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The Evolution of Animal Personalities

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Introduction

In many animal species, individuals of the same sex, age, and size differ consistently in whole suites of correlated behavioral tendencies, comparable with human personalities (Clark and Ehlinger 1987; Digman 1990; Gosling 2001; Sih et al. 2004a). Individual birds, for example, often differ consistently in the way they explore their environment, and these differences are associated with differences in boldness and aggressiveness (Groothuis and Carere 2005). In rodents such as mice and rats, individuals differ consistently in the way they deal with environmental challenges, and such differences encompass exploration, attack, avoidance, and nest-building behavior (Koolhaas et al. 1999). Interestingly, personality differences are often associated with morphological (Ehlinger and Wilson 1988), physiological (Korte et al. 2005), and cognitive (Reddon and Hurd 2009) differences among individuals (see also chapter 12). In this chapter we focus on the evolutionary causes of animal personalities (Wilson 1998; Buss and Greiling 1999; Dall et al. 2004). What are the factors promoting the evolution of personalities? And how do these factors shape the structure (what type of traits are associated with each other?) and the ontogenetic stability of personalities?

Understanding the evolution of animal personalities (henceforth personalities) requires a shift in our thinking about animal behavior (Wilson 1998). While behavioral ecologists have traditionally "atomized" the organism into single behavioral traits that are studied in isolation (Gould and Lewontin 1979), the study of personalities requires a more holistic approach for at least two reasons. First, personalities refer to suites of correlated traits (Sih et al. 2004a, b) that are stable across part of the ontogeny of individuals (different authors use different criteria for such stability, ranging from weeks to years, Sih and Bell 2008). Consequently, interdependencies between multiple different traits (e.g., the relationship between the boldness of an individual and its aggressiveness and exploration behavior) and the same trait expressed at different points during ontogeny (e.g., the relationship between juvenile and adult aggressiveness) have to be taken into account. Second, on a proximate level, trait correlations are often caused by genetic (Mackay 2004), hormonal (Ketterson and Nolan 1999), or cognitive (Rolls 2000) mechanisms affecting multiple traits at the same time. In order to understand the evolution of such trait correlations, we need an approach that integrates mechanisms and adaptation (Tinbergen 1963).

Personalities refer to differences in suites of correlated behavioral traits that are stable over part of the ontogeny of individuals. In some cases, personality differences are associated with differences in state (McNamara and Houston 1996), that is, with differences in the morphological (Ehlinger and Wilson 1988), physiological (Koolhaas et al. 1999), or cognitive (Howard et al. 1992) characteristics or with environmental conditions (Wilson 1998) that individuals face. Some state differences are readily observable (e.g., differences in size, sex, or position in dominance hierarchy) while others are less conspicuous (e.g., differences in nutrition, stress responsiveness, or experience).

The state of an individual may affect the cost and benefits of its actions, and thus its optimal behavior (McNamara and Houston 1996; Houston and McNamara 1999; Clark and Mangel 2000). In such cases, individuals benefit from adjusting their behavior to their current state by expressing state-dependent behavior (condition-dependent behavior, phenotypic plasticity). Importantly for personalities, single states often affect the costs and benefits of multiple behavioral traits at the same time (McNamara and Houston 1996). Differences in states thus provide a potentially powerful explanation for differences in suites of correlated behavioral traits.

Explaining personalities in terms of differences in state, however, requires us to provide answers to two basic questions. First, why do individuals differ in states in the first place? In many cases, the maintenance of such differences seems puzzling. Why, for example, should individuals differ in physiological characteristics such as stress responsiveness (Aron and Aron 1997; Koolhaas et al. 1999) or basal metabolic rate (Careau et al. 2008)? Second, why are such differences stable over time? Many states (e.g., energy reserves, experience, parental investment received, future fitness expectation) are affected by many different factors, including an individual's own behavior. Such states are potentially highly variable over time. Why, then, should differences in states be stable over time and what are the mechanisms that give rise to such stability?

Differences in state provide a plausible explanation for personality differences (Dall et al. 2004; Sih and Bell 2008), but only a partial one. Personality differences can also be observed for individuals that do not seem to differ in states relevant to the observed behavioral differences. In fact, many empirical studies that report personality differences control for state differences among individuals (Verbeek et al. 1994; Dingemanse et al. 2002; 2007; Bell 2007). The observation of personalities among individuals that do not differ in states is particularly puzzling. First, why should individuals differ in their response to the same problem (e.g., how to explore the environment) when facing identical costs and benefits associated with behavioral actions? Should we not rather expect that any given problem has a unique optimal behavioral solution? Second, why are the responses to different problems sometimes correlated with each other (Clark and Ehlinger 1987; Digman 1990; Gosling 2001; Sih et al. 2004a)? Why should a bold individual, for example, be more aggressive than a shy conspecific, and why should bold individuals tend to remain bold throughout ontogeny? Such limited plasticity seems especially surprising since behavior, in contrast to many morphological features, is often thought to be highly plastic (but see DeWitt et al. 1998), and such plasticity would indeed seem to be advantageous (Wilson 1998; Dall et al. 2004).

