bout when individuals take turns being the lead individual. In particular, investigators have been interested in whether the dynamics of predator inspection fit a simple TFT model, where individuals cooperate as long as their partner cooperates (inspects), but defect (stop inspecting) when the partner defects. In that context, a given individual's behavior during predator inspection could depend on its: (1) cooperative tendency, (2) schooling tendency, (3) social sensitivity, and also (4) boldness per se. Boldness can be measured by the individual's tendency to do predator inspection even when alone. Schooling tendency can be assayed by looking at group size preferences when offered a choice between groups of different size. Social sensitivity has at least two elements—individuals should reduce their tendency to inspect if the partner has recently defected, but also increase their tendency to inspect if the partner resumes being cooperative.

Cooperativeness should be assessed after accounting statistically for these other behavioral tendencies. Overall behavior and interaction dynamics should depend on the interplay between these different behavioral tendencies for both individuals. Later in this chapter, we discuss quantitative methods for examining multiple behavioral tendencies in more detail.

G. DISPERSAL

Dispersal behavior can have critical effects on various ecological and evolutionary processes (Clobert *et al.*, 2001). In particular, in modern habitats that are often fragmented, there is considerable interest in how dispersal and movements among patches affect metapopulation and metacommunity dynamics (Holyoak *et al.*, 2005), as well as species invasions. Most theory in these aspects of spatial ecology emphasizes the importance of the amount and pattern of dispersal; however, few include much, if any, mechanistic details on the biology of dispersal. One potentially very important factor is individual variation in dispersal behavior (Benard and McCauley, 2008) and its relationship to a general behavioral type; that is, how dispersal is part of an overall behavioral syndrome. The dispersal process involves three stages each of which can be influenced by individual variation in behavioral type (Baguette and Van Dyck, 2007): (1) leaving a source patch, (2) moving through a matrix of unsuitable habitat, and (3) settling into a new patch.

The relationship between behavioral type and the tendency to leave a source patch depends on the ecological and social pressures involved in inducing dispersal. If dispersal is not a direct response to stressful conditions in the source patch, but is instead active and "voluntary," then dispersers might tend to be the more bold individuals, individuals with less fear of the unknown. Even when all or most individuals have strong incentives to leave, if the costs of dispersal are also high, we still might expect dispersers to be more bold than average. Indeed, some studies have found that dispersers tend to be more bold or exploratory than average (Dingemanse *et al.*, 2003; Fraser *et al.*, 2001; Rehage and Sih, 2004; Whybrow, 2005). In contrast, if individuals are driven to disperse by high predation risk, then it might be the more timid ones that opt to leave, dispersers might tend to be the less bold (more fearful) individuals. Alternatively, if dispersal is induced by interference competition and aggression, then dispersers might be the unaggressive, subordinate individuals that are driven out by more aggressive dominants. On the other hand, in marmots, it is the most aggressive (disagreeable) individuals that are forced to leave the social group (Armitage, 1986). Finally, even without aggression, at high density, asocial individuals (that avoid conspecifics) might be overrepresented among the dispersers (Cote and Clobert, 2007). The main points are

that we expect nonrandom dispersal by behavioral type to be common and that the particular behavioral type that disperses more should be predictable given the ecological or social scenario.

Recent work on the spread of western bluebirds in the United States highlights many of these points. As the range of Western bluebirds has expanded, they have displaced native Mountain bluebirds. Duckworth and Badyaev (2007) showed that aggressiveness is heritable in Western bluebirds and it is the especially aggressive Western bluebirds which disperse into new areas, outcompeting the Mountain bluebirds. However, over generations, the aggressiveness of Western bluebirds in their new range decreased rapidly in an evolutionary response to selection for reduced aggressiveness, probably because more aggressive males provide less parental care and therefore have lower reproductive success (Duckworth, 2006). This study shows that different behavioral types are favored at different stages of invasion: the aggressive Western bluebirds disperse, while less aggressive individuals are favored after establishment.

Ecological selection pressures in the matrix habitat between patches can also represent a strong, selective filter that favors some behavioral types over others. And, settlement and successful establishment in a new patch can depend on behavioral type. Highly social individuals should be attracted to conspecifics and should thus be less likely to colonize empty habitats, as compared to asocial individuals. Asocial individuals might thus be particularly important in metapopulation dynamics and the spread of invasions. Finally, after settling, the new disperser's behavioral type could play an important role in determining its establishment and impact on the colonized community. In order to establish in a new habitat, dispersers typically need to cope with novel selection pressures—often, new predators, competitors, or prey. The ability to cope with new challenges might require problem solving that is associated with low neophobia. Interestingly, broad, comparative analyses of birds suggest that invasive species tend to be non-neophobic species that often discover new foraging innovations (Sol *et al.*, 2002, 2005). Overall, we suggest that assays that document individual variation in boldness, aggressiveness (as compared to affiliative tendency), neophobia, and dispersal tendency could help understand major patterns in spatial ecology.

VI. Future Prospects

A. Game Theory and Effects of Social Group Composition

Game theory assumes that in social groups, the fitness of behavioral types (e.g., of hawks vs doves or of territorials vs satellites) is frequency-dependent; that is, it depends on the mix of behavioral types in the group

(Dugatkin and Reeve, 1998; Maynard Smith, 1982; Sinervo and Calsbeek, 2006). This basic scenario holds for many theoretical behavioral dichotomies—for example, hawk/dove, producer/scrounger, cooperator/defector, as well as for more complex games like rock/scissors/paper. Although this is a fundamental tenet of game theory that has guided our thinking on social behavior for the last 35 years, surprisingly few studies have experimentally manipulated the frequency of behavioral types to examine actual effects on fitness or on behavioral dynamics (e.g., Beauchamp et al., 1997; Flynn and Giraldeau, 2001). The exception involves morphologically based alternative mating types (AMTs), for example, larger territorial individuals versus smaller satellites. Here, because behavioral types are easy to identify, studies have indeed examined frequency-dependent fitnesses associated with the different types. But even here, few experimental studies have manipulated the relative frequency of these AMTs (Bleay et al., 2007; Warner and Hoffman, 1980). A possible explanation for this disconnect between decades of theory and empirical work is the fact that until recently, relatively few studies have quantified individual variation in behavioral type in order to identify "hawks" and "doves," a prerequisite for experimentally creating groups with different mixes of hawks and doves. Now that behavioral syndromes are receiving more attention, a key issue should be to better understand how the behavior and fitness of different behavioral types depends on the group's social composition [mix of behavioral types in the group (e.g., Sih and Watters, 2005)].

Social selection theory (Wolf et al., 1998) provides a quantitative framework for relating both individual traits and the group's social composition to individual fitness. The basic idea extends the regression approach for quantifying natural selection and sexual selection on traits (e.g., Arnold and Wade, 1984a,b). Wolf et al. (1998) incorporated effects of the individual's group social composition by adding the social group's mean trait value as an independent variable in the regression equation of traits (individual and group) on fitness. The method partitions out natural and sexual selection gradients (relationships between the individual's traits and fitness) from social selection gradients (the relationship between the interacting group's mean trait value and individual fitness). Selection on a focal trait then also depends on social selection—the product of the social selection gradient and the covariance between the individual's trait and the social group's trait. In frequency-dependent games, individual fitness should depend on the interaction between the individual's trait and the group's social composition. This is handled by adding an interaction term into the regression equation.

