

Risk Attitudes in a Changing Environment: An Evolutionary Model of the Fourfold Pattern of Risk Preferences

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A striking feature of human decision making is the fourfold pattern of risk attitudes, involving risk-averse behavior in situations of unlikely losses and likely gains, but risk-seeking behavior in response to likely losses and unlikely gains. Current theories to explain this pattern assume particular psychological processes to reproduce empirical observations, but do not address whether it is adaptive for the decision maker to respond to risk in this way. Here, drawing on insights from behavioral ecology, we build an evolutionary model of risk-sensitive behavior, to investigate whether particular types of environmental conditions could favor a fourfold pattern of risk attitudes. We consider an individual foraging in a changing environment, where energy is needed to prevent starvation and build up reserves for reproduction. The outcome, in terms of reproductive value (a rigorous measure of evolutionary success), of a one-off choice between a risky and a safe gain, or between a risky and a safe loss, determines the risk-sensitive behavior we should expect to see in this environment. Our results show that the fourfold pattern of risk attitudes may be adaptive in an environment in which conditions vary stochastically but are autocorrelated in time. In such an environment the current options provide information about the likely environmental conditions in the future, which affect the optimal pattern of risk sensitivity. Our model predicts that risk preferences should be both path dependent and affected by the decision maker's current state.

Keywords: risk proneness, risk aversion, cumulative prospect theory, reproductive success, temporal autocorrelation

Risk refers to situations in which the state of the world is uncertain, but the probability of possible states is known. Decision making under risk is a widely discussed topic in many fields of research, from economics to machine learning, and normative theories of how to make decisions under risk are well characterized (Dall, 2010; Houston & McNamara, 1999; Mangel & Clark, 1988; Sutton & Barto, 1998; von Neumann & Morgenstern, 1944). However, everyday decision making in individuals seems to deviate consistently from normative economic predictions (Thaler, 1980).

Decision making under risk is often studied by offering the participant a choice between two hypothetical options: either a gain (or loss) with some probability p between 0 and 1, or a smaller gain (or loss) with certainty. Attitudes to risk can be inferred from the participant's choices when the expected values (means) of the two options are equal. The participant is said to be risk neutral if

they are indifferent between the two options, risk averse if they prefer the certain ("safe") option and risk seeking if they prefer the probabilistic ("risky") option. According to an influential body of empirical work, people tend to be risk averse in the realm of gains and risk seeking in the realm of losses (Kahneman & Tversky, 1979).

One striking feature of human decision making under risk is the so-called "fourfold pattern" of risk preferences (Markowitz, 1952; Tversky & Kahneman, 1992), summarized in Table 1. When the nonzero outcome of the risky option becomes unlikely (i.e., when p is low), the above pattern of choice reverses: the same individuals typically become risk seeking for gains and risk averse for losses (Kahneman & Tversky, 1979; Tversky & Kahneman, 1992). Everyday examples of these effects are seen when individuals play the lottery and overvalue long-shot gambles (Golec & Tamarkin, 1998) but are also willing to pay insurance premiums, behavior that expected utility theory does not readily explain (Friedman & Savage, 1948). Markowitz (1952) uncovered a similar fourfold pattern based on the magnitudes (rather than the probabilities) of the outcomes, arguing that individuals are risk averse for gambles involving large gains or small losses and risk seeking for gambles involving small gains or large losses (Scholten & Read, 2014). Thus, attitudes toward risk appear to be strongly dependent on the probabilities and amounts involved.

