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Consistent Individual Behavioral Variation: What Do We Know and Where Are We Going?

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Abstract

The study of individual behavioral variation, sometimes called animal personalities or behavioral types, is now a well-established area of research in behavioral ecology and evolution. Considerable theoretical work has developed predictions about its ecological and evolutionary causes and consequences, and studies testing these theories continue to grow. Here, we synthesize the current empirical work to shed light on which theories are well supported and which need further refinement. We find that the major frameworks explaining the existence of individual behavioral variation, the pace-of-life syndrome hypothesis and state-dependent feedbacks models, have mixed support. The consequences of individual behavioral variation are well studied at the individual level but less is known about consequences at higher levels such as among species and communities. The focus of this review is to reevaluate and reestablish the foundation of individual behavioral variation research: What do we know? What questions remain? And where are we going next?



1. INTRODUCTION

Individuals are unique. Consistent individual behavioral variation has been traditionally ignored as noise around some evolutionary optimum. But over the past several decades, there has been a growing appreciation that individual behavioral variation may be not just the incidental, raw material for natural selection but also the product of it, making the generation and maintenance of this variation itself worthy of study. This realization arose nearly simultaneously across several different research fields. For example, in the animal sciences, researchers noticed how some individuals actively attempted to escape stressors, whereas others froze in the face of threat (Koolhaas et al. 1999), and an individual's tendency to struggle under restraint and respond to handling was described as their temperament (Burrow 1997). In behavioral ecology, some individuals were consistently more aggressive to conspecifics or more active than expected under threat of predation (Sih et al. 2004a). Collectively, in the past 20 years or so, most organismal biological fields recognized that individuals not only differ in their behavior but do so consistently, and that these individual differences could provide insights into the animal's welfare, ecology, and evolution, as well as into human behavior.

Here, we focus on the study of consistent individual behavioral variation within behavioral ecology and evolution. The purpose of this review is to assess where we stand as a field, to evaluate what questions we have asked and what questions we have answered, and to highlight what work still lies ahead. First, we explain what individual behavioral variation is and what advances in the methods are used to study it. Then, we evaluate what progress has been made on understanding the ecological and evolutionary drivers and the consequences of individual behavioral variation.

1.1. What Is Consistent Individual Behavioral Variation?

Within behavioral ecology, the study of individual behavioral variation as a broad topic of interest was established with the publication of a series of papers in the early 2000s (Dall et al. 2004; Réale et al. 2007; Sih et al. 2004a,b). These papers reviewed evidence that individuals often behave differently from each other and that they do so in a manner that is consistent over time and sometimes across contexts (for an even earlier review, see Clark & Ehlinger 1987). These papers outlined the potential ecological and evolutionary importance of such variation, and in doing so, they inspired a generation of empirical and theoretical behavioral ecologists.

One of the first stumbling blocks, common to any new field, was the establishment of common terminology. The seminal papers that established the study of consistent individual behavioral variation as a topic of interest used different terms. The highly influential papers by Sih et al. (2004a,b) used the terms behavioral types and behavioral syndromes to describe an individual's (consistent) expression of behavior and correlations among behaviors across individuals at the population level, respectively. Dall et al. (2004) used personality differences and Réale et al. (2007) used temperament. Though there are broad similarities among these terms in what they attempt to describe, there is a lack of precision in how these terms are used, which has led to an understandable criticism of the field (Carter et al. 2013, Dall & Griffith 2014, Dingemanse & Wright 2020). However, now as the study of individual behavioral variation has matured, the field appears to be coalescing around a common terminology.

We find the term consistent individual behavioral variation (or differences) to be most useful, as it operationally describes the general phenomenon. Importantly, within this broader umbrella term, more specific components of behavioral variation can be precisely defined by their relationship to statistical terms. For example, the behavioral variance within a population can be partitioned into its among-individual and within-individual variance components (**Figure 1**).

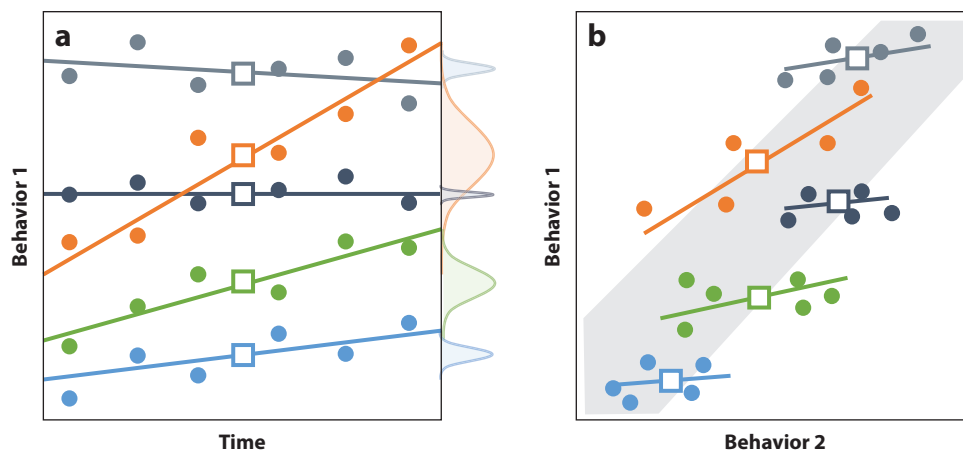


Figure 1

Patterns of consistent individual behavioral variation. (a) Individuals, represented by different colors, are repeatedly observed for the same behavior over time (*circles*). Individuals can change their behavior over time (*colored lines*) but still differ in their average behavior (*squares*), leading to among-individual variation. Individuals can also vary in their own behavior over time, leading to within-individual variation (*colored distributions on right*). (b) Individuals are observed engaging in several behaviors simultaneously multiple times. Individuals' averages of each behavior can correlate, leading to among-individual correlations (indicated by the *gray background*). An individual's expression of a behavior at a given time can also correlate with that same individual's expression of the other behavior, leading to within-individual correlations (*colored lines*). Note that the direction of the among- and within-individual correlations is independent and thus not necessarily always expected to be in the same direction.