These are the questions we address in this chapter. We will organize our discussion under the two main themes of variation and correlation, reflecting two main aspects of personalities. We first focus on the causes of variation within populations. In particular, we discuss how random causes, frequency-dependent selection, spatiotemporal variation in the environment, and non-equilibrium dynamics can give rise to variation in behavior and states underlying behavior. We then focus on the two types of behavioral correlations that define personalities, that is, correlations over time and across contexts. In particular, we will discuss the role of the architecture of behavior, stable state differences, and social conventions in causing stable behavioral correlations.

Causes of variation

Individuals can differ substantially in their behavioral responses when confronted with the same problem (e.g., how to explore the environment, how to respond to a predator), and such behavioral variation is a key feature of personalities (Clark and Ehlinger 1987; Digman 1990; Gosling 2001; Sih et al. 2004a). Behavioral variation can take various forms. In some cases, variation has a broad unimodal distribution (e.g., as in the case of variation in many human personality traits, Nettle 2006), while in other situations a small number of discrete variants coexist (e.g., variation in mating strategies, Gross 1996). As discussed above, behavioral variation may or may not be associated with variation in states among individuals. Moreover, behavioral variation may or may not be associated with genetic variation (Wilson 1994; Bouchard and Loehlin 2001).

In this section we focus on the ultimate causes of the emergence and maintenance of behavioral variation. Since our focus is on adaptive behavioral differences, we will not discuss processes that give rise to nonadaptive behavioral variation such as, for example, mutation. As we have emphasized above, adaptive behavioral variation is often caused by variation in states and state-dependent behavior, and we briefly discuss the two main routes to state differences among individuals, evolved vs. random state differences. We then discuss two basic and well-studied mechanisms that can give rise to adaptive variation in behavior, frequency-dependent selection and spatiotemporal variation in the environment. We conclude this section by discussing how non-equilibrium dynamics can give rise to variation among individuals.

DIFFERENCES IN STATES

State differences among individuals are ubiquitous: pick any two individuals within a population and typically you find that these individuals differ in some aspects of their morphological, physiological, cognitive, or environmental condition. These state differences are an important source of adaptive behavioral differences. In many situations, aspects of the state of an individual are under the direct control of that individual. Individuals typically have, for example, the option to choose among different environmental conditions (e.g., habitats, social environments) or the opportunity to fine-tune certain aspects of their physiology (e.g., stress responsive system, basal metabolic rate). Why should individuals that do not initially differ in states make different decisions? At first sight, one would perhaps expect that there is one optimal option among different states. State differences among individuals, however, need not always reflect adaptation. In many situations, aspects of the state of an individual are affected by factors that are not under the individual's control. Differences in states arise whenever these factors differ between individuals. One individual, for example, grows up in a rich environment while another grows up in a poor environment. One individual finds a high-quality food source and thus increases its nutritional condition while another one does not find such a food source. One individual gets infected by a parasite while another one does not. Examples of state differences caused by such random factors abound.

FREQUENCY-DEPENDENT SELECTION

In groups of foraging animals, individuals typically have the choice between two different behavioral roles (Giraldeau and Beauchamp 1999): either search for food sources on their own ("producers") or exploit food sources discovered by others ("scroungers"). In this case, the benefits associated with a phenotype depend on the frequency of that phenotype in the population (Barnard and Sibly 1981): the higher the frequency of scroungers in a group, the less beneficial this role becomes, since more scroungers compete for fewer resources. Such situations give rise to so-called negative frequency-dependent selection (Maynard Smith 1982), a form of selection that is known to be an important source of variation within populations (Heino et al. 1998; Dugatkin and Reeve 2000; Sinervo and Calsbeek 2006).

In situations with negative frequency-dependence selection, selection acts to increase the frequency of rare phenotypes within populations. In its simplest form, as in the producer-scrounger example above (Barnard and Sibly 1981), this rarity advantage gives rise to two phenotypes that coexist in stable frequencies within a population. Moreover, whenever individuals have the choice between more than two phenotypes, negative frequency dependence can give rise to situations in which any number of phenotypes can coexist in stable frequencies. When negative frequency dependence interacts with positive frequency dependence, as for example in the so-called rock-paper-scissors games (Maynard Smith 1982), selection can give rise to a dynamic equilibrium in which multiple phenotypes coexist at continuously changing frequencies (Sinervo and Lively 1996; Sinervo and Calsbeek 2006).

Negative frequency-dependent selection can, as in the producer-scrounger situation, give rise to adaptive behavioral variation among individuals that do initially not differ in states. The same process can also give rise to adaptive state differences among individuals. For example, the benefits of a particular physiological or cognitive architecture (e.g., particular level of stress responsiveness, particular learning rule) might depend on how common this architecture is in the population, thus promoting the coexistence of different architectures (Wolf et al. 2008). Similarly, the benefits of being in a particular environment (e.g., territory, habitat, or social position) might depend on the frequency with which other individuals choose this environment, thus promoting the coexistence of individuals in different environmental states (Ens et al. 1995; Wilson 1998).

