

# An Evolutionary Model of Bounded Rationality and Intelligence

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**Most economic models assume individuals are intelligent, rational, and maximize their own self-interest. However, mounting evidence suggests that humans often make seemingly random and suboptimal decisions. We reconcile this conflict by demonstrating, in an evolutionary model, that natural selection is capable of generating both types of behavior; the type that emerges depends on whether reproductive outcomes are correlated or independent across individuals in any given generation. If they are correlated, behaviors such as risk aversion, loss aversion, probability matching, and randomization can emerge and eventually become dominant throughout the entire population. If they are independent, individually optimal risk-neutral behaviors will become dominant instead. This framework implies a natural definition of intelligence: any behavior that increases an individual’s reproductive success. We show how intelligence can emerge via selection, why it may be bounded, and why such bounds typically imply the coexistence of multiple levels and types of intelligence.**

Most economic theories assume that individuals behave rationally, maximizing their own self-interest subject to resources constraints. This framework has led to numerous breakthroughs in economic science, including expected utility theory (1) (an axiomatic formulation of rational behavior under uncertainty), the notion of “rational expectations” (2) (individual expectations are formed to be mutually consistent with those arising from economic equilibria), and the “efficient markets hypothesis” (3, 4) (market prices fully reflect all available information). While other alternatives have been proposed, such as heuristic approximation (“satisficing”) and bounded rationality (5), the vast majority of current economic models still assume the ideal of a fully rational and optimizing individual, often referred to as *Homo economicus*. The influence of this paradigm goes far beyond academia—it underlies current macroeconomic and monetary policies, and has also become an integral part of the rules and regulations that govern financial markets today (6, 7).

However, there is mounting empirical and experimental evidence, including the recent financial crisis, suggesting that humans do not always behave rationally, but often make seemingly random and suboptimal decisions (8). These behavioral anomalies are especially pronounced when elements of risk and probability are involved, and two of the most well-known are probability matching (9, 10) (the tendency to choose randomly between heads and tails when asked to guess the outcomes of a series of independent biased-coin tosses, where the randomization matches the probability of the biased coin), and loss aversion (11) (the tendency to take greater risk when choosing between two potential losses, and less risk when choosing between two potential gains). Both behaviors are clearly suboptimal from the individual’s perspective, yet they have been observed in thousands of geographically diverse human subjects over several decades. Such anomalous behaviors have also been observed in many non-human subjects including ants, bees, fish, pigeons, and primates, which suggests that they may have a common and ancient origin, and an evolutionary role that belies their apparent shortcomings.

Accordingly, several evolutionary models have been proposed to explain these counterintuitive behaviors (12–14), as well as a variety of other social customs including altruism, cooperation, subterfuge, self-deception, kin selection, and reciprocity (15–19). The fields of sociobiology and, more recently, evolutionary psychology have expanded the reach of evolution to even broader domains such as language, culture, and religion (17, 20–23). However, it is unclear how these behaviors relate to standard economic theories of individual rationality, why they emerge in some instances and not others, and what part intelligence plays in such behaviors.

Here we address these issues through a simple evolutionary model of binary choice (14) in which rational economic behavior can be reconciled with several prominent violations of rationality such as probability matching, loss aversion, and randomization. The key feature is the interaction between individual behavior and the stochastic environment in which reproductive success is determined. If all individuals behave identically and deterministically, choosing the course of action that leads to the highest expected number of offspring, this can lead to extinction if reproductive uncertainty is perfectly correlated across individuals in a given generation, i.e., if all individuals occupy the same ecological niche. For example, if all individuals choose to forage in the same higher-yielding patch, the first time that patch becomes barren, the entire population will be wiped out. In such environments, randomizing behavior such as probability matching (10) may be favored by natural selection over any type of deterministic behavior. What we observe as irrational behavior may indeed be irrational from the individual’s perspective, but not from the population’s perspective and it is the latter that is the outcome of natural selection. However, if reproductive success is statistically independent across individuals in a given generation—corresponding to situations in which each individual occupies its own unique niche—we show that natural selection favors individually optimal deterministic behavior instead.

Such a framework provides a natural definition of “intelligence”: any behavior that is pos-

itively correlated with reproductive success. If achieving such correlation imposes biological costs on an individual—for example, because it requires attention, memory, planning, and other cognitive faculties—these costs imply an upper bound on the degree of intelligence that emerges through selection. This yields an evolutionary foundation for “bounded rationality” (5), a heuristics-based alternative to rational economic behavior.

Consider a population in which each individual (not necessarily human) is faced with a single decision in its lifetime, to choose action  $a$  or  $b$ , and this choice implies a certain number of offspring  $x_a$  or  $x_b$ , respectively, where  $x_a$  and  $x_b$  are random variables with joint distribution function  $\Phi(x_a, x_b)$ . Let individual  $i$ 's behavior be represented by a binary variable  $I_i$  which equals 1 if  $a$  is chosen and 0 if  $b$  is chosen. Suppose that  $i$  chooses  $a$  with probability  $f$  and chooses  $b$  with probability  $1-f$  where the probability  $f$  is any value between 0 and 1, including the two endpoints (thus capturing purely deterministic behavior as well). The parameter  $f$  represents the behavioral “phenotype” of an individual, and we assume that this behavior is completely “mindless” in the sense that the individual's decision  $I_i$  is statistically independent of any other variables in its environment, including the behaviors of others and the outcomes  $(x_a, x_b)$ . The assumption of independence also implies the absence of any strategic interactions between individuals, since  $i$ 's choice has no impact on  $j$ 's reproductive outcomes.

If we assume that the offspring of type- $f$  individuals are also of the same type, and we start with an equal number of all types of individuals in the population, we can explore the evolution of behavior by identifying the value of  $f$  that exhibits the highest geometric growth rate (or “fitness”), which we denote by  $f^*$ . Over time,  $f^*$  individuals will dominate the population at an exponentially fast rate, hence the behavior  $f^*$  will have “emerged” through the forces of natural selection. We call  $f^*$  the “growth-optimal” behavior to emphasize this fact. The particular value of  $f^*$  depends critically on the properties of  $\Phi(x_a, x_b)$ , which is a highly compact representation of the biological features of the individual, its random environmental

circumstances, and the uncertain impact of behavior on fecundity. Although such a model of evolution, in which individuals live for one period and engage in asexual reproduction with no mutation, is clearly stylized, it does capture the essence of how natural selection shapes behavior. Extensions to biologically more realistic features such as imperfect hereditary transmission of  $f$ , sexual reproduction, and multiple rounds of offspring within a single lifetime can easily be accommodated via constraints on  $\Phi$  and more sophisticated relationships between the  $f$  of an offspring and its parents, but at the expense of analytical tractability and transparency.

Despite the simplicity of this framework, its behavioral implications are surprisingly rich. If we assume that  $\Phi(x_a, x_b)$  is independently and identically distributed (IID) from one generation to the next, but is *identically distributed* across a given generation—implying that all individuals in a given generation are part of the same ecological niche and will produce the same number of random offspring  $x_j$  if they choose action  $j$ ,  $j = a, b$ —we can compute the geometric growth rate of each subpopulation of type  $f$  by applying the Law of Large Numbers over many generations (see SI), which yields  $\lim_{T \rightarrow \infty} \log n_T(f)/T \equiv \alpha(f) = E[\log(fx_a + (1-f)x_b)]$ , where  $n_T(f)$  denotes the number of individuals of type  $f$  in generation  $T$ . By maximizing this growth rate  $\alpha(f)$  with respect to  $f$ , we can determine the behavior  $f^*$  that emerges through natural selection. The solution has three parts. We find that  $f^* = 1$  if  $E[x_a/x_b] > 1$  and  $E[x_b/x_a] < 1$ , where these inequalities imply that the reproductive success of  $a$  is unambiguously higher than that of  $b$ . Conversely,  $f^* = 0$  if  $E[x_a/x_b] < 1$  and  $E[x_b/x_a] > 1$ . However, if  $E[x_a/x_b] \geq 1$  and  $E[x_b/x_a] \geq 1$ , then  $f^*$  is strictly greater than 0 and less than 1, and is given by the value that satisfies the equality  $E[x_a/(f^*x_a + (1-f^*)x_b)] = E[x_b/(f^*x_a + (1-f^*)x_b)]$ . In this case, the behavior that yields the fastest growth rate involves randomizing with probability  $f^*$ , where  $f^*$  is the value that equates the expected ratio of the number of offspring from each choice to the average number of offspring across the two choices.