Numerous descriptive and mechanistic models have been put forward to account for the fourfold pattern, including security-potential/aspiration theory (Lopes & Oden, 1999), the transfer of attention exchange model (Birbaum, 2008), the priority heuristic (Brandstätter, Gigerenzer, & Hertwig, 2006; Katsikopoulos &

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Table 1
The Fourfold Pattern of Risk Attitudes

	Gains	Losses
High probability or large amount	Risk averse	Risk seeking
Low probability or small amount	Risk seeking	Risk averse

Note. When the likelihood of the non-zero outcome is high or the amount to be won or lost is large (there is not a clear boundary for this and it may vary across individuals), individuals in general are risk averse for gains but risk seeking for losses. On the other hand, when the likelihood of the nonzero outcome is low or the amount to be won or lost is small, the pattern of preference may reverse such that some individuals become risk seeking for gains and risk averse for losses. (Based on Markowitz, 1952 and Tversky & Kahneman, 1992).

Gigerenzer, 2008), stochastic expected utility theory (Blavatsky, 2007), decisions by sampling (Stewart, Chater, & Brown, 2006) and ordinary Bayesian decision making (Fennell & Baddeley, 2012). These are all descriptive explanations, in that they assume a particular decision-making process to reproduce empirical observations. A prominent example is prospect theory (Kahneman & Tversky, 1979; Tversky & Kahneman, 1992), a descriptive model of decision making that purports to capture many of the systematic divergences that humans make from expected utility theory (EUT). To account for the fourfold pattern, prospect theory invokes a probability weighting function for decisions, such that individuals are assumed to overweight low-probability events (behaving as if the probability is greater than it actually is) and underweight highly likely events (behaving as if the probability is less than it actually is). The distorted probabilities and hypothetical value functions are used to improve the predictive power of the model, with no consideration of why it might be beneficial to make decisions in this way.

Our approach here is very different. We make no a priori assumptions about the utility and probability weighting functions used in decision making. Instead, we take a normative perspective and ask whether the fourfold pattern of risk preferences can be understood in adaptive terms. Specifically, we seek to identify conditions under which the fourfold pattern may enhance fitness, where fitness is the expected lifetime reproductive success of the decision maker. To do so, we build an evolutionary model that links behavior directly to reproductive success.

Our model is based on risk-sensitive foraging theory, which was developed by behavioral ecologists as an explanatory framework for how animals should choose optimally between risky foraging options (Houston & McNamara, 1999; Kacelnik & Bateson, 1996; Kacelnik & El Mouden, 2013; McNamara & Houston, 1992; Real & Caraco, 1986; Stephens, 1981). Recently there have been several attempts to use this framework to provide an evolutionary account of human risk preferences and other patterns described by prospect theory. For example, McDermott, Fowler, and Smirnov (2008) attempted to explain risk aversion in gains and risk seeking in losses (the first row of Table 1) using risk-sensitive foraging theory, and claimed that this pattern of risk attitudes is ecologically rational (sensu: Goldstein & Gigerenzer, 2002). Similar claims have been made by Aktipis and Kurzban (2004) and Mishra and colleagues (Mishra, 2014; Mishra & Fiddick, 2012; Mishra, Gregson, & Lalumière, 2012). However, these claims are based on an incorrect characterization of fitness and therefore fail to explain

observed risk preferences (Houston, Fawcett, Mallpress, & McNamara, 2014).

Here we identify a scenario in which the fourfold pattern is in fact rational, in that it arises from a strategy that maximizes the expected lifetime reproductive success of the decision maker. Specifically, this is the case when environmental conditions change stochastically over time, affecting the options available to the decision maker, and the pattern of change shows autocorrelation (see definition below). Because of this autocorrelation, the options available to the decision maker and/or the outcomes of its choices provide information about the likely conditions in the near future (Fawcett et al., 2014), which can affect the consequences of risk-based choice. We demonstrate this principle by modeling an individual foraging in an environment in which its background rate of energetic gain (or loss) changes stochastically over time. We explore various patterns of environmental change and identify conditions under which we might expect a fourfold pattern of risk attitudes to evolve. Our study represents an important advance over previous evolutionary approaches to decision making under risk (e.g., McDermott et al., 2008) in that it provides a logical account of choice based on expected lifetime reproductive success (Houston et al., 2014) and addresses the reversal of risk preferences at very low probabilities, capturing the key features of the fourfold pattern.