Negative frequency-dependent selection is a common phenomenon in social interactions (Maynard Smith 1982, Svensson and Sheldon 1998; Dugatkin and Reeve 2000). It occurs, for example, in interactions between individuals in which adopting a different phenotype confers an advantage over the interacting partner. Such situations occur in agonistic interactions, as for example hawk-dove–like encounters (Maynard Smith 1982), in which the aggressive hawk strategy is beneficial whenever the opponent plays dove, whereas the nonaggressive dove strategy is beneficial whenever the opponent plays hawk. They also occur in more cooperative interactions, when social partners benefit from diversifying into different behavioral roles that complement each other (Clark and Ehlinger 1987). The benefits of such behavioral complementarity can be caused by various mechanisms. Choosing different behavioral roles may help, for example, to avoid competition between partners, to reap the benefits of behavioral specialization, or to reduce the risk associated with a certain strategy.

Negative frequency dependence can also be caused more indirectly (Kokko and Lopez-Sepulcre 2007) via competition for different types of resources that have density-dependent benefits (i.e., the benefits of a resource decrease with the number of individuals that compete for that type of resource). Such density dependence gives rise to negative frequency dependence: the more individuals compete for a particular type of resource (e.g., a territory, habitat, mate), the less beneficial it becomes. Density-dependent resource competition can thus promote the coexistence of individuals that exploit different resources (Wilson 1998).

Negative frequency-dependent selection can thus give rise to adaptive variation in states and/or behavior among individuals. In principle, this variation might or might not be associated with genetic variation (Maynard Smith 1982; Wilson 1994). Consider, for example, a situation in which two phenotypes coexist with frequencies of 30% and 70% (e.g., producer and scroungers, individuals with a low and a high basal metabolic rate, or slow and fast learners). This phenotypic variation can arise in a population of genetically identical individuals that adopt each of the phenotypes randomly but with the same probability (choose one phenotype in 30%, the other in 70% of the cases), as for example in the case of environmental sex determination, where mixed broods arise despite the fact that individuals do not differ genetically with respect to sex determination. However, variation can also arise in a genetically polymorphic population in which a fixed proportion of individuals adopts each of the phenotypes (30% of the individuals choose one phenotype, 70% the other). Individual differences in foraging behavior in the larvae of the fruitfly (*Drosophila melanogaster*) provide a good example of the latter situation (Fitzpatrick et al. 2007). In natural populations, a dimorphism in foraging strategies can be observed ("rover" vs. "sitter" individuals). This dimorphism is based on a single major gene polymorphism that is maintained by negative frequency-dependent selection; both the rover and the sitter allele attain their highest relative fitness when rare in the population.

SPATIOTEMPORAL VARIATION IN THE ENVIRONMENT

Natural selection shapes the phenotype of individuals to match their environment, and in many natural situations, the environment and thus the optimal phenotype varies in space or in time. What is the expected evolutionary outcome in such a situation? In particular, should we expect that, as it is often thought to be the case (Nettle 2006; Koolhaas et al. 2007; Penke et al. 2007), environmental variation promotes phenotypic variation within populations? And if so, should we expect that such phenotypic variation is associated with genetic variation? The answers to these questions depend on the situation (Hedrick 1976; 1986; Seger and Brockmann 1987; Moran 1992; Leimar 2005) and, in particular, on whether the population faces spatial or temporal variation in the environment (for an alternative classification, see Frank and Slatkin 1990 and Donaldson-Matasci et al. 2008) and on how well individuals can match their phenotype to their environment.

To understand the importance of phenotype-environment matching, consider first a situation in which individuals can match their phenotype to their environment in an error- and cost-free manner, be it via habitat choice, habitat tracking and limited migration (i.e., the environment is chosen to match the phenotype), phenotypic plasticity (i.e., the phenotype is chosen to match the environment), or a combination of these processes. In such a situation evolution is expected to result in perfect phenotype-environment matching. No variation is maintained within each environment. This example is certainly extreme and unrealistic (DeWitt et al. 1998); it illustrates, however, that environmental variation can give rise to phenotypic variation only within environments in situations with limited phenotype-environment matching.

Consider now the most basic scenario of spatial variation. A population inhabits an environment with two types of habitats, so that different phenotypes are favored within each habitat. As we have just seen, if perfect phenotype-environment matching is possible, no variation within environments can be maintained. This is different in situations in which there is an intermediate degree of phenotype-environment matching, that is, in situations where habitat choice (or habitat tracking) or phenotypic plasticity is possible but not perfect. Individuals might, for example, make errors when choosing habitats. In such situations, phenotypic variation can be maintained both at a population level and within each habitat (Seger and Brockmann 1987). The reason for this is as follows. Since some degree of phenotype-environment matching is possible, coexisting genotypes (or phenotypes of a plastic genotype) experience different environments, and each genotype will, on average, experience more often the environment in which it is favored. Variation within environments arises since phenotype-environment matching is not perfect. The resulting phenotypic variation can in principle be due to plasticity, genetic polymorphism, or a combination of both factors.

