

# Heterogeneous responsiveness to environmental stimuli

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## Abstract

Individuals of a species cope with environmental variability through behavioral adjustments driven by individuals' responsiveness to environmental stimuli. Three key empirical observations have been made for many animal species: The coexistence of different degrees of responsiveness within one species; the consistency of an individual's degree of responsiveness across time; and the correlation of an individual's degree of responsiveness across contexts. Taking up key elements of existing approaches, we provide one unifying explanation for all three observations, by identifying a unique evolutionarily stable strategy of an appropriately defined game within a stochastic environment that has all three features. Coexistence is explained by a form of negative frequency dependence. Consistency and correlation is explained through potentially small, individual, differences of states animals have and the resulting differential advantages they can get from it. Our results allow us to identify a variety of testable implications.

# Heterogeneous responsiveness to environmental stimuli

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**Individuals of a species cope with environmental variability through behavioral adjustments driven by individuals' responsiveness to environmental stimuli. Three key empirical observations have been made for many animal species: The coexistence of different degrees of responsiveness within one species; the consistency of an individual's degree of responsiveness across time; and the correlation of an individual's degree of responsiveness across contexts. Taking up key elements of existing approaches, we provide one unifying explanation for all three observations, by identifying a unique evolutionarily stable strategy of an appropriately defined game within a stochastic environment that has all three features. Coexistence is explained by a form of negative frequency dependence. Consistency and correlation is explained through potentially small, individual, differences of states animals have and the resulting differential advantages they can get from it. Our results allow us to identify a variety of testable implications.**

game theory | reactivity | behavioural ecology | individual differences

**A** first step to understand how resilient different species are to an increase in the variability of their environment is to understand the driving mechanisms behind their ability to deal with the already volatile environments that they have always lived in. We build a game-theoretic model to identify potential mechanisms leading to an evolutionary stable strategy that exhibits the key empirical observations that have been made in the literature on the responsiveness to environmental stimuli in a stochastic environment. The model also delivers additional testable implications. The model provides specific quantitative frequency predictions of the distribution of environmental responsiveness as a function of a few parameters of the environment. Owing to the stylized nature of the game theoretic model, these quantitative predictions should be taken with a grain of salt, but could at least be the starting point for additional exploration. The model, however, also provides a range of robust qualitative predictions. The model, in general, predicts a continuum of different degrees of environmental responsiveness. It also predicts that the exact stochastic nature does not affect the distribution of environmental responsiveness. This implies that any potential changes to the stochastic process that generates these individuals' environment does at least not affect the distribution of these individuals' degree of responsiveness. Finally, when there is idiosyncratic noise in the individuals' observation of their environment, the model predicts that the equilibrium responsiveness increases when the observation noise increases. More observation noise, in some sense, forces individuals to overreact to environmental stimuli.

**Building blocks from the existing literature** It is well documented that individuals differ in the degree of responsiveness to external stimuli, a phenomenon sometimes referred to as behavioral

plasticity, see e.g., (1). This difference in environmental responsiveness constitutes the main characteristic of personalities, and personalities have been observed in more than 100 species, see e.g., the survey by (2). Three key observations have been made for many animal species, as, for instance, highlighted by (3) (see also (4)): The coexistence of different degrees of responsiveness within one species; the consistency of an individual's degree of responsiveness across time; and the consistency, or often referred to as correlation, of an individual's degree of responsiveness across contexts.\*

A few theoretical approaches explain one or more of these three observations. The theory of biological sensitivity to context, as in (6, 7), and (8) explains the coexistence of different degrees of environmental responsiveness with differences in individuals' experiences in their early development, where different experiences lead to different behavior. The theory of differential sensitivity as in (9) interprets the difference of behaviour as a way to hedge future generations against the uncertainty in the environment, recently formalised by (10) and (11). Since the future is inherently unpredictable, parents have offspring with different degrees of environmental responsiveness so that for every environment there are at least some offspring that are able to cope with the environment.† A third theoretical approach is built around the idea

\*The "suite of correlated behaviors [...] reflecting the individual consistency across [...] situations" has been referred to as a "behavioral syndrome" by (5).

†The two theories are not exclusive. (6), also (1) argue in favor of an integration of the two theories.

## Significance Statement

There is a pressing need to better understand how individuals in a population deal with rapid change (notably human-induced) such as biodiversity loss or climate change. A first step to understand how resilient different species are to an increase in variability is to understand what the driving mechanisms are behind their ability to deal with the already volatile environments they have always lived in. Here, we use ingredients from various theories to build a simple game-theoretical model to explain the heterogeneity of animal responsiveness to environmental stimuli. The model provides additional testable predictions: the proportion of responsive individuals is affected by the amplitude but not by the stochasticity of the environment; the proportion of responsive individuals is higher the more noisy the animals' information about the environment; the distribution of the degree of responsiveness has a specific testable form.