Among-individual variation describes how different individuals are from each other in their average behavior, whereas within-individual variation describes how consistent individuals generally are in repeated expressions of behavior. Consistent individual behavioral variation exists when there is sizeable among-individual variation; that is, the behavior is repeatable (Bell et al. 2009). When one is speaking about a particular individual, it is most straightforward to refer to its average behavior or, if necessary, its behavioral type. Individuals can also covary in how they express more than one behavior. For example, if the most aggressive individuals in a population are also generally the most active ones, there is among-individual covariation in aggression and activity. This type of correlation between behaviors among individuals has been called a behavioral syndrome (Sih et al. 2004a); however, among-individual correlation is more precise (reviewed by Garamszegi et al. 2012). This is because behaviors can also covary within individuals (i.e., within-individual correlation) if both behaviors are measured repeatedly and simultaneously. For example, when a particular individual is more aggressive, it may also be more active than when that same individual is less aggressive (**Figure 1**).

Linking different aspects of behavioral variation to statistical concepts has been a major advance in the field because the hypotheses used to explain consistent individual behavioral variation are focused on different levels of biological variation (Brommer 2013, Dingemanse & Dochtermann 2013, Niemelä & Dingemanse 2018b). Among-individual (co)variation in behavior is thought to be generated by (semi)permanent genetic, maternal, developmental, or long-lasting environmental effects. In contrast, within-individual (co)variation is often the more flexible portion of behavior and thus is more likely to be influenced by short-term environmental changes or attributed to measurement error. Precision in how we communicate about different aspects of behavioral

variation is critical for our effort to be precise in the hypotheses we generate and experiments we perform about its causes and consequences.

1.2. How Do We Measure Consistent Individual Behavioral Variation?

The behavior of an individual is multifaceted. At any given moment, an individual could exhibit several different behavioral responses, for example, the speed with which they move and also the location of where that movement occurs. Additionally, the same behavioral response, like movement speed, can be expressed across different contexts, such as during foraging and during mating. Researchers must therefore make important decisions about which behavioral responses to measure, under what contexts, and most importantly, how this behavioral expression may provide insight into the behavioral decisions an individual is making.

1.2.1. Defining behavior. Now that there appears to be a growing consensus about the terminology to describe consistent individual behavioral variation, the next stumbling block has been what to call and how to interpret the behaviors we measure. Réale et al. (2007) proposed five broad categories of behavior: boldness, exploration, activity, aggression, and sociability. Importantly, Réale et al. (2007) are clear that these descriptions should be viewed as a working tool; however, in reality this categorization has instead become the de facto model for the structure of behavioral variation across all animals (Koski 2014). This has led to the conflation of behavioral variables or responses (i.e., what we measure) with behavioral axes of variation or traits (sensu human personality traits of, e.g., extraversion or neuroticism). We argue that in most situations it is only speculation to assume that two different behavioral responses (e.g., latency to leave a refuge and distance traveled in an open field) are expressions of the same underlying trait (e.g., two measurements of boldness) or different traits (one measuring boldness and the other measuring exploration; see Carter et al. 2012, Peralas et al. 2017). Instead, Réale et al. (2007) should rightly be interpreted as a hypothesis for the structure of behavioral traits. Until we know which behavioral responses are expressions of which traits, operational definitions are most precise. Define the behaviors by what is measured, for example, latency to leave a refuge or distance traveled in an open field, and leave the interpretation of the behavioral response for the discussion. This will improve precision and clarity in the field and limit the opportunity for jingle-jangle fallacies that can impede progress (Carter et al. 2013).

1.2.2. Observing behavior. The most important methodological consideration when studying individual differences in behavior is the need for repeated measurements on the same individuals, as this is the only way to estimate the among- and within-individual components of behavioral variation (Dingemanse & Wright 2020, Niemelä & Dingemanse 2018b). Combining these two components then allows us to estimate a behavior's repeatability, that is, the proportion of variation that is attributable to among-individual differences, which is now the most common metric used to identify the presence of consistent individual behavioral variation. It is worthwhile to note that reporting the among- and within-individual variance components in addition to repeatability estimates is encouraged (Dochtermann & Royauté 2019). The seminal paper by Bell et al. (2009) demonstrated that, by and large, behavior is generally repeatable (mean repeatability across all behaviors was 0.37), meaning that individual identity does explain a significant portion of behavioral variation within a population. However, this result also suggests that most behavioral variation (0.63) is not explained by individual identity, highlighting the importance of considering environmental variation and measurement error (Dingemanse & Wright 2020, Niemelä & Dingemanse 2017).

Once a researcher has chosen the most appropriate behavioral response(s) to measure, the next step is to observe and quantify the animal's behavior. This can be done under controlled settings in the laboratory or under more natural conditions in the field. The advantages of working in the laboratory are that the researcher can easily keep track of individuals and have better control over the environment that the animal experiences, therefore limiting confounding environmental variation (but too much standardization can be a bad thing too; Richter et al. 2009). An individual's behavior can be observed in standardized behavioral assays. The most common assays are open-field, emergence, novel object, and preference tests (e.g., Perals et al. 2017). The exact design of each assay often varies according to the species and the specific behaviors the researchers are interested in. The major assumption of standardized assays is that the behavior expressed under these conditions is representative of behavior that individual would express in the wild. This may (e.g., Dhellemmes et al. 2021) or may not (e.g., Laskowski et al. 2015) be the case, and validating such standardized assays is important for any study whose authors wish to generalize their findings beyond a laboratory setting.

Observing animals in the field increases the likely ecological validity of the expressed behavioral variation. Here, species that reliably use the same sites, such as birds that use nest boxes, are especially amenable, as researchers can find the same individuals repeatedly to observe their behavior directly or capture the animals to measure their behavior in more standardized assays (e.g., Dingemanse et al. 2012). Researchers have also developed in situ assays in which wild animals are able to interact with devices such as foraging tasks (e.g., Aplin et al. 2014) or model predators or conspecifics (e.g., Mathot et al. 2015). Technological advances in global positioning systems and radio tags have dramatically improved our ability to observe behavior digitally, which can provide detailed information about animal movement patterns in the wild (e.g., Hertel et al. 2021). However, field studies have drawbacks too, as with less experimental control comes the potential for confounding variables that may affect behavior in uncontrollable, unexpected, or unmeasurable ways (e.g., pseudopersonality; Niemelä & Dingemanse 2017).