A good example of adaptive variation caused by spatial variation in the environment is provided by the bluegill sunfish (*Lepomis macrochirus*) that inhabit North American freshwater lakes (Ehlinger and Wilson 1988). In these populations, consistent individual differences in foraging tactics (e.g., hover duration, pattern of movement) have been described. It turns out that these differences can be associated with differences in habitat use: the most efficient foraging tactic depends on whether an individual is in littoral or open water zones, and individuals that employ different tactics are preferentially (but not exclusively, thus phenotype-environment matching is not perfect) found in the habitat that fits their foraging tactic best. Interestingly, differences in foraging tactics are associated with rather subtle morphological differences (e.g., fin size, fin placement) between individuals, which again tend to favor one habitat over the other. We will return to this point below when discussing the causes of consistency. Spatial variation need not correspond to differences in the abiotic environment, as above, but can be induced by variation in the biotic environment of individuals. It has been suggested, for example, that variation in boldness within animal species can be maintained by the fact that different habitats vary in their degree of risk (Wilson 1998).

In addition to spatial variation, temporal variation in environmental conditions has also been suggested as contributing to the maintenance of personality differences. Contrary to the intuition of many biologists, however, it is not always the case that temporal variation will result in the coexistence of different strategies. Exactly as with spatial variation, the evolutionary effects of temporal fluctuations depend on population regulation, the degree of phenotype-environment matching, the costs of plasticity, and many other details of the biological system under consideration. To grasp this, consider a simple scenario of temporal fluctuations. Within a generation, all individuals within a population face the same environment, but the environment varies across generations, and different environments favor different phenotypes. As we have seen above, whenever individuals can adjust their phenotype to their current environment in an error- and cost-free manner, no variation is maintained within environments. However, unlike for spatial variation, genetic variation cannot be maintained in situations with limited phenotype-environment matching, at least as long as generations are non-overlapping (see the discussion of bet-hedging below for how purely phenotypic variation can be maintained in such a scenario). This is because all genotypes face exactly the same environment, there is no frequency dependence, and among any number of potential genotypes there will always be one that achieves the highest (geometric mean) fitness (Seger and Brockmann 1987). Many species, however, are iteroparous and have overlapping generations; in this situation then, temporal fluctuations can maintain genetic polymorphisms (Ellner and Hairston 1994). As we model species where the lifetime of individuals (and thus the generation overlap) progressively increase, temporal fluctuations tend to average out within the lifetime of a single individual and the model comes closer and closer to a temporal analogue of a spatial model without habitat choice, which can maintain genetic polymorphisms through local density dependence (Levene 1953).

A well-known feature of temporally fluctuating environments, with or without overlapping generations, is that so-called bet-hedging genotypes are selectively favored (Seger and Brockmann 1987); these are genotypes that switch during development stochastically between two or more phenotypes. A single bet-hedging genotype thus gives rise to a mixture of phenotypes (e.g., aggressive and nonaggressive individuals, individuals with a low and a high stress responsiveness; see Bergmüller and Taborsky 2010). This can be seen as a risk-spreading strategy, since no matter how the environment turns out, some of the bet-hedging phenotypes are well adapted. A diversifying bet-hedger can reduce its variance in fitness in an optimal way and thereby increase its geometric mean fitness. Bet-hedging can thus explain the coexistence of different personalities; however, since the variation caused by bet-hedging is only phenotypic (i.e., all phenotypes have the same genotype), bet-hedging alone cannot account for the observation that personalities are moderately heritable (Bouchard and Loehlin 2001).

In summary, in species with non-overlapping generations, temporal fluctuations can maintain only phenotypic variation. In species with overlapping generations, genetic variation can be maintained as well, but bet-hedging strategies are selectively favored (Leimar 2005). As should have been clear from the above discussion, however, the mere presence of temporal variation is by no means sufficient for explaining variation. To give an example, Dingemanse and colleagues (2004) studied a population of great tits (*Parus major*) for which environmental conditions (masting of beeches) varied across years. They found that different behavioral types were favored depending on the environmental condition, which in turn explained the maintenance of variation in this population (for other examples in which temporal variation in environmental conditions may explain personality variation, see Réale and Festa-Bianchet 2003 and chapter 7).

NON-EQUILIBRIUM DYNAMICS

Until now our analysis has been based on the premise that natural selection gives rise to an equilibrium in which strategies coexist in stable frequencies. It is not at all clear, however, that the dynamics of selection will lead to such an equilibrium. There are plenty of examples where the dynamics of frequency-dependent selection (e.g., Weissing 1991), competition (e.g., Huisman and Weissing 1999), and sexual selection (e.g., Van Doorn and Weissing 2006) lead to oscillations and often even chaotic dynamics. This has important implications since non-equilibrium conditions generally have a much higher potential for maintaining variation than the long-term constancy induced by equilibrium conditions (e.g., Huisman et al. 2001; Van Doorn and Weissing 2006).