Variation in social group composition (e.g., the mix of more vs less aggressive animals in a social group) likely affects not just the fitness of each behavioral type but also the actual behavior expressed by different

individuals. When a group of highly aggressive individuals are put together, some will remain highly aggressive, while others will substantially reduce their aggressiveness, that is, individuals will likely vary in behavioral plasticity. The behavioral syndrome view suggests new ways of thinking about behavioral plasticity in a game context. Most simple game theory models assume that individuals have either pure behavioral types (e.g., no plasticity, pure hawks, or pure doves) or no behavioral types [i.e., all individuals follow the same optimal probabilistic or condition-dependent ESS (Dugatkin and Reeve, 1998; Maynard Smith, 1982)]. In contrast, behavioral syndrome studies suggest that many real animals show some, but limited (less than optimal), plasticity; for example, both shy and bold individuals alter their boldness depending on the context (are less bold when predators are present), but within limits that allow us to identify some individuals as being consistently more shy versus more bold. Using a reaction norm framework, the simple behavioral syndrome approach posits that males differ in average behavior, but have similar behavioral plasticity (parallel reaction norms). In reality, animals appear to differ substantially in both mean behavioral type and behavioral plasticity (Koolhaas *et al*., 1999).

Only a few studies have examined effects of the group's social composition on behavioral plasticity within groups. Some found that individuals do not retain their behavioral types when they are placed in a social group (Mottley and Giraldeau, 2000). Other studies show that behavioral types are largely maintained (e.g., aggressive individuals stay relatively aggressive, or AMTs do not modify their behavior) regardless of the group's social composition (Sih and Watters, 2005; van Erp-van der Kooij *et al*., 2003). However, even in these studies, where most individuals maintained their behavioral type, some individuals showed substantial behavioral plasticity. For example, Sih and Watters, (2005) created groups of water striders that differed in average male aggressiveness. They found that although, in general, hyperaggressiveness was only seen in groups made up primarily of highly aggressive males, one hyperaggressive male emerged in a group that was created by putting together very unaggressive males. Apparently, one male that was unaggressive in a mixed social background became much more aggressive when it was surrounded by males that were all relatively passive. Clearly, more study is needed to better understand variation among behavioral types in their social plasticity in response to the group's social composition.

Finally, if the fitness of behavioral types depends on the group's social composition, then individuals should choose group social compositions that favor them (i.e., they should exhibit adaptive social situation choice). Alternatively, individuals might exhibit nonadaptive social preferences; for example, through imprinting, individuals might prefer associating with

their own behavioral type even when this is not adaptive. In any case, patterns of social situation choice should have important effects on selection and evolution. As noted above, social selection theory emphasizes that the covariance between individual traits and group traits (e.g., a tendency for aggressive individuals to interact with other aggressive individuals) is a key to how social selection influences selection on individual traits. Phenotype-dependent social situation choice is a likely mechanism generating this covariance. In general, adaptive situation choice can generate diversity both by driving the evolution of specialization (and ultimately, speciation) and by allowing the maintenance of variation (Wcislo, 1989; Wilson and Yoshimura, 1994). For example, if bold individuals do well in habitat X, but not Y, and vice versa for shy individuals, then both can do well and persist if they each prefer their optimal habitats. Social situation choice, however, is made more complicated by the fact that the sum of individual social situation choices determines the observed social compositions in different groups. Hawks that prefer to associate with doves might not be able to do so if doves avoid associating with hawks. Further study of behavioral type-dependent social situation choice should prove insightful.

B.   BEHAVIOR AS THE OUTCOME OF MULTIPLE BEHAVIORAL SYNDROMES

In the above discussion of cooperation, as with other behaviors, behavioral expression by each individual, and behavioral dynamics in an interaction, probably depend on multiple behavioral axes. This is, in fact, a familiar concept in human personality studies. Our behavior in any given situation is thought to reflect five main personality axes—the Big Five (extraversion, neuroticism, agreeableness, openness, and conscientiousness) with multiple subfactors within each of these five main factors (McCrae and Costa, 1999). The Big Five is a quantitative, statistical construct that emerged from factor analysis. Behavioral assays (often, questionnaires) assign a subject a score (from 0 to 100) on each of the five factors. Thus, in principle, it is possible to quantify the relative contribution of each of the Big Five to variation in actual behavior in a given context. Along similar lines, some detailed studies in behavioral genetics have partitioned out how behavior in a standardized laboratory assay (e.g., the open field assay) reflects multiple statistical factors [e.g., activity per se, exploratory tendency vs fear or anxiety (Henderson et al., 2004)].

Quantitative analysis of the role of multiple behavioral axes in explaining overall behavior and fitness outcomes should be an exciting future step for behavioral ecology. For example, in a mating context, one could quantify individual variation among a group of males in activity, aggressiveness, and social sensitivity (Fig. 3). Ideally, each of these axes would be assessed in
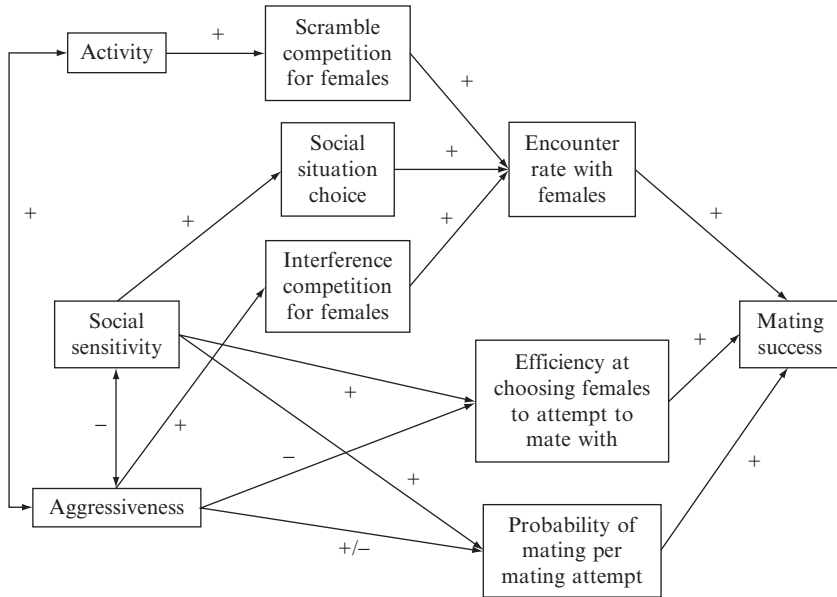
F IG . 3. Multiple pathways for how multiple behavioral tendencies might influence mating success. On the left are three behavioral axes: activity, social sensitivity, and aggressiveness. All three influence encounter rates with females. Social sensitivity and aggressiveness also affect variation among males in their efficiency of choosing suitable females to court, and probability of mating given a mating attempt. See the text for details.

multiple contexts, of which mating is only one. Each of these behavioral tendencies could then play a role in governing behavior and success in multiple stages that lead up to overall mating success. First, males must encounter females. Depending on the social system, either more active or more aggressive males might encounter females more. In systems with ''scramble competition'' for finding females, more active males should, on average, be better scramble competitors. In systems with interference competition for access to females, more aggressive males should outcompete other males in agonistic contests and might thus encounter more females. In general, males that have higher social sensitivity should exercise adaptive social situation choice that should enhance their encounter rates with females. For example, they might actively leave sites with an unfavorable sex ratio and prefer sites with more females per male. Social sensitivity should also help males to efficiently choose appropriate females to court (Sih and Watters, 2005). Inappropriate choices could include the wrong species, gender, or age class, or females that are of either low quality or too high quality (females that will very likely reject the focal male). Finally,

social sensitivity might be associated with higher courtship ability that enhances the probability of mating per mating attempt (Patricelli *et al.*, 2002, 2006). More aggressive displays could not only increase the probability of mating per mating attempt but also be associated with inappropriate mating attempts and unwanted sexual coercion (Ophir *et al.*, 2005; Sih and Watters, 2005).