This result is surprising to economists because it seems inconsistent with the maximization

of self-interest, as well as the deterministic behavior implied by expected utility theory (*I*). Suppose  $E[x_a] > E[x_b]$  and  $\text{Var}[x_a] = \text{Var}[x_b]$  so that action  $a$  leads to a larger number of offspring on average for the same level of risk; from an individual’s perspective, the “rational” action would be to always select  $a$ ,  $f = 1$ . However, such individually rational behavior will eventually be dominated by the faster-growing  $f^*$ -types, hence it cannot persist over time. The growth-optimal behavior  $f^*$  may be viewed as a primitive version of “altruism”, i.e., behavior that is suboptimal for the individual but which promotes the survival of the population. A numerical example of this counterintuitive phenomenon is provided in SI.

Now suppose we change our assumption that individuals all belong to the same ecological niche, and assume that  $\Phi(x_a, x_b)$  is IID across individuals in each generation, as well as from one generation to the next. This corresponds to the situation in which each individual occupies its own unique niche, receiving a separate and independent random draw for  $x_a$  or  $x_b$  from the same respective distributions as others. In this case, the Law of Large Numbers applies across individuals within each generation as well as over time, and the growth rate of type- $f$  individuals is given by  $\log(f\mu_a + (1-f)\mu_b)$ , where  $\mu_i \equiv E[x_i]$ ,  $i = a, b$ . This function contains no random variables and attains its maximum at  $f^* = 0$  or  $1$ , depending on whether  $\mu_a < \mu_b$  or  $\mu_a > \mu_b$ , respectively. Because individuals are already well diversified across statistically independent niches, they can all engage in identical behavior—individually optimal behavior—even within a single generation without the risk of extinction due to the statistical independence of reproductive outcomes across individuals.

When Nature yields systematic environmental shocks to an entire population’s reproductive success, the population must engage in random behavior to ensure that some of its members will survive. However, when Nature imposes idiosyncratic shocks across the population, deterministic behavior can persist because the chances of all individuals experiencing bad draws becomes infinitesimally small as the population size grows. This distinction between systematic and

idiosyncratic environments is the key to reconciling seemingly irrational behavior with *Homo economicus*: the former emerges from systematic environments, and the latter from idiosyncratic ones. Apparently, “Nature abhors an undiversified bet”, hence the type of environmental risk to fecundity determines the type of behavior that has greatest fitness. This may seem obvious to evolutionary biologists but it has profound consequences, including a natural definition of intelligent behavior and bounded rationality.

Recall that the individuals in our model are mindless in the sense that their behaviors are assumed to be statistically independent of all other variables. Suppose we relax this assumption by allowing individual decisions to be correlated with other variables such as  $x_a$  and  $x_b$ . Specifically, let  $I_i$  be correlated with  $x_a$  and  $x_b$ . As before, consider an initial population with equal numbers of individuals of all types  $f$ , and with arbitrary correlations between  $I_i$  and  $x_a$  and  $x_b$  so that no single value is overrepresented. Applying the Law of Large Numbers, we see that the growth rate for individuals of type  $f$  with correlations  $\rho = \text{Corr}[I_i, (x_a - x_b)]$  is given by  $\alpha(f, \rho) = \log(f\mu_a + (1-f)\mu_b + \rho\sigma\sqrt{f(1-f)})$ , where  $\sigma$  is the standard deviation of  $x_a - x_b$ . In this case, the growth rate is equal to the growth rate of the mindless population plus an extra term  $\rho\sigma\sqrt{f(1-f)}$  that reflects the impact of correlation between an individual’s decision and the number of offspring. Several implications follow immediately from this expression.

First, subpopulations with negative correlation between behavior and  $x_a - x_b$  clearly cannot survive in the long run; their growth rates are less than the no-correlation case, and correspond to counter-productive behavior in which decisions coincide with lower-than-average reproductive outcomes more often than not, i.e., choosing  $a$  when  $x_a - x_b$  is lower than average and choosing  $b$  when the reverse is true. By the same logic, subpopulations with positive correlation will grow faster, and individuals with the highest correlations  $\rho^*$  will dominate the population. We suggest that these cases may be considered primitive forms of “intelligence”—behavior that yields improved fitness.

The subpopulation with the largest  $\rho$  will grow fastest and come to dominate the population. For example, certain senses such as hearing and eyesight are so highly correlated with reproductive success that they become universally represented in the population. By optimizing  $\alpha(f, \rho)$  with respect to  $f$  and  $\rho$  to yield  $f^*$  and  $\rho^*$ , we arrive at the growth-optimal level of intelligence and behavior that emerges from the population (see SI):  $\rho^* = 1$  and  $f^* = \text{Prob}(x_a > x_b)$ . Perfect positive correlation always dominates imperfect correlation, and despite the presence of idiosyncratic reproductive risk, the growth-optimal behavior involves probability matching, albeit a different kind in which  $f^*$  matches the probability of  $x_a$  exceeding  $x_b$ .

If there is no biological cost to attaining  $\rho^* = 1$ , then perfect correlation will quickly take over the entire population, and because we have assumed no mutation from one generation to the next, all individuals will eventually possess this trait. However, it seems plausible that positive correlation would be associated with positive cost. For example, by using certain defense mechanisms such as chemical repellants or physical force, animals can fend off predators. This behavior increases their expected number of offspring, but the physiological cost of defense may decrease this expectation, hence the evolutionary success of such behavior depends on the net impact to fitness. If we define a cost function  $c(\rho)$ , then we can express the “net” impact of correlation by deducting this cost from the correlation itself to yield the following asymptotic growth rate of type- $f$  individuals:  $\alpha(f, \rho) = \log(f\mu_a + (1-f)\mu_b + [\rho - c(\rho)]\sigma\sqrt{f(1-f)})$ . With plausible conditions on  $c(\cdot)$  and  $\Phi(x_a, x_b)$ , there is a unique solution  $(f^*, \rho^*)$  to  $\alpha^* = \max_{\{f, \rho\}} \alpha(f, \rho)$ . Because  $\rho$  is subject to a nonlinear constraint that depends on  $f$ , explicit expressions for  $(f^*, \rho^*)$  are not as simple as the no-intelligence case (see SI for details). However, the structure of the solution is qualitatively identical and intuitive:  $f^*$  reduces to three possibilities, either 0 or 1 if correlation is too “expensive” to achieve, or the probability-matching solution  $f^* = \text{Prob}(x_a > x_b)$  if the cost function  $c(\rho)$  is not too extreme. This growth-optimal solution is an example of bounded rationality—bounded in the sense that higher levels of  $\rho$

might be achievable but at too high a cost  $c(\rho)$ . The behavior that eventually dominates the population is good enough, where “good enough” now has a precise meaning: they attain the maximum growth rate  $\alpha^*$ . In other words,  $f^*$  is an example of satisficing.

If the cost of intelligence is influenced by other biological and environmental factors  $\mathbf{x} = [x_1 \cdots x_n]$ , then the multivariate cost function  $c(\rho, \mathbf{x})$  will almost certainly induce a multiplicity of solutions to the growth-optimization problem. This implies a multitude of behaviors and levels of intelligence that can coexist because they yield the same maximum population growth rate  $\alpha^*$ . The set of behaviors  $f^*(\mathbf{x})$  and intelligence  $\rho^*(\mathbf{x})$  that emerge from the population will be a function of  $\mathbf{x}$  and given implicitly by the solution to  $\alpha^* = \max_{\{f, \rho\}} \alpha(f, \rho)$ . This provides a direct link between adaptive behavior and the environment, which is the basis for models of social evolution and evolutionary psychology (15, 17, 24, 25).