C.K. designed research, J.C. reviewed literature, J.C. and C.K. performed research, J.C., M.G. and C.K. wrote the paper.

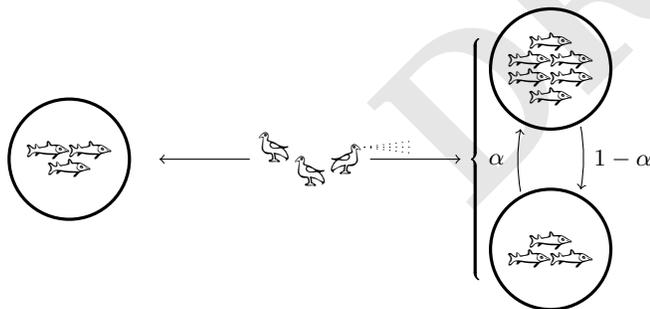
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of “negative frequency dependence.” The more individuals are responsive to environmental stimuli the less the benefits of being responsive. Negative frequency dependence is a cornerstone for explanations of the coexistence of different degrees of environmental responsiveness in the seminal models of (12), (13), (14). See (15) for a review of earlier models. While negative frequency dependence is able to explain coexistence, consistency and correlation are often explained by an individual’s state (e.g., morphology, phenotype, size, etc.), as in (16) and (15).<sup>‡</sup> However, the recent meta analysis by (17) shows a weak link between state and personalities (individuals’ state can only explain between 3 and 8% of the personality differences).

We study individual responsiveness to environmental stimuli for the specific problem of foraging from multiple food sources, which allows us to additionally build on the existing game-theoretic literature on the *ideal free distribution* of (18), see e.g., the survey of (19): individuals allocate themselves proportionally to the amount of food available at each food source. We enrich these game-theoretic models by embedding them in a stochastic environment, which allows us to incorporate the salient features of the three approaches mentioned above. We do this in a few steps of varying complexity.

**Modelling strategy and main results** The basic model (in Section 1) is sketched in Figure 1. To illustrate the model we use fish-feeding birds as an example, with the simplifying condition that they do not show any social behavior (such as flocking or swarming). Individuals have to choose to forage from one of two food sources, one providing a fixed amount of food, the other a random amount of food. All individuals who go to the same food source are assumed to share the available food there equally. In the basic model the random food source can only have two possible levels of food availability.



**Fig. 1.** A graphical sketch of the basic model. The birds are the players, who choose which food source to go to: fixed food source A on the left or stochastic food source B on the right, with  $\alpha$  the probability of high food availability. The bird’s scanning indicates that players make their decision based on observing the food availability at the stochastic source.

Our first main result (Proposition 1) is that, under a mild condition, the game always has a unique symmetric Nash equilibrium strategy, and this strategy exhibits coexistence of responsive and non-responsive individuals.<sup>§</sup> This coexistence is in terms of the equilibrium being in completely mixed

<sup>‡</sup>(12) explain consistency and correlation with a “positive-feedback mechanism:” responsiveness is less costly for individuals that have been responsive before. (14) explain consistency and correlation by small variations of individuals’ metabolism (which is a form of state).

<sup>§</sup>We use the definition of an ESS as extended from that of (20) to symmetric  $n$ -player games by (21), see also (22). In Proposition 2 we show that our games are *stable games* in the sense of (23). This implies that the unique symmetric Nash equilibrium of these games is asymptotically stable

strategies. This has two possible interpretations. Either all individuals truly randomize between being responsive and not being responsive. Under this interpretation we would not obtain consistency and correlation. Or, alternatively, the individuals playing the game are randomly chosen from a larger population to play this game and an appropriate fraction of individuals is responsive and another is non-responsive. This could be interpreted to at least allow for consistency and correlation. In Section 3 we introduce small perturbations to the game theoretic model by allowing an individual’s food source preference, and the individual’s (small) cost of being responsive, to be a little bit idiosyncratic. This is essentially the idea of (30) *purification* and the idea of *threshold decisions* of (31). The mixed strategy equilibrium (or ESS) corresponds in the so modified game to an equilibrium in which every individual actually uses a pure strategy of either being responsive or not. This pure strategy choice depends to some extent on this individual’s idiosyncratic preference or cost and would thus be stable across time and, to a lesser extent, also across contexts.

We not only show that there is a unique symmetric Nash equilibrium with the desired features, but also provide an analytic expression for the equilibrium pure strategy frequencies as a function of the parameters of the problem. This allows us to derive additional testable predictions of our model. Acknowledging that our model is a highly simplified account of reality, some of these predictions may well hold beyond the narrower confines of our model. In particular, and perhaps most striking: the unique equilibrium does not change with the stochasticity of the environment, at least when the cost of cognition is negligible. In other words, the equilibrium does not depend on the probability of the state of food availability at the random food source. This implies that changes to the stochastic process of the environment may not push behavior out of equilibrium. Individuals’ strategies are already sufficiently complex to allow essentially immediate and automatic adaptation to such changes. Of course, this does not imply that individuals are not affected if, for instance, high food availability becomes rarer. Only their strategy is unaffected, not necessarily the amount of food they can consume.