Although, in theory, distinct behavioral axes should be uncorrelated (e.g., the Big Five in human personality study are orthogonal factors from a factor analysis), in reality, in any given sample, these axes might be correlated. For example, aggressiveness might be negatively correlated to social sensitivity (see earlier references). In principle, one could use path analysis (see Sih *et al.*, 2002) to quantify correlations among behavioral axes and the relative effects of each of these behavioral axes in determining overall mating success via multiple pathways.

VII. Summary

After placing the study of behavioral syndromes into historical perspective and clarifying some misconceptions about the term, the aim of this chapter is to illustrate some of the important questions that come into focus when viewing animal behavior through ''behavioral syndromes lenses.'' In general, we see two particularly exciting research directions. One of these focuses on trying to understand variation in behavioral syndromes. The other applies the behavioral syndromes approach to topics of interest to behavioral ecologists that have not historically focused on individual variation: For any given behavior, do individuals behave consistently differently from each other? If so, are those differences correlated across contexts?

The next major task in studies of behavioral syndromes themselves is to quantify and explain the patterns of variation in behavioral syndromes. As a first step, for example, we would like to know which behaviors tend to occur in clusters and which tend to be independent? When do correlations break down over ontogenetic and evolutionary time? Then, the challenge is to explain those patterns from both a proximate and ultimate perspective—how does selection act on differences in the lability of proximate mechanisms to produce variable correlations?

At the same time, we expect that the next major wave of studies on behavioral syndromes will apply these ideas to understand topics of interest to behavioral ecologists, things like mate choice, cooperation, and group living. We described several relatively understudied axes of behavioral variation, for example environmental and social sensitivity, learning,

choosiness, cooperativeness, etc, all of which could offer new insights into long-standing questions. Along the way, we highlighted other priorities for research such as consideration of nonbehavioral traits such as physiology and morphology as part of an integrated phenotype and the inclusion of conceptual (e.g., dynamic programming, network theory, and path analysis) and empirical (e.g., genomics) tools.

Acknowledgments

References

Amlacher, J., and Dugatkin, L. A. (2005). Preference for older over younger models during mate-choice copying in young guppies. *Ethol. Ecol. Evol.* **17,** 161–169.

Andersson, M., and Simmons, L. W. (2006). Sexual selection and mate choice. *Trends Ecol. Evol.* **21,** 296–302.

Arendt, J. (1997). Adaptive intrinsic growth rates: An integration across taxa. *Q. Rev. Biol.* **72,** 149–177.

Armbruster, W. S., and Schwaegerle, K. E. (1996). Causes of covariation of phenotypic traits among populations. *J. Evol. Biol.* **9,** 261–276.

Armitage, K. B. (1986). Individuality, social behavior, and reproductive success in yellow-bellied marmots. *Ecology* **65,** 1186–1193.

Arnold, S. J., and Wade, M. J. (1984a). On the measurement of natural and sexual selection—Theory. *Evolution* **38,** 709–719.

Arnold, S. J., and Wade, M. J. (1984b). On the measurement of natural and sexual selection—Applications. *Evolution* **38,** 720–734.

Arnqvist, G., and Henriksson, S. (1997). Sexual cannibalism in the fishing spider and a model for the evolution of sexual cannibalism based on genetic constraints. *Evol. Ecol.* **11,** 255–273.

Aron, E. N. (1996). ''The Highly Sensitive Person: How to Thrive When the World Overwhelms You.'' Carol Publishing Group, New York City.

Baguette, M., and Van Dyck, H. V. (2007). Landscape connectivity and animal behavior: Functional grain as a key determinant for dispersal. *Landscape Ecol.* **22,** 1117–1129.

Bateson, P. P. G., Barker, D., Clutton-Brock, T., Deb, D., D'Udine, B., Foley, R. A., Gluckman, K., Godfrey, K., Kirkwood, T., Mirazon Lahr, M., McNamara, J. M., Metcalfe, N. B., *et al.* (2004). Developmental plasticity and human health. *Nature* **430,** 419–421.

Beauchamp, G., Giraldeau, L. A., and Ennis, N. (1997). Experimental evidence for the maintenance of foraging specializations by frequency-dependent choice in flocks of spice finches. *Ethol. Ecol. Evol.* **9,** 105–117.

Bell, A. M. (2005). Differences between individuals and populations of threespined stickleback. *J. Evol. Biol.* **18,** 464–473.

Bell, A. M. (2007). Future directions in behavioral syndromes research. *Proc. R. Soc. Biol. Sci. Ser. B* **274,** 755–761.

Bell, A. M., and Sih, A. (2007). Exposure to predation generates personality in threespined sticklebacks. *Ecol. Lett.* **10,** 828–834.

Bell, A. M., and Stamps, J. A. (2004). The development of behavioural differences between individuals and populations of stickleback. *Anim. Behav.* **68,** 1339–1348.

Bell, A. M., Backstrom, T., Huntingford, F. A., Pottinger, T. G., and Winberg, S. (2007). Variable behavioral and neuroendocrine responses to ecologically-relevant challenges in sticklebacks. *Physiol. Behav.* **91,** 15–25.

Benard, M.F., and McCauley, S.J. (2008). Integrating across life-history stages: Consequences of natal habitat effects on dispersal. *Am. Nat.* **171,** 553–567.

Bennett, A. J., Lesch, K. P., Heils, A., Long, J. C., Lorenz, J. G., Shoaf, S. E., Champoux, M., Suomi, M. V., Linnoila, M. V., and Higley, J. D. (2002). Early experience and serotonin transporter gene variation interact to influence primate CNS function. *Mol. Psychiatry* **7,** 118–122.

Benus, R. F., and Rondigs, M. (1996). Patterns of maternal effort in mouse lines bidirectionally selected for aggression. *Anim. Behav.* **51,** 67–75.

Benus, R. F., Koolhaas, J. M., and Van Oortmerssen, G. A. (1987). Individual differences in behavioural reaction to a changing environment in mice and rats. *Behaviour* **100,** 105–122.

Benus, R. F., Den Daas, S., Koolhaas, J. M., and Van Oortmerssen, G. A. (1990). Routine formation and flexibility in social and non-social behaviour of aggressive and nonaggressive male mice. *Behaviour* **112,** 176–193.

Benus, R. F., Bohus, B., Koolhaas, J. M., and van Oortmerssen, G. A. (1991). Heritable variation for aggression as a reflection of individual coping strategies. *Experientia* **47,** 1008–1019.

Bergmuller, R., Russell, A., Johnstone, R., and Bshary, R. (2007). On the further integration of cooperative breeding and cooperation theory. *Behav. Processes* **76,** 170–181.

Biro, P. A., and Stamps, J. A. (2008). Are animal personality traits linked to life-history productivity? *Trends Ecol. Evol.* **23,** 361–368.

Bjelvenmark, J., and Forsgren, E. (2003). Effects of mate attraction and male-male competition on paternal care in a goby. *Behaviour* **140,** 55–69.

Bleay, C., Comendant, T., and Sinervo, B. (2007). An experimental test of frequency-dependent selection on male mating strategy in the field. *Proc. R. Soc. B-Biol. Sci.* **274,** 2019–2025.

Boogert, N. J., Reader, S. M., and Laland, K. N. (2006). The relation between social rank, neophobia and individual learning in starlings. *Anim. Behav.* **72,** 1229–1239.

Boyce, W. T., and Ellis, B. J. (2005). Biological sensitivity to context. I. An evolutionary-developmental theory of the origins and functions of stress reactivity. *Dev. Psychopathol.* **17,** 271–301.

Bressler, E. R., and Balshine, S. (2006). The influence of humor on desirability. *Evol. Hum. Behav.* **27,** 29–39.