The simplicity and generality of our framework suggest that the behaviors we have derived are likely to be quite primitive on an evolutionary timescale, and that most species will have developed the necessarily biological apparatus to engage in such behavior under the right environmental conditions. However, evolution can also produce more sophisticated behaviors such as overconfidence (26), altruism and self-deception (24), and state-dependent strategies like the Hawk-Dove game (27), which emerge as a result of more complex environmental conditions. For example, if we assume that one individual’s action can affect the reproductive success of another individual, e.g.,  $i$ ’s fecundity is influenced by  $j$ ’s selection of  $a$  or  $b$ , individuals engaging in strategic behavior will reproduce more quickly than those with simpler behaviors such as probability matching or loss aversion. In a resource-constrained environment in which one individual’s choice can affect another individual’s reproductive success, strategic interactions such as reciprocity and cooperation will likely emerge (16, 19). Time varying environmental conditions  $\Phi_t(x_a, x_b)$ , mutation through sexual reproduction, and multiple reproductive cycles within a single lifetime (iteroparity) are other extensions that would introduce additional richness and

complexity into our framework.

However, we have purposefully assumed an unconstrained stable stochastic environment with no strategic considerations to see what kinds of behavior are truly primitive. We find a surprisingly complex and subtle range of behaviors—behaviors that do not always conform to common economic intuition about rationality—can arise and persist via natural selection. While it is nearly self-evident that the critical determinant of which behavior emerges from a given population is the interaction between the biological features of the individuals and the nature of the environment, our simple framework shows just how powerful environmental forces can be in shaping fundamental aspects of decisionmaking. If we seek to understand the origin of intelligence and the limits of rational behavior, we may find more useful answers by studying current and past environments rather than our genes.

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## Supplementary Information

**The General Model** We first present our general model, which encompasses the possibility of variation in outcomes across individuals within a generation, as well as across generations, and also the possibility of intelligent behavior. In the following sections we consider several special cases giving rise to the results stated in the accompanying paper.

Each individual in a population is faced with a single decision in its lifetime, choosing action  $a$  or  $b$ , and this choice results in a certain number of offspring,  $x_a$  or  $x_b$ , respectively. The quantities  $x_a$  and  $x_b$  are random variables with a joint distribution  $\Phi(x_a, x_b)$ . The behavior of individual  $i$  is represented by a 0/1 Bernoulli trial,  $I$ , with probability  $f$ , i.e.,  $a$  is chosen with probability  $f$  (in which case  $I = 1$ ), and  $b$  is chosen with probability  $1 - f$  (in which case  $I = 0$ ). When we wish to specify the outcomes applicable to a particular individual,  $i$ , for any of these variables, we add a subscript  $i$ . Similarly, when we wish to specify a particular generation,  $t$ , we add the subscript  $t$ .

We assume that an individual with a choice function  $I$  has offspring with the identical choice function  $I$ . We are interested in the growth of the population of individuals with a specific choice function over time, and we write  $n_t$  for the number of such individuals in generation  $t$ . In general, we have

$$n_t = \sum_{i=1}^{n_{t-1}} (I_{it}x_{ait} + (1 - I_{it})x_{bit}),$$

where the sum runs over all individuals in generation  $t - 1$ . We assume that although all the individuals have the same function  $I$ , the random variable for each individual is independent of all the others. We also assume that the distributions  $\Phi_{it}$  are independent and identically distributed across individuals  $i$  and times  $t$ . Under these assumptions, the value of  $n_t$  can be

expressed as

$$n_t \stackrel{p}{=} n_{t-1} (\mathbb{E} [I_t x_{at}] + \mathbb{E} [(1 - I_t) x_{bt}])$$

$$\stackrel{p}{=} n_{t-1} (\mathbb{E} [I_t] \mathbb{E} [x_{at}] + \mathbb{E} [1 - I_t] \mathbb{E} [x_{bt}] + \text{Cov} (I_t, x_{at}) + \text{Cov} (1 - I_t, x_{bt})) \quad (1)$$

where the expectations and covariances in (1) are calculated for a typical individual having offspring at time  $t$ . No subscript,  $i$ , is needed to index these individuals since all members of the population have the same expectation of outcomes and the same choice function  $I_t$ . The symbol  $\stackrel{p}{=}$  denotes equivalence in probability, and this equivalence (1) follows from the Law of Large Numbers.<sup>1</sup> Introducing some new notation, we can rewrite (1) as

$$n_t \stackrel{p}{=} n_{t-1} \left( f \mu_{at} + (1 - f) \mu_{bt} + \sqrt{f(1 - f)} (\sigma_{at} \rho_{at} + \sigma_{bt} \rho_{bt}) \right), \quad (2)$$

where  $\mu_{at}$  and  $\mu_{bt}$  represent the common expected values for  $x_{ait}$  and  $x_{bit}$  for each individual  $i$  at time  $t$ , where  $\sigma_{at}$  and  $\sigma_{bt}$  represent the corresponding standard deviations, and where  $\rho_{at}$  and  $\rho_{bt}$  represent the common correlations at time  $t$  of each  $x_{ait}$  and  $x_{bit}$  with  $I_{it}$  and  $1 - I_{it}$ , respectively. Because all of these values are the same across all individuals having offspring at time  $t$ , the subscript  $i$  is not necessary in any of the terms in (2). It is also convenient to write

$$n_t \stackrel{p}{=} n_{t-1} \left( f \mu_{at} + (1 - f) \mu_{bt} + \sigma_t \rho_t \sqrt{f(1 - f)} \right), \quad (3)$$

where  $\rho_t$  is the common correlation of  $I_{it}$  with  $y_{it} = x_{ait} - x_{bit}$  for each individual  $i$  having offspring at time  $t$ , and where  $\sigma_t$  is the common standard deviation of  $y_{it}$  for such individuals.

We use backward recursion to find that

$$n_T \stackrel{p}{=} n_0 \prod_{t=1}^T \left( f \mu_{at} + (1 - f) \mu_{bt} + \sigma_t \rho_t \sqrt{f(1 - f)} \right),$$

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<sup>1</sup>In particular, the sums over the sample population converge almost surely to the unrestricted means and covariances. This follows since the variance of each relevant random variable must be bounded, provided that there is an upper bound on the possible number of offspring a single individual may have.

where  $n_0$  is the number of individuals in the population at time  $t = 0$ . From this we deduce that

$$\frac{1}{T} \log n_T \xrightarrow{p} \mathbb{E} \left[ \log \left( f\mu_{at} + (1-f)\mu_{bt} + \sigma_t \rho_t \sqrt{f(1-f)} \right) \right], \quad (4)$$

where the expectation is taken with respect to the continuous limit of the distribution of the random variable values over times  $t$ .<sup>2</sup>

It is convenient to introduce a new notation for the right-hand side of (4), namely

$$\alpha = \mathbb{E} \left[ \log \left( f\mu_{at} + (1-f)\mu_{bt} + \sigma_t \rho_t \sqrt{f(1-f)} \right) \right]. \quad (5)$$

In what follows, we seek to identify the values of  $I$  that give rise to the maximum value for  $\alpha$ , since individuals with such values will dominate the population over time in a sense made precise by the following proposition.

**Proposition 1** *Suppose that two different choice functions,  $I_1$  and  $I_2$ , give rise to values  $\alpha_1$  and  $\alpha_2$ , with the property that  $\alpha_1 > \alpha_2$ . Individuals with the choice function  $I_1$  will become exponentially more numerous over time, since*

$$\lim_{T \rightarrow \infty} \frac{n_T(I_2)}{n_T(I_1)} \xrightarrow{p} \lim_{T \rightarrow \infty} e^{T(\alpha_2 - \alpha_1)} = 0.$$

In the following sections, we consider the parameters giving rise to maximal values for  $\alpha$  under various specific assumptions about the nature of the distributions  $\Phi_{it}$ .