Another testable prediction can be derived from an extension of our basic model, presented in Section 4, in which individuals only receive (private) noisy information about the state of food availability. At least for small amounts of noise, the equilibrium responsiveness increases when the noise increases. More noise, in some sense, forces individuals to overreact to environmental stimuli. A final testable prediction, again derived from an extension of our basic model and presented in Section 5, is that for more general distributions of food availability, one would expect to see a continuum of degrees of responsiveness to environmental stimuli. See e.g., (32) for empirical support for this finding.

## 1. The basic model

In this section we present the simplest possible model of interest for our problem. Each of  $n < \infty$  individuals can go to one of two food sources A or B. Food source A has a fixed amount of food normalized to  $n$  units of nutrition to facilitate an easier comparison when we vary the number of individuals  $n$ . Food

under most plausible behavioral adjustment dynamics, such as the replicator dynamics of (24), the Smith dynamics (25), the projection dynamics (26), as well as all dynamics of the class of target dynamics (among them the BNN (27), Best response (28) and Logit (29) dynamics).

152 source  $B$  has a stochastic amount of food  $n \cdot X$ , with  $X$  drawn  
 153 from a Bernoulli distribution with  $X = \eta$  with probability  $\alpha$   
 154 and  $X = \lambda$  with probability  $1 - \alpha$ .

155 Before making their choice of food source, individuals can,  
 156 in principle, inform themselves about the state of food source  
 157  $B$ ; individuals can choose to learn whether  $X = \lambda$  or  $X = \eta$ .  
 158 Individuals, thus, have six strategies at their disposal in this  
 159 simple model. They can choose to be informed or to be  
 160 uninformed. If uninformed they can then choose to go to food  
 161 source  $A$  or  $B$ . If informed they have the choice to ignore their  
 162 information and go to  $A$  or  $B$  regardless of the information  
 163 they have received, or they can react to the information in  
 164 one of two ways. They can be, what we term, *responsive* by  
 165 going to  $A$  when  $X = \lambda$  and going to  $B$  when  $X = \eta$ , or, what  
 166 we term *counter-responsive* by doing the opposite.

167 We assume that the choice of becoming informed bears an  
 168 arbitrarily small cost  $c > 0$ , where arbitrarily small means that  
 169 we ultimately investigate the limit case when  $c$  tends to zero.  
 170 The assumption of positive costs implies that the two strategies  
 171 of getting informed and then ignoring the information are  
 172 strictly dominated by the strategy of not getting informed and  
 173 going to the same food source. By virtue of saving on the small  
 174 positive cost  $c$  the latter strategies provide a strictly higher  
 175 payoff in both states  $X = \lambda$  and  $X = \eta$  regardless of what the  
 176 other individuals do. We are thus left with four pure strategies.  
 177 We denote the set of strategies by  $S = \{A, B, R, C\}$ , for always  
 178 going to food source  $A$ , always to  $B$ , being responsive, and  
 179 being counter-responsive, respectively.

180 We allow individuals to choose randomly. We come back  
 181 to the interpretation of random choice in Section 3. Let  $\Delta(S)$   
 182 denote the set of all mixed strategies, that is the set of all  
 183 probability distributions over  $S$ . A pure strategy  $s \in S$  can  
 184 be identified as the mixed strategy that attaches probability 1  
 185 on pure strategy  $s$ .

186 We assume throughout the paper that all individuals who  
 187 go to the same food source share the available food at this  
 188 source equitably. This implies that the payoff to an individual  
 189 who goes to one of the two food sources only depends on  
 190 the number of other individuals,  $k$ , that go to food source  $A$   
 191 (which implies that  $n - 1 - k$  others go to food source  $B$ ). The  
 192 payoff to an individual who goes to food source  $A$  is given by  
 193  $\frac{n}{k+1}$ ; the payoff to an individual who goes to  $B$  is given by  
 194  $\frac{nX}{n-k}$ .

195 Given that individuals can choose mixed strategies, that  
 196 is can choose randomly, we need to compute individuals' ex-  
 197 pected payoffs given these random choices. To do so, consider  
 198 an arbitrary individual who is facing that all other  $n - 1$  indi-  
 199 viduals choose a given (mixed) strategy  $\sigma \in \Delta(S)$  with  $\sigma(s)$   
 200 the probability that pure strategy  $s$  is chosen. Denote by  $N_s$   
 201 the random variable that is the number of opponents who  
 202 end up choosing pure strategy  $s \in S$  (given the probability of  
 203 choosing  $s$  is  $\sigma(s)$ ). The tuple  $(N_A, N_B, N_R, N_C)$  is then multi-  
 204 nomially distributed with parameters  $n - 1$  and probability  
 205 vector  $(\sigma(A), \sigma(B), \sigma(R), \sigma(C))$ .

