Evolutionary emergence of responsive and unresponsive personalities

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Edited by Brian Skyrms, University of California, Irvine, CA, and approved August 29, 2008 (received for review June 16, 2008)

In many animal species, individuals differ consistently in suites of correlated behaviors, comparable with human personalities. Increasing evidence suggests that one of the fundamental factors structuring personality differences is the responsiveness of individuals to environmental stimuli. Whereas some individuals tend to be highly responsive to such stimuli, others are unresponsive and show routine-like behaviors. Much research has focused on the proximate causes of these differences but little is known about their evolutionary origin. Here, we provide an evolutionary explanation. We develop a simple but general evolutionary model that is based on two key ingredients. First, the benefits of responsiveness are frequency-dependent; that is, being responsive is advantageous when rare but disadvantageous when common. This explains why responsive and unresponsive individuals can coexist within a population. Second, positive-feedback mechanisms reduce the costs of responsiveness; that is, responsiveness is less costly for individuals that have been responsive before. This explains why individuals differ consistently in their responsiveness, across contexts and over time. As a result, natural selection gives rise to stable individual differences in responsiveness. Whereas some individuals respond to environmental stimuli in all kinds of contexts, others consistently neglect such stimuli. Interestingly, such differences induce correlations among all kinds of other traits (e.g., boldness and aggressiveness), thus providing an explanation for environment-specific behavioral syndromes.

architecture of behavior | behavioral flexibility | behavioral syndromes | individual differences | reactivity

Empirical findings in >100 species, ranging from insects to mammals, suggest that personalities are a widespread phenomenon in the animal kingdom (1–9). Individuals differ profoundly from each other in their behavior, and these differences are often consistent over time and extend to various contexts. In birds, fish, and rodents, for example, some individuals are consistently more aggressive than others, and aggressive individuals differ from nonaggressive individuals in many other respects like foraging behavior or the exploration of novel environments (5). From an adaptive point of view, both the coexistence of behavioral types and the consistency of individuals are poorly understood (10, 11).

Many researchers believe that a fundamental factor structuring personality differences is the degree to which individual behavior is guided by environmental stimuli (6–8, 12–21). Whereas some individuals pay attention to environmental stimuli and quickly adapt their behavior to the prevailing conditions, others show more rigid, routine-like behavior. Such differences in responsiveness (also termed coping style, reactivity, flexibility, plasticity) have been documented in many organisms including birds [e.g., great tits (12), spice finches (13), and zebra finches (14)] and mammals [e.g., rats and mice (7), pigs (20), and humans (15, 16)].

In both mice and rats (21), individuals differ substantially in their responsiveness to environmental changes in a maze task. Some individuals quickly form a routine, are not influenced by minor environmental changes, and perform relatively badly when confronted with a changing maze configuration. Others omit forming a routine, are strongly influenced by minor changes, and perform relatively well when confronted with changing maze configurations. Similarly, some great tits readily adjust their foraging behavior to a change in the feeding situation, whereas others stick to formerly successful habits (12). The finding that humans and other primates differ in their susceptibility to environmental influences (15, 16) might also be interpreted along these lines.

These observations raise two important questions. First, why do responsive and unresponsive individuals coexist within a population? Should we not expect a single "optimal" phenotype? And second, why are differences in responsiveness consistent across contexts and over time? Should we not expect that individuals adjust their responsiveness to the needs of the prevailing situation? In this article, we develop a simple but general evolutionary model to address these questions.

First, we address the coexistence problem. Our crucial insight is that for many realistic scenarios, the benefits of responsiveness are negatively frequency-dependent. As a consequence, responsiveness spreads when rare but is selected against when common. This explains coexistence. Second, we address consistency. We show that stable individual differences in responsiveness arise whenever the costs of responsiveness are lower for those individuals that have been responsive before. We argue that many processes like learning or training give rise to such positive feedbacks thus explaining consistency. Interestingly, our results illustrate that individual differences at the level of behavioral organization (here, the responsiveness to environmental stimuli) can induce correlative associations among all kinds of otherwise unrelated traits.

Coexistence of Responsive and Unresponsive Individuals

Basic Scenario. We consider a population of individuals that face environmental uncertainty. By assessing the prevailing environmental state and adequately responding to it, individuals can typically increase their payoff. Yet, such a responsive strategy involves costs (22) such as, for example, the time and energy costs of sampling the environment, the mortality cost induced by collecting information, or the costs of building and maintaining the required sensory machinery.