**The Case of No Intelligence** We say that a member of the population exhibits intelligence if its behavior correlates positively with outcomes, i.e., if  $\rho > 0$ . If  $\rho = 0$ , however, then we say

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<sup>2</sup>Note that to apply the Law of Large Numbers here we assume that the terms  $\log \left( f\mu_{at} + (1-f)\mu_{bt} + \sigma_t \rho_t \sqrt{f(1-f)} \right)$  have bounded variance. This assumption is valid provided that the distribution of the argument of the logarithm does not have positive mass in arbitrarily small neighborhoods of zero.

that no intelligence is present.<sup>3</sup> In this situation, we can write  $\alpha = \alpha(f)$ , and we write  $f^*$  for the value of  $f$  that gives rise to the maximum value of  $\alpha$ . Also, we can write the expression for  $\alpha$  from (5) as

$$\alpha(f) = E[\log(f\mu_{at} + (1-f)\mu_{bt})].$$

The value  $f^*$  that maximizes this expression for  $\alpha$  is characterized by the following proposition.

**Proposition 2** *If intelligence is not present in a population, the growth-optimal behavior  $f^*$  is given by*

$$f^* = \begin{cases} 1 & \text{if } E[\mu_{at}/\mu_{bt}] > 1 \text{ and } E[\mu_{bt}/\mu_{at}] < 1 \\ \text{solution to (7)} & \text{if } E[\mu_{at}/\mu_{bt}] \geq 1 \text{ and } E[\mu_{bt}/\mu_{at}] \geq 1 \\ 0 & \text{if } E[\mu_{at}/\mu_{bt}] < 1 \text{ and } E[\mu_{bt}/\mu_{at}] > 1 \end{cases} \quad (6)$$

where  $f^*$  is defined implicitly in the second case of (6) by:

$$E\left[\frac{\mu_{at}}{f^*\mu_{at} + (1-f^*)\mu_{bt}}\right] = E\left[\frac{\mu_{bt}}{f^*\mu_{at} + (1-f^*)\mu_{bt}}\right] \quad (7)$$

and the expectations are taken with respect to the joint distributions across time  $t$  for  $\mu_{at}$  and  $\mu_{bt}$ , as these distributions are implied by the  $\Phi_{it}$ .

**Proof.** The result can be seen by computing the first and second derivatives of  $\alpha$ . Because the second derivative is strictly negative, there is exactly one maximum value obtained in the interval  $f \in [0, 1]$ . The values of the first derivative of  $\alpha(f)$  at the endpoints of the interval are  $\alpha'(0) = E[\mu_{at}/\mu_{bt}] - 1$  and  $\alpha'(1) = 1 - E[\mu_{bt}/\mu_{at}]$ . If  $\alpha'(0)$  and  $\alpha'(1)$  are both positive or both negative, then  $\alpha(f)$  increases or decreases, respectively, throughout the interval and the maximum value is attained at  $f = 1$  or  $f = 0$ , respectively. Otherwise,  $f = f^*$  is the unique point in the interval for which  $\alpha'(f) = 0$ , where  $f^*$  is defined in (7), and it is at this

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<sup>3</sup>The case  $\rho < 0$  would correspond to “intelligence” that leads to a less favorable outcome than no intelligence, and so we exclude this case from consideration.

point that  $\alpha(f)$  attains its maximum value. The expression (6) summarizes the results of these observations for the various possible values of  $E[\mu_{at}/\mu_{bt}]$  and  $E[\mu_{bt}/\mu_{at}]$ . Note that the case  $E[\mu_{at}/\mu_{bt}] \leq 1$  and  $E[\mu_{bt}/\mu_{at}] \leq 1$  is not considered because this set of inequalities implies that  $\alpha'(0) \leq 0$  and  $\alpha'(1) \geq 0$ , which is impossible, since  $\alpha''(f)$  is strictly negative.

**Numerical Example of Probability Matching** The emergence of probability matching is most easily seen through a simple numerical example of our model in which  $\mu_{at}$  and  $\mu_{bt}$  are negatively correlated Bernoulli trials. Consider an environment in which it is sunny and rainy with probability  $p=75\%$  and  $1-p=25\%$ , respectively. Individuals must decide where to build their nests, in the valley (choice  $a$ ) or on a plateau (choice  $b$ ). During sunny days, nesting on a plateau will yield  $\mu_{at} = 0$  offspring because of the heat of the sun and lack of water, whereas nesting in the valley yields  $\mu_{at} = 3$  offspring because of the valley's shade and the streams that run through it. During rainy days, the exact opposite outcomes are realized: nesting in the valley yields  $\mu_{at} = 0$  because the valley will flood, drowning all offspring, but nesting on a plateau yields  $\mu_{at} = 3$  because the rain clouds provide both water and protection from the sun. In this environment, the behavior that maximizes the survival probability of an individual's offspring is to choose  $a$  all the time ( $f = 1$ ) since the probability of sunshine is 75%. However, such behavior cannot survive—the first time it rains, all individuals of type  $f = 1$  will be eliminated from the population. In fact, the behavior yielding the highest growth rate is  $f^* = 0.75$ ; hence, “probability matching” behavior (10, 12, 14) is evolutionarily dominant in this special case.

For other values of the outcomes of  $\mu_{at}$  and  $\mu_{bt}$ ,  $f = p$  may not yield the highest rate of growth, but  $f^*$  can nevertheless be strictly greater than 0 and less than 1, so that randomizing behavior will still persist. When faced with environmental randomness that affects the entire population in the same manner (recall our “single-niche” assumption), and where the type of randomness yields extreme outcomes for different behaviors, deterministic behavior cannot sur-

vive because at some point, an extreme outcome will occur, wiping out that subpopulation. The only way to survive is to randomize, and the subpopulation that grows fastest in this type of environment is one in which  $f^* = p$ . For concreteness, Table (I) contains a numerical simulation of this example.

**A Universal Measure and a Cost of Intelligence** As we have noted, the case of no intelligence corresponds to no correlation, i.e.,  $\rho_t = 0$ , while the case of intelligence corresponds to positive correlation, i.e.,  $\rho_t > 0$ , with higher values representing more intelligence. The correlation  $\rho_t$  cannot necessarily assume any value in the range  $[0, 1]$ , however, and it is in fact constrained by the choice of  $f$ . More specifically,  $\rho_t$  can assume all values in the range  $[0, \rho_{t,\max}(f)]$  but no values outside this range, where  $\rho_{t,\max}(f)$  is a function dependent on  $f$  and the  $\Phi_{it}$ . A precise value for  $\rho_{t,\max}$  is calculated in Proposition 3, below. Because the upper bound for  $\rho_t$  depends upon  $f$ , the measure  $\rho_t$  is difficult to use as a universal representation of underlying intelligence. We therefore introduce the additional variable  $\gamma$ , defined as

$$\gamma = \frac{\rho_t}{\rho_{t,\max}(f)}. \quad (8)$$

This is a universal representation of intelligence in the sense that it represents the fraction of the maximum possible correlation achievable, and this fraction remains constant even as the maximum possible correlation varies with  $f$ .

In the case in which there is no variation in the  $\Phi_{it}$  across time, then the values of  $\rho_t$  and  $\rho_{t,\max}(f)$  are the same for all  $t$ , and we write these common value as  $\rho$  and  $\rho_{\max}(f)$ . This is the case we considered in our main paper, and there we simply used  $\rho$  as the measure of intelligence instead of  $\gamma$ , since the two measures are the same up to a constant rescaling factor that is common across all generations. For purposes of this Supplementary Information, however,

we deal with the more general situation in which we must use  $\gamma$  instead of  $\rho$  as the universal measure of intelligence.