Brodie, E. D. I. (1992). Correlational selection for color pattern and antipredator behavior in the garter snake, *Thamnophis ordinoides*. *Evolution* **46,** 1284–1298.

Brooks, R., and Endler, J. A. (2001). Female guppies agree to differ: Phenotypic and genetic variation in mate-choice behavior and the consequences for sexual selection. *Evolution* **55,** 1644–1655.

Budaev, S. V., Zworykin, D. D., and Mochek, A. D. (1999). Individual differences in parental care and behaviour profile in the convict cichlid: A correlation study. *Anim. Behav.* **58,** 195–202.

Capitanio, J. P., Mendoza, S. P., and Lerche, N. W. (1998). Individual differences in peripheral blood immunological and hormonal measures in adult male rhesus macaques (*Macaca mulatta*): Evidence for temporal and situational consistency. *Am. J. Primatol.* **44,** 29–41.

Careau, J., Thomas, M., Humphries, M., and Reale, D. (2008). Energy metabolism and animal personality. *Oikos.* **117,** 641–653.

Carere, C., Welink, D., Drent, P. J., Koolhaas, J. M., and Groothuis, T. G. G. (2001). Effect of social defeat in a territorial bird (Parus major) selected for different coping styles. *Physiol. Behav.* **73,** 427–433.

Carere, C., Groothuis, T. G. G., Mostl, E., Daan, S., and Koolhaas, J. M. (2003). Fecal corticosteroids in a territorial bird selected for different personalities: Daily rhythm and the response to social stress. *Horm. Behav.* **43,** 540–548.

Caspi, A., Roberts, B. W., and Shiner, R. L. (2005). Personality development: Stability and change. *Annu. Rev. Psychol.* **56,** 453–484.

Champagne, F. A., and Meaney, M. J. (2006). Stress during gestation alters postpartum maternal care and the development of the offspring in a rodent model. *Biol. Psychiatry* **59,** 1227–1235.

Champoux, M., Bennett, A., Shannon, C., Higley, J. D., Lesch, K. P., and Suomi, S. J. (2002). Serotonin transporter gene polymorphism, differential early rearing, and behavior in rhesus monkey neonates. *Mol. Psychiatry* **7,** 1058–1063.

Clark, C. W. (1994). Antipredator behavior and the asset-protection principle. *Behav. Ecol.* **5,** 159–170.

Clark, A. B., and Ehlinger, T. J. (1987). Pattern and adaptation in individual behavioral differences. *In* ''Perspectives in Ethology'' (P. P. G. Bateson and P. H. Klopfer, Eds.), pp. 1–47. Plenum Press, New York.

Clark, M. M., and Galef, B. G. (1999). A testosterone-mediated trade-off between parental and sexual effort in male mongolian gerbils (*Meriones unguiculatus*). *J. Comp. Psychol.* **113,** 388–395.

Clobert, J., Danchin, E., Dhondt, A. A., and Nichols, J. D. (2001). ''Dispersal.'' Oxford University Press, New York.

Cote, J., and Clobert, J. (2007). Social personalities influence natal dispersal in a lizard. *Proc. R. Soc. B-Biol. Sci.* **274,** 383–390.

Cox, J. G., and Lima, S. L. (2006). Naivete and an aquatic-terrestrial dichotomy in the effects of introduced predators. *Trends Ecol. Evol.* **21,** 674–680.

Crowley, P. H., Travers, S. E., Linton, M. C., Cohen, S. L., Sih, A., and Sargent, R. C. (1991). Mate density, predation risk and the seasonal sequence of mate choices: A dynamic game. *Am. Nat.* **137,** 567–596.

Cummings, M., and Mollaghan, D. (2006). Repeatability and consistency of female preference behaviours in a northern swordtail, *Xiphophorus nigrensis*. *Anim. Behav.* **72,** 217–224.

Curio, E. (1976). ''The Ethology of Predation.'' Springer-Verlag, Berlin.

Dall, S. R. X., Houston, A. I., and McNamara, J. M. (2004). The behavioural ecology of personality: Consistent individual differences from an adaptive perspective. *Ecol. Lett.* **7,** 734–739.

Davis, J. M., and Stamps, J. A. (2004). The effect of natal experience on habitat preferences. *Trends Ecol. Evol.* **19,** 411–416.

De Ridder, E., Pinxten, R., and Eens, M. (2000). Experimental evidence of a testosterone-induced shift from paternal to mating behaviour in a facultatively polygynous songbird. *Behav. Ecol. Sociobiol.* **49,** 24–30.

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

Dingemanse, N. J., Both, C., van Noordwijk, A. J., Rutten, A. L., and Drent, P. J. (2003). Natal dispersal and personalities in great tits (Parus major). *Proc. R. Soc. Lond.– Ser. B Biol. Sci.* **270,** 741–747.

Dingemanse, N. J., Both, C., Drent, P. J., and Tinbergen, J. M. (2004). Fitness consequences of avian personalities in a fluctuating environment. *Proc. R. Soc. Lond. Ser. B* **271,** 847–852.

Dingemanse, N. J., Thomas, D. K., Wright, J., Kazem, A. J. N., Koese, B., Hickling, R., and Dawnay, N. (2007). Behavioural syndromes differ predictably between twelve populations of three-spined stickleback. *J. Anim. Ecol.* **76,** 1128–1138.

Dingle, H. (2001). The evolution of migratory syndromes in insects. *In* ''Insect Movement: Mechanisms and Consequence. Proceedings of the Royal Entomological Society's 20th Symposium'' (I. P. Woiod, D. R. Reynolds, and C. D. Thomas, Eds.), pp. 159–181. CABI Publishers, New York.

Diorio, J., and Meaney, M. J. (2007). Maternal programming of defensive responses through sustained effects on gene expression. *J. Psychiatry Neurosci.* **32,** 275–284.

Dochtermann, N. A., and Jenkins, S. H. (2007). Behavioral syndromes in Merriam's kangaroo rats (*Dipodomys merriami*): A test of competing hypotheses. *Proc. R. Soc. B-Biol. Sci.* **274,** 2343–2349.

Drent, P. J., Van Oers, K., and Van Noordwijk, A. J. (2003). Realised heritability of personalities in the great tit (Parus major). *Proc. R. Soc. Lond. Ser. B.* **270,** 45–51.

Duckworth, R. A. (2006). Behavioral correlations across breeding contexts provide a mechanism for a cost of aggression. *Behav. Ecol.* **17,** 1011–1019.

Duckworth, R. A., and Badyaev, A. V. (2007). Coupling of dispersal and aggression facilitates the rapid range expansion of a passerine bird. *Proc. Natl. Acad. Sci. USA* **104,** 15017–15022.

Duckworth, R. A., Badyaev, A. V., and Parlow, A. F. (2003). Elaborately ornamented males avoid costly parental care in the house finch (*Carpodacus mexicanus*): A proximate perspective. *Behav. Ecol. Sociobiol.* **55,** 176–183.

Dugatkin, L. A., and Alfieri, M. (1991). Tit-for-Tat in guppies: The relative nature of cooperation and defection during predator inspection. *Evol. Ecol.* **5,** 300–309.

Dugatkin, L. A., and Godin, J. G. J. (1993). Female mate copying in the guppy (*Poecilia reticulata*): Age-dependent effects. *Behav. Ecol.* **4,** 289–292.

Dugatkin, L. A., and Reeve, H. K. (1998). ''Game Theory and Animal Behavior.'' Oxford University Press, New York.

Dukas, R. (1998). Constraints on neural processing and their effects on behavior. *In* ''Cognitive Ecology: The Evolutionary Ecology of Information Processing and Decision Making'' (R. Dukas, Ed.). University of Chicago Press, Chicago.