A good example for non-equilibrium coexistence is the covariation of dispersal and colonizing ability observed in many species (e.g., Chitty 1967; Duckworth and Badyaev 2007). In such species, some individuals disperse while others are philopatric, potentially reflecting a bet-hedging strategy. Dispersers typically have a phenotype that allows them to colonize unoccupied space, but this same phenotype is selectively disadvantageous under crowded conditions (e.g., Duckworth and Kruuk 2009). Such a "colonizer" phenotype could probably not persist under constant and stable equilibrium conditions. In a perturbed environment, however, where empty spaces are created once in a while, the colonizers can flourish because they can exploit these opportunities. Once the empty spaces are filled, however, the settlers succumb to their own success, since they create an environment that can be more efficiently exploited by alternative phenotypes that do better under crowded conditions. At each point in space, there is ongoing directional selection, but in the population as a whole both types of strategies can stably coexist (Duckworth and Badyaev 2007).

Causes of correlations

Up to now we have focused on the causes of behavioral differences in response to environmental problems (e.g., how to explore an environment, how to respond to a predator). Personalities, however, entail much more than simple behavioral differences among individuals (Clark and Ehlinger 1987; Digman 1990; Gosling 2001; Sih et al. 2004a). First, personalities refer to behavioral differences that are stable through part of the ontogeny of individuals (time-consistency of behavior), that is, individuals that score relatively high (low) in a given behavioral situation often tend to score relatively high (low) in the same situation at later points in time. Second, personalities refer to differences that extend to whole suites of correlated behaviors, that is, correlated variation in functionally different contexts (e.g., antipredator behavior is correlated with agonistic behavior). Both types of correlations indicate behavioral inflexibilities (Wilson 1998; Dall et al. 2004) in the sense that the behavior that an individual exhibits at one point in time and in one particular context is predictive of the same individual's behavior at later points in time and in different contexts. Why did evolution give rise to such behavioral inflexibilities when a flexible structure of behavior would seem to be more advantageous? To answer this question, we first need to explore why, in some cases, evolution gives rise to architectures of behavior that result in apparently maladaptive behavioral correlations. We then focus on state variables as a cause of behavioral correlations in general and discuss two main sources for the stability of state differences over time, that is, stable state differences and positive feedback mechanisms. We conclude this section by discussing how social conventions can give rise to adaptive behavioral correlations.

ARCHITECTURE OF BEHAVIOR

On a proximate level, the behavioral phenotype of an individual is affected by its architecture of behavior, that is, the genetic, physiological, neurobiological, and cognitive systems underlying behavior. This architecture, in turn, gives rise to behavioral correlations whenever multiple traits are affected by a common underlying mechanism. Such common mechanisms are ubiquitous. Examples include pleiotropic genes (Mackay 2004), hormones (Ketterson and Nolan 1999), and neurotransmitters (Bond 2001) that affect multiple traits at the same time; emotions (Rolls 2000); and simple behavioral rules that are used for a variety of different but related problems (Todd and Gigerenzer 2000).

It has been shown, for example, that the consistency of aggressiveness through ontogeny in the three-spined stickleback (*Gasterosteus aculeatus*) is caused by pleiotropic genes (Bakker 1986). Pleiotropic genes are also thought to be responsible (Riechert and Hedrick 1993; Maupin and Riechert 2001) for the positive correlation between agonistic behavior, antipredator behavior, and superfluous killing in an American desert spider (*Agelenopsis aperta*). The negative correlation between mating effort and parental effort in several bird species is mediated by the hormone testosterone (McGlothlin et al. 2007). And finally, the fearfulness of an individual affects its reaction to a range of potentially threatening situations, including persistent dangers in its habitat, novelty, and interactions with conspecifics (Boissy 1995).

Behavioral correlations can thus be the result of a relatively rigid architecture of behavior. The resulting behavioral associations appear adaptive in some cases (see below). In others, however, they give rise to apparently maladaptive behaviors (Sih et. al 2004b). It might, for example, be advantageous for a female spider to show high levels of aggression toward territorial intruders, but she might also kill and consume all potential mates during courtship and as a consequence be left unmated at the time of egg laying (Arnqvist and Henriksson 1997). Similarly, it might be advantageous for salamander larvae to be active in the absence of predatory cues but not advantageous if the larvae are also active in the presence of such cues (Sih et al. 2003). In other words, rigid behavioral architectures can explain behavioral correlations at the proximate level, but from an ultimate perspective, one is tempted to ask why such rigid behavioral architectures persist over evolutionary time. Especially in cases where a rigid architecture gives rise to apparently maladaptive behavior, one would expect evolution to uncouple unfavorable behavioral associations.