Once the animal is observed, the researcher now needs to extract the relevant behavioral responses. With video observations, this is often done by hand with the aid of behavioral coding software (e.g., BORIS; Friard & Gamba 2016) with which the researcher watches the video and scores when the animal performs different actions. One of the biggest developments in the field is the widening use of more automated tracking software, which has improved the speed and accuracy with which researchers can extract behavioral data from videos (e.g., DeepLabCut; Mathis et al. 2018).

1.2.3. Analyzing behavior. Advances in statistical methods have also contributed to the expansion and robustness of the study of consistent individual behavioral variation. In particular, the application of quantitative genetic methods and the linkage of key terms to statistical definitions have reduced confusion, improved study design, and revealed more nuanced patterns of biological variation (Barbosa & Morrissey 2021, Dochtermann & Roff 2010). In particular, mixed-effects models have allowed researchers to appropriately partition behavioral variance at the among-individual (variance from individual identity) and within-individual (residual variance) levels while still accounting for important fixed effects (e.g., different treatments or environmental factors) of interest (Dingemanse et al. 2010) (**Figure 1**). Several papers explain how to apply mixed-effects models to estimate variance components across different levels and test hypotheses about the biological processes generating patterns of variation (e.g., Dingemanse & Dochtermann 2013, O'Dea et al. 2022). Such methods, quickly becoming the gold standard, allow researchers to partition variance appropriately and uncover interesting and previously underappreciated patterns of biological variation (e.g., Westneat et al. 2015).



2. EVOLUTIONARY AND ECOLOGICAL DRIVERS OF INDIVIDUAL VARIATION

In a proximate sense, repeatable variation in individual behavior stems from variation in any of the mechanisms underlying behavioral expression. The proximate mechanisms include genetic variation (reviewed by van Oers & Mueller 2010, Dochtermann et al. 2019) and environmental variation, both of which can lead to changes in or interactions with epigenetic variation (reviewed by Jablonka 2013, Ledón-Rettig et al. 2013), gene expression (reviewed by Bell & Aubin-Horth 2010), and neurological, hormonal, and metabolic processes (for a few key reviews, see Carere et al. 2010, Cummings 2015, Godwin & Thompson 2012, Lipshutz et al. 2019, Young & Wang 2004). Reviewing the literature on proximate mechanisms of consistent individual behavioral variation is beyond the scope of this review; our goal in the next sections is to focus on the ultimate mechanisms, that is, the evolutionary and ecological drivers that shape individual behavioral variation.

The interest in consistent individual behavioral variation stemmed from the realization that it might be the product rather than simply the raw material of natural selection. This realization has generated a multitude of hypotheses about the evolutionary and ecological processes that can generate and/or maintain such variation in populations. There have been several retractions in this field in the past few years (**Supplemental Table 1**), and it is particularly important to (re)assess support for these hypotheses on the basis of current empirical work. Although we have structured the hypotheses by whether they operate on evolutionary or ecological timescales, there are feedbacks between the two, so delineations between them are fluid. We list a few of the leading review articles for each hypothesis in **Figure 2** for interested readers.

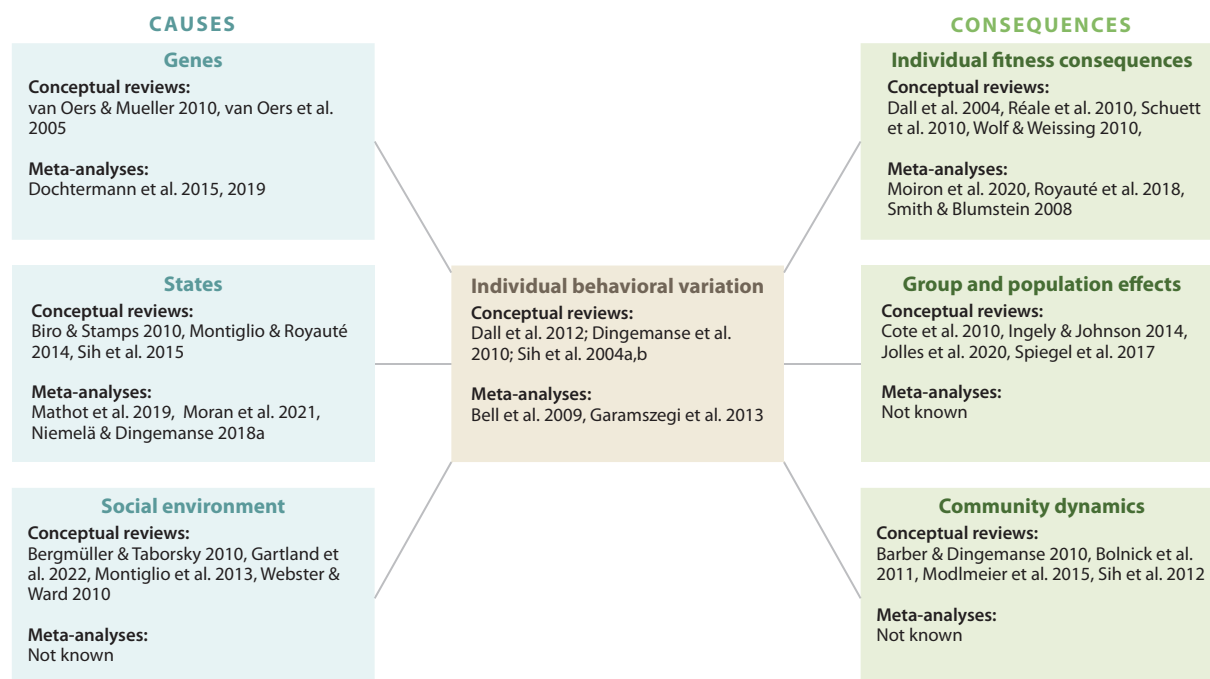


Figure 2

The study of consistent individual behavioral variation has enjoyed considerable empirical and conceptual interest for the past two decades. This provides a summary of several key reviews and meta-analyses for understanding patterns of individual behavioral variation in nonhuman animals and its ecological and evolutionary causes and consequences.