Emlen, D. J. (1997). Alternative reproductive tactics and male-dimorphism in the horned beetle (Coleoptera: Scarabaeidae). *Behav. Ecol. Sociobiol.* **41,** 335–341.

Endler, J. A. (1995). Multiple-trait coevolution and environmental gradients in guppies. *Trends Ecol. Evol.* **10,** 22–29.

Falconer, D. S., and Mackay, T. F. C. (1996). ''Introduction to Quantitative Genetics.'' Longman, Essex, England.

Flynn, R. E., and Giraldeau, L. A. (2001). Producer-scrounger games in a spatially explicit world: Tactic use influences flock geometry of spice finches. *Ethology* **107,** 249–257.

Forstmeier, W., and Birkhead, T. R. (2004). Repeatability of mate choice in the zebra finch: Consistency within and between females. *Anim. Behav.* **68,** 1017–1028.

Fraser, D. F., Gilliam, J. F., Daley, M. J., Le, A. N., and Skalski, G. T. (2001). Explaining leptokurtic movement distributions: Intrapopulation variation in boldness and exploration. *Am. Nat.* **158,** 124–135.

Freeman-Gallant, C. R., and Rothstein, M. D. (1999). Apparent heritability of parental care in Savannah Sparrows. *Auk* **116,** 1132–1136.

Galef, B. G., and Giraldeau, L. A. (2001). Social influences on foraging in vertebrates: Causal mechanisms and adaptive functions. *Anim. Behav.* **61,** 3–15.

Galsworthy, M. J., Paya-Cano, J. L., Monleon, S., and Plomin, R. (2002). Evidence for general cognitive ability (g) in heterogeneous stock mice and an analysis of potential confounds. *Genes Brain Behav.* **1,** 88–95.

Giles, N., and Huntingford, F. A. (1984). Predation risk and inter-population variation in antipredator behaviour in the threespined stickleback. *Anim. Behav.* **32,** 264–275.

Gladwell, M. (2000). ''The Tipping Point: How Little Things Can Make a Big Difference.'' Little Brown and Company, New York.

Godin, J. G. J., Herdman, E. J. E., and Dugatkin, L. A. (2005). Social influences on female mate choice in the guppy, Poecilia reticulata: Generalized and repeatable trait-copying behaviour. *Anim. Behav.* **69,** 999–1005.

Gosling, S. D. (2001). From mice to men: What can we learn about personality from animal research? *Psychol. Bull.* **127,** 45–86.

Gould, S. J., and Vrba, E. S. (1982). Exaptation; a missing term in the science of form. *Paleobiology* **8,** 4–15.

Hamilton, W. D. (1964). The genetic evolution of social behavior. *J. Theor. Biol.* **7,** 17–18.

Healy, S., and Braithwaite, V. (2000). Cognitive ecology: A field of substance? *Trends Ecol. Evol.* **15,** 22–26.

Henderson, N. D. (1990). Quantitative genetic analysis of neurobehavioral phenotypes. *In* ''Developmental Behavior Genetics: Neural, Biometrical and Evolutionary Approaches'' (M. E. Hahn, J. K. Hewit, N. D. Henderson, and R. H. Benno, Eds.), pp. 283–297. Oxford University Press, New York.

Henderson, N. D., Turri, M. G., DeFries, J. C., and Flint, J. (2004). QTL analysis of multiple behavioral measures of anxiety in mice. *Behav. Genet.* **34,** 267–293.

Hessing, M. J. C., Hagelso, A. M., Van Beek, J. A. M., Wiepkeme, P. R., Schouten, W. G. P., and Krukow, R. (1993). Individual behavioural characteristics in pigs. *Appl. Behav. Sci.* **37,** 285–295.

Holyoak, M., Leibold, M. A., and Holt, R. D. (2005). ''Metacommunities: Spatial Dynamics and Ecological Communities.'' The University of Chicago Press, Chicago, IL.

Huntingford, F. A. (1976a). The relationship between anti-predator behaviour and aggression among conspecifics in the three-spined stickleback. *Anim. Behav.* **24,** 245–260.

Huntingford, F. A. (1976b). The relationship between inter- and intra-specific aggression. *Anim. Behav.* **24,** 485–497.

Jang, Y. W., and Greenfield, M. D. (2000). Quantitative genetics of female choice in an ultrasonic pyralid moth, *Achroia grisella*: Variation and evolvability of preference along multiple dimensions of the male advertisement signal. *Heredity* **84,** 73–80.

Jawer, M. (2005). Environmental sensitivity: A neurobiological phenomenon? *Semin. Integr. Med.* **3,** 104–109.

Jennions, M. D., and Petrie, M. (1997). Variation in mate choice and mating preferences: A review of causes and consequences. *Biol. Rev. Camb. Philos. Soc.* **72,** 283–327.

Johnson, J., and Sih, A. (2005). Pre-copulatory sexual cannibalism in fishing spiders (*Dolomedes triton*): A role for behavioral syndromes. *Behav. Ecol. Sociobiol.* **58,** 390–396.

Johnson, J. C. (2003). Pre-copulatory sexual cannibalism in fishing spiders: The ecology of an extreme sexual conflict (thesis). *In* ''Biological Sciences''. University of Kentucky.

Johnson, S. D., and Steiner, K. E. (2000). Generalization versus specialization in plant pollination systems. *Trends Ecol. Evol.* **15,** 140–143.

Kendler, K. S., and Greenspan, R. J. (2006). The nature of genetic influences on behavior: Lessons from ''simpler'' organisms. *Am. J. Psychiatry* **163,** 1683–1694.

Ketterson, E. D., and Nolan, V. (1999). Adaptation, exaptation, and constraint: A hormonal perspective. *Am. Nat.* **154,** S4–S25.

Ketterson, E. D., Nolan, V., Wolf, L., and Ziegenfus, C. (1992). Testosterone and avian life historieseffects of experimentally elevated testosterone on behavior and correlates of fitness in the dark-eyed junco (Junco-Hyemalis). *Am. Nat.* **140,** 980–999.

Kirkpatrick, M., and Dugatkin, L. A. (1994). Sexual selection and the evolutionary effects of copying mate choice. *Behav. Ecol. Sociobiol.* **34,** 443–449.

Kokko, H. (1998). Should advertising parental care be honest? *Proc. R. Soc. Lond. Ser. B-Biol. Sci.* **265,** 1871–1878.

Kokko, H., Jennions, M. D., and Brooks, R. (2006). Unifying and testing models of sexual selection. *Annu. Rev. Ecol. Syst.* **37,** 43–66.

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

Koolhaas, J. M., De Boer, S. F., and Buwalda, B. (2006). Stress and adaptation. *Curr. Dir. Psychol. Sci.* **15,** 109–112.

Kortet, R., and Hedrick, A. (2007). A behavioural syndrome in the field cricket Gryllus integer: Intrasexual aggression is correlated with activity in a novel environment. *Biol. J. Linn. Soc.* **91,** 475–482.

Kummer, H., and Goodall, J. (1985). Conditions of innovative behaviour in primates. *Philos. Trans. R. Soc. London Ser. B* **308,** 203–214.

Laland, K. N., and Reader, S. M. (1999a). Foraging innovation is inversely related to competitive ability in male but not in female guppies. *Behav. Ecol.* **10,** 270–274.

Laland, K. N., and Reader, S. M. (1999b). Foraging innovations in the guppy. *Anim. Behav.* **57,** 331–340.

Lande, R., and Arnold, S. J. (1983). The measurement of selection on correlated characters. *Evolution* **37,** 1210–1226.