We suppose that a member of a population has a particular value of  $f \in [0, 1]$  and a particular value of  $\gamma \in [0, 1]$ , and that these attributes are passed on to all offspring of an individual. In terms of  $f$  and  $\gamma$ , the expression for  $\alpha$  in (5) can be written

$$\alpha = \mathbb{E} \left[ \log \left( f\mu_{at} + (1-f)\mu_{bt} + \sigma_t \gamma \rho_{t,\max}(f) \sqrt{f(1-f)} \right) \right]. \quad (9)$$

We also consider the possibility that  $\gamma$  has a cost,  $c(\gamma)$ , associated with it, and that once this cost is factored in, the expression for  $\alpha$  becomes

$$\alpha = \mathbb{E} \left[ \log \left( f\mu_{at} + (1-f)\mu_{bt} + \sigma_t (\gamma - c(\gamma)) \rho_{t,\max}(f) \sqrt{f(1-f)} \right) \right]. \quad (10)$$

We assume that  $c(0) = 0$  and  $c(\gamma) > 0$  for  $\gamma > 0$ . We also assume that  $\gamma - c(\gamma) > 0$  for sufficiently small values of  $\gamma$  and that  $\gamma - c(\gamma) < 0$  for values of  $\gamma$  sufficiently close to 1. Thus, at least some small amount of intelligence is beneficial, but high costs make the choice of  $\gamma = 1$  prohibitively expensive. In addition, we make the further assumption that  $c$  is twice continuously differentiable and that  $c'(\gamma) > 0$  and  $c''(\gamma) > 0$ . Because of this assumption, there is a unique value of  $\gamma^*$  that maximizes  $\gamma - c(\gamma)$ .

$$\gamma^* = \text{unique } \gamma \text{ such that } c'(\gamma) = 1. \quad (11)$$

It is convenient to introduce some additional notation related to the distribution of the  $y_{it}$ , which is given by the function  $\Phi_{it}$ . We write  $\varphi_t$  for the probability that  $y_{it} > 0$  for individuals in generation  $t$ , i.e.,

$$\varphi_t = \text{Prob}(y_{it} > 0). \quad (12)$$

This value is thus the probability that choice  $a$  is superior to choice  $b$  in generation  $t$ . In addition, we write  $\delta_t^+$  and  $\delta_t^-$  for the expected value of  $y_{it}$  conditional on either  $y_{it} > 0$  or  $y_{it} \leq 0$ ,

respectively. That is,

$$\delta_t^+ = \mathbb{E}[y_{it}|y_{it} > 0] \quad \text{and} \quad \delta_t^- = \mathbb{E}[y_{it}|y_{it} \leq 0]. \quad (13)$$

The values of  $\varphi_t$ ,  $\delta_t^+$ , and  $\delta_t^-$  are constant across all individuals in generation  $t$  because the functions  $\Phi_{it}$  are independent and identical across individuals in generation  $t$ . In much of what follows, we also find it convenient to make the following assumption about the independence of  $y_{it}$  and  $I_{it}$ , conditional on the sign of  $y_{it}$ . This assumption may be violated in a fully general case, but it allows us to simplify our analysis and obtain more tractable formulas while still retaining a rich framework in which to operate.

**A 1** *For all  $i$  and  $t$ , conditional on the sign of  $y_{it}$ , the distribution of  $y_{it}$  and the distribution of  $I_{it}$  are independent. Thus,*

$$\mathbb{E}[I_{it}y_{it}|y_{it} > 0] = \delta_t^+ \mathbb{E}[I_{it}|y_{it} > 0] \quad \text{and} \quad \mathbb{E}[I_{it}y_{it}|y_{it} \leq 0] = \delta_t^- \mathbb{E}[I_{it}|y_{it} \leq 0].$$

*In other words, the value of  $I_{it}$  can only depend upon the sign of  $y_{it}$ , and thus the question of whether  $a$  or  $b$  is the superior choice, and not upon additional information about the degree of the superiority of one choice over the other.*

Under assumption A1, and using Propositions 3 and 4, which are proven in the section *Upper Bound on Correlation*, below, we can rewrite (10) as

$$\alpha = \mathbb{E} \left[ \log \left( f\mu_{at} + (1-f)\mu_{bt} + \left( \delta_t^+ - \delta_t^- \right) (\gamma - c(\gamma)) (\min(f, \varphi_t) - f\varphi_t) \right) \right]. \quad (14)$$

We seek the values of  $f$  and  $\gamma$  that maximize  $\alpha$ , as defined in (14). If the optimal value occurs when  $f = 0$  or  $f = 1$ , then the amount of intelligence is clearly irrelevant, since the term involving intelligence vanishes and behavior is simply deterministic. If the optimal value occurs when  $f \in (0, 1)$ , then the optimal amount of intelligence is clearly  $\gamma = \gamma^*$ , as defined above. The nature of the optimal choice of  $f$  is derived in Propositions 5 and 6, in the case of no systematic variation across generations, and Proposition 7, in the general case.

**Upper Bound on Correlation** In this section we consider the restrictions on the possible values for  $\rho_t$ . The value of  $\rho_t$  is subject to constraints that depend upon the nature of the distributions  $\Phi_{it}(x_a, x_b)$ , as well as on the value of  $f$  for the population. The next proposition makes this dependence clear, when assumption A1 holds.

**Proposition 3** *Under assumption A1, the value of  $\rho_t$  is given by*

$$\rho_t = \text{Corr}(I_{it}, y_{it}) = \text{Corr}(I_{it}, H(y_{it})) \left( \frac{\delta_t^+ - \delta_t^-}{\sigma_t / \sqrt{\varphi_t(1 - \varphi_t)}} \right), \quad (15)$$

where  $H(y_{it})$  is the Heaviside function, which is 1 when  $y_{it} > 0$  and 0 otherwise. The values of  $\delta_t^+$ ,  $\delta_t^-$ , and  $\varphi_t$  are as defined in (13) and (12). The correlation between  $I_{it}$  and  $H(y_{it})$  may be also be written as

$$r_t \stackrel{\text{def}}{=} \text{Corr}(I_{it}, H(y_{it})) = \frac{(\pi_t - \varphi_t f)}{\sqrt{\varphi_t(1 - \varphi_t)} \sqrt{f(1 - f)}}, \quad (16)$$

where

$$\pi_t = \text{Prob}(I_{it} = 1 \text{ and } y_{it} > 0). \quad (17)$$

The value of  $r_t$  and that of  $\pi_t$  are the same for each individual  $i$  in a given generation  $t$ .

**Proof.** The result follows directly from the definition of correlation. We have

$$\begin{aligned} \text{Corr}(I_{it}, y_{it}) &= \frac{\text{E}[I_{it}y_{it}] - \text{E}[I_{it}]\text{E}[y_{it}]}{\text{Std}(y_{it})\text{Std}(I_{it})} \\ &= \frac{\pi_t \delta_t^+ + (f - \pi_t) \delta_t^- - f(\varphi_t \delta_t^+ + (1 - \varphi_t) \delta_t^-)}{\sigma_t \sqrt{f(1 - f)}} \\ &= (\pi_t - \varphi_t f) \frac{\delta_t^+ - \delta_t^-}{\sigma_t \sqrt{f(1 - f)}} \end{aligned}$$

$$\begin{aligned}
&= \left( \frac{\pi_t - \varphi_t f}{\sqrt{f(1-f)}\sqrt{\varphi_t(1-\varphi_t)}} \right) \left( \frac{\delta_t^+ - \delta_t^-}{\sigma_t/\sqrt{\varphi_t(1-\varphi_t)}} \right) \\
&= \text{Corr}(I_{it}, H(y_{it})) \left( \frac{\delta_t^+ - \delta_t^-}{\sigma_t/\sqrt{\varphi_t(1-\varphi_t)}} \right),
\end{aligned}$$

which proves (15).