2.1. Evolutionary Drivers: Which Mechanisms Generate or Maintain Consistent Individual Behavioral Variation over Multigenerational Timescales?

From the evolutionary perspective, a behavioral strategy that increases an individual's fitness will be amplified in a population over multigenerational timescales, assuming selection pressure remains in the same direction. Because individual behavioral variation has fitness consequences (Section 3), the question is, How is among-individual behavioral variation maintained in a population; why don't all individuals behave the same way? Two general classes of drivers have been proposed to answer this question: (a) life-history trade-offs and the pace-of-life syndrome (POLS) hypothesis, and (b) fluctuating or heterogeneous selection pressures. The key difference between the two explanations is that trade-offs predict that multiple strategies can coexist by achieving similar fitness at a given time, whereas fluctuating selection predicts that there may be a single optimal strategy at any given point but that this strategy changes over time or space.

2.1.1. Life-history trade-offs and the pace-of-life syndrome hypothesis. An individual's fitness is determined largely by the number of fertile offspring that an individual produces; however, investment in current reproduction is predicted to come at the cost of greater mortality risk and a reduction in future reproduction. This trade-off between current reproduction and future reproduction can lead to the maintenance of individual behavioral variation, as individuals that prioritize current reproduction are predicted to also exhibit faster behavioral strategies (i.e., greater activity, aggression, exploration) compared with slower individuals that prioritize longer life span for future reproduction (reviewed by Dingemanse & Wolf 2010). In this way, the modern POLS hypothesis builds on classic life-history theory to predict that among-individual behavioral variation can be maintained as part of a suite of coevolved life-history, physiological, and behavioral traits that allow individuals with different strategies to achieve similar fitness over their lifetimes (Réale et al. 2010).

Although the POLS hypothesis has been widely used to explain among-individual behavioral variation, empirical studies testing this hypothesis report mixed results. This empirical work has now been well summarized by two recent meta-analyses that found that correlations between behavioral traits and life-history traits were generally not in the direction predicted by the POLS hypothesis (Moiron et al. 2020, Royauté et al. 2018) (see Section 3 for more discussion of the consequences of individual behavior on fitness). The modern POLS hypothesis was developed largely as a verbal model and is agnostic about the mechanisms generating the relationships among traits. As Mathot & Frankenhuis (2018) point out, little formal modeling has been developed since the seminal paper by Réale et al. (2010), leading to a lack of precision about which traits we expect to be related to each other and at which level of analysis (i.e., genetic versus phenotypic) these relationships should occur. The confusion between levels of biological variation has been especially problematic, as most empirical research is done at the phenotypic (i.e., individual) level, whereas life-history trade-offs are predicted to occur at the genetic level.

The most conclusive support for the POLS hypothesis would therefore be evidence of genetic correlations between individual behavioral traits and life-history traits. Indeed, there is evidence for negative genetic correlations among life-history traits (Roff 1996), but thus far, fewer studies have investigated genetic correlations between behavioral traits and life-history traits. One of the few examples of this type of correlation was done with mouse lemurs (*Microcebus murinus*) and a negative genetic correlation between emergence latency and growth rate was found (Zablocki-Thomas et al. 2019). However, another study, with crickets (*Gryllus integer*), found no clear genetic correlations between behavioral traits and life-history traits (Niemelä et al. 2013). The direction of genetic correlation may also depend on the behavioral traits measured; for instance, genetically



more exploratory crickets (*Gryllus bimaculatus*) showed shorter life span, but genetically more aggressive individuals showed longer life span (Santostefano et al. 2017a). A major need moving forward is a clear reevaluation of the POLS hypothesis to refine its predictions about the expected relationships between (which) behaviors and (which) life-history traits and the level of analysis [Dammhahn et al. (2018) open an entire special issue on the topic; Laskowski et al. 2021]. It will also be useful to identify the underlying genetic mechanisms, such as pleiotropy or linkage disequilibrium, to test under which conditions selection is likely to (de)couple the relationship between behavioral traits and life-history traits.

2.1.2. Fluctuating or heterogeneous selection. Trade-offs are predicted to allow multiple different behavioral strategies to achieve similar fitness, thus maintaining variation in the population. Alternatively, selection may instead favor a single optimal strategy at any given time, but if this optimum changes more quickly than the population can track it, this can also lead to the maintenance of variation. These selective pressures can vary over time or space as a function of an environmental gradient, such as the social environment, in the case of density- or frequency-dependent selection.

A modest number of empirical examples have investigated how selection may change over time or space and how it maintains individual behavioral variation (reviewed by Dingemanse & Réale 2013). In particular, populations with long-term monitoring programs are critical for measuring fluctuating selection pressures on behavioral traits of interest. Work on European great tits (Dingemanse et al. 2004, Nicolaus et al. 2016, Quinn et al. 2009), Siberian chipmunks (Le Cœur et al. 2015), red squirrels (Boon et al. 2007), and bighorn sheep (Réale & Festa-Bianchet 2003) has found evidence of selection on different behavioral traits that varies across years. Mouchet et al. (2021) expanded from single-population studies to show that spatial variation in selection pressures across multiple populations of great tits may be even stronger than temporal variation in selection within a single population. These empirical studies suggest two different links may occur between individual behavior and fitness. On the one hand, when resources are scarce and/or density is low, behaviors associated with greater exploration and higher aggression can help individuals increase fitness through defending territories with valuable resources; in contrast, these individuals may incur too many unnecessary costs when resources are abundant. On the other hand, when competition is high, the POLS hypothesis may predict that slow individuals with low exploration and aggression could have higher reproductive success because they produce few bigger offspring, which are more competitive than many offspring produced by fast individuals, and vice versa when competition is low.