The Model

We consider a forager in an environment in which conditions (e.g., food availability) fluctuate over time. The forager's energetic reserves are denoted by x (where $x = 0, 1, 2, \dots$). Time is divided into discrete steps of unit length and in each time step the forager's reserve level changes by an amount d , which is an environmental state variable that can take both positive and negative values; thus in some environmental states the forager is gaining energy, whereas in others it is losing energy. In addition to the change d , the forager experiences stochastic gains and losses (metabolic "noise") that are independent of the current environmental state (this has a smoothing effect that is necessary to avoid grid effects; see Appendix A for technical details).

The environmental state variable (d) changes stochastically but is positively autocorrelated in time, meaning that the occurrence of a given environmental state at time t increases the chances of the same state occurring at $t + 1$ (compared with the long-term average probability of that environmental state). In the results shown we consider four possible states of d : -8 , -2 , 2 , and 8 , representing very bad, moderately bad, moderately good, and very good environmental conditions, respectively. The transition matrix \mathbf{D} is then a 4×4 matrix giving the probabilities α_{ij} of the environmental state changing from a value d_i at time t to a value d_j at time $t + 1$:

$$\mathbf{D} = \begin{matrix} & d_j = -8 & d_j = -2 & d_j = +2 & d_j = +8 \\ \begin{matrix} d_i = -8 \\ d_i = -2 \\ d_i = +2 \\ d_i = +8 \end{matrix} & \begin{bmatrix} 1-3E & E & E & E \\ E & 1-3E & E & E \\ E & E & 1-3E & E \\ E & E & E & 1-3E \end{bmatrix} & \end{matrix} \quad (1)$$

where $0 < E < 1/3$. Note that this transition matrix represents a stationary Markov chain.

The transition probabilities depend only on the current state of the environment and not on how long it has been in that state. Here we are particularly interested in scenarios where $E < 0.25$, such that the environment is more likely to stay in the same state than to switch to any other specific state. This positive autocorrelation implies that the current state of the environment is indicative of its likely future state. The lower the value of E , the stronger the positive autocorrelation, so the longer the environment tends to persist in its current state and the more informative the current conditions are about the conditions the forager will experience in the future.

Under these conditions, we are interested in the *reproductive value* of the forager given its current energetic state (x) and the current environmental state (d). This is a fitness-related measure developed in behavioral ecology that can be used to compare the outcomes of different decisions in a common currency (McNamara & Houston, 1986). For the purpose of this model, reproductive value can be simplified to the expected future number of offspring produced by the forager during the remainder of its life (Houston & McNamara, 1999), which will depend on x and d .

If the forager's reserves ever reach 0, it dies, has a reproductive value of 0 and can no longer gain or lose reserves. In addition there is a fixed background probability of mortality per time step, m_B , which is independent of energetic reserves. Background mortality is not necessary for the effects we observe but is known to affect optimal risk sensitivity (e.g., McNamara, Merad, & Houston, 1991), so we also explore the consequences of changing this parameter. We assume that the forager can only reproduce (and hence gain units of reproductive value) if it builds up sufficient reserves. If the forager's energetic reserves ever reach (or overshoot) some upper threshold L , it reproduces and is awarded an immediate fitness pay-off of Z reproductive units, but loses an amount of energetic reserves c (where $c \geq \max(d)$). The forager's life then continues at this new reserve level and it can reproduce again if it crosses the reproductive threshold again. Reproduction in the form of this pay-off Z upon reaching the upper threshold is the only means by which fitness is gained in the model and the forager continues accruing units of reproductive value in this way until it dies.