LeBas, N. R., Hockham, L. R., and Ritchie, M. G. (2003). Nonlinear and correlational sexual selection on 'honest' female ornamentation. *Proc. R. Soc. B-Biol. Sci.* **270,** 2159–2165.

Liker, A., and Barta, Z. (2002). The effects of dominance on social foraging tactic use in house sparrows. *Behaviour* **139,** 1061–1076.

MacColl, A. D. C., and Hatchwell, B. J. (2003). Heritability of parental effort in a passerine bird. *Evolution* **57,** 2191–2195.

Mackay, T. F. C. (2004). The genetic architecture of quantitative traits: Lessons from *Drosophila. Curr. Opin. Genet. Dev.* **14,** 253–257.

Maestripieri, D., Higley, J. D., Lindell, S. G., Newman, T. K., McCormack, K. M., and Sanchez, M. M. (2006). Early maternal rejection affects the development of monoaminergic systems and adult abusive parenting in rhesus macaques (Macaca mulatta). *Behav. Neurosci.* **120,** 1017–1024.

Maestripieri, D., Lindell, S. G., and Higley, J. D. (2007). Intergenerational transmission of maternal behavior in rhesus macaques and its underlying mechanisms. *Dev. Psychobiol.* **49,** 165–171.

Magellan, K., and Magurran, A. E. (2007). Behavioural profiles: Individual consistency in male mating behaviour under varying sex ratios. *Anim. Behav.* **74,** 1545–1550.

Magrath, M. J. L., and Elgar, M. A. (1997). Paternal care declines with increased opportunity for extra-pair matings in fairy martins. *Proc. R. Soc. London Ser. B-Biol. Sci.* **264,** 1731–1736.

Magrath, M. J. L., and Komdeur, J. (2003). Is male care compromised by additional mating opportunity? *Trends Ecol. Evol.* **18,** 424–430.

Magurran, A. E. (1986). Predator inspection behaviour in minnow shoals: Differences between populations and individuals. *Behav. Ecol. Sociobiol.* **19,** 267–273.

Magurran, A. E. (1993). Individual differences and alternative behaviours. *In* ''Behaviour of Teleost Fishes'' (T. J. Pitcher, Ed.), 2nd ed., pp. 441–477. Chapman & Hall, New York.

Mangel, M., and Stamps, J. (2001). Trade-offs between growth and mortality and the maintenance of individual variation in growth. *Evol. Ecol. Res.* **3,** 583–593.

Marchetti, C., and Drent, P. J. (2000). Individual differences in the use of social information in foraging by captive great tits. *Anim. Behav.* **60,** 131–140.

Matzel, L. D., Han, Y. R., Grossman, H., Karnik, M. S., Patel, D., Scott, N., Specht, S. M., and Gandhi, C. C. (2003). Individual differences in the expression of a ''general'' learning ability in mice. *J. Neurosci.* **23,** 6423–6433.

Matzel, L. D., Townsend, D. A., Grossman, H., Han, Y. R., Hale, G., Zappulla, M., Light, K., and Kolata, S. (2006). Exploration in outbred mice covaries with general learning abilities irrespective of stress reactivity, emotionality, and physical attributes. *Neurobiol. Learn. Mem.* **86,** 228–240.

Maynard Smith, J. (1982). ''Evolution and the Theory of Games.'' Cambridge University Press, Cambridge.

McCrae, R. R., and Costa, P. T., Jr. (1999). A five-factor theory of personality. *In* ''Handbook of Personality: Theory and Research'' (L. A. Pervin and O. P. John, Eds.), 2nd ed., pp. 139–153. Guilford Press, New York.

McElreath, R., and Strimling, P. (2006). How noisy information and individual asymmetries can make ''personality'' an adaptation: A simple model. *Anim. Behav.* **72,** 1135–1139.

McElreath, R., Luttbeg, B., Fogarty, S. P., Brodin, T., and Sih, A. (2007). Evolution of animal personalities. *Nature* **450,** E5.

McGlothlin, J. W., Parker, P. G., Nolan, V., and Ketterson, E. D. (2005). Correlational selection leads to genetic integration of body size and an attractive plumage trait in dark-eyed juncos. *Evolution* **59,** 658–671.

McNamara, J. M., Gasson, C. E., and Houston, A. I. (1999). Incorporating rules for responding into evolutionary games. *Nature* **401,** 368–371.

McNamara, J. M., Barta, Z., Fromhage, L., and Houston, A. I. (2008). The coevolution of choosiness and cooperation. *Nature* **451,** 189–192.

Meaney, M. J. (2001). Maternal care, gene expression, and the transmission of individual differences in stress reactivity across generations. *Annu. Rev. Neurosci.* **24,** 1161–1192.

Mery, F., and Kawecki, T. J. (2003). A fitness cost of learning ability in *Drosophila* melanogaster. *Proc. R. Soc. London Ser. B-Biol. Sci.* **270,** 2465–2469.

Mery, F., and Kawecki, T. J. (2004). The effect of learning on experimental evolution of resource preference in *Drosophila melanogaster. Evolution* **58,** 757–767.

Mery, F., and Kawecki, T. J. (2005). A cost of long-term memory in *Drosophila. Science* **308,** 1148.

Mery, F., Belay, A. T., So, A. K. C., Sokolowski, M. B., and Kawecki, T. J. (2007). Natural polymorphism affecting learning and memory in *Drosophila. Proc. Natl. Acad. Sci. USA* **104,** 13051–13055.

Metcalfe, N. B., and Monaghan, P. (2001). Compensation for a bad start: Grow now, pay later? *Trends Ecol. Evol.* **16,** 254–260.

Milinski, M. (1987). Tit-for-Tat in sticklebacks and the evolution of cooperation. *Nature* **325,** 433–435.

Mischel, W. (2004). Toward an integrative science of the person. *Annu. Rev. Psychol.* **55,** 1–22.

Mitchell, D. P., Dunn, P. O., Whittingham, L. A., and Freeman-Gallant, C. R. (2007). Attractive males provide less parental care in two populations of the common yellowthroat. *Anim. Behav.* **73,** 165–170.

Moretz, J., Martins, E., and Robison, B. (2007). Behavioral syndromes and the evolution of correlated behavior in zebrafish. *Behav. Ecol.* **18,** 556–562.

Morris, M. R., Nicoletto, P. F., and Hesselman, E. (2003). A polymorphism in female prefer-ence for a polymorphic male trait in the swordtail fish Xiphophorus cortezi. *Anim. Behav.* **65,** 45–52.

Morris, M. R., Rios-Cardenas, O., and Tudor, M. S. (2006). Larger swordtail females prefer asymmetrical males. *Biol. Lett.* **2,** 8–11.

Mottley, K., and Giraldeau, L. A. (2000). Experimental evidence that group foragers can converge on predicted producer-scrounger equilibria. *Anim. Behav.* **60,** 341–350.

Nakagawa, S., Gillespie, D. O. S., Hatchwell, B. J., and Burke, T. (2007). Predictable males and unpredictable females: Sex difference in repeatability of parental care in a wild bird population. *J. Evol. Biol.* **20,** 1674–1681.

Neff, B. D., and Sherman, P. W. (2004). Behavioral syndromes versus Darwinian algorithms. *Trends Ecol. Evol.* **19,** 621–622.

Nunes, S., Fite, J. E., and French, J. A. (2000). Variation in steroid hormones associated with infant care behaviour and experience in male marmosets (*Callithrix kuhlii*). *Anim. Behav.* **60,** 857–865.

Ophir, A. G., Persaud, K. N., and Galef, B. G. (2005). Avoidance of relatively aggressive male Japanese quail (*Coturnix japonica*) by sexually experienced conspecific females. *J. Comp. Psychol.* **119,** 3–7.