206 Given  $\sigma$ , let  $R_{A\lambda}$  denote the random variable that is the  
 207 food share available at food source  $A$  in state  $\lambda$ . Let food shares  
 208  $R_{A\eta}, R_{B\lambda}, R_{B\eta}$ , be defined analogously. These (random) food

shares are given by

$$\begin{aligned} R_{A\lambda} &= \frac{n}{N_A + N_R + 1} \\ R_{A\eta} &= \frac{n}{N_A + N_C + 1} \\ R_{B\lambda} &= \frac{\lambda \cdot n}{N_B + N_C + 1} \\ R_{B\eta} &= \frac{\eta \cdot n}{N_B + N_R + 1}. \end{aligned}$$

We can, then, express an individual's expected payoffs from  
 choosing pure strategy  $s \in S$ , when all others use mixed  
 strategy  $\sigma$ , as follows.

$$\begin{aligned} u(A, \sigma) &= \alpha \mathbf{E}[R_{A\eta}] + (1 - \alpha) \mathbf{E}[R_{A\lambda}] \\ u(B, \sigma) &= \alpha \mathbf{E}[R_{B\eta}] + (1 - \alpha) \mathbf{E}[R_{B\lambda}] \\ u(R, \sigma) &= \alpha \mathbf{E}[R_{B\eta}] + (1 - \alpha) \mathbf{E}[R_{A\lambda}] - c \\ u(C, \sigma) &= \alpha \mathbf{E}[R_{A\eta}] + (1 - \alpha) \mathbf{E}[R_{B\lambda}] - c. \end{aligned} \quad [1]$$

In the above expression,  $\mathbf{E}$  denotes the expectation with respect  
 to the randomness created by mixed strategy  $\sigma$ .

We extend an individual's payoff function to mixed strate-  
 gies by taking expectations. That is

$$u(\sigma', \sigma) = \sum_{s \in S} u(s, \sigma) \sigma'(s).$$

A strategy  $\sigma \in \Delta(S)$  is a *symmetric Nash equilibrium*, see  
 (33), if  $u(\sigma, \sigma) \geq u(\sigma', \sigma)$  for all  $\sigma' \in \Delta(S)$ .

## 2. Results for the basic model

The following proposition (with proof in the appendix) is the  
 main result for the basic model for the limit case where the  
 cost of cognition (or being responsive) is negligible. It proves  
 that there is a unique symmetric Nash equilibrium of this  
 game, shows that in this equilibrium there is heterogeneity  
 in individual's responsiveness to environmental stimuli, and  
 provides an exact analytic expression for the frequency of  
 responsive individuals. This equilibrium responsiveness fre-  
 quency, finally, is shown to be independent of the stochasticity  
 $\alpha$  in the environment.

**Proposition 1.** *Under the assumption that  $\frac{1}{n} < \lambda < \eta < n$ ,  
 the game in the basic model, in the limit as cognition cost  
 $c \rightarrow 0$  and the number of individuals  $n \rightarrow \infty$ , has a unique  
 limiting symmetric Nash equilibrium, in which  $\sigma(A) = \frac{1}{1+\eta}$ ,  
 $\sigma(B) = \frac{\lambda}{1+\lambda}$ ,  $\sigma(R) = \frac{\eta-\lambda}{(1+\lambda)(1+\eta)}$ , and  $\sigma(C) = 0$ .*

The intuition behind the key insight of this result is as  
 follows. First, we notice that no pure strategy can be an  
 equilibrium. If everyone always goes to food source  $A$ , it  
 would be best to go to food source  $B$ . If everyone goes to  $B$ ,  
 it would be best to go to  $A$ . If everyone is responsive, then  
 it would be best to be counter-responsive, so as to always  
 be at the food source where no one else is and not have to  
 share food at all. If everyone is counter-responsive, for the  
 same reason it is best to be responsive. One can then show,  
 in fact, that in a Nash equilibrium there must be a mix of  
 strategies  $A$ ,  $B$ , and  $R$  (and, interestingly, no  $C$ ). This means  
 that, in equilibrium, we have the coexistence of responsive and  
 unresponsive individuals. This also implies that all individuals  
 must be indifferent between always going to  $A$ , always going  
 to  $B$ , and to being responsive. This can only be achieved if the  
 realized food share at each food source is the same, regardless  
 of the state of the food availability at the random food source.

255 The exact equilibrium frequencies can then be derived from  
 256 this argument. Finally, this finding then also explains why the  
 257 frequency of responsive individuals does not depend on the  
 258 exact stochastic nature of the environment.