The evolution of a more flexible behavioral architecture might in principle be prevented for two types of reasons. First, a more flexible architecture might be advantageous (i.e., an individual with such an architecture would achieve a higher fitness than an individual with a more rigid architecture) but not attainable by evolution. Such a situation can occur because the evolutionary transition from one complex phenotype (here: rigid architecture) to another complex phenotype (more flexible architecture) is typically not possible in one step but requires several intermediate steps. A more flexible architecture of behavior might, for example, require a novel hormonal system that cannot directly (i.e., with a small number of mutations) emerge from the present hormonal system. The architectures associated with these intermediate hormonal systems, however, might be disadvantageous to the individual. In other words, the evolution of a more flexible behavioral architecture might be prevented by the crossing of an adaptive valley of the fitness landscape. Such a situation occurs if the current behavioral correlations correspond to a local peak in the fitness landscape, reflecting the fact that the involved traits are to some extent well adapted to each other.

Second, a more flexible behavioral architecture might not be advantageous. In such situations, evolution is expected to give rise to adaptive behavioral canalization (e.g., West-Eberhard 2003; Edgell et al. 2009). Such a situation can occur if a more flexible architecture is associated with costs (costs of plasticity such as the costs associated with the acquisition of information, DeWitt et al. 1998) that are not outweighed by the corresponding benefits. In both cases, correlations can persist even though they give rise to behavioral traits that, when viewed in isolation from their architectural basis, might appear maladaptive.

STABLE STATE VARIABLES

Many aspects of an individual's state affect the cost and benefits of multiple behavioral traits at the same time (McNamara and Houston 1996). State differences in combination with state-dependent behavior (condition-dependent behavior, phenotypic plasticity) thus provide an explanation for adaptive behavioral correlations of apparently unrelated behavioral traits. However, state differences do not immediately explain why individuals should be consistent over time. Put differently, why should initial state differences among individuals be relatively stable over time? In this section we discuss two main determinants of consistency of states, inherently stable state variables and positive feedback mechanisms between state and behavior.

Inherently stable state variables. As discussed above, random causes, frequency-dependent selection, and spatiotemporal variation can give rise to populations with variation in states among individuals. Whenever a change of state among these variants is associated with substantial costs, such situations can result in consistent differences in state and, consequently, consistent differences in whole suites of (state-dependent) traits that are affected by this state. In some situations, differences in states are associated with differences in morphological and physiological characteristics that are costly to change. Consider, for example, sex differences. In many animal species, frequency-dependent selection maintains two sexes at constant proportions within populations. These equilibrium proportions, however, can in principle be maintained in populations in which individuals change their sex over time. Such a sex change, however, is often associated with substantial costs to the individual (caused by the necessary morphological and physiological changes). We thus typically observe stable (life-long) sex differences among individuals, which are, in turn, associated with whole suites of correlated behavioral traits. In humans (Costa et al. 2001), for example, women typically score higher than males on traits related to the agreeableness axis (e.g., cooperativeness, empathy, trust), while in many other animal species, sex differences exist in parental care and courtship behavior (Kelley 1988).

In some situations, evolution gives rise to populations in which individuals are distributed into a small number of discrete size classes (Brockmann 2001). A change among these variants is typically associated with substantial costs, which in turn favors consistency in size and thus consistency in behavioral traits that are affected by body size. A common phenomenon, for example, is the use of fighting and sneaking as alternative mating tactics depending on body size, as observed in dung beetles, bees, and many other species (Gross 1996).

Morphological and physiological differences, which can be changed only with substantial costs, need not be as conspicuous as in the case of sex or size differences. As discussed above (Ehlinger and Wilson 1988), within populations of bluegill sunfish (*Lepomis macrochirus*) individuals differ in morphological characteristics that are functional either in the littoral or in open water zone (e.g., fin size, fin placement). Such (stable) differences are associated with consistent differences in behavioral traits such as foraging tactics. Interestingly, the underlying morphological differences are not obvious to an observer; in fact, sunfish have been studied for many years without any recognition of the adaptive nature of these differences (Wilson 1998).

Inherently stable state differences need not be associated with morphological and physiological characteristics that are costly to change. In some cases stability is caused, at least in part, by factors external to the individual. Human societies, for example, encompass a large diversity of professions (e.g., teachers, managers, bureaucrats). Although it is in principle possible for an individual to change its profession, such changes are typically very costly to the individual (e.g., in terms of required training or education). As a result, individuals typically stick to their profession, once chosen. Differences in professions, in turn, are often associated with consistent differences in suites of correlated behavioral traits. Human leaders, for example, are more extrovert and more conscientious than nonleaders (Judge et al. 2002); entrepreneurs are more conscientious and open, but less neurotic and agreeable, than managers (Zhao and Seibert 2006).

Self-reinforcing feedback loops. Many aspects of an individual's state are much more labile than the ones discussed above. Consider, for example, the energy reserves of an individual, the experience that an individual has with a certain situation, or the future fitness expectations of an individual. These states are, like many others, labile since they can easily be changed by many different factors, including the individual's own behavior. Labile states can, like the inherently stable states, affect multiple behavioral traits at the same time, thus explaining suites of correlated behavioral traits. But why should labile states be stable over time?