Under this set-up, using an iterative method explained in Appendix A, we can calculate the forager's reproductive value for any current energetic state and current environmental state, $U_D(x, d)$. This represents the forager's expected future number of offspring before it dies. A key feature of our approach is that we do not assume any particular function relating reproductive value to the state variables x and d ; rather, this emerges from our calculations and is influenced by the pattern of environmental change. We then use this measure to identify the optimal risk preference, as explained below.

Risk Preference

The expected risk preference of the forager can be determined for any situation (i.e., for any combination of x and d) by offering it a hypothetical gamble: a one-off stochastic option that can be chosen as an alternative to the background deterministic rate of energetic gain (d). The change in reproductive value as a result of accepting this option can be computed and compared with that experienced under the background rate. We assume that the for-

ager is sensitive to differences in reproductive value, that is, that it has evolved to maximize the expected total quantity of offspring produced in its lifetime. Therefore, if there is a difference between the background and alternative options in terms of reproductive value, we expect the forager to choose the one that yields the higher reproductive value.

We assume that the gamble offered is related to the current environmental state d . Specifically, the alternative option is a probabilistic gain or loss, R , with probability $p = d/R$ and therefore has the same expected energetic value as the current background deterministic change in reserves d (because $d = pR$). Thus, large gains and losses are assumed to be less likely than small gains and losses, as is known to be the case for gambles faced by humans in a wide variety of real-world contexts (Pleskac & Hertwig, 2014). $U_S(x, d, R)$ represents the expected reproductive value associated with this stochastic option for an individual in state (x, d) , that is, the average result of a change in reserves of size R with probability p and zero change in reserves with probability $(1 - p)$. See Equation A6 in Appendix A for an explanation of how we compute this.

The difference in reproductive value Ψ from choosing the stochastic option over the deterministic option (when both options give an equal expected change in reserves, $pR = d$) is:

$$\Psi(x, d, R) = U_S(x, d, R) - U_D(x, d). \quad (2)$$

Equation 2 essentially represents the expected benefit, in terms of reproductive value, from gambling. When $\Psi > 0$, the forager is expected to be risk seeking, as its change in reproductive value from choosing the risky (stochastic) option is greater than that from choosing the fixed (deterministic) option. Conversely, when $\Psi < 0$, the reproductive value from choosing the fixed option is greater than that from choosing the risky option and therefore we should expect to see risk-averse behavior.

Results

The default parameter values for our model are shown in Table 2. These parameters are held constant unless stated otherwise.

Figure 1a shows the predicted risk preference, in terms of the benefit of selecting the risky option over the fixed option (Ψ), for an individual with intermediate reserves ($x = 50$) in each of the four environmental states in a moderately autocorrelated environment ($E = 0.05$), with varying sizes of the stochastic gain/loss (R). Preference values above zero indicate risk-seeking behavior, whereas those below zero indicate risk aversion. Note that as R changes (movement along the horizontal axis), the probability of the gain/loss (p) also changes (such that $p = d/R$).

Our model predicts risk-seeking behavior under very bad ($d = -8$) and moderately good ($d = 2$) conditions and risk aversion under very good ($d = 8$) and moderately bad ($d = -2$) conditions. For an equivalent magnitude of potential gains or losses, this corresponds to a tendency to accept gambles for low-probability gains and high-probability losses, but to decline gambles for high-probability gains and low-probability losses. For example, considering a potential gain or loss of $R = \pm 30$ (see black arrows on Figure 1a), the probability of this outcome under extreme conditions ($d = \pm 8$) is 0.267; the forager should accept the gamble in very bad conditions ($d = -8$) but refuse it in very good conditions ($d = 8$). Under moderate conditions ($d = \pm 2$) the

Table 2
 Default Parameter Values for the Model and Summary of Sensitivity Analysis