The value of  $\pi_t$  does not depend upon the choice of individual  $i$  because the functions  $\Phi_{it}$  and  $I_{it}$  are independent and identically distributed across individuals in generation  $t$ . The lack of dependence of  $r_t$  on the choice of individual  $i$  within a given generation can be seen by noting that

$$r_t = \text{Corr}(I_{it}, H(y_{it})) = \frac{\pi_t - \varphi_t f}{\sqrt{f(1-f)}\sqrt{\varphi_t(1-\varphi_t)}},$$

and observing that the right-hand side of this equation does not depend upon the choice of individual  $i$ . ■

An implication of the formula in (15) is that the possible values for  $\rho_t$  cannot necessarily be arbitrarily close to 1. The range of possible values for  $\rho_t$  is made more precise by the following proposition.

**Proposition 4** *Under assumption A1. the range of possible values for  $\pi_t$  when intelligence is present is*

$$f\varphi_t < \pi_t \leq \min(f, \varphi_t). \quad (18)$$

*The corresponding range of possible values for  $r_t$  is*

$$0 < r_t \leq r_{t,\max}, \quad \text{where} \quad r_{t,\max} = \frac{\max(f, \varphi_t) - \varphi_t f}{\sqrt{f(1-f)}\sqrt{\varphi_t(1-\varphi_t)}}. \quad (19)$$

*The inequality  $r_t < 1$  holds whenever  $f \neq \varphi_t$ . The corresponding range of possible values for  $\rho_t$  is*

$$0 < \rho_t \leq \rho_{t,\max}, \quad \text{where} \quad \rho_{t,\max} = r_{t,\max} \frac{\delta_t^+ - \delta_t^-}{\sigma_t/\sqrt{\varphi_t(1-\varphi_t)}}. \quad (20)$$

The inequality  $\rho_{t,\max} < 1$  holds unless  $r_t = 1$  and both  $E[y_{it}^2|y_{it} > 0] = (E[y_{it}|y_{it} > 0])^2$  and  $E[y_{it}^2|y_{it} \leq 0] = (E[y_{it}|y_{it} \leq 0])^2$ .

**Proof.** From the definition of  $\pi_t$  in (17), it is clear that  $\pi$  must be bounded above by  $\min(f, \varphi_t)$ . Also, because intelligence only occurs when  $\rho_t > 0$ , the formulas in (15) and (16) show that it must also be the case that  $\pi_t$  is bounded below by  $f\varphi_t$ , and this suffices to prove (18).

The range of possible values for  $r_t$  can be derived by substituting the limits of the possible range for  $\pi_t$  into the expression for  $r_t$  in (16), and the range of possible values for  $\rho_t$  follows from (15).

To obtain an upper bound on  $\rho_{t,\max}$ , it is useful to proceed by first deriving a lower bound for  $\sigma_t$ . Note that Hölder's Inequality shows that

$$\begin{aligned} \sigma_t^2 &= E[y_{it}^2] - (E[y_{it}])^2 = \varphi_t E[y_{it}^2|y_{it} > 0] + (1 - \varphi_t) E[y_{it}^2|y_{it} \leq 0] \\ &\quad - (\varphi_t E[y_{it}|y_{it} > 0] + (1 - \varphi_t) E[y_{it}|y_{it} \leq 0])^2 \\ &\geq \varphi_t (E[y_{it}|y_{it} > 0])^2 + (1 - \varphi_t) (E[y_{it}|y_{it} \leq 0])^2 \\ &\quad - (\varphi_t E[y_{it}|y_{it} > 0] + (1 - \varphi_t) E[y_{it}|y_{it} \leq 0])^2 \\ &= \varphi_t(1 - \varphi_t) (\delta_t^+ - \delta_t^-)^2. \end{aligned}$$

The expectations are all taken with respect to a particular individual within generation  $t$  and are also independent of the specific choice of individual within the generation. Also, the conditions for equality in Hölder's inequality show that equality only holds for our lower bound on  $\sigma_t^2$  when both  $E[y_{it}^2|y_{it} > 0] = (E[y_{it}|y_{it} > 0])^2$  and  $E[y_{it}^2|y_{it} \leq 0] = (E[y_{it}|y_{it} \leq 0])^2$ . The lower bound on  $\sigma_t^2$  can be re-written as

$$\frac{\delta_t^+ - \delta_t^-}{\sigma_t / \sqrt{\varphi_t(1 - \varphi_t)}} \leq 1,$$

and this the upper bound on  $\rho_{t,\max}$  described in the proposition. ■

**Intelligence and No Variation Across Generations** We now consider the case in which there may be intelligence, so that it is possible to have  $\gamma > 0$ , but we assume that there is no variation in the distribution of possible outcomes across generations. Thus, we have  $\mu_{at} = \mu_a$ ,  $\mu_{bt} = \mu_b$ ,  $\delta_t^+ = \delta^+$ ,  $\delta_t^- = \delta^-$ , and  $\varphi_t = \varphi$ . In this case, we can write the expression for  $\alpha$  from (9) as

$$\alpha = \log \left( f\mu_a + (1 - f)\mu_b + (\gamma - c(\gamma)) (\min(\varphi, f) - \varphi f) (\delta^+ - \delta^-) \right). \quad (21)$$

Note that we do not take the expectation of the logarithm in this expression for  $\alpha$ , since the value of the logarithm is constant across generations under the current assumptions. The values of  $f$  and  $\gamma$  that maximize  $\alpha$  in the case in which intelligence is costless (so that  $c(\gamma) \equiv 0$ ) are characterized by the following proposition.

**Proposition 5** *Under assumption A1, and under the further assumptions that intelligence has no cost and that there is no variation in outcome possibilities across generations, the values of  $f$  and  $\gamma$  at which  $\alpha$  is maximized are  $f = \varphi$  and  $\gamma = 1$ , provided that  $\varphi \in (0, 1)$ . If  $\varphi$  is either 0 or 1, then  $\alpha$  is maximized when  $f = \varphi$ , and the value of  $\gamma$  is irrelevant.*

**Proof.** The expression for  $\alpha$  in (21) is maximized when the argument of the logarithm is maximized, and this can be written

$$e^\alpha = f\mu_a + (1 - f)\mu_b + \gamma (\min(\varphi, f) - \varphi f) (\delta^+ - \delta^-).$$

The partial derivative of  $e^\alpha$  with respect to  $\gamma$  is

$$\frac{\partial e^\alpha}{\partial \gamma} = (\min(\varphi, f) - \varphi f) (\delta^+ - \delta^-),$$

and this value is greater than 0 provided that  $f \notin \{0, 1\}$ , since  $\delta^+ - \delta^- > 0$ . Thus, if  $f \notin \{0, 1\}$ ,  $e^\alpha$  is a strictly increasing function of  $\gamma$ , and the maximum value of  $e^\alpha$  for any fixed value of  $f \in (0, 1)$  is obtained when  $\gamma = 1$ .

The partial derivative of  $e^\alpha$  with respect to  $f$  is

$$\frac{\partial e^\alpha}{\partial f} = \varphi(1 - \gamma)\delta^+ + (1 - \varphi(1 - \gamma))\delta^-,$$

when  $f > \varphi$ , and

$$\frac{\partial e^\alpha}{\partial f} = (1 - (1 - \varphi)(1 - \gamma))\delta^+ + (1 - \varphi)(1 - \gamma)\delta^-,$$

when  $f < \varphi$ . When  $\gamma = 1$ , the expressions for  $\partial e^\alpha / \partial f$  becomes simply  $\delta^-$  or  $\delta^+$ , when  $f > \varphi$  and  $f < \varphi$ , respectively. Because  $\delta^- < 0$  and  $\delta^+ > 0$ ,  $e^\alpha$  obtains its maximum for  $f \in (0, 1)$  is at  $f = \varphi$  and  $\gamma = 1$ .