Fig. 1 shows the structure of a simple model that captures the key ingredients of this scenario. Individuals have a choice between the two options L ("left") and R ("right"). The payoffs from these options depend on the environment, which can be in either of two states that occur with probability s_i ($i = 0$ or 1). Accordingly, we denote the payoffs from choosing L and R as a_i

Author contributions: M.W., G.S.v.D., and F.J.W. designed research; M.W., G.S.v.D., and F.J.W. performed research; and M.W. and F.J.W. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

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This article contains supporting information online at www.pnas.org/cgi/content/full/0805473105/DCSupplemental.

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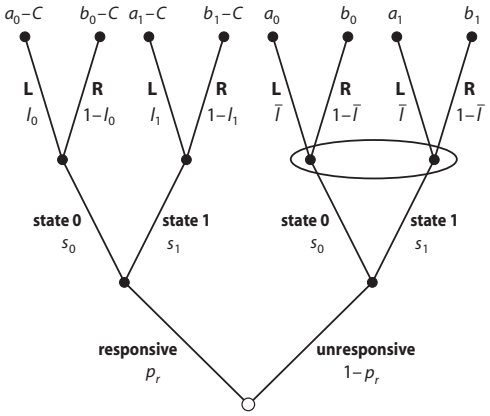

Fig. 1. Setup of the one-stage model. We consider a scenario where individuals can find themselves in either of two states, where state i occurs with probability s_i. Individuals have the choice between two options L and R. The payoffs associated with these options, a_i and b_i, depend on the state of the environment $i = 0,1$ and, in addition, on the strategy established in the population. An individual follows the responsive strategy with probability p_r. Responsive individuals can distinguish between the two states and make their behavior dependent on the current state. Accordingly, the probability l_i with which a responsive individual chooses option L depends on the state i. In contrast, unresponsive individuals cannot distinguish between the two states and have to use the same probability $\bar{l}$ in both states. Although responsiveness allows more flexible behavior, it is costly and reduces the payoff by C.

and b_i, respectively. Before choosing between L and R, individuals choose whether or not to adopt a responsive strategy. Responsive individuals get to know the current state and can therefore make their behavior dependent on this information; that is, choose L with probability l_0 or l_1, depending on the state of the environment. Yet, responsiveness is costly and reduces the payoff by C. In contrast, unresponsive individuals cannot distinguish between the two states and have to use the same probability $\bar{l}$ in both states.

Benefits of Responsiveness. In view of the cost of responsiveness C, the responsive strategy can only spread if the benefits of responsiveness exceed these costs. The benefits of responsiveness are given by the excess payoff E of a responsive over an unresponsive individual. What determines this excess payoff? In state i, a responsive individual plays strategy l_i and thus obtains the payoff $l_i a_i + (1 - l_i)b_i$. This payoff will typically exceed the payoff of an unresponsive individual, $\bar{l}a_i + (1 - \bar{l})b_i$, that has to use the general-purpose strategy $\bar{l}$. The payoff difference in state i is therefore $(l_i - \bar{l})(a_i - b_i)$, and the benefits of responsiveness are thus given by

$$E = \sum_i s_i(l_i - \bar{l})(a_i - b_i).$$

Hence, the responsive strategy spreads whenever $E > C$, and the unresponsive strategy spreads whenever $E < C$.

Frequency Dependence. From now on, we make the crucial assumption that the payoffs a_i and b_i are negatively frequency-dependent, that is, the excess payoff of choosing L over R in state i, $a_i - b_i$, decreases with the frequency f_i of individuals that choose option L in state i ($f_i = p_r\, l_i + (1 - p_r)\bar{l}$). As we discuss below, this is a realistic assumption. In the supporting information (SI), we demonstrate that frequency dependence at the level of the choices between L and R gives rise to benefits of responsiveness that are negatively frequency dependent, that is

$$\frac{dE}{dp_r} < 0. \qquad [1]$$

The intuition for this result is as follows. Consider a situation where in state i, it is advantageous to choose option L ($a_i > b_i$). Hence, responsive individuals choose L ($l_i = 1$), whereas unresponsive individuals have to stick to the general-purpose strategy $\bar{l}$. However, the payoff difference between L and R decreases with the frequency of individuals that choose option L. As a consequence, the benefits of responsiveness in state i decrease with the frequency of responsive individuals.