Parameter	Description	Default value	Range of values over which fourfold pattern holds (given default values of other parameters)
L	Reproductive threshold	100	$L \geq 70$
d	Possible environmental states, determining change in energy reserves per time step	$[-8, -2, 2, 8]$	See Appendix B (Sections 2–4)
μ	Mean metabolic noise	0	$\mu \approx 0$
σ	SD of the metabolic noise	3	$\sigma \geq 1$
Z	Number of offspring produced per reproductive event	1	$Z > 0$
c	Loss of energetic reserves during reproduction	10	$0 < c < 85$
E	Transition probability between state d_i and state d_j where $i \neq j$	0.05	$0.0002 < E < 0.1$
m_B	Background mortality (state-independent probability of death at each time step)	0	$m_B < 0.001$

probability drops to 0.067, and the preferences reverse: the forager should refuse the gamble in moderately bad conditions ($d = -2$) but accept it in moderately good conditions ($d = 2$). This predicted pattern of risk attitudes corresponds to the fourfold pattern laid out by Tversky and Kahneman (1992).

The predicted risk preferences also fit well with the fourfold pattern identified by Markowitz (1952), according to which individuals are risk seeking for small potential gains and large potential losses, but risk averse for large potential gains and small potential losses. Note that the potential gain or loss (R) from the gamble is bigger under extreme conditions ($d = \pm 8$) than it is under moderate conditions ($d = \pm 2$), given a fixed probability (p) of that outcome (see white arrows on Figure 1a). Taking $p = .2$, for example, the amount at stake in the gamble is $R = \pm 40$ under extreme conditions; the forager should accept the gamble in very bad conditions ($d = -8$) but refuse it in very good conditions ($d = 8$). Under moderate conditions ($d = \pm 2$) the amount at stake drops to $R = \pm 10$, and the preferences reverse: the forager should refuse the gamble in moderately bad conditions ($d = -2$) but accept it in moderately good conditions ($d = 2$).

The strength of the risk preferences predicted are strongly dependent on the forager's reserve level (Figure 1b). Nevertheless, the fourfold pattern holds over a fairly broad range of reserves (see Figure 1b) except for reserve levels close to the upper ($x = L$) or lower ($x = 0$) boundary, where the opportunity to reproduce or the threat of starvation is imminent and taking the gamble may result in the forager hitting that boundary. Whether it is better to be risk seeking or risk averse is determined by the curvature of the reproductive value functions (shown in Figure B1, Appendix B). When $d = 8$ and $d = -2$, the value functions are concave (i.e., decreasing in slope) over most of the range of reserve levels, which implies a preference for fixed over variable outcomes, that is, risk aversion. In contrast, when $d = 2$ and $d = -8$, the value functions are convex (i.e., increasing in slope) over most of the range of reserve levels, which implies a preference for variable over fixed outcomes, that is, risk-seeking behavior (see Houston et al., 2014).

Positive temporal autocorrelation is the critical feature driving this pattern of risk preferences. In an autocorrelated world, the gamble offered to the forager reflects the conditions it is likely to experience in the near future, which affects whether it should accept or decline the gamble. The fourfold pattern begins to break down as autocorrelation becomes weak. For $E > 0.1$ the current environmental state is only weakly predictive of the future envi-

ronmental state, and as E approaches 0.25 (zero autocorrelation) the shapes of the value functions become essentially equivalent (see Figure B3, Appendix B), so the fourfold pattern disappears (see Figure 2). At the opposite extreme, when $E < 0.0002$ it is highly unlikely that the environmental state will switch in the near future. Individuals in bad environmental conditions are then very likely to die before conditions improve, whereas those in good conditions are likely to reproduce many times before conditions worsen. In this scenario, risk preferences in a one-off gamble have little effect on reproductive success. Between these extremes of very weak or very strong autocorrelation, the fourfold pattern holds for a wide range of transition probabilities (see Figure 3).