Overli, O., Sorensen, C., Pulman, K. G. T., Pottinger, T. G., Korzan, W., Summers, C. H., and Nilsson, G. E. (2007). Evolutionary background for stress-coping styles: Relationships between physiological, behavioral, and cognitive traits in non-mammalian vertebrates. *Neurosci. Biobehav. Rev.* **31,** 396–412.

Pampoulie, C., Lindstrom, K., and St Mary, C. M. (2004). Have your cake and eat it too: Male sand gobies show more parental care in the presence of female partners. *Behav. Ecol.* **15,** 199–204.

Patricelli, G. L., Uy, J. A. C., Walsh, G., and Borgia, G. (2002). Male displays adjusted to female's response - Macho courtship by the satin bowerbird is tempered to avoid fright-ening the female. *Nature* **415,** 279–280.

Patricelli, G. L., Coleman, S. W., and Borgia, G. (2006). Male satin bowerbirds, *Ptilonor-hynchus violaceus*, adjust their display intensity in response to female startling: An experiment with robotic females. *Anim. Behav.* **71,** 49–59.

Penke, L., Denissen, J. J. A., and Miller, G. F. (2007). The evolutionary genetics of personality. *Eur. J. Pers.* **21,** 549–587.

Peters, A. (2002). Testosterone and the trade-off between mating and paternal effort in extrapair-mating superb fairy-wrens. *Anim. Behav.* **64,** 103–112.

Pfeffer, K., Fritz, J., and Kotrschal, K. (2002). Hormonal correlates of being an innovative greylag goose (*Anser anser*). *Anim. Behav.* **63,** 687–695.

Pigliucci, M., and Preston, K. (2004). ''Phenotypic Integration: Studying the Ecology and Evolution of Complex Phenotypes.'' Oxford University Press, Oxford.

Pitcher, T. (1992). Who dares, wins: The function and evolution of predator inspection behaviour in shoaling fish. *Netherlands Journal of Zoology*, **42,** 371–391.

Plomin, R., and Dunn, J. (1986). ''The Study of Temperament: Changes, Continuities and Challenges.'' Erlbaum, Hillsdale, NJ.

Qvarnstrom, A. (1997). Experimentally increased badge size increases male competition and reduces male parental care in the collared flycatcher. *Proc. R. Soc. London Ser. B-Biol. Sci.* **264,** 1225–1231.

Reader, S. M. (2003). Innovation and social learning: Individual variation and brain evolution. *Anim. Biol.* **53,** 147–158.

Real, L. A. (1993). Toward a cognitive ecology. *Trends Ecol. Evol.* **8,** 413–417.

Reale, D., Reader, S. M., Sol, D., McDougall, P. T., and Dingemanse, N. J. (2007). Integrating animal temperament within ecology and evolution. *Biol. Rev.* **82,** 291–318.

Reaney, L., and Backwell, P. (2007). Risk-taking behavior predicts aggression and mating success in a fiddler crab. *Behav. Ecol.* **18,** 521–525.

Rehage, J. S., and Sih, A. (2004). Dispersal characteristics and boldness: A comparison of Gambusia species of varying invasiveness. *Biol. Invasions* **6,** 379–391.

Reichard, M., Le Comber, S. C., and Smith, C. (2007). Sneaking from a female perspective. *Anim. Behav.* **74,** 679–688.

Reinhold, K., Reinhold, K., and Jacoby, K. J. (2002). Dissecting the repeatability of female choice in the grasshopper *Chorthippus biguttulus*. *Anim. Behav.* **64,** 245–250.

Reznick, D. (1983). The structure of guppy life histories—The tradeoff between growth and reproduction. *Ecology* **64,** 862–873.

Riechert, S. E., and Hammerstein, P. (1983). Game-theory in the ecological context. *Annu. Rev. Ecol. Syst.* **14,** 377–409.

Riechert, S. E., and Hedrick, A. V. (1993). A test for correlations among fitness-linked behavioural traits in the spider *Agelenopsis aperta*. *Anim. Behav.* **46,** 669–675.

Roberts, B. W., Walton, K. E., and Viechtbauer, W. (2006). Patterns of mean-level change in personality traits across the life course: A meta-analysis of longitudinal studies. *Psychol. Bull.* **132,** 1–25.

Roff, D. A. (1992). "The Evolution of Life Histories: Theory and Analysis." Chapman & Hall, New York.

Roff, D. A. (1995). The estimation of genetic correlations from phenotypic correlations: A test of Cheverud's conjecture. *Heredit* **74,** 481–490.

Ros, A. F. H., Bruintjes, R., Santos, R. S., Canario, A. V. M., and Oliveira, R. F. (2004). The role of androgens in the trade-off between territorial and parental behavior in the Azorean rock-pool blenny, Parablennius parvicornis. *Horm. Behav.* **46,** 491–497.

Sapolsky, R. M., Romero, L. M., and Munck, A. U. (2000). How do glucocorticoids influence stress responses? Integrating permissive, suppressive, stimulatory and preparative actions. *Endocr. Rev.* **21,** 55–89.

Schlichting, C. D., and Pigliucci, M. (1998). "Phenotypic Evolution: A Reaction Norm Perspective." Sinauer, Sunderland, MA.

Schwagmeyer, P. L., and Mock, D. W. (2003). How consistently are good parents good parents? Repeatability of parental care in the house sparrow, *Passer domesticus*. *Ethology* **109,** 303–313.

Shettleworth, S. J. (1998). "Cognition, Evolution and Behavior." Oxford University Press, Oxford.

Shuster, S. M. (1989). Male alternative reproductive strategies in a marine isopod crustacean—the use of genetic markers to measure differences in fertilization success among alpha-males, beta-males and gamma-males. *Evolution* **43,** 1683–1698.

Sih, A. (1992). Prey uncertainty and the balancing of antipredator and feeding needs. *Am. Nat.* **139,** 1052–1069.

Sih, A., and Christensen, B. (2001). Optimal diet theory: When does it work and when and why does it fail? *Anim. Behav.* **61,** 379–390.

Sih, A., and Watters, J. V. (2005). The mix matters: Behavioural types and group dynamics in water striders. *Behaviour* **142,** 1417–1431.

Sih, A., Lauer, M., and Krupa, J. J. (2002). Path analysis and relative importance of male-female conflict, female choice and male-male competition in water striders. *Anim. Behav.* **63,** 1079–1089.

Sih, A., Kats, L. B., and Maurer, E. F. (2003). Behavioral correlations across situations and the evolution of antipredator behaviour in a sunfish-salamander system. *Anim. Behav.* **65,** 29–44.

Sih, A., Bell, A. M., and Johnson, J. C. (2004a). Behavioral syndromes: An ecological and evolutionary overview. *Trends Ecol. Evol.* **19,** 372–378.

Sih, A., Bell, A. M., Johnson, J. C., and Ziemba, R. (2004b). Behavioral syndromes: An integrative overview. *Q. Rev. Biol.* **79,** 241–277.

Sih, A., Bell, A. M., and Johnson, J. C. (in press). Behavioral syndromes. *In* "Evolutionary Behavioral Ecology" (D. F. Westneat and C. W. Fox, Eds.). Oxford University Press, Oxford

Sinervo, B., and Lively, C. M. (1996). The rock-paper-scissors game and the evolution of alternative male strategies. *Nature* **380,** 240–243.

Sinervo, B., and Calsbeek, R. (2006). The developmental, physiological, neural, and genetical causes and consequences of frequency-dependent selection in the wild. *Annu. Rev. Ecol. Syst.* **37,** 581–610.

