



# How noisy information and individual asymmetries can make ‘personality’ an adaptation: a simple model

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Recent attention has been drawn to the existence of individual differences in correlated behaviour across contexts, animal ‘personality’ (Gosling 2001, *Psychological Bulletin*, **127**, 45–86) and behavioural syndromes (Sih et al. 2004b, *Quarterly Review of Biology*, **79**, 241–277). The causes of these patterns of behaviour are subjects of debate. Here, we present a very simple model of how adaptively managing noisy information, combined with differences in individual state, can lead to evolutionarily stable differences in how individuals respond to environmental cues. When information is very noisy, behavioural syndromes are most likely, but as long as there is some error, some types of individuals display the same behaviour in all contexts. In extreme cases, very few individuals display flexible behaviour, and different stable behavioural types dominate the population.

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Behavioural ecologists sometimes observe stable behavioural variation among individuals within contexts, as well as consistent behaviour within individuals across contexts. Some individuals tend to be aggressive in many contexts, while others tend to be timid, for example. The recognition of correlated behaviours across contexts, even where optimal behaviour in each context is plausibly distinct, has spawned a search for evolutionary explanations of animal ‘personality’ (Gosling 2001) and behavioural syndromes (Sih et al. 2004b). Reviews of cases of stable behavioural types within a population, as well as discussions of how these phenomena fit into existing evolutionary theory (Gosling 2001; Dall et al. 2004; Sih et al. 2004a, b), have generated debate over whether these patterns result from constraints or adaptive strategies (see e.g. Neff & Sherman 2004).

In this short paper, we derive a game theoretic model of how stable interindividual behavioural types can emerge as an adaptive response to (1) imperfect information

about what context an individual is in and (2) differences in individual state that affect payoffs in the different contexts. The model we develop here is similar in framing to that of Sih (1992): individuals sometimes encounter predators, and so they need to evolve a foraging strategy that manages the risk of predation with the gains to foraging. In the human sciences, this effect is sometimes called the ‘smoke detector principle’ (Nesse & Williams 1994). However, by incorporating differences in individual state, we show that different stable behavioural types can emerge at equilibrium. ‘State’ can refer to size, experience, skill sets, or any asymmetry that affects fitness payoffs. In their review of the behavioural syndromes literature, Sih et al. (2004b) specifically call for models of this kind.

In the remainder of the paper, we first explain the model verbally, then we present the formal model and its analysis, and finally we discuss the results and possible variations on the model.

## Verbal Summary of the Model

One reason for across-context consistency in behaviour may be that cues that indicate which context an individual is in are noisy. Some noise will always exist, because cues are never perfectly correlated with phenomena. Sudden warm weather might predict rain and

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a shadow over head might predict a predator, but neither is perfect. Because of this noise, mistakes are inevitable when guessing which behaviour is optimal in the current context. If errors are common enough, individuals may be better off always behaving the same way across contexts. Thus noise limits the value of phenotypic plasticity.

The argument above may generate consistency across contexts, but why would some individuals be consistently one way, while other individuals behave consistently another? That is, if individual 1 always does X, in both situations A and B, why would individual 2 always do Y, in A and B? One possible answer is that if individuals 1 and 2 have asymmetries in ability that lead them to rank the fitness payoffs in A and B differently, they may opt to behave in opposite manners in both contexts.

Suppose for example that in a particular species, individuals come in two types: big and small. Imagine individuals have the opportunity to forage in a context in which predators are sometimes present. They must assess whether it is safe to continue foraging, because the predator is absent, or unsafe and flee. Assume big individuals are harder to eat, so if they continue to forage in the presence of a hungry predator, their expected payoff is higher than that of small individuals, who are easy to swallow. Now if cues from the predator about its presence or aggression level are noisy, what should each type of individual do on average? If there is sufficient noise in the cues, it will pay to always assume the predator is hungry and avoid foraging. You can eat later, when the predator is not around, or you can forage someplace safe. However, if big individuals cannot be eaten very easily, then it may pay them to usually ignore cues and try to forage anyway. That is, for big individuals, the cost of missing out on a meal may be greater than the expected cost of being attacked, while for small individuals, the cost of missing a meal is small relative to the cost of being attacked.

In the next section, we formalize the above argument, using a continuous range of states, rather than just 'big' and 'small'. However, keep in mind that state in the model could refer to many kinds of asymmetry, not just an obvious morphological one. In the discussion, we present some other ambiguous contexts in which the model might apply.

## Formal Model

Assume that each individual in a large well-mixed population has state  $x \geq 0$ . We use state here in the same sense as Houston & McNamara (1999) to refer to any aspect of the individual that can be measured and is needed to understand the strategic options, payoffs and dynamics of behaviour (a state variable). This might be any asymmetry, including differences in acquired skill or experience, age, energy reserves, or immune status. We do not model how differences in state arise, but rather what their consequences can be. We will imagine  $x$  to be body size, for the sake of the story that frames the model. It is possible, though, that differences in skill or experience could arise from otherwise identical individuals. These asymmetries in state would then have the same effect within the

model. Thus the model will apply beyond obvious morphological differences.

We consider how individuals behave when foraging in a particular location. There are other situations in which individuals may forage, but in the one we consider, sometimes a predator is present. Thus there are two contexts, predator absent and predator present. There is a chance  $p$  that a predator is actually present. Individuals can assess the environment for a cue (visual, chemical or otherwise) that a predator is present. A proportion  $f$  of the time, the cue is false. Individuals can either forage or run away in response to a cue. We assume that the payoff to successfully foraging (when a predator is really absent) is  $F(x)$ . When a predator is present, there is a chance  $E(x)$  that an individual escapes being eaten, in which case that individual's fitness is unchanged,  $w_0$ . The rest of the time, prey do not escape and they are eaten. We write specific forms for  $F(x)$  and  $E(x)$  later. For now, it is enough to assume that  $\partial E(x)/\partial x > 0$  and  $F(x) > 0$ . That is, larger individuals are less likely to be eaten and successful foraging increases fitness.

We are interested in two thresholds: (1) the size  $x$  at which always running away is better than responding to the cue, and (2) the size  $x$  at which always foraging is better than responding to the cue. The fitness of an individual of size  $x$  who never forages (NF; never in this context, but there are other contexts in which it is safe to forage) is simply:

$$W(\text{NF}|x) = w_0.$$

The fitness of an individual of size  $x$  who responds (R) to cues about the presence of a predator is instead:

$$W(\text{R}|x) = p\{(1-f)w_0 + fE(x)w_0\} + (1-p)\{(1-f)(F(x) + w_0) + fw_0\}.$$

Thus the individual never forages, provided that:

$$E(x) < 1 - \left(\frac{F(x)}{w_0}\right) \left(\frac{1-f}{f}\right) \left(\frac{1-p}{p}\right). \quad (1)$$

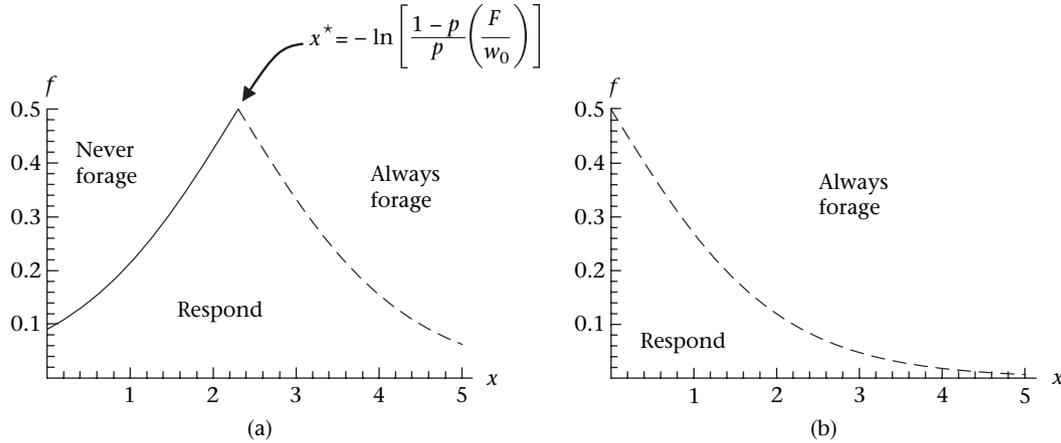
Similarly, an individual of size  $x$  who always forages (AF) has fitness:

$$W(\text{AF}|x) = pE(x)w_0 + (1-p)(F(x) + w_0).$$

Thus always foraging has higher fitness than responding when:

$$E(x) > 1 - \left(\frac{F(x)}{w_0}\right) \left(\frac{f}{1-f}\right) \left(\frac{p}{1-p}\right). \quad (2)$$

Using the two conditions above, we can deduce the range of states that lead to 'personality' outcomes; when some individuals consistently behave one way while others behave in other ways. It is easier to see the possibilities once we assume some functional form for  $E(x)$ . Let  $E(x) = 1 - \exp(-x)$ , which means that individuals with  $x = 0$  are always caught and individuals of increasing size are caught less. Since size  $x$  is measured on an arbitrary scale, this costs us little in terms of generality. Let  $F(x) = F > 0$ . Solving expressions (1) and (2) for  $f$  gives



**Figure 1.** Plots of the two boundary conditions for  $f$ , as a function of size  $x$ , assuming  $E(x) = 1 - \exp(-x)$ . The solid line is the boundary for never forage (NF). Values of  $f$  above this line make NF an evolutionarily stable strategy (ESS). The dashed line is the boundary for always forage (AF). Above this line, is an ESS. (a)  $p = 0.5$ ,  $w_0/F = 10$ . Three types of individuals exist: the smallest individuals always run away, mid-sized individuals respond to cues, and the largest always forage. The more error in  $f$ , the greater the range of sizes that lead to fixed behaviours. At  $f = 0.5$ , there is no information, small individuals always run and large individuals always forage. No one responds to cues. (b)  $p = 0.5$ ,  $w_0/F = 1$ . Foraging is sufficiently better than forgoing the opportunity that selection does not favour timid individuals. However, above a certain size, always forage is still an ESS.

two functions of  $x$  that yield threshold values of error. Figure 1 plots these two boundary conditions. When the value of foraging is low relative to the outside option ( $w_0$ ), small individuals may be better off running away. But even if the value of foraging is high, large individuals may be better off always foraging, rather than trying to respond to cues.

The two boundary conditions for  $f$  intersect where:

$$x = x^* = -\ln \left[ \frac{1-p}{p} \left( \frac{F}{w_0} \right) \right].$$

This expression helps us understand how the base-rate presence of the predator and the relative value of foraging affect the regions of invariant behaviour. As  $p$  increases, predators are more common, and the value of  $x^*$  increases. This is a result of selection favouring the general assumption that predators are around, even if undetected. Thus, a greater range of sizes of  $x$  will be selected to never forage (left of the first boundary in Fig. 1a). Increasing the ratio  $F/w_0$  reduces the value of  $x^*$ , because when foraging is valuable, a greater range of sizes for  $x$  will be selected to always forage.

## DISCUSSION

We think that this model, like many formal arguments, is best seen as a proof of the logical consistency of a hypothesis. If (1) information about the world is noisy and (2) individuals vary in state, and that state has consequences for the payoffs to actions, then selection may favour individuals in different states ignoring cues about context and behaving as if they had 'personality'. Furthermore, this source of consistent behavioural differences across contexts is an adaptation, not a side-effect of any constraint, other than the fact that information about the world is prone to error. Selection of course acts

on strategies, not behaviour, and so while any given instance of behaviour may appear maladaptive, 'personality' as it exists in this model is not a maladaptation, once the full range of contexts and outcomes is considered.

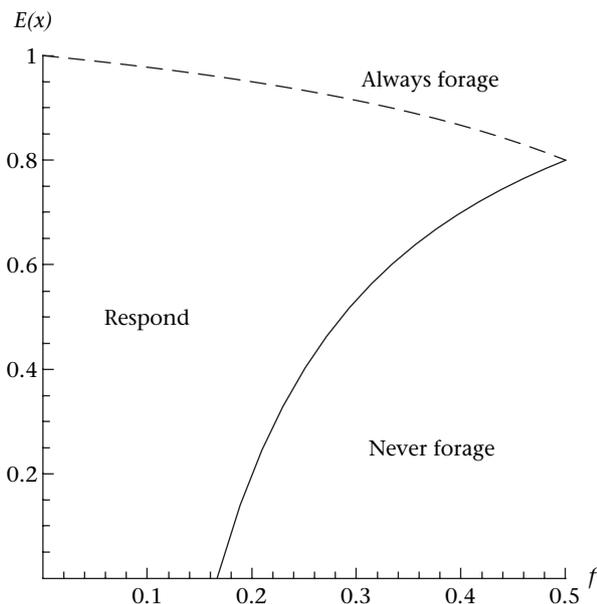
We used a foraging example, in which individuals differ in body size, to frame the model. However, many other adaptive contexts could be wrapped around the same abstractions. In some cases, the two contexts may be apparently more different than simply foraging when a predator is absent versus when it is present. For example, it is not always clear if a conspecific wishes to mate with or feed on a potential mate. Cues might be available that allow distinguishing between these two contexts, but mistakes are likely and deception is possible. If individual state affects the expected costs and benefits of forgoing mating or potentially being consumed, then consistent across-context differences could arise, as they do in the foraging framework of the model. The important issue is whether contexts that seem obviously different to the behavioural ecologist are always obviously different to the organism of study.

Another concern is whether this model can apply to cases in which individuals are very similar in state yet nevertheless display behavioural syndromes. This model of course may not apply in such cases. However, since many aspects of an organism's state are hard to observe, it is not clear whether obvious aspects of state being the same precludes hidden states, such as immune condition or experience, from generating similar outcomes. For example, if past experience generates some individuals who are good at escape behaviour and others who are better at avoiding detection, then these differences in state could also affect payoffs while foraging and again generate predictable differences in behaviour across contexts. Also, if the scale at which state is measured transforms into functional outcomes in a very nonlinear way, then even

small differences in size or age or experience could produce big differences in behaviour.

One interesting case is to rearrange the model to generate personality from individual differences in awareness or in the ability to process cues, rather than from state differences that affect escape probabilities. Assume all individuals have the same  $x$ , such that we now plot expressions (1) and (2) as a function of individual differences in  $f$ , the noise in information about predator presence. These differences in state  $f$  might arise from experience in observing cues, subtle differences in sensory ability, or investments in attention. We plot the system from this point of view in Fig. 2. If accuracy of information could arise from investment in 'information foraging', then it might be possible to derive cases in which two coexisting strategies are (1) foraging for accurate information and (2) responding to cues and forgoing information foraging and instead behaving inflexibly.

A number of changes to the model are possible. If the minimum value of  $E(x)$  is not zero and the maximum value does not approach one, then the broad deductions above can change. We could let  $E(x) = (E_{\max} - E_{\min})(1 - \exp(-x)) + E_{\min}$ , for example. If  $E_{\max}$  is small enough, selection may favour monotypic populations in which only one strategy, perhaps an invariant one, is present. The same kind of monotypic population can result from certain forms of  $F(x)$ , the value of foraging. If large individuals get less from foraging, perhaps  $F(x) = F \exp(-x)$ , then we again get a situation in which there is a threshold amount of error above which everyone in the population



**Figure 2.** Individual differences in the ability to extract noiseless information may also lead to persistent differences in behaviour across contexts. Here we plot conditions 1 and 2 as functions of  $f$ , the error in cues about predators. Individuals who can extract accurate information, on the left side of the plot, are likely to respond to cues. With increasing noise, individuals may either always forage or never forage, depending upon the details. Pictured,  $w_0/F = 5$ ,  $p = 0.5$ .

avoids foraging. Below this amount, everyone responds to cues. It may seem more reasonable to assume that the value increases with size, as in  $F(x) = F(1 - \exp(-x))$ , which means that larger individuals gain more from foraging, perhaps because they are hungrier, or because they are better competitors. While this changes the precise results, it has little effect on the intuitions we presented above.

Another obvious extension is to consider a continuous behaviour. In such a model, error is likely to distort behaviour from the perfect-information optimum. For example, models by both Tufto (2000) and Luttbegg & Warner (1999) produce lack of response to cues or biasing of response as a result of uncertainty about environmental state. Neither of these models incorporates behavioural syndromes specifically, but either type of problem could be extended to include variation in individual state, as in the model we present here.

Finally, some of our colleagues have asked us how the model would work in the case of more dynamic states, such as explicit experience, that change as the individual behaves. We have not made such a model, but we imagine that some dynamic states could lead to self-reinforcing divergence, as when individuals invest in special skills that make them better competitors at one task but worse at others. This is to say that we find no obvious reason that dynamic state models could not produce the same kind of effect we outline here.

How important this kind of adaptation is for explaining the cases of behavioural syndromes and animal personality in the literature is hard to say. However, a first important step in understanding animal 'personality' is to have a number of deductively valid hypotheses to challenge with the data from a number of experimental systems. See for example Dall et al. (2004) for other ideas. We also note that the idea we have modelled here is conceptually very like Haselton's (Haselton & Buss 2000) theory of error management in the psychology of human mating (state in our model is conceptually like sex in theirs), for which there is a growing empirical literature suggesting the idea is of explanatory value.

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