Given a suitable level of positive autocorrelation ($0.0002 < E < 0.1$), the fourfold pattern is robust to changes in the other parameter values (see final column of Table 2). For example, the same pattern of risk preferences is observed when the loss of energetic reserves at reproduction, c , is increased from 10 to 70 energetic units (results not shown). Raising background mortality increases the preference for risk across all environmental states (see Figure B6, Appendix B), but the fourfold pattern is preserved until background mortality exceeds 1 in 1,000 per time step (with other parameters kept at their default values). As the best and worst environmental states become more extreme, the risk preferences diverge (Figure B7, Appendix B), strengthening the fourfold pattern. Provided that the d values for the four environmental states remain symmetric around zero, those values can be modified extensively before the pattern is lost. For example, a similar fourfold pattern is observed when the environmental states are $d = [-9, -8, 8, 9]$, $d = [-2, -1, 1, 2]$, or $d = [-9, -1, 1, 9]$, although the range of parameter space over which the pattern holds may vary (see Figure B4 and B5, Appendix B). Thus, an individual in environmental state $d = -8$ has a preference for risk when $d = -8$ is the worst possible state to be in, but prefers the fixed option when there is a worse state of $d = -9$. This demonstrates that the pattern is fairly insensitive to the magnitude of the background gains and losses, but instead depends on whether there are better or worse states that the environment may switch to in the future.

We have focused on a situation in which transitions to all other environmental states are equally likely (i.e., α_{ij} is constant for all $j \neq i$), but the fourfold pattern extends to other patterns of change as long as the transition matrix is centrosymmetric (i.e., the probabilities of moving inward toward the intermediate states or out-