Coexistence. Because the benefits of responsiveness $E(p_r)$ are negatively frequency-dependent, they will be highest in a population of unresponsive individuals ($p_r = 0$) and lowest in a population of responsive individuals ($p_r = 1$). We have seen that responsive individuals can invade a population of unresponsive individuals whenever $E(0) > C$, whereas unresponsive individuals can invade a population of responsive individuals whenever $C > E(1)$. Accordingly, both strategies can spread when rare whenever

$$E(0) > C > E(1) \qquad [2]$$

leading to the coexistence of responsive and unresponsive individuals. In the *SI*, we show that $E(0)$ and $E(1)$ can readily be calculated. $E(0)$ is given by $E(0) = s_0 s_1 \Delta$, where $\Delta = \Sigma_i |a_i - b_i|$ is the total payoff difference in a population of unresponsive individuals. $E(1)$ is equal to zero whenever, in a population of responsive individuals, a mixed evolutionarily stable strategy (ESS) would be played in any of the environmental states.

Example I: Coexistence in a Patch-Choice Game. We now illustrate this result and its consequences for a situation where the options L and R correspond to the alternatives in a patch-choice game, where each individual has the choice between two patches. The payoff an individual obtains in any of the two patches is given by $a_i = A_i/f_i$ and $b_i = B_i/(1 - f_i)$, where A_i and B_i are state-dependent baseline values of the two patches, and f_i is the frequency of individuals that choose patch A in state i.

Fig. 2*A* illustrates that negative frequency dependence on the level of the patch-choice game gives rise to benefits of responsiveness that are negatively frequency-dependent. Responsive individuals (green line) always obtain a payoff that is as least as high as that of unresponsive individuals (red line) because they can choose the better patch in each environment. However, as predicted by our analysis above (Eq. **1**), the payoff difference between responsive and unresponsive individuals (black line), that is, the benefit of responsiveness, decreases with the frequency of responsive individuals. Whether decreasing benefits of responsiveness give rise to the coexistence of responsive and unresponsive individuals depends on the strength of this decrease and on the cost of responsiveness (see Eq. **2**). For the chosen parameter values of A_i and B_i, we expect coexistence whenever the cost of responsiveness C is between $E(1) = 0$ and $E(0) = 0.5$ (right axis). For any of these equilibria, one can readily calculate the corresponding ESS behavior of responsive and unresponsive individuals in the patch-choice game. This is illustrated in Fig. 2*C*, which shows how these strategies change with the cost of responsiveness.

To test these predictions, we implemented our assumptions in individual-based computer simulations in which trait frequencies change over time under the influence of natural selection (see *Appendix*, below). The simulation results are in perfect agreement with our analytical predictions. For any value of $C < 0.5$, the population converges to the predicted mixture of responsive and unresponsive individuals; Fig. 2*B* shows two simulations for the scenario depicted in Fig. 2*A* (C = 0.2), one starting from an