Slater, P. J. B. (1981). Individual differences in animal behavior. *In* "Perspectives in Ethology" (P. P. G. Bateson and P. H. Klopfer, Eds.), pp. 35–49. Plenum, New York.

Smith, H. G. (1995). Experimental demonstration of a trade-off between mate attraction and paternal care. *Proc. R. Soc. London Ser. B-Biol. Sci.* **260,** 45–51.

Sol, D., Timmermans, S., and Lefebvre, L. (2002). Behavioural flexibility and invasion success in birds. *Anim. Behav.* **63,** 495–502.

Sol, D., Lefebvre, L., and Rodriguez-Teijeiro, J. D. (2005). Brain size, innovative propensity and migratory behaviour in temperate Palaearctic birds. *Proc. R. Soc. B-Biol. Sci.* **272,** 1433–1441.

Stamps, J. A. (1991). Why evolutionary issues are reviving interest in proximate behavioral mechanisms. *Am. Zool.* **31,** 338–348.

Stamps, J. A. (2007). Growth-mortality tradeoffs and 'personality traits' in animals. *Ecol. Lett.* **10,** 355–363.

Stamps, J. A., Krishnan, V. V., and Reid, M. L. (2005). Search costs and habitat selection by dispersers. *Ecology* **86,** 510–518.

Stephens, D. W. (1991). Change, regularity, and value in the evolution of animal learning. *Behav. Ecol.* **2,** 77–89.

Stephens, D. W., and Krebs, J. R. (1986). "Foraging Theory." Princeton University Press, Princeton, NJ.

Stevenson-Hinde, J., Sitillwell-Barnes, R., and Zunz, M. (1980). Subjective assessment of rhesus monkeys over four successive years. *Primates* **21,** 66–82.

Storey, A. E., Delahunty, K. M., McKay, D. W., Walsh, C. J., and Wilhelm, S. I. (2006). Social and hormonal bases of individual differences in the parental behaviour of birds and mammals. *Can. J. Exp. Psychol.-Revue Canadienne De Psychologie Experimentale* **60,** 237–245.

Sundstrom, L. F., Petersson, E., Hojesjo, J., Johnsson, J. I., and Jarvi, T. (2004). Hatchery selection promotes boldness in newly hatched brown trout (*Salmo trutta*): Implications for dominance. *Behav. Ecol.* **15,** 192–198.

Suomi, J. S. (1987). Genetic and maternal contributions to individual differences in Rhesus monkey biobehavioral development. *In* "Psychobiological Aspects of Behavioral Development" (N. Krasnagor, Ed.), pp. 397–419. Academic Press, New York.

Trivers, R. L. (1971). The evolution of reciprocal altruism. *Q. Rev. Biol.* **46,** 35–57.

Valone, T. (2007). From eavesdropping on performance to copying the behavior of others: A review of public information use. *Behav. Ecol. Sociobiol.* **62,** 1–14.

Van Duyse, E., Pinxten, R., and Eens, M. (2000). Does testosterone affect the trade-off between investment in sexual/territorial behaviour and parental care in male great tits? *Behaviour* **137,** 1503–1515.

van Erp-van der Kooij, E., Kuijpers, A. H., Van Eerdenburg, F. J., Dieleman, S. J., Blankenstein, D. M., and Tielen, M. J. M. (2003). Individual behavioural characteristics in pigs—influences of group composition but no differences in cortisol responses. *Physiol. Behav.* **78,** 479–488.

van Oers, K., de Jong, G., van Noordwijk, A. J., Kempenaers, B., and Drent, P. J. (2005). Contribution of genetics to the study of animal personalities: A review of case studies. *Behaviour* **142,** 1185–1206.

Veenema, A. H., Blume, A., Niederle, D., Buwalda, B., and Neumann, I. D. (2006). Effects of early life stress on adult male aggression and hypothalamic vasopressin and serotonin. *Eur. J. Neurosci.* **24,** 1711–1720.

Veiga, J. P., Moreno, J., Arenas, M., and Sanchez, S. (2002). Reproductive consequences for males of paternal vs territorial strategies in the polygynous spotless starling under variable ecological and social conditions. *Behaviour* **139,** 677–693.

Verbeek, M. E. M., Drent, P. J., and Wiepkema, P. R. (1994). Consistent individual differences in early exploratory behaviour of male great tits. *Anim. Behav.* **48,** 1113–1121.

Verbeek, M. E. M., Boon, A., and Drent, P. J. (1996). Exploration, aggressive behaviour and dominance in pair-wise confrontations of juvenile male great tits. *Behaviour* **133,** 945–963.

Warner, R. R., and Hoffman, S. G. (1980). Population density and the economics of territorial defense in a coral reef fish. *Ecology* **61,** 772–780.

Watters, J. V. (2005). Can the alternative male tactics 'fighter' and 'sneaker' be considered 'coercer' and 'cooperator' in coho salmon? *Anim. Behav.* **70,** 1055–1062.

Wcislo, W. T. (1989). Behavioral environments and evolutionary change. *Annu. Rev. Ecol. Syst.* **20,** 137–169.

Weaver, I. C. G., Cervoni, N., Champagne, F. A., D'Alessio, A. C., Sharma, S., Seckl, J. R., Dymov, M., Szyf, M., and Meaney, M. J. (2004). Epigenetic programming by maternal behavior. *Nat. Neurosci.* **7,** 847–854.

Westneat, D. F., and Sargent, R. C. (1996). Sex and parenting: The effects of sexual conflict and parentage on parental strategies. *Trends Ecol. Evol.* **11,** 87–91.

Whybrow, P. C. (2005). ''American Mania. When More is not Enough.'' Norton and Company, New York.

Wilson, D. S. (1998). Adaptive individual differences within single populations. *Philos. Trans. R. Soc. London Ser. B* **353,** 199–205.

Wilson, D. S., and Yoshimura, J. (1994). On the coexistence of specialists and generalists. *Am. Nat.* **144,** 692–707.

Wilson, D. S., Clark, A. B., Coleman, K., and Dearstyne, T. (1994). Shyness and boldness in humans and other animals. *Trends Ecol. Evol.* **11,** 442–446.

Winberg, S., and Nilsson, G. E. (1993). Roles of brain monoamine neurotransmitters in agonistic behaviour and stress reactions, with particular reference to fish. *Comp. Biochem. Physiol. C Comparative Pharmacology and Toxicology* **106,** 597–614.

Wingfield, J. C., Hegner, R. E., Dufty, A. M., and Ball, G. F. (1990). The challenge hypothesis—Theoretical implications for patterns of testosterone secretion, mating systems, and breeding strategies. *Am. Nat.* **136,** 829–846.

Wolf, J. B., Brodie, E. D. I., Cheverud, J. M., Moore, A. J., and Wade, M. J. (1998). Evolutionary consequences of indirect genetic effects. *Trends Ecol. Evol.* **13,** 64–69.

Wolf, M., van Doorn, G. S., Leimar, O., and Weissing, F. J. (2007a). Life history tradeoffs favour the evolution of personality. *Nature* **447,** 581–585.

Wolf, M., van Doorn, G. S., Leimar, O., and Weissing, F. J. (2007b). Wolf *et al.* reply. *Nature* **450,** E5–E6.

Worden, B. D., Skemp, A. K., and Papaj, D. R. (2005). Learning in two contexts: The effect of interference and body size in bumblebees. *J. Exp. Biol.* **208,** 2045–2053.

Wright, J. (2007). Cooperation theory meets cooperative breeding: Exposing some ugly truths about social prestige, reciprocity and group augmentation. *Behav. Processes* **76,** 142–148.

Zahavi, A. (1975). Mate selection–selection for a handicap. *J. Theor. Biol.* **53,** 205–214.