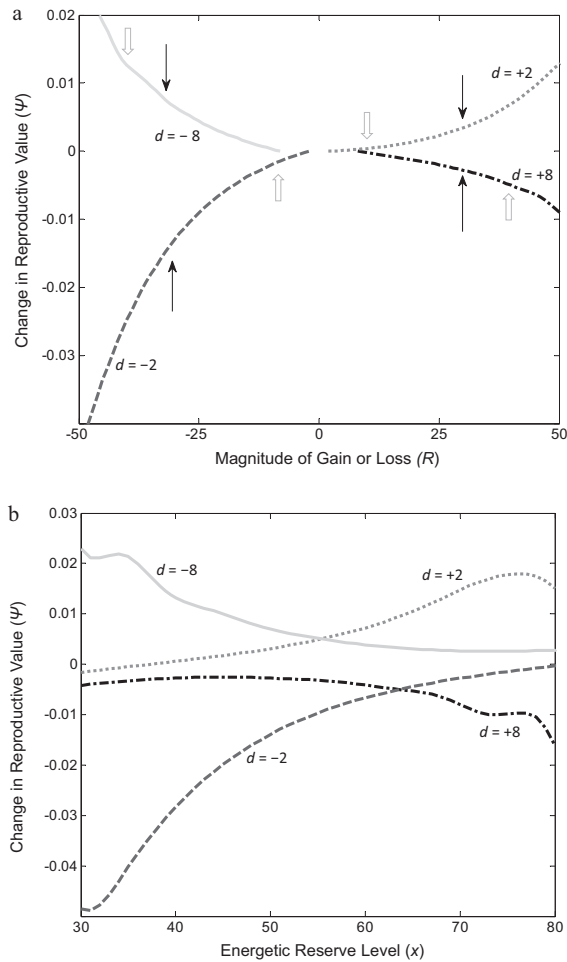


Figure 1. (a) The change in reproductive value (Ψ) from taking a one-off stochastic option instead of the current background deterministic option d under very good ($d = 8$), moderately good ($d = 2$), moderately bad ($d = -2$) and very bad ($d = -8$) environmental conditions, for a forager with intermediate reserves ($x = 50$) in an environment showing moderate positive autocorrelation ($E = 0.05$). Each point on a given line represents a different gamble opportunity (differing in magnitude, R , and probability, p , of the outcome). Moving along the line away from 0 increases $|R|$ and decreases p (holding the expected value equivalent to d). Points above 0 on the vertical axis ($\Psi > 0$) represent a preference for risk (greater reproductive value associated with taking the stochastic option over the deterministic option), whereas points below 0 ($\Psi < 0$) represent an aversion to risk. See Table 2 for parameter values. The black arrows on this figure indicate gambles offering a potential gain or loss of $R = \pm 30$ with a probability of either $p = .267$ (for $d = \pm 8$) or $p = .067$ (for $d = \pm 2$). The white arrows indicate gambles offering a potential gain or loss of either $R = \pm 10$ (for $d = \pm 2$) or $R = \pm 40$ (for $d = \pm 8$) with a probability of $p = .2$. (b) The change in reproductive value (Ψ) from taking a one-off stochastic option (with a potential gain or loss of $R = \pm 30$) instead of the current background deterministic option d under very good ($d = 8$), moderately good ($d = 2$), moderately bad ($d = -2$), and very bad ($d = -8$) environmental conditions, for varying levels of energy reserves in an environment showing moderate positive autocorrelation ($E = 0.05$).

ward toward more extreme states are symmetric about the center). For example, when transitions can only occur between adjacent environmental states (between -8 and -2 , between -2 and 2 and between 2 and 8), we observe similar effects (Figure B8 and B9,

Appendix B). The fourfold pattern is less prevalent when the switching rate is asymmetric across positive and negative environmental states. The pattern is still observed in some situations in which the values of the environmental states (d) are asymmetric but the mean change in energetic reserves across the four states is zero (e.g., $d = [-7, -3, 1, 9]$ and $d = [-8, -2, 4, 6]$), but it typically disappears when the mean change deviates significantly from zero (e.g., $d = [-8, -2, 7, 8]$ and $d = [-8, -7, 2, 8]$). A similar effect is seen when mean metabolic noise deviates significantly from zero; negative values of μ favor risk seeking in all environmental states, whereas positive values favor risk aversion in all environmental states. In general, ubiquitous risk seeking is observed across all environmental states when the long-term average change in energy reserves is negative, and universal risk aversion is observed when it is positive. Thus even when the forager is in a very good environmental state (e.g., $d = 8$), if it faces a net energetic loss in the long term (i.e., averaging across all states), it should be risk seeking according to our model.

Discussion

Previous attempts to explain human risk preferences from an evolutionary perspective (e.g., Aktipis & Kurzban, 2004; McDermott et al., 2008) have claimed that risk-seeking behavior is adaptive at low reserves whereas risk-averse behavior is adaptive at high reserves. Our model demonstrates that in a stochastic foraging environment in which conditions are autocorrelated over time, risk preferences may be much more complex. Using a rigorous evolutionary approach based on reproductive value, we have shown that optimal risk preferences can be strongly influenced by the options currently available, because these provide information about the likely future conditions and hence the need to take risks (see Fawcett et al., 2014). Under this

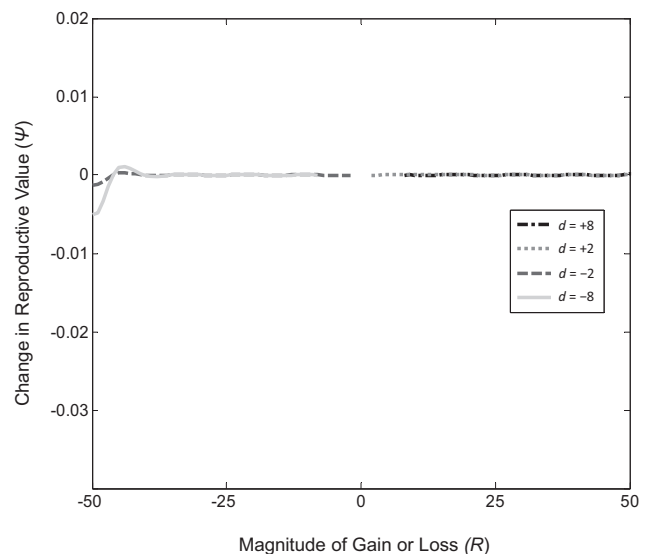


Figure 2. The change in reproductive value (Ψ) from taking a one-off stochastic option instead of the current background deterministic option d under very good ($d = 8$), moderately good ($d = 2$), moderately bad ($d = -2$), and very bad ($d = -8$) environmental conditions, for a forager with intermediate reserves ($x = 50$) in an environment showing zero autocorrelation ($E = 0.25$). See Figure 1 for more details.