259 It is well known that a necessary condition for a strategy to  
 260 be an evolutionarily stable strategy (ESS) in the sense of (20),  
 261 and for our context in the sense of (21), is that the strategy  
 262 in question is a symmetric Nash equilibrium strategy. It is  
 263 also well known, see e.g., (34), that Nash equilibria are the  
 264 only candidates for asymptotically stable rest points under  
 265 most deterministic behavioral adjustment (or evolutionary)  
 266 dynamics, with the replicator dynamics of (24) the first and  
 267 most prominent example. The following result shows that  
 268 the unique symmetric Nash equilibrium that we identified in  
 269 Proposition 1 is indeed an ESS as well as asymptotically stable  
 270 under many behavioral adjustment dynamics.

271 **Proposition 2.** *Under the assumption that  $\frac{1}{n} < \lambda < \eta < n$ ,*  
 272 *the unique equilibrium of the game in the basic model, in the*  
 273 *limit as cognition cost  $c \rightarrow 0$  and the number of individuals*  
 274  *$n \rightarrow \infty$ , is an ESS, is asymptotically stable under the replicator*  
 275 *dynamics (24), the Smith (25) and the projection dynamics*  
 276 *(26), as well as the class of target dynamics which comprises,*  
 277 *among others, the BNN (27), Best-response (28) and Logit*  
 278 *dynamics (29).*

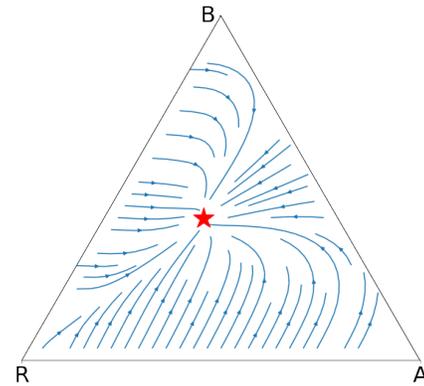
279 The key insight to prove this Proposition is that all games  
 280 in our class of games are stable games in the sense of (23), as  
 281 we prove in the Appendix. All results then follow from this  
 282 fact.

283 Some of these findings can be seen in Figure 2, which depicts  
 284 the phase diagram of the replicator dynamics. The only  
 285 difference between Figures 2.a and 2.b is that the stochasticity  
 286 parameter  $\alpha$  changes. This has no effect on the equilibrium  
 287 itself, but does affect somewhat the out of equilibrium dynam-  
 288 ics. It can also be seen that not only is the unique equilibrium  
 289 asymptotically stable, but also in fact a global attractor under  
 290 the replicator dynamics: All solution paths eventually  
 291 converge to the equilibrium.

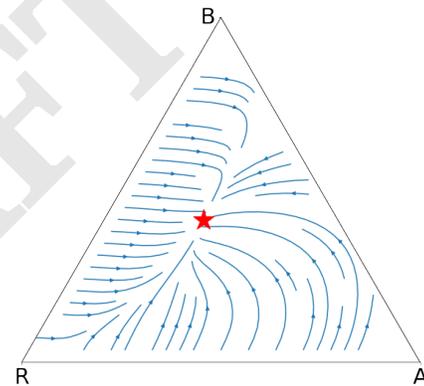
292 We finally highlight that, if the cost of cognition,  $c$ , is non-  
 293 negligible, then the equilibrium frequencies not only depend  
 294 on this cost, but also depend on  $\alpha$ , the stochastic nature of  
 295 the environment. By the known fact, see e.g., (35), that the  
 296 (symmetric) Nash equilibrium correspondence is upper-hemi-  
 297 continuous in the space of games, small changes to  $c$  and  $\alpha$   
 298 can, however, only lead to small changes in the equilibrium  
 299 frequencies.

### 300 3. Consistency and Correlation

301 Suppose that the  $n$  individuals play the same game given in  
 302 our basic model over and over again for many periods of time.  
 303 Suppose that, at every point in time, they play the unique  
 304 symmetric equilibrium given in Proposition 1. An outside  
 305 observer would note that when the amount of food available at  
 306  $B$  is high ( $X = \eta$ ) more individuals are to be found at source  
 307  $B$  than when it is low ( $X = \lambda$ ). They would also observe that  
 308 the food share each individual receives is the same regardless  
 309 of which source the individuals go to. The outside observer  
 310 would conclude that some individuals must be responsive to  
 311 the stochastic food availability at source  $B$ . But if they were to  
 312 trace each individual, they would realize that each individual  
 313 is sometimes responsive and sometimes not responsive. There



(a)  $\alpha = 0.7, \lambda = 0.7, \eta = 3$



(b)  $\alpha = 0.4, \lambda = 0.7, \eta = 3$

**Fig. 2.** Phase diagram of the replicator dynamics for different parameter values. The cost of cognition  $c$  is always zero. The equilibrium is denoted by a red star.

314 is no internal consistency in the individuals' behavior. Each  
 315 animal randomizes at each point in time. This is no surprise,  
 316 because the unique equilibrium is in mixed (or randomized)  
 317 strategies. However, we must point out that this is inconsistent  
 318 with empirical findings.