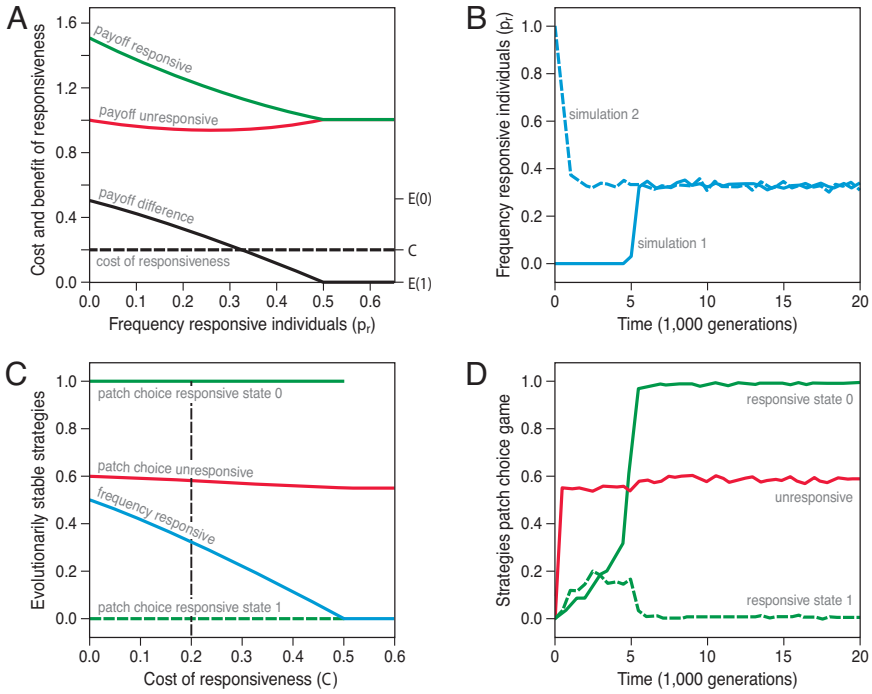

Fig. 2. Coexistence of responsive and unresponsive individuals due to frequency-dependent selection, illustrated for a situation where the options *L* and *R* correspond to the alternatives in a patch-choice game. (*A*) Dependence of payoffs on the proportion of responsive individuals in the population. Responsive individuals always obtain a payoff that is at least as high as the payoff to unresponsive individuals. The benefits of responsiveness (i.e., the excess payoff of responsive individuals, black line) decreases from a value $E(0) = 0.5$ in a population of unresponsive individuals to $E(1) = 0$ in populations with a high proportion of responsive individuals. The benefits of responsiveness exactly balance the cost of responsiveness at $p_r = 0.32$. (*B*) Two individual-based simulations illustrating that, independent of the initial conditions, natural selection gives rise to the stable mixture of responsive and unresponsive individuals predicted by *A*. (*C*) Dependence of the evolutionarily stable strategies on the cost of responsiveness. The dashed black line indicates the configuration in *A* and *B*. (*D*) Individual-based simulation showing the evolution of behavior in the patch-choice game. At equilibrium, responsive individuals exhibit a state-dependent pure strategy: ''always choose patch *L* state 0'' and ''always choose patch *R* in state 1.'' Unresponsive individuals employ a mixed strategy.

ancestral population of responsive individuals and the other from an ancestral population of unresponsive individuals. Fig. 2*D* illustrates that also the behavior of responsive and unresponsive individuals in the patch-choice game is in perfect agreement with our analytical predictions. Unresponsive individuals (red line) evolve an intermediate tendency to choose between the two patches ($\bar{l}^* = 0.58$), whereas responsive individuals (green lines) flexibly employ the two extreme strategies ''always choose patch *A*'' ($l_0^* = 1$) and ''always choose patch *B*'' ($l_1^* = 0$), depending on the state of the environment.

Consistent Individual Differences in Responsiveness

Positive Feedbacks and Consistency. Empirical evidence suggests that individuals that are responsive to environmental stimuli at one point in time and in one context tend to be responsive at later points in time and in different contexts as well (6, 7). Why should natural selection give rise to such consistency? Consider first the extreme case where being responsive once reduces the cost of further responsiveness to zero. In this case, it is obvious that previously responsive individuals should be responsive anew, because they can reap the benefits of responsive behavior without incurring additional cost. Hence, responsiveness is consistent within and across contexts. This is an extreme scenario, because early responsiveness has a very strong feedback on the cost of later responsiveness. However, we now show that even the tiniest feedback is sufficient to induce consistent individual differences in responsiveness.

To investigate the effect of such feedbacks, we now consider a two-stage scenario. In each of the stages, individuals face the choice between adopting a responsive or an unresponsive strategy. The two stages might either represent the same context at different points in time (e.g., patch choice early and late in the season) or different contexts (e.g., a patch choice and aggressive encounters). In both stages, individuals face a choice between two options (say *L* and *R* in stage 1 and say *L′* and *R′* in stage 2), where the payoffs are again negatively frequency-dependent and depend on the state of the environment. For simplicity, we assume that the environmental states in both stages are uncorrelated. Individuals that are responsive in any of the two stages get to know the environmental state in that stage and can fine tune their behavior accordingly. The fitness of an individual is given by the sum of payoffs obtained in both stages reduced by the cost of responsiveness. As above, the cost of responsiveness in the first stage is given by *C*. We assume that the cost of responsiveness in the second stage is smaller for individuals that were responsive in the first stage (C_r) than for those individuals that were unresponsive in the first stage (C_{ur}). In the *SI*, we show that even the smallest cost reduction gives rise to consistency in responsiveness: At the ESS, individuals that are responsive in the first stage have a higher tendency to be responsive in the second stage ($p_r|_r$) than individuals that are unresponsive in the first stage ($p_r|_{ur}$), that is

$$p_r^*|_r > p_r^*|_{ur}. \qquad [3]$$

In fact, as we presently show, even a very small feedback gives rise to strong consistency in responsiveness across stages.