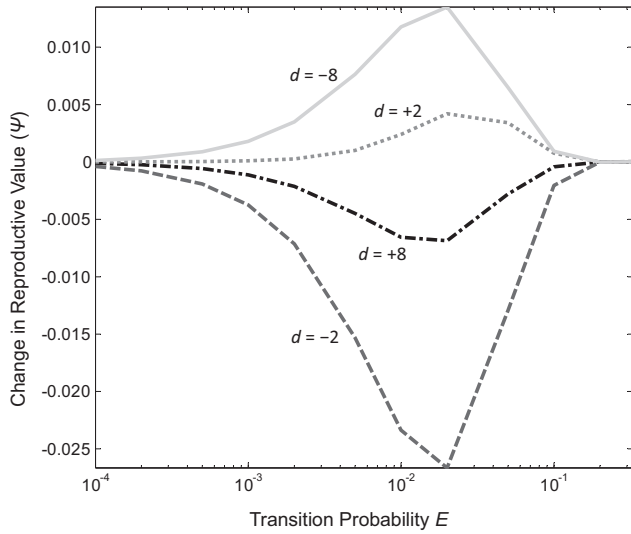


Figure 3. The change in reproductive value (Ψ) from taking a one-off stochastic option (with a potential gain or loss of $R = \pm 30$) instead of the current background deterministic option d under very good ($d = 8$), moderately good ($d = 2$), moderately bad ($d = -2$), and very bad ($d = -8$) environmental conditions, for a forager with intermediate reserves ($x = 50$), in relation to the transition probability (E). All other parameters are held constant at their default values (see Table 2).

scenario, selection can favor a fourfold pattern of risk preferences. Our evolutionary model predicts a preference for fair gambles over certainty for unlikely gains and likely losses, but an aversion to gambling for likely gains and unlikely losses, as described by Tversky and Kahneman (1992). It also predicts the stake-dependent fourfold pattern described by Markowitz (1952), namely risk aversion for gambles involving large gains or small losses and risk seeking for gambles involving small gains or large losses. To the best of our knowledge, our model provides the first functional (adaptive) explanation for both of these reported patterns of decision making.

To understand why the fourfold pattern is adaptive in our model, it is important to consider how environmental conditions now and in the near future affect the probabilities of reaching the reproductive threshold and avoiding the starvation boundary. When environmental conditions are very good (8 in our default setup), the forager shows risk aversion. Here the forager is in the most favorable situation and is likely to reach the reproductive threshold before conditions change, without having to take risks. Under very bad environmental conditions (-8 in our default setup), in contrast, the forager should be risk seeking. This is the environmental state most likely to deplete the forager's reserves to the starvation boundary; to maximize its chances of surviving until conditions improve, it typically pays the forager to gamble. For the intermediate states, however, the preferences reverse. In the moderately good environmental state (2 in our default setup), the forager's reserves are increasing but at a slower rate than in the best environmental state (8), and when a switch occurs it is more likely that conditions will worsen (probability $2E$) than improve (probability E). Therefore, the forager needs to take a risk to maximize its chances of reaching the reproductive threshold before conditions change. Conversely, in the moderately bad environmental

state (-2 in our default setup), the forager's reserves are decreasing but at a slower rate than in the worst environmental state (-8), and when a switch occurs it is more likely that conditions will improve (probability $2E$) than worsen (probability E). In this situation the forager should avoid taking