319 A slight change to the basic model is able to accommodate  
 320 the common empirical finding that over time typically the  
 321 same individuals are responsive. This modification is based  
 322 on the idea of *purification* of (30), which is very similar to the  
 323 idea of *threshold decisions* as provided in (31). The idea is  
 324 that individuals differ a little bit in terms of their personal  
 325 preferences and actually make a pure strategy choice that is,  
 326 however, dependent on their own personal preferences that  
 327 only they themselves know. As a consequence, while the  
 328 equilibrium looks mixed to other individuals, each individual  
 329 actually plays a pure strategy. We adapt the model according  
 330 to this idea by replacing the payoff function  $u$  of the original  
 331 model with a slightly perturbed payoff function  $v_\theta$  that is

essentially equal to  $u$  plus a small idiosyncratic (individual-specific) preference or perturbation term:

$$\begin{aligned} v_\theta(A, \sigma) &= u(A, \sigma) + \theta_A \\ v_\theta(B, \sigma) &= u(B, \sigma) + \theta_B \\ v_\theta(R, \sigma) &= u(R, \sigma) + \alpha\theta_B + (1 - \alpha)\theta_A + \theta_R \\ v_\theta(C, \sigma) &= u(C, \sigma) + \alpha\theta_A + (1 - \alpha)\theta_B + \theta_R, \end{aligned}$$

where the vector  $\theta = (\theta_A, \theta_B, \theta_R)$  is i.i.d. drawn from some arbitrary full support continuous joint distribution  $F$  (with density  $f$ ) over  $\Theta = [-\epsilon, \epsilon]^3$ , for a small  $\epsilon > 0$ . It is assumed that an individual's realized  $\theta$  is that individual's private information, unknown to other individuals. We have deliberately chosen the same preference perturbation  $\theta_R$  for pure strategies  $C$  and  $R$ , as it seems more natural to have an idiosyncratic perturbation of the cost of being responsive rather than for how one is responsive. However, it does not matter what we assume for pure strategy  $C$  as long as the payoff perturbation is small, as pure strategy  $C$  provides a strictly lower payoff than the other three strategies in the equilibrium given in Proposition 1, and small payoff perturbations cannot change that.

(30) has shown that almost any equilibrium of a complete information game, such as our basic game, is such that for any nearby incomplete information game with payoff perturbations given by the joint distribution  $F$  has a nearby equilibrium and that this nearby equilibrium is essentially in pure strategies.<sup>¶</sup> In such a nearby equilibrium there is a parameter region for  $\theta \in \Theta$  for which an individual strictly prefers to play  $A$ , another region for which an individual strictly prefers to play  $B$ , and a final region in which an individual strictly prefers to play  $R$ . The set of  $\theta$ 's for which an individual is indifferent between two or three of the three strategies has measure zero. See the Supporting Information for more details. Finally, such purified equilibria can also shown to be dynamically stable under a suitably defined behavioral adjustment dynamics as in (36), see (37).

Suppose now that the  $n$  individuals play the resulting equilibrium of the same slightly perturbed game repeatedly over many time periods. It is then a question of whether the perturbation parameters  $\theta$  remain the same for each individual over time or not. Suppose that they do. Then an outside observer would not only observe all that the observer would have observed that we described above, but also that it would be the same individuals who always go to food source  $A$ , the same individuals who always go to food source  $B$ , and the same who are responsive.

This model is also flexible enough to generate a strong consistency over time and a weaker, but some, consistency across contexts, depending on how these consistencies are interpreted. Consider the bird example again. One could imagine that  $\theta_R$  is an individual bird's specific parameter that does not change over time nor across contexts. On the other hand the parameters  $\theta_A$  and  $\theta_B$  might be constant for one season, but could be different in another season, when the bird's nest location (or the location of the food sources) changes.

As an example of why the perturbed model may be appropriate for our purposes, consider birds who every day have to decide to go to food source  $A$  or  $B$  from their nesting place.

<sup>¶</sup>(30) calls such equilibria *regular* and shows that all finite complete information games have a regular equilibrium. As our equilibrium is unique it must be regular.

Then the location of their nesting place gives rise to their  $\theta$ . An approach could be that  $\theta_A$  and  $\theta_B$  are proportional to the distance that the bird's nest is from the two food sources, respectively, while  $\theta_R$  could be more of a personal characteristic of the bird, measuring how much/less cognitively able this bird is relative to other birds.

One could obtain equilibrium purification even by introducing a payoff-irrelevant personal and privately know characteristic, such as an individual's prior experiences in life, with individuals playing different pure strategies depending on their personal prior experiences. This means that, as pointed out e.g., in (3), (16) and (15), the purification threshold could also be based on an individual's state or their life history.