Example II: Consistency and Behavioral Syndromes. We now illustrate this result and its consequences for a situation where individuals have to choose a patch in the first stage (as above) and are involved in aggressive encounters in the second stage.

EVOLUTION

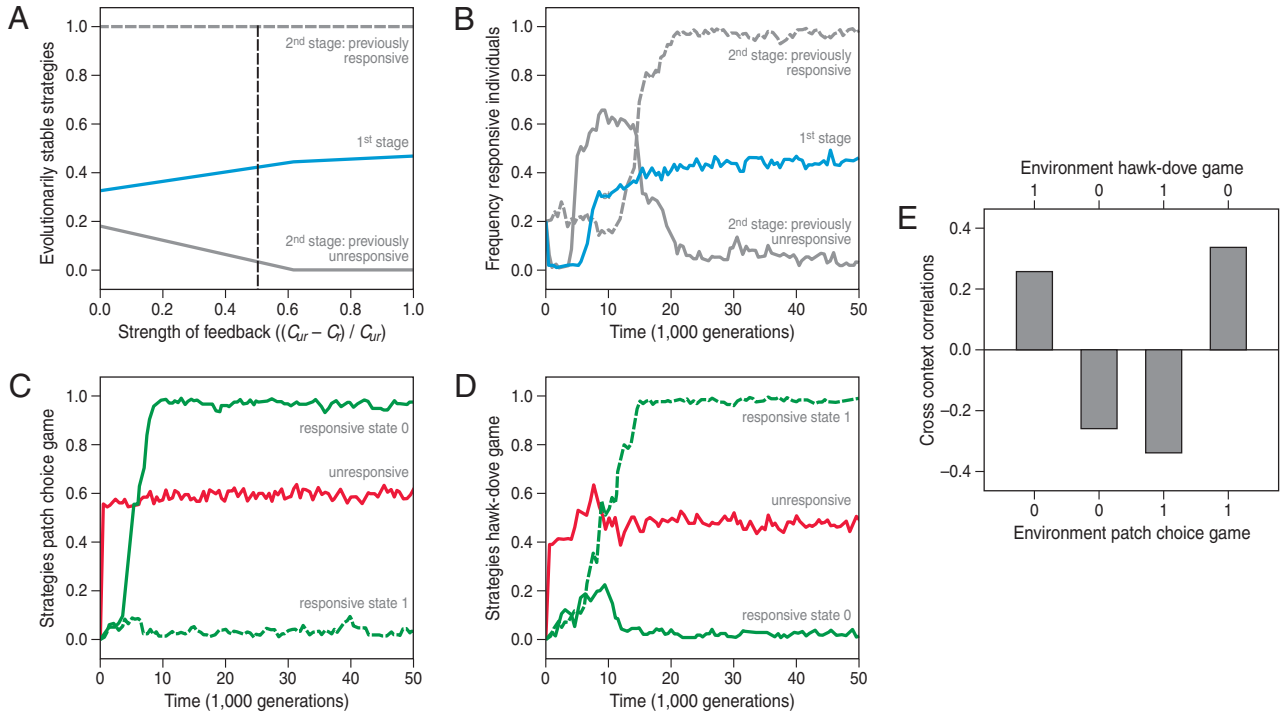

Fig. 3. Evolution of consistent individual differences in responsiveness due to positive feedbacks. (*A*) Evolutionarily stable responsiveness illustrating that, independent of the strength of feedback, individuals that are responsive in the first stage (here patch-choice game) show high levels of responsiveness in the second stage (here a hawk–dove game), whereas previously unresponsive individuals show low levels of responsiveness in the second stage. The dashed black line indicates the configuration in the individual based simulations *B*–*E*. (*B*) Typical simulation illustrating the evolution of consistent individual differences in responsiveness. (*C* and *D*) In both the patch choice context (*C*) and in the hawk–dove context (*D*), unresponsive individuals evolve a mixed strategy, whereas responsive individuals evolve the pure strategies that are used dependent on the state of the environment. (*E*) For each combination of environmental states in the two stages, a correlation results between the behavioral choices (patch choice and hawk–dove game), induced by the fact that individuals differ consistently in their responsiveness and that responsive individuals play a pure strategy in either state. The sign and the strength of these correlations depend on the combination of states in both contexts.

Aggressive encounters are modeled as a hawk–dove (23) game (L' = "hawk" and R' = "dove"): Individuals fight for a resource of value V, and aggressive hawks risk injury, reducing their payoff by D. Now we assume that the resource value is either V_0 or V_1, depending on the state of the environment.

Fig. 3A depicts how the ESS level of responsiveness depends on the strength of the feedback. For any degree of cost reduction, first-stage responsiveness is represented by the blue line, and second-stage responsiveness of previously responsive and unresponsive individuals is depicted by the dashed and solid gray lines, respectively. Note that for strong feedbacks, all individuals play a pure strategy in the second stage: Previously responsive individuals are always responsive, whereas previously unresponsive individuals are never responsive. Remarkably a dichotomy of similar strength already occurs at very weak feedbacks. In other words, the smallest cost reduction gives rise to consistent individual differences. Our individual-based simulations (Fig. 3*B*) are in perfect agreement with these analytical predictions.

Behavioral Syndromes. As in the one-stage game considered above, at the ESS, unresponsive individuals play a general-purpose mixed strategy in both stages, whereas responsive individuals adapt their behavior to the prevailing conditions and choose a pure strategy (Fig. 3 *C* and *D*). Notice that, for a given combination of environmental states, all responsive individuals play the same combination of pure strategies in both stages. At the population level, this induces a correlation between the behavioral choices in stage 1 and stage 2. In other words, consistent individual differences in responsiveness induce behavioral correlations that might be interpreted as behavioral syndromes (1, 5). Note that this cross-context correlation reflects consistency in the behavior of responsive individuals rather than an intrinsic link between the two contexts. This is also reflected by the fact that the sign and the strength of these correlations depend on the environment (Fig. 3*E*).

Discussion

Frequency Dependence. Our explanation for the coexistence of responsive and unresponsive individuals is based on the insight that the benefits of responsiveness are negatively frequency-dependent. Frequency dependence at the level of responsiveness is caused by our assumption that the payoffs at the level of the behavioral choices (e.g., patch choice, aggressive encounters) are frequency-dependent. This assumption is realistic. For example, behavior in social interactions (e.g., aggressive or cooperative behavior) has frequency-dependent payoffs almost by definition, because the outcome depends on the behavior of all participants (23–25). Other forms of frequency dependence arise whenever individuals compete for limited resources as, for example, in a foraging context. In these situations, individual behavior impacts on the environment, which, in turn, feeds back on the individuals (26). Next to such ecological mechanisms, a variety of other mechanisms can also lead to frequency dependence (27).

Emergence of Polymorphism. In our model, frequency-dependent selection gives rise to polymorphism. This may reflect our assumption that individuals face a binary choice between adopting a responsive or an unresponsive tactic. In some situations, it is indeed reasonable to view responsiveness as an all-or-nothing decision; in others, however, responsiveness is better viewed as

a continuous trait. For example, individuals may vary in their degree of sampling on a scale from superficial to thorough. Alternatively, individuals may vary their rate of sampling as in situations where individuals differ in their tendency to interrupt their "normal" behavior to sample.

When responsiveness varies continuously, negative frequency dependence may result in either a monomorphism with an intermediate degree of responsiveness or a polymorphism where individuals differ in their responsiveness. The evolutionary outcome will reflect the shape of the tradeoff individuals face. Intuitively, polymorphism is favored when the costs and benefits associated with responsiveness give rise to a convex tradeoff, whereas monomorphism is favored by concave tradeoffs (28). Interestingly, the coexistence of responsive and unresponsive phenotypes has been suggested in other contexts as, for example, the coexistence of plastic and canalized developmental strategies (29) or the coexistence of generalists and specialists (30).

Positive Feedbacks. Our model explains consistency in responsiveness by a positive-feedback mechanism. Previously responsive individuals have a higher tendency to be responsive again because they face lower costs (or higher benefits) than previously unresponsive individuals. Remarkably, the smallest such asymmetry translates into a strong positive association of responsiveness across stages.

It is highly plausible that positive feedbacks act within contexts as, for example, in the case when responsive individuals get better at being responsive (e.g., assessing cues) with repeated experience (31). Cross-context feedbacks might seem less likely, but they can be caused by various mechanisms. We give three examples. First, the cost of responsiveness may consist of a context-independent part (e.g., screening the environment) and a context-specific part (e.g., screening for specific cues). With respect to a second context, the context-independent part represents fixed costs that do not have to be paid again. Second, individuals that are responsive in one context may build up knowledge and skills that can be used in a different context. If, for example, individuals get better in interpreting environmental cues, the costs are lower for experienced than for inexperienced individuals. Third, information gathered in one context may prove useful for assessing the state of the environment in a different context, that is, information acquired in one context may spill over to a different context.

Responsiveness and Behavioral Flexibility. In the empirical literature, differences in responsiveness are also referred to as differences in flexibility, plasticity, and reactivity. These categories are often used synonymously (e.g., refs. 7 and 8). However, this is not always adequate. Whereas responsiveness refers to the propensity of an individual to adjust its behavior to the prevailing environmental conditions, behavioral flexibility refers to the tendency of an individual to show varying behavior when confronted with the same context repeatedly. One might think that responsive individuals are flexible (i.e., show varying behavior) and unresponsive individuals are rigid (i.e., show the same behavior). Our analysis shows, however, that this relation is more ambiguous.

Consider a situation where individuals are repeatedly confronted with the same context under uncertainty. Both responsive and unresponsive individuals will appear flexible to an observer. Responsive individual are flexible because they play a state-dependent pure strategy and thus change their behavior with the environmental state. Yet, unresponsive individuals are also flexible because they play a mixed strategy and hence change their behavior due to randomization. There is, however, a crucial difference between the two strategies: Only responsive individuals vary their behavior systematically in response to the environmental conditions.

The relation between responsiveness and flexibility is not always as ambiguous. We give two examples. First, consider the above scenario where individuals are repeatedly confronted with the same context but now assume that there is a cost associated with changing behavior (e.g., switching patches might be costly). Such a cost has a differential effect on responsive and unresponsive individuals. Whereas responsive individuals change their behavior only when it pays to, unresponsive individuals do not improve their payoff by changing behavior. Consequently, whenever there is a cost associated with changing behavior, unresponsive individuals should rigidly stick to the behavior once chosen, whereas responsive individuals should keep changing their behavior flexibly whenever the environmental state changes. Note that in such a case, unresponsive individuals still mix between both alternatives on a population level: Some consistently choose option L, whereas others choose option R.

Second, consider a situation where individuals, instead of choosing between two discrete alternative L and R, face a choice between a continuum of alternatives. For example, instead of choosing between an aggressive hawk and a nonaggressive dove strategy, individuals might choose an intensity of aggression that varies continuously between a minimum level L and a maximum level R. In this case, the mixed strategy of unresponsive individuals does not correspond to a randomization but to an intermediate intensity of aggression. Thus, when confronted with such a context repeatedly, unresponsive individuals rigidly show the same intermediate level of aggression, whereas responsive individuals flexibly exhibit maximal and minimal levels of aggression, depending on the state of the environment.

Implications for Understanding Animal Personalities. The defining feature of animal personalities is that individual behavior is correlated over time and across contexts. Such correlations, or behavioral syndromes (1, 5), seem puzzling because a more flexible structure of behavior should be advantageous. Current explanations fall into two classes. According to the "constraints view," trait correlations result from constraints on the architecture of behavior (5). This view emphasizes seemingly nonadaptive aspects of behavior and limited plasticity. However, it remains unclear why the underlying constraints are not removed by natural selection. Interestingly, our model exemplifies that a flexible architecture may invade the constrained one, without necessarily going to fixation.

According to the "adaptive view," trait correlations are the result of natural selection. Particular combinations of traits appear together because they work well together (32–37). For example, the boldness–aggressiveness syndrome has been explained in terms of differences in energy reserves (33), differences in future fitness expectations (36), and differences in growth rates (37). Although being in the realm of the adaptive view, our results provide a different type of explanation. Individual differences at the level of the behavioral organization can give rise to correlative associations of all kinds of otherwise unrelated behaviors.

Consider the above scenario where evolution gives rise to a correlation between the patch choice behavior of individuals and their aggressiveness (Fig. 3*E*). Suppose, for the sake of the argument, that the patches differ in their riskiness (e.g., presence of a predator) such that patch choice might be interpreted as a choice between being bold and being shy. In this case, the correlation pattern in Fig. 3*E* resembles an environment-specific boldness–aggressiveness syndrome that has been found in natural populations of sticklebacks (38, 39). Notice, however, that this correlation is not caused by an intrinsic link between boldness and aggressiveness. Rather it is caused by the fact that the coexisting responsive and unresponsive individuals employ different decision rules to choose between the behavioral alternatives. Whereas responsive individuals use a fine-tuned rule that conditions the behavior on the prevailing conditions, unresponsive individuals employ a general-purpose rule that does

not distinguish between these conditions. Trait correlations do not, therefore, necessarily reflect an inherent connection between the associated traits but can be a byproduct of stable individual differences at the level of behavioral organization.

Appendix

Here, we give the setup of the individual-based simulations. The analytical results are derived in the *SI*. We simulated a spatially heterogeneous metapopulation with many "islands" (i.e., local patches). The islands differ in their environmental conditions for the choice situations (L vs. R): For the patch choice (hawk–dove) context in stage 1 (stage 2) a fraction s_0 (s_0') of the islands is in state 0, and the remaining islands are in state 1. For the two-stage scenario, the environmental conditions for each of the stages are drawn independently from each other. In all our simulations, we studied populations of 5,000 individuals that are distributed among 50 islands.

After birth, individuals disperse to a random island. Individuals are haploid and characterized by a suite of heritable traits corresponding to (*i*) the tendency to choose the responsive strategy in each of the stages and (*ii*) the tendency to choose option L in each of the stages. Each of these traits is encoded by a separate gene locus; for the two-stage scenario, separate loci encode the behavior in the first and in the second stage. After obtaining the payoff (see below), individuals mate at random within each island, reproduce, and then die. Each island contributes equally to the total offspring generation; within islands, the relative contribution of an individual to the offspring generation is proportional to its net payoff. During reproduction, mutations occur with probability $\mu = 1 \times 10^{-3}$. Whenever a mutation occurs, it has a small effect on a random locus: It changes the strategy of an individual by a value that is drawn from a normal distribution with mean 0 and standard deviation 0.1, with the constraint that it remains in the interval from 0 to 1.

For the one-stage scenario (Fig. 2), individuals face a situation as depicted in Fig. 1. We assume that the options L and R represent the behavioral alternatives in a patch-choice game. For an island with environmental state i, the payoff that an individual obtains in any of the two patches is given by $a_i = A_i/f$ and $b_i = B_i/(1 - f)$, where A_i and B_i are state-dependent baseline values, and f is the frequency of individuals that choose patch L in this island. All simulations are based on $A_0 = 0.8, B_0 = 0.2, A_1 = 0.3, B_1 = 0.7, C = 0.2$, and $s_0 = 0.5$.

For the two-stage scenario (Fig. 3), individuals face a situation as depicted in Fig. 1 twice. We assume that the options represent the behavioral alternatives in a patch-choice game in the first stage and the alternatives in a hawk–dove game in the second stage. In the hawk–dove game, individuals within an island are paired at random and fight for a resource with a value V_i that depends on the island's state of the environment for the hawk–dove game. Payoffs are obtained as in the standard hawk–dove game (23): When two hawks meet, one gets V_i, and the other gets $-D$; when two doves meet, both get $V_i/2$; when a hawk meets a dove, the hawk gets V_i, and the dove gets 0. Fig. 3 is based on $V_0 = 2, V_1 = 8, D = 10$ for the hawk–dove game, $C = 0.2$, $C_{ur} = 0.2$, $C_r = 0.1$ for the cost of responsiveness, and $s_0 = 0.5$, $s_0' = 0.5$.

ACKNOWLEDGMENTS. We thank T. W. Fawcett, O. Leimar, D. S. Wilson, and an anonymous referee for numerous helpful suggestions and D. Visser for preparing the figures. G.S.v.D. was supported by a Rubicon grant from the Netherlands Organisation for Scientific Research.

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