If  $\varphi$  is 0 or 1, then the value of  $f$  that maximizes  $\alpha$  and  $e^\alpha$  is clearly  $f = \varphi$ , and the value of  $\gamma$  is irrelevant, since intelligence is irrelevant for an optimal outcome in this situation. ■

Proposition 5 shows that, when  $c(\gamma) \equiv 0$ , more intelligence, i.e., a higher  $\gamma$  value, is always desirable, except in situations in which behavior is completely deterministic, i.e.,  $f$  is equal to 0 or 1. This result makes sense when intelligence is costless, but to make the situation more realistic, we also consider the situation in which an intelligence level of  $\gamma$  is associated with a cost  $c(\gamma) \neq 0$  of the type described in *A Universal Measure and a Cost of Intelligence* above. The next proposition characterizes the values of  $f$  and  $\gamma$  that maximize  $\alpha$  when there is no variation across generations and when there is such a cost to intelligence.

**Proposition 6** *Under assumption A1, and under the further assumptions that there is no variation in outcome possibilities across generations and that there is a cost  $c(\gamma)$  of intelligence of the type described in A Universal Measure and a Cost of Intelligence above, the values of  $f$  and*

$\gamma$  that maximize  $\alpha$  are characterized in the following way. If  $\mu_b > \mu_a$  and  $\varphi \in (0, 1)$ , then

$$f^* = \begin{cases} \varphi & \text{if } \gamma^* - c(\gamma^*) > \frac{\mu_b - \mu_a}{\delta^+ + \mu_b - \mu_a}; \\ [0, \varphi] & \text{if } \gamma^* - c(\gamma^*) = \frac{\mu_b - \mu_a}{\delta^+ + \mu_b - \mu_a}; \text{ and} \\ 0 & \text{if } \gamma^* - c(\gamma^*) < \frac{\mu_b - \mu_a}{\delta^+ + \mu_b - \mu_a}. \end{cases} \quad (22)$$

Here  $\gamma^*$  is as defined in (11). If  $\mu_b < \mu_a$  and  $\varphi \in (0, 1)$ , then

$$f^* = \begin{cases} \varphi & \text{if } \gamma^* - c(\gamma^*) > \frac{\mu_a - \mu_b}{\mu_a - \mu_b - \delta^-}; \\ [\varphi, 1] & \text{if } \gamma^* - c(\gamma^*) = \frac{\mu_a - \mu_b}{\mu_a - \mu_b - \delta^-}; \text{ and} \\ 1 & \text{if } \gamma^* - c(\gamma^*) < \frac{\mu_a - \mu_b}{\mu_a - \mu_b - \delta^-}. \end{cases} \quad (23)$$

If  $\mu_a = \mu_b$  then  $f^* = \varphi$ , and if  $\varphi \in \{0, 1\}$ , then  $f^* = \varphi$ . In all cases for which  $f^* \notin \{0, 1\}$ , the optimal choice of  $\gamma$  is  $\gamma^*$ . If, however,  $f^* \in \{0, 1\}$ , then intelligence is unimportant, and the choice of  $\gamma$  does not matter.

**Proof.** The proof follows from a straightforward analysis of the partial derivatives of  $e^\alpha$  with respect to  $\gamma$  and  $f$ . The derivative of  $e^\alpha$  with respect to  $\gamma$  is

$$\frac{\partial e^\alpha}{\partial \gamma} = (1 - c'(\gamma)) (\min(\varphi, f) - \varphi f) (\delta^+ - \delta^-),$$

and for any value of  $f \in (0, 1)$ , this partial derivative is zero exactly when  $\gamma = \gamma^*$ . Thus, if the optimal value of  $f$  is in the interior of the interval  $[0, 1]$ , the optimal value of  $\gamma$  is  $\gamma^*$ .

When  $\gamma = \gamma^*$ , the partial derivative of  $e^\alpha$  with respect to  $f$  can be written

$$\frac{\partial e^\alpha}{\partial f} = \mu_a - \mu_b + (\delta^+ - \delta^-)(\gamma^* - c(\gamma^*))(1 - \varphi), \quad (24)$$

when  $f < \varphi$ , and

$$\frac{\partial e^\alpha}{\partial f} = \mu_a - \mu_b + (\delta^+ - \delta^-)(\gamma^* - c(\gamma^*))(-\varphi), \quad (25)$$

when  $f > \varphi$ . When  $\mu_b > \mu_a$  and  $\varphi \in (0, 1)$ , the expression in (25) is always negative, and so  $e^\alpha$  is decreasing in  $f$  in the region  $f \in [\varphi, 1]$ . Also, the sign of (24) is positive, zero, or negative, according to whether  $\gamma^* - c(\gamma^*)$  is larger, equal to, or less than, respectively, the value of  $\frac{\mu_b - \mu_a}{\delta^+ + \mu_b - \mu_a}$ . In these three situations, the function  $e^\alpha$  is increasing, constant, or decreasing, respectively, in the region  $f \in [0, \varphi]$ . These observations lead directly to the results in (22).

The remaining results of the proposition follow from similar analysis of the partial derivative of  $e^\alpha$  with respect to  $f$  in the various cases described. ■

**Example of Optimal Choice with Intelligence** In this section, we provide an illustrative example of our model in the case of no variation across generations and the possibility of intelligence in behavior.

For purposes of our example, we assume a cost function of a particular type, namely

$$c(\gamma) = \kappa \frac{\gamma^2}{1 - \gamma},$$

where  $\kappa > 0$  is a parameter that can be chosen higher to indicate a greater cost to intelligence, or lower to indicate the reverse situation. This function  $c(\gamma)$  can also be written

$$c(\gamma) = \kappa \left( -\gamma - 1 + \frac{1}{1 - \gamma} \right), \quad (26)$$

and it is straightforward to check that it satisfies all of our requirements for a cost function for  $\gamma \in [0, 1]$ . Specifically,  $\gamma - c(\gamma) > 0$  for small values of  $\gamma$ , and  $\gamma - c(\gamma) < 0$  for values of  $\gamma$  sufficiently close to 1. Also,  $c(\gamma)$  is twice continuously differentiable, is increasing, and is convex. For this cost function, the value of  $\gamma^*$  defined in (11) can be written

$$\gamma^* = 1 - \sqrt{\frac{\kappa}{1 + \kappa}}.$$

Also, the value of  $\gamma^* - c(\gamma^*)$ , which is needed to determine the cases specified in Proposition 6, can be written

$$\gamma^* - c(\gamma^*) = 1 + 2 \left( \kappa - \sqrt{\kappa(1 + \kappa)} \right).$$

The values of  $\gamma^*$  and  $\gamma^* - c(\gamma^*)$  are plotted as functions of  $\kappa$  in Figure (1).

The result of Proposition 6 is illustrated in Figure (2). We assume that  $\mu_b > \mu_a$ , and we use the horizontal axis to indicate the size of the ratio  $r = \delta^+ / (\mu_b - \mu_a)$ . We use the vertical axis to indicate the value of  $\kappa$ . For any  $r$  and  $\kappa$  values, Proposition 6 can be used to determine the optimal  $f$  value, namely  $f^*$ . The value of  $f^*$  is either 0 or  $\varphi$ , except when  $\gamma^* - c(\gamma^*) = 1/(1+r)$ , and in this special case the value of  $f^*$  may be anywhere between 0 and  $\varphi$ . The deterministic value 0 is possible while the deterministic value 1 is not simply because we have assumed that  $\mu_b > \mu_a$ . As the figure indicates, a sufficiently high cost of intelligence, as indicated by a high  $\kappa$  value, corresponds to the deterministic choice  $f^* = 0$  and no use of intelligence. When intelligence has a low enough cost for a given ratio value, however, the optimal choice is  $f^* = \varphi$ , which is the same frequency for  $f$  as occurs in probability matching.