In addition to density-dependent selection patterns, the behavioral strategies of other individuals can generate frequency-dependent selection pressures. In particular, negative frequency-dependent selection occurs when the least-common strategy in a population is favored. This pattern of selection has been used in theoretical work as a potential explanation for the generation and maintenance of among-individual behavioral variation (reviewed by Dingemanse & Wolf 2010) but has generally had little empirical testing. One of the few examples is that Kurvers et al. (2012) found no evidence for negative frequency-dependent benefits in groups of foraging geese (*Branta leucopsis*) based on the individual's boldness behavior. A set of papers found evidence for negative frequency-dependent selection in fruit flies (*Drosophila melanogaster*), but only under certain environmental conditions: Individuals with the rare behavioral strategy showed higher survival than those with the common strategy, but only under high population densities (aggressive behavior; Kilgour et al. 2018) or low nutrient conditions (foraging behavior; Fitzpatrick et al. 2007). Although few studies have explicitly tested the negative frequency-dependent selection hypothesis in the context of consistent individual behavioral variation per se, the large literature

on game theories (e.g., producer-scrrounger and hawk-dove games; Maynard Smith 1982) supports the general prediction that the success of a particular behavioral tactic often decreases as it becomes more common in the group.

Last, variation in predation pressure has been implicated as a key factor affecting patterns of among-individual behavioral variation. Currently, several examples show that behavioral variation, and specifically among-individual correlations in behavior, differs between populations that experience relatively heavy predation pressure and those that do not (Bell 2005; Dhellemmes et al. 2020; Dingemanse et al. 2007, 2020). Spatial variation in an important selective pressure, like predation, could then maintain variation in the larger population over evolutionary timescales. In addition to acting on evolutionary timescales, predation pressure may also be a key ecological driver, as direct exposure to predation generates stronger among-individual behavioral correlations within a single population (Bell & Sih 2007). What is still unclear is what exactly is the target of selection: Are predators generating correlational selection on two independent behavioral traits (i.e., boldness and aggression), or are the predators selecting for a single underlying trait of which both behavioral measures are expressions, or does predation pressure drive behavioral plasticity that subsequently shapes the correlated behavior?

2.2. Ecological Drivers: Which Mechanisms Amplify or Decrease Personality Variation Within Generations?

Even though individuals often behave consistently over time, individuals can and do adjust their behavioral expression to their current environment. So how do current environmental conditions shape consistent individual behavioral variation? Here, we focus this question by reviewing the empirical evidence for the ecological drivers of individual behavioral variation.

2.2.1. State-dependent feedbacks. A major ecological hypothesis explaining why individuals exhibit consistency in their behavior over time is that behavioral expression may be linked to more slowly changing state variables, and this link drives individual differences through feedbacks between their behavior and states. State variables are diverse and broad, and they can be intrinsic, such as an individual's body condition, its energetic rates, or its residual reproductive value, or extrinsic, such as an animal's parasite load or its position in a dominance hierarchy (reviewed by Sih et al. 2015). Importantly, states and behavior are expected to be bidirectionally linked, such that changes in state, for example, can lead to changes in behavior that then will lead to further changes in state. Positive feedbacks are most useful for explaining the maintenance (or generation) of individual behavioral variation, as negative feedbacks are expected to erode variation over time.

The most commonly investigated state variables are metabolic rates, hormone levels, and aspects of body size and condition. In fact, sufficient empirical work has investigated the links between these putative state variables and behavioral variation for several meta-analyses to be performed. Holtmann et al. (2017) compiled estimates of repeatability of several putative state variables and found that metabolic rates tend to have higher repeatabilities than hormone levels do, suggesting that metabolic rates may more likely be state variables that affect individual behavior. The meta-analysis by Niemelä & Dingemanse (2018a) found that variation in several putative intrinsic state variables, including body size, body condition, metabolic rates, and hormone levels, explained a small (approximately 5%) but significant portion of the among-individual variation in behavior and that metabolic rates had a slightly higher correlation generally. The meta-analysis by Mathot et al. (2019) explored the relationship between behavioral variation and metabolic rates in particular and found stronger positive relationships between metabolic rates



and behaviors that are likely to be related to energy intake or expenditure. Altogether, the data point to (aspects of) metabolism being more likely to be linked to (some) aspects of behavioral variation, than other suggested state variables such as hormone levels or body size. However, this linkage is likely modest at best and more complicated than a simple one-to-one relationship, which is not surprising given all the demands an individual faces.

Pathogens and social status are two extrinsic factors that have been proposed as key state variables influencing behavior. With pathogens, parasites, and contaminants, there are likely complex interactions between individual behavior, likelihood of exposure, and subsequent effects of infection on an individual's intrinsic state and behaviors (reviewed by Kortet et al. 2010, Montiglio & Royauté 2014). For example, individuals that exhibit greater activity may increase their exposure to pathogens or contaminants, and if infection lowers energy reserves, this could lead to negative feedbacks, such that those individuals reduce their activity. Alternatively, it is also possible that if infection instead reduces that individual's expected future reproduction, it may then increase its activity to reproduce as quickly as possible (positive feedback loop). Similar complex interactions and feedbacks might occur between an individual's social status, other intrinsic state variables, and the individual's behavior (e.g., Cornwallis & Birkhead 2008, Favati et al. 2014). Increasing social status in a dominance hierarchy often gives the individual greater access to resources, which can influence body size, energy reserves, and future reproductive potential, all of which may influence later behavior. The role of social interactions is discussed in more detail in Section 2.2.2.

Importantly, most research testing state-dependent hypotheses is generally correlative (reviewed by Biro & Stamps 2010), which limits our interpretation of causality. As opposed to a causal feedback mechanism in which one trait directly affects the other, states and behavior may instead be linked through underlying genetic correlations. For example, in Atlantic salmon (*Salmo salar*), transgenic individuals with increased growth rate were more likely to forage in the presence of predators (Abrahams & Sutterlin 1999). The most rigorous tests of state-dependent feedbacks would involve direct manipulations to states or behaviors to test whether this leads to changes in the other trait and, importantly, to subsequent feedbacks between them. Manipulation of an individual's energy status is the most common method for testing state-dependent feedbacks. Experimental studies commonly find that changes in energy states lead to behavioral change; a recent meta-analysis of studies that conducted experimental manipulations of an individual's nutritional or energetic state found that reduced nutritional condition led to increased risk-taking behavior (Moran et al. 2021), suggesting a potential negative feedback loop if risk-taking behavior increases their energetic states, which should erode variation among individuals. Another example of a potential negative feedback loop was found in Belding's ground squirrels (*Urocitellus beldingi*); when individuals were in better body condition, they were more likely to reduce their exploration and activity levels than when they were in worse body condition (Dosmann et al. 2015). In contrast, Sakai (2020) showed that clonal geckos (*Lepidodactylus lugubris*) reared on restricted diets (lower body condition) exhibited lower risk-taking behavior, though this effect dissipated as the animals aged. However, not all experimental manipulations were successful at altering behavior. In red knots (*Calidris canutus*), gizzard mass (as a proxy of energy reserved) is correlated with individual exploration, but direct manipulations of gizzard mass did not influence exploration level (Bijleveld et al. 2014), demonstrating that there is not a strong causal link between this measure of energy reserves and individual behavior in this species. Another experimental study using red knots did find positive feedback between gizzard mass and foraging effort, but it only weakly explained individual variation in behavior and in states (Mathot et al. 2017).