#### 4. Imperfect private signals of food availability

In our basic model, individuals can learn the state of food availability at the food sources perfectly. In this section we study how the results change if this learning is imperfect. To do so we suppose that each individual, when they learn, receive a noisy signal about the actual level of food availability at food source B. Individuals  $i$  receive conditionally independent (and identically distributed) signals  $s_i \in \{l, h\}$  such that  $P(s_i = h|X = \eta) = P(s_i = l|X = \lambda) = 1 - \epsilon$ , with  $\epsilon < \frac{1}{2}$ . In words, in the high state  $\eta$  the high signal  $h$  is more likely than the low signal  $l$  and in the low state  $\lambda$  the low signal  $l$  is more likely than the high signal  $h$ . The signal is, thus, informative about the true state.

In this case, (random) food shares are given by

$$\begin{aligned} R_{A\lambda} &= \frac{n}{N_{A\lambda} + 1} \\ R_{A\eta} &= \frac{n}{N_{A\eta} + 1} \\ R_{B\lambda} &= \frac{\lambda \cdot n}{N_{B\lambda} + 1} \\ R_{B\eta} &= \frac{\eta \cdot n}{N_{B\eta} + 1}, \end{aligned}$$

where, given strategy  $\sigma$  (used by all opponents),  $N_{A\lambda}$  follows a binomial distribution with  $n - 1$  trials and success probability  $\sigma(A) + (1 - \epsilon)\sigma(R) + \epsilon\sigma(C)$ . Similarly,  $N_{A\eta}$ ,  $N_{B\lambda}$ ,  $N_{B\eta}$  are also binomially distributed with  $n - 1$  trials and success probabilities  $\sigma(A) + (1 - \epsilon)\sigma(C) + \epsilon\sigma(R)$ ,  $\sigma(B) + (1 - \epsilon)\sigma(R) + \epsilon\sigma(C)$ , and  $\sigma(B) + (1 - \epsilon)\sigma(C) + \epsilon\sigma(R)$ , respectively.

Payoffs are as described in Equation 1. All the arguments of the proof of Proposition 1 go through and, ultimately, we obtain that the game has a unique symmetric Nash equilibrium,  $\sigma$ , that is also an ESS (and all other results of Proposition 2 apply) with

$$\begin{cases} \sigma(R) = \frac{\eta - \lambda}{(1 - 2\epsilon)(1 + \eta)(1 + \lambda)} \\ \sigma(A) = \frac{1}{1 + \eta} - \epsilon \frac{\eta - \lambda}{(1 - 2\epsilon)(1 + \eta)(1 + \lambda)} \\ \sigma(B) = \frac{\lambda}{1 + \lambda} - \epsilon \frac{\eta - \lambda}{(1 - 2\epsilon)(1 + \eta)(1 + \lambda)}. \end{cases}$$

The key new insight is that the higher the error probability  $\epsilon$  the higher the fraction (or probability) of responsive individuals in equilibrium.

#### 5. General distributions of food source availability

Recall that, in the basic model food source B is assumed to be Bernoulli distributed (i.e., with only two possible levels of available food at that source). In this section we consider an arbitrary distribution for the food availability at food source B.

Let  $X$ , the available quantity of food at food source B, be distributed according to some distribution with cdf  $F$  with everywhere positive density  $f$  on the interval  $\chi = [x_L, x_H]$  with  $0 \leq x_L < x_H \leq \infty$ . To make the analysis tractable we simplify the model in two ways. First, we set the cost of being responsive,  $c = 0$ .<sup>†</sup> Second, we assume that all individuals learn the value of  $X$ , and allow individuals to only use monotone strategies: An individual's strategy can be described by a cutoff value  $y \in \chi$  such that the individual goes to food source A if and only if  $x < y$ . Otherwise the individual goes to food source B. This implies that the strategy space is identical to  $\chi$  and the set of mixed strategies is the set  $\Delta(\chi)$  of all probability distributions over  $\chi$ . A fully mixed symmetric Nash equilibrium strategy, which can be described by a cdf  $G$  on  $\chi$  must satisfy that any individual is indifferent between using any pure strategy in  $\chi$ , i.e., between using any cut-off  $y \in \chi$ .

We then get the following result.

**Proposition 3.** *In the model of this section, for any  $n$ , there is a unique completely mixed symmetric equilibrium. In the limit as  $n$  tends to infinity, the equilibrium probability that an individual uses cut-off reactivity  $y$  is given by the cdf  $G(y) = \frac{y}{1+y}$ , with  $G(x_L) = \frac{x_L}{1+x_L}$  the probability of an individual always going to food source B,  $1 - G(x_H) = \frac{1}{1+x_H}$  the probability of an individual always going to food source A, and  $G(y) - G(x) = \frac{y-x}{(1+x)(1+y)}$  the probability that an individual adopts a degree of responsiveness in the interval  $[x, y]$ .<sup>\*\*</sup>*

This finding is consistent with those in the basic model. For example, the strategy called  $B$  in the previous model is here similar of choosing the cut off  $x_L$  (since  $x_L$  is the minimum possible value of the stochastic source). The equilibrium frequency of this strategy in the basic model is given by  $\frac{\lambda}{1+\lambda}$ , which is equivalent to  $\frac{x_L}{1+x_L}$ , as  $x_L$  is the smallest possible value of the stochastic source.