In some situations the state and behavior of individuals are linked by a positive feedback (Sih et al. 2004a, b; Wolf et al. 2008): initial state differences give rise to differences in behavior, which act to stabilize or even increase the initial state differences. Such positive feedback mechanisms, in turn, can give rise to consistent individual differences in labile states and behavioral traits that are associated with these states. An important positive feedback is the feedback between behavior and an individual's experience. Individuals often get better at certain activities with increased experience (Rosenzweig and Bennett 1996); in other words, learning, training, and skill formation reduce the costs or increase the benefits of the same action when this action is repeated, which in turn favors consistency in this behavior (Wolf et al. 2008). Positive feedbacks via experience can give rise to consistent individual differences in single behavioral traits. Animals often learn how to recognize predators (Griffin 2004), which in turn makes it less costly to explore and forage a risky habitat for individuals that did this before. Under such conditions, whenever variation in risk-taking behavior is maintained within populations (Wilson 1998; Wolf et al. 2007), positive feedback acts to promote consistent individual differences in risk-taking behavior. Positive feedbacks can also give rise to consistent differences in suites of correlated behavioral traits. Experience gained in one context, for example, can affect the cost and benefits of behavioral actions in another context and thus give rise to a cross-context association of behavioral traits. Individuals that learn to assess the strength of conspecific competitors might, for example, at the same time get better at assessing the risk associated with predators.

Positive feedback does not need to act via behavior directly. The costs and benefits of behavioral traits that are related to resource acquisition (e.g., aggression, boldness), for example, often depend on an individual's characteristics, such as its resource-holding potential, and this interaction can give rise to a positive feedback loop (Sih and Bell 2008). An individual's physical strength, for example, enhances its fighting ability, which in turn may result in more resources being available to the individual (e.g., access to food and better nutrition) that further enhance its strength.

Positive feedback can also act via physiological characteristics of the individual. It has been suggested, for example, that in many animal species, deviations from a once-chosen growth rate are costly to the individual (Stamps 2007; Biro and Stamps 2008). Compensatory growth, for example, often comes at the cost of increased risk of disease, higher mortality rates, or decreased physiological capacity later in life (Mangel and Munch 2005). Similarly, deviations from a once-chosen basic metabolic rate or stress responsiveness might be costly to the individual. In such situations, a once-chosen physiological characteristic (growth rate, basic metabolic rate, stress responsiveness) affects the costs and benefits of future physiological characteristics such that maintaining a once-chosen set-up is advantageous. This, in turn, favors consistency in suites of traits that are associated with these characteristics. Differences in growth rates, for example, affect the cost and benefits of many traits that are related to food intake, such as aggression and boldness (Stamps 2007).

SOCIAL CONVENTIONS

An adaptive association of different behaviors does not necessarily reflect an underlying state variable that affects the costs and benefits of these behaviors. Rather, behavioral traits (be it the same trait expressed at different points during ontogeny or different traits) can get associated with each other because individuals in a population follow an adaptive behavioral rule (or convention) that favors the association of these traits. When an individual is confronted with another individual in a social interaction, for example, its behavior may be dependent on the behavioral history of the other individual. For example, when A and B interact in a hawk-dove–like encounter (Maynard Smith 1982), individuals might follow the rule "if the opponent played hawk before, choose dove; otherwise choose hawk." Such an eavesdropping strategy (Johnstone 2001) makes sense whenever there is some consistency in the behavior of individuals. Just as consistency favors eavesdropping, so eavesdropping favors consistency whenever it is beneficial for individuals to be predictable (but see Dall et al. 2004; McNamara et al. 2008). This interaction between consistency and eavesdropping can thus give rise to populations in which individuals follow a behavioral rule that favors consistency and, as a result, individuals show consistent behavior.

Do such conventions arise in natural situations? The so-called winner-loser effect (Chase et al. 1994) might be a good example of that. It is well known that winners of previous contests are more likely to win again (and losers are more likely to lose again), even against different opponents and in situations in which there are no asymmetries between the opponents. According to a survey across several taxa (Rutte et al. 2006), when there are no other asymmetries between opponents, the probability of winning a subsequent contest is almost doubled for previous winners, but is reduced more than five times for previous losers even against different opponents. Winner-loser effects are currently not well understood, but one possible explanation is that an individual's prior success acts as a "random historical asymmetry" that is used to settle the conflict (Parker 1974; Maynard Smith and Parker 1976; Hammerstein 1981; Van Doorn et al. 2003a, b). Social conventions that favor consistency are not limited to aggressive interactions.

An influential idea in explaining cooperation is that individuals should make their behavior dependent on an image score of the other individual (Nowak and Sigmund 1998; Leimar and Hammerstein 2001), a measure of how cooperative the other individuals has been in the past. Such image scoring can, in turn, favor consistency in cooperative behavior.

Conclusions

In this chapter, we have provided an overview of the mechanisms that promote the evolution of personalities. We focused on two basic questions: which factors promote adaptive behavioral variation within populations, and which factors promote adaptive correlations between behavioral traits across contexts or over time (table 9.1).