Altogether, there is evidence that individual behavior is linked with individual states, especially aspects of energy reserves or metabolism. So far, most manipulative evidence suggests the presence of negative feedbacks between state variables and behavior. However, given that negative

feedbacks are expected to erode the differences among individuals over time, just the presence of negative feedbacks does not adequately explain the continued maintenance of individual behavioral variation.

2.2.2. Social interactions. Social interactions and the social environment generally are well-known influencers of individual behavior (reviewed by Gartland et al. 2022, Webster & Ward 2011). The social niche specialization hypothesis predicts that, through repeated interactions with conspecifics, individual behavioral variation increases as a result of competition avoidance (Bergmüller & Taborsky 2010, Montiglio et al. 2013). Indeed, in one of the first explicit empirical tests of this hypothesis, foraging sticklebacks exhibited consistent individual differences in behavior, but only when these differences helped the animals avoid competition (Laskowski & Bell 2013). The emergence of social hierarchies is a classic example of social niche differentiation, and evidence shows that individual behavior can often (but not always, e.g., Devost et al. 2016) predict social position or dominance (reviewed by Briffa et al. 2015).

The social niche specialization hypothesis predicts that among-individual behavioral variation should become stronger with repeated social interactions. Several empirical papers explicitly testing this prediction in social spiders were recently retracted (**Supplemental Table 1**); however, there are numerous other tests of this hypothesis. In support of this prediction, a recent study of field crickets (*G. bimaculatus*) did find that social interactions increased among-individual variation in aggression (Jäger et al. 2019). However, perhaps more studies found no effect of increasing social familiarity on individual behavioral variation (Bierbach et al. 2017, Carter et al. 2014, Laskowski & Bell 2014). In fact, there is also evidence for the opposite effect of social interactions on behavior: Studies of fish (Jolles et al. 2016) and birds (McCune et al. 2018) found that individuals were more likely to adjust their behavior to that of their group-mates as a result of social experience, thus decreasing among-individual behavioral variation and potentially increasing among-group variation (Munson et al. 2021). Altogether, social interactions are important drivers of behavioral expression generally (reviewed by Gartland et al. 2022, Webster & Ward 2011). Current evidence does not strongly support the prediction that repeated social interactions lead to greater individual behavioral divergence; in fact, in some species they may lead to the opposite: greater behavioral conformity. Whether we should expect social interactions to lead to behavioral divergence, conformity, or no effect at all likely depends on the ecology of the species. Social niches might be expected to play a stronger role in species that maintain stable group membership over time than in species with more fluid membership in which repeated interactions with the same individuals are less common.

Indirect genetic effects have the potential to alter how individuals respond to each other; they could be another factor that explains why effects of social interactions on individual behavior vary (reviewed by Schneider et al. 2017). For example, if individuals possess genetic variants that increase their own aggressive behavior and reduce the aggressive behavior of their opponents (e.g., Santostefano et al. 2017b), this may lead to social niche differentiation. However, if the indirect genetic effect is in the same direction as the direct genetic effect, for example, a genotype that increases (or reduces) one's aggression also increases (or reduces) aggression of other individuals, then this could lead to synergistic effects in which among-individual variation will be reduced in favor of behavioral conformity. For example, in honey bees (*Apis mellifera*), allele frequency of a colony predicts the aggressiveness level at the colony level, but an individual's genotype could not predict an individual's aggressiveness (Avalos et al. 2020), suggesting behavioral conformity within a colony through indirect genetic effects. In *Drosophila simulans*, individuals show opposite behavioral responses if they interact with another individual with the same genotype (Jaffe et al. 2020), leading to social niche differentiation; however, individuals show more similar behavioral



responses when they interact with an individual with a different genotype, leading to behavioral conformity.

2.2.3. Individual behavioral variation in the absence of genetic and environmental variation. Evolutionary and ecological models often rely on either genetic or environmental variation to generate behavioral variation. However, a growing number of studies have shown that individual behavioral variation arises even in the absence of variation in genetic and environmental factors (Bierbach et al. 2017, Freund et al. 2013, Schuett et al. 2011, Werkhoven et al. 2021). It is unlikely that any experiment can completely eliminate environmental variation [in fact, the lack of environmental variation may contribute to the stochasticity of some phenotypic expression (Richter et al. 2009)], and stochastic molecular or biological processes are inevitable during development. But such micro-environmental variation and developmental noise are not generally appreciated as major drivers of individual behavioral variation in behavioral ecology [but more so in other fields (Vogt 2015)]. These findings highlight the fact that our understanding of the factors driving the emergence of individual behavioral variation will likely remain incomplete if we do not understand how this variation is shaped during development (Stamps & Groothuis 2010).

Regardless of the mechanisms initially generating behavioral variation even among otherwise identically treated, genetically identical animals, an intriguing evolutionary hypothesis is that such variation could itself be adaptive. In the bet-hedging hypothesis, diversifying phenotypes of the same genotype ensures that at least some offspring could survive given unpredictable environmental fluctuations (Simons 2011). Bet-hedging strategies function at the genotype level: Individuals with the same genotype show different phenotypes (high among-individual variation) given the same environmental conditions. Testing for bet-hedging can be challenging because complete tests would require fitness to be tracked over many generations, but some observations may imply a potential adaptive bet-hedging strategy. For example, in *D. melanogaster*, a study found that some genotypes generated more behavioral variation than did other genotypes (Ayroles et al. 2015). Developmental noise itself could be the mechanism for bet-hedging, as genotypes may differ in stochastic epigenetic modifications during development (Herman et al. 2014).