**Intelligence and Variation Across Generations** The final case we consider is the one in which individuals may be intelligent and in which there may be variation in outcomes over time. The following proposition describes nature of the optimal choice of  $f$  and  $\gamma$  in this setting under certain assumptions.

**Proposition 7** *Under assumption A1, and under the further assumptions that the distribution of  $\varphi_t$  is smooth and that intelligence has a cost of the type described in A Universal Measure and a Cost of Intelligence above, the maximal value of  $\alpha$  occurs when  $\gamma = \gamma^*$ . In addition, if the optimal choice of  $f$  is in the interior of the interval  $[0, 1]$ , then this choice is defined implicitly by the equation*

$$\mathbb{E} \left[ \frac{\mu_{at} - \mu_{bt} + (\gamma^* - c(\gamma^*)) (\delta_t^+ - \delta_t^-) (H(\varphi_t - f) - \varphi_t)}{f^* \mu_{at} + (1 - f^*) \mu_{bt} + (\gamma^* - c(\gamma^*)) (\delta_t^+ - \delta_t^-) (\min(\varphi_t, f) - \varphi_t f)} \right] = 0,$$

where  $H$  is the Heaviside function, and where the expectations are taken with respect to the joint distributions across time  $t$  for  $\mu_{at}$  and  $\mu_{bt}$ , as these distributions are implied by the  $\Phi_{it}$ .

**Proof.** The optimality of the choice  $\gamma = \gamma^*$  follows from consideration of the derivative of  $\alpha$  with respect to  $\gamma$ . The optimality of  $f$  described in the proposition follows from the fact that the second derivative of  $\alpha$  with respect to  $f$  is continuous and strictly negative, since  $\varphi_t$  has a smooth distribution. Also, because the optimal value of  $f$  is assumed to occur in the interior of the interval  $[0, 1]$ , it follows that this value is the unique place at which the derivative with respect to  $f$  vanishes, when  $\gamma = \gamma^*$ .

Generation	$f = .20$	$f = .50$	$f^* = .75$	$f = .90$	$f = 1$
1	21	6	12	24	30
2	12	6	6	57	90
3	6	12	12	144	270
4	18	9	24	387	810
5	45	18	48	1,020	2,430
6	96	21	108	2,766	7,290
7	60	42	240	834	21,870
8	45	54	528	2,292	65,610
9	18	87	1,233	690	196,830
10	9	138	2,712	204	590,490
11	12	204	6,123	555	1,771,470
12	36	294	13,824	159	5,314,410
13	87	462	31,149	435	15,943,230
14	42	768	69,954	1,155	0
15	27	1,161	157,122	3,114	0
16	15	1,668	353,712	8,448	0
17	3	2,451	795,171	22,860	0
18	3	3,648	1,787,613	61,734	0
19	9	5,469	4,020,045	166,878	0
20	21	8,022	9,047,583	450,672	0
21	6	12,213	6,786,657	1,215,723	0
22	0	18,306	15,272,328	366,051	0
23	0	27,429	34,366,023	987,813	0
24	0	41,019	77,323,623	2,667,984	0
25	0	61,131	173,996,290	7,203,495	0

Table 1: Simulated population sizes for binary-choice model with five subpopulations in which individuals choose  $a$  with probability  $f$  and  $b$  with probability  $1 - f$ , where  $f = 0.20, 0.5, 0.75, 0.9, 1$ , and the initial population is 10 for each  $f$ . Reproductive uncertainty is systematic and also binary, with  $\text{Prob}(\mu_a = 3, \mu_b = 0) = 0.75$  and  $\text{Prob}(\mu_a = 0, \mu_b = 3) = 0.25$ . In this setting, probability matching  $f^* = 0.75$  is the growth-optimal behavior.

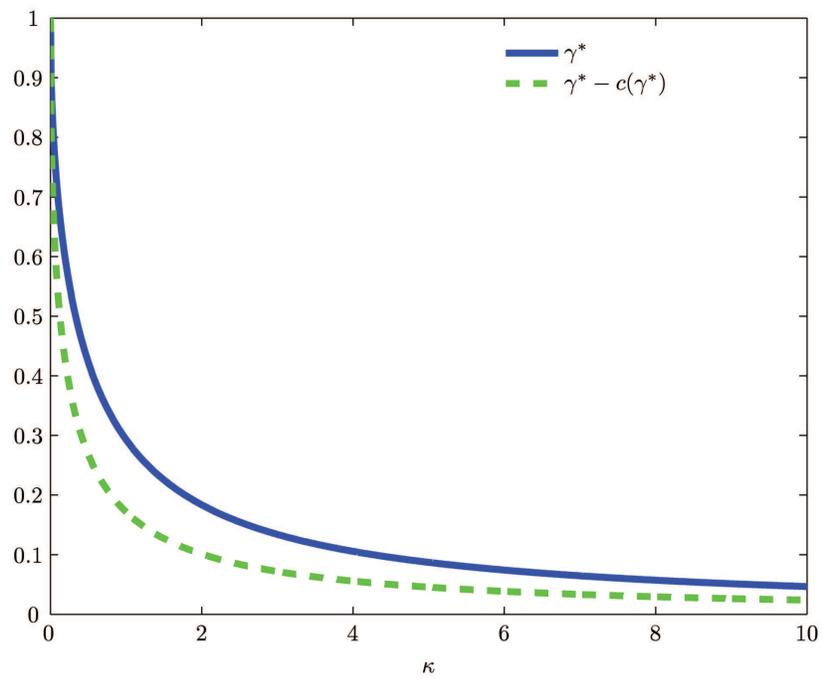


Figure 1: The figure shows the values of  $\gamma^*$  and  $\gamma^* - c(\gamma^*)$  as functions of  $\kappa$ , the cost of intelligence parameter in (26).

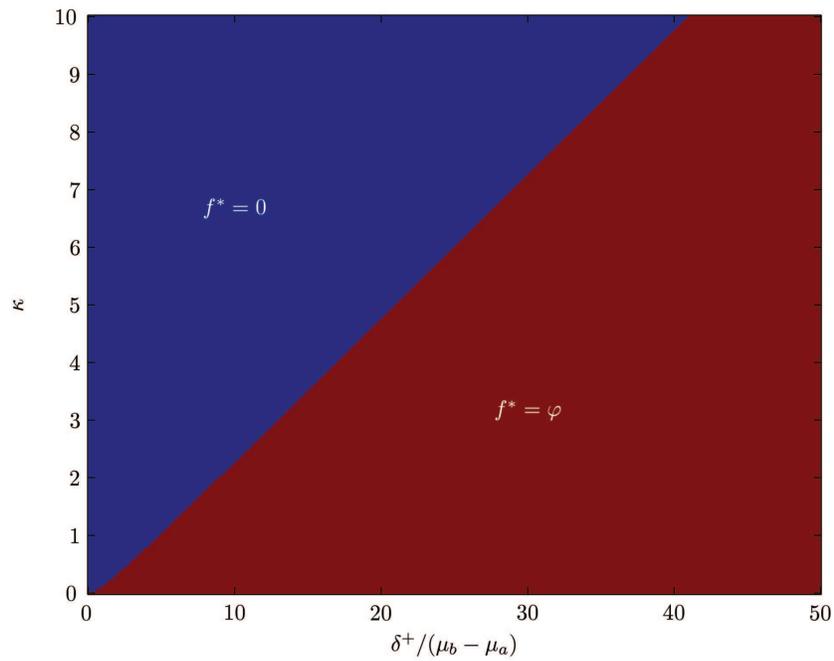


Figure 2: The figure shows the values for  $f^*$  for particular values of  $\kappa$  and  $r = \delta^+ / (\mu_b - \mu_a)$ . The region toward the upper left corresponds to relatively costly intelligence and deterministic behavior of the form  $f^* = 0$ . The region toward the lower right corresponds to relatively cheap intelligence and probability matching of the form  $f^* = \varphi$ . On the line between the two large regions, any value for  $f^*$  between 0 and  $\varphi$  is optimal.