Factors promoting variation and correlations can interact in various ways (figure 9.1). Random causes, frequency-dependent selection, spatiotemporal variation, and non-equilibrium dynamics can give rise to variation in states among individuals. Whenever such states affect the cost and benefits of behavioral traits, state differences promote state-dependent behavior and thus adaptive behavioral variation; whenever the costs and benefits of multiple behavioral traits are affected at the same time, the result is adaptive behavioral variation that is correlated across contexts. In principle, behavioral variation should be stable as long as the underlying variation in states is stable. Whenever states are very costly to change and thus inherently stable (e.g., sex and size differences), variation is expected to be stable. In the case of labile states (e.g., energetic state, experience with a certain behavior), variation can be stabilized via positive feedback mechanisms between behavior and states: variation in states gives rise to variation in behavior that acts to stabilize or increase initial state differences.

Spatiotemporal variation, frequency-dependent selection, and non-equilibrium dynamics can give rise to behavioral variation that is not associated with underlying state differences and state-dependent behavior (e.g., producers and scroungers, hawks and doves). Such variation can be stabilized over time via positive feedback mechanisms: the initial variation in behavior gives rise to differences in states that act to stabilize the behavioral differences (e.g., producers gain experience that makes producing more beneficial). Such feedbacks can also extend to multiple behavioral traits, thus giving rise to adaptive behavioral correlations (e.g., experience gained in the producer-scrounger context can affect the cost and benefits of behavior in different contexts). Alternatively, behavioral variation in single

Table 9.1. Causes of adaptive behavioral variation, of adaptive behavioral correlations across contexts, and of adaptive behavioral consistency over time.

(a) Causes of adaptive behavioral variation
- State differences[1]
- Frequency-dependent selection
- Spatiotemporal variation
- Non-equilibrium dynamics

(b) Causes of adaptive behavioral correlations across contexts
- Architecture of behavior
- States[1] affecting behavior in multiple contexts
- Social conventions favoring the association of traits

(c) Causes of adaptive time-consistency in behavior
- Architecture of behavior
- Inherently stable states[1]
- Labile states[1] that are stabilized via positive feedbacks
- Social conventions favoring time-consistency

[1] In combination with state-dependent behavior.

or multiple behavioral traits can be stabilized via social conventions, which favor consistency in behavior.

The analysis presented here suggests that personalities, and animal behavior in general, require a holistic approach to be fully understood. Rather than "atomizing the organism" (Gould and Lewontin 1979) into single behavioral traits that are studied in isolation, studying multiple different traits in concert is necessary: behavior in one context (e.g., antipredator, mating, fighting, parental care) can often be understood only when taking the interdependencies with past and future behavior in the same and other contexts into account. The understanding of personalities also requires an integration of mechanism and adaptation (Tinbergen 1963). As we have emphasized above, behavioral correlations are often caused by the architecture of behavior, that is, by the genetic, physiological, neurobiological, and cognitive systems underlying behavior. In order to understand such correlations, we thus have to understand the coevolution of behavior and its underlying mechanisms. Finally, personalities in themselves may have consequences for the evolutionary process (Wilson 1998; Dall et al. 2004). For example, in social contexts, the existence of variation in one trait often selects for variation in another trait. Variation in cooperativeness, for example, can select

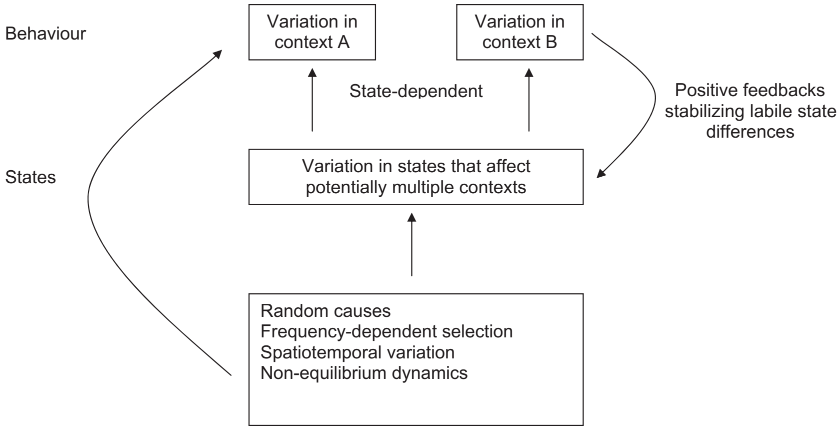

Figure 9.1. Random causes, frequency-dependent selection, spatiotemporal variation, and non-equilibrium dynamics can act on states or directly on behavior. Differences in states in combination with state-dependent behavior can give rise to adaptive behavioral differences. Behavioral differences, in turn, can be stabilized via positive feedback mechanisms between behavior and states.

for variation in choosiness, which in turn selects for cooperativeness (McNamara et al. 2008). Variation in cooperativeness can thus trigger a coevolutionary process of cooperativeness and choosiness that gives rise to very different evolutionary outcomes (here: high levels of cooperation) when compared with situations without such initial variation.

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