3. EVOLUTIONARY AND ECOLOGICAL CONSEQUENCES OF INDIVIDUAL VARIATION

Interest in consistent individual behavioral variation has been spurred, at least in part, by the potential consequences it can have for ecological and evolutionary processes (reviewed by Wolf & Weissing 2012). There has been considerable theoretical and conceptual effort to explore these consequences across multiple levels—from determining individual fitness to influencing population dynamics and species interactions and, finally, to affecting community- and ecosystem-level processes. Specifically, an individual's consistent behavioral response may influence its own fitness, role in a group, or interactions with other individuals (hetero- or conspecific), whereas the average behavior or the magnitude of among-individual variation within a population may influence group-, species-, and community-level dynamics. The greatest empirical effort thus far has been devoted to understanding how individual behavior influences individual fitness and population dispersal. Although it is of considerable conceptual interest, far less empirical work has been done testing how individual behavioral variation may influence processes at the community level.

3.1. Individual-Level Consequences

Individual behavior is predicted to have consequences for individual growth, survival, and reproductive success. Particularly, the POLS hypothesis predicts that riskier behaviors can increase



growth and early reproductive success but that they would do so at a cost to survival and future reproductive success (Réale et al. 2010). An early meta-analysis by Smith & Blumstein (2008) supported this prediction by showing that bolder behavior increased reproductive success but incurred greater mortality risks, especially among males. A more recent meta-analysis that partitioned the among- and within-individual-level correlations between risky behaviors and survival (Moiron et al. 2020) showed that among-individual variation in risky behaviors did explain a small but significant portion of the variation in survival ($\sim 6\%$), but that individuals that exhibited riskier behavior lived longer in studies that had been conducted in the wild, which is the exact opposite direction predicted by the POLS hypothesis. This result appears counterintuitive at first. However, classic life-history theory may provide an explanation: Life-history trade-offs, such as those predicted by the POLS hypothesis, are expected only when there is strong among-individual variation in resource allocation. However, if there is stronger among-individual variation in resource acquisition, this can instead lead to the appearance of a positive correlation at the among-individual level (van Noordwijk & de Jong 1986). Laskowski et al. (2021) suggested that because some behaviors are more likely to be associated with resource acquisition as opposed to resource allocation, positive as opposed to negative relationships between behavior and life-history traits such as survival could be expected.

3.2. Group- and Population-Level Consequences

Individual behavior modulates how conspecifics interact (reviewed by Gartland et al. 2022, Webster & Ward 2011) and thus can have important consequences on group and collective behavior (reviewed by Jolles et al. 2020). Indeed, considerable empirical work now shows that groups differ in their group foraging patterns (e.g., Dyer et al. 2009), collective behavior (e.g., Jolles et al. 2017), and social networks on the basis of the individuals that compose those groups. In regard to social networks, a general pattern seems to emerge in which shyer individuals have fewer but stronger social contacts than do bolder individuals that typically have more but weaker social contacts (Aplin et al. 2013, Pike et al. 2008, Snijders et al. 2014). This pattern means that bolder individuals might play especially important roles in spreading information or disease within groups given their more dispersive social networks. Consequences of individual behavior within a group context have special implications in social and eusocial species as reviewed by Jandt et al. (2014). It is important to note, however, that several empirical papers that have explored the consequences of individual behavior on task specialization and colony success in species of social spiders have been recently retracted (**Supplemental Table 1**).

There has also been considerable empirical work testing how individual behavior can influence dispersal, which can be critical for gene flow, population dynamics, and range expansions (reviewed by Cote et al. 2010a). For example, Duckworth & Badyaev (2007) found that the most dispersive western bluebirds (*Sialia mexicana*) were also the most aggressive, which allowed these individuals to outcompete the local mountain bluebirds and thus advance their overall range. Other work with mosquitofish (*Gambusia affinis*) demonstrated that less social individuals were more likely to disperse farther (Cote et al. 2010b). However, a follow-up study found that the relationship disappeared if the animals were measured under the threat of predation (Cote et al. 2013). This result may be of particular importance for those interested in the influence of individual behavioral variation on invasion dynamics (Carere & Gherardi 2013, Chapple et al. 2012). For example, if invaders are released from native predators in their introduced range, and if behavior-dependent dispersal is stronger when predators are absent, this might allow invaders to expand their ranges especially quickly.



If individual behavior drives differences in dispersal, this could then lead to nonrandom distributions of individuals across the landscape. Such habitat-matching is predicted to be common (reviewed by Jacob et al. 2015). There is also considerable evidence that individual behavior can drive differences in movement patterns and habitat use across a wide variety of taxa (reviewed by Spiegel et al. 2017). Importantly, behaviorally mediated habitat use coupled with assortative mating preferences sets the stage for potential speciation implications (reviewed by Ingley & Johnson 2014). Several examples show not only that individuals often prefer mates with similar behavioral responses (reviewed by Schuett et al. 2010) but also that these assortative pairs often also enjoy higher reproductive success (e.g., Ariyomo & Watt 2012, Gabriel & Black 2012).

3.3. Consequences for Species Interactions and Communities

Individual behavior can also influence how different species interact with each other. There has been a particular focus on the role of behavior in mediating the outcome of predator–prey interactions (reviewed by Toscano et al. 2016) (see **Supplemental Table 1**). In particular, functional responses, which describe intake rates of predators across prey density, provide a useful link between individual behavior and species interactions. Functional responses can be used to predict the potential stability of predator–prey interactions over ecological timescales, and if behavior influences predator foraging strategies (reviewed by Araújo et al. 2011), then individual variation in predator behavioral strategies can alter how we expect species to interact (reviewed by Bolnick et al. 2011).

Classic ecological theory often uses the expected outcome of the average individual in a population to characterize the interaction between two species. However, if instead a curvilinear interaction function (like a functional response) is averaged over all individuals in the population (all of which exhibit different behaviors), then the expected outcome can be quite different. This is known as Jensen's inequality, and theoretical work shows that this phenomenon can lead to quantitatively and qualitatively different predictions about trophic interactions (reviewed by Bolnick et al. 2011). Nevertheless, empirical testing of the influence of individual behavioral variation per se on food webs is still limited. Sommer & Schmitz (2020) provide one of the few examples and show that grasshoppers (*Melanoplus femurrubrum*) that exhibit different consistent behaviors also differ in how they respond to predation threat (from spiders), generating differential effects on lower trophic levels. It is noteworthy that a few key examples that claimed to show that individual behavior altered trophic interactions have been retracted or have editorial concerns (see **Supplemental Table 1**). In contrast, a recent paper found that the individual behavior of the predatory European perch (*Perca fluviatilis*) in mesocosms did not appear to directly influence trophic interactions within aquatic food webs. Instead, the behavior of the predators did influence the lower trophic levels via an indirect effect through predator growth (Laskowski et al. 2022).

Interactions that occur between hosts and parasites are a special type of species interaction. The potential consequences of individual behavioral variation on pathogen or parasite exposure and infection have received growing attention (Coats et al. 2010, Kortet et al. 2010). Disentangling cause from consequence is difficult, as individual behavior will influence infection and transmission probabilities and then, in turn, infections may alter behavior, including individual behavioral variation specifically (Coats et al. 2010, Ezenwa et al. 2016). Boyer et al. (2010) demonstrated a unidirectional effect of individual behavior on parasite load: In Siberian chipmunks (*Tamias sibiricus*) an individual's activity and exploration predicted its tick load, but not vice versa, demonstrating that the animal's behavior drove its exposure to parasites. Understanding host–parasite dynamics will be closely linked with work on social networks and state-dependent feedback loops (Sih et al. 2018).

3.4. Consequences for Management and Conservation

Finally, individual behavioral variation can have important consequences for management and conservation practices. Arlinghaus et al. (2017) and Mittelbach et al. (2014) review how individual behavioral variation and human-induced behavioral change, for example, as a result of hunting or harvesting, can substantially affect future ecological and evolutionary processes and managerial decisions. Both groups suggest that generally, intensive harvesting should select for less active, shyer individuals remaining in the populations. As a counterpoint, Geffroy et al. (2015) suggest that nature-based, nonconsumptive tourism could instead lead to decreased fearfulness in populations as the animals become accustomed to human interactions, which may influence their interactions with natural predators, as they may not flee as quickly as they should.

4. WHERE ARE WE GOING NEXT?

It has been nearly two decades since the publication of the seminal papers that established the study of consistent individual behavioral variation as a topic of general interest in ecology and evolution. Since then, the field has grown strong conceptual and theoretical interest, and consistent individual behavioral variation has become a unifying theme across many disciplines within broader ecological and evolutionary research (**Figure 2**). Empirical work has quickly accumulated, generating the opportunity for meta-analyses to make general conclusions to test different hypotheses. By reevaluating and reestablishing what we know about the field's foundations, we can better see where we need to go next.

SUMMARY POINTS

1. Clarifying terminology with operational definitions and the adoption of mixed modeling statistical techniques have increased the precision with which we talk about and investigate individual behavioral variation.
2. The structure and relationships among behavioral responses that consistently differ among individuals are still largely unclear. Although we have hypotheses about what we think are the fundamental axes of behavioral variation, this structure can be uncovered only through comprehensive, comparative behavioral data collection.
3. Modest evidence suggests that some behaviors, especially those linked with energy acquisition and expenditure, are linked to metabolism, energy reserves, or both. Most evidence suggests that if state-dependent feedbacks do exist, they are likely negative, so it remains unclear whether such feedbacks suffice to explain long-lasting differences in individual behavioral variation.
4. The pace-of-life syndrome hypothesis lacks support for its general predictions at the among-individual level; the field is currently in the process of refining this hypothesis to make its predictions more specific about particular behaviors and levels of analysis.
5. There is relatively strong evidence to demonstrate that individual behavioral variation has consequences for individual fitness, especially survival. Current data also generally support that selection pressures fluctuate over time and especially across space.
6. Social interactions clearly influence individual behavior, but current evidence suggests that repeated social interactions are most likely to lead to weaker among-individual



behavioral variation through conformity rather than increasing such variation, though this relationship may vary according to species ecology.

7. Empirical evidence to support theoretical predictions about the consequences of individual behavioral variation on species interactions and communities is largely absent.

FUTURE ISSUES

1. What is the structure, or what are the axes of variation, of individual behavioral variation? Is this structure conserved across taxa or does it vary according to some aspect of species ecology?
2. Which behaviors are most likely to be linked in state-dependent feedbacks, and what is the nature of these feedbacks? How do these feedbacks interact with trade-offs in other costly traits, such as life-history traits?
3. What role do stochastic processes such as developmental noise contribute to the emergence of individual behavioral variation? What mechanisms do individuals use to shape their behavioral decisions over their lifetimes?
4. How does the presence of individual behavioral variation contribute to species interactions? Are these effects mediated through changes in other processes, such as changes in individual state variables or social networks?

DISCLOSURE STATEMENT

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- Carere C, Maestripieri D. 2013. *Animal Personalities: Behavior, Physiology, and Evolution*. Chicago: Univ. Chicago Press
- Stoffel MA, Nakagawa S, Schielzeth H. 2017. rptR: repeatability estimation and variance decomposition by generalized linear mixed-effects models. *Methods Ecol. Evol.* 8:1639–44
- An introduction to repeatability estimation with rptR: <https://cran.r-project.org/web/packages/rptR/vignettes/rptR.html>. This vignette provides a tutorial on how to estimate repeatability of repeated measures data using the rptR package in R.
- Wilson AJ, Réale D, Clements MN, Morrissey MM, Postma E, et al. 2010. An ecologist's guide to the animal model. *J. Anim. Ecol.* 79:13–26
- WAMwiki, the wild animal models wiki: <https://www.wildanimalmodels.org>. This wiki page is associated with Wilson et al. (2010), providing specific examples with accompanying code on how to run animal models in several different statistical programs, including R and ASReml.