## 6. Discussion

We built a stylized game theoretic model of foraging behavior in a stochastic environment. For every parameter specification within certain bounds, this model has a unique symmetric Nash equilibrium, that is also the unique ESS and asymptotically stable under a variety of evolutionary dynamics. This equilibrium has the three key features identified in the literature of *coexistence* of differing degrees of environmental responsiveness, *consistency* of individual environmental responsiveness over time, and *correlation* of individual environmental responsiveness across contexts.

By explicitly studying the phenomenon of heterogeneous responsiveness to environmental stimuli in a foraging setting, we are able to identify the push towards the ideal free distribution of (18), satisfied in the equilibrium of our game, as a possible driving force of this heterogeneity. We derive explicit analytical expressions for the equilibrium frequencies of responsive and non-responsive behavior, at least when the cost of cognition (needed to respond to environmental stimuli)

<sup>†</sup> In a setting in which individuals can have different degrees of responsiveness, as we have here, one might want to assume that the cost of responsiveness varies with the degree of responsiveness. We shall not pursue this here, however.

<sup>\*\*</sup> The distribution with cdf  $G(y) = \frac{y}{1+y}$  is the distribution of a random variable  $Y$  such that its reciprocal (or inverse)  $\frac{1}{Y}$  has exactly the same distribution. One could call  $G$  the inversion invariant distribution.

is negligible or at least relatively small. This allows us to perform comparative statics as to how the equilibrium frequencies change when some of the model parameters change. For instance, we find that, at least when cognition costs are negligible, the exact stochastic nature of the environment does not affect the equilibrium. This finding suggests that changes in the stochastic environmental process would at least not be so disruptive as to push behavior out of equilibrium. Put differently, equilibrium strategies are already complex enough to allow for automatic adaptation to such changes in the stochastic environmental process. In the remainder of this section we discuss some of the limitations of our approach.

**Cost of cognition** We have only explored the case of zero, and by a continuity argument, also of small cost of cognition. For larger cost of cognition, generally, equilibrium behavior will depend on the stochastic nature of the environment and the equilibrium will not satisfy the ideal free distribution. While it would be interesting to do so, we have not explored this issue. However, for most species, it is not unreasonable to assume a relatively small cost of cognition (38–41).

**Noisy information** Another insight that we can derive from an extension of our model is that the higher the noise in the environmental stimuli the more responsive individuals become in equilibrium. This is under the assumption of individuals receiving private and stochastically independent noisy information about the state of the environment. We have not explored the perhaps sometimes more interesting case of correlated information, such as all individuals receiving the same public information. In such a setting, the ideal free distribution would at best hold in expectation, and there would be a positive variance of food *share* availability at the random source. Another, empirically relevant, informational setting is one where not all individuals receive the same quality of information (perhaps not all are equally close to the source of information). One would then expect individuals to infer additional information about the state of the environment from other individuals' behavior. If, for instance, there are many birds flying out to a specific point at sea, another bird might follow based on the idea that there is information in that behavior. This will certainly be the case for socializing birds, which display behavior of forming flocks and swarms. Such behavior would add another layer of complexity to the game.

**The number of food sources** Our model only has two food sources. This keeps the analysis mathematically tractable, but comes at the cost of a possible oversimplification. Introducing an arbitrary number of stochastic food sources would, indeed, make the analysis more complicated. However, given our results, one would conjecture that in any (evolutionary stable) equilibrium of such a modified game, the ideal free distribution holds, at least when costs of cognition are negligible: all food sources would have equal food shares, and this would be true for all states. This alone would already imply that equilibrium behavior would not depend on the exact stochastic nature of the environment. This would also imply that any (evolutionary stable) equilibria would again satisfy coexistence, and for slightly perturbed models, consistency and correlation. The only difference is that one would not necessarily expect a unique equilibrium and it would be harder to characterize these explicitly.

549 **Generalizing** We focused here on foraging choice as a concrete  
 550 setting in which one would expect the coexistence, consistence  
 551 and correlation of different responsiveness to external stim-  
 552 ulti. However, our results could possibly be generalized to  
 553 different context where there is a resource to share among  
 554 individuals, with a resource distributing at different point, and  
 555 some of them stochastic. Such contexts are social interactions,  
 556 mating behaviour, division of labour (42), space-use (43), or  
 557 niche specialisation (42, 44, 45). Those last studies shows  
 558 similar concepts (state dependence, frequency dependence, so-  
 559 cial awareness, environmental heterogeneity) applied to niche  
 560 specialisation. In particular, increasing evidence show a link  
 561 between specialisation and personality. It is hypothesized that  
 562 personality implies specialization (46, 47) or the other way  
 563 around (44, 48). Finally and more speculatively, our results  
 564 might even be translatable to the issue of stem cell differentia-  
 565 tion, which might arise from competition over resources, see  
 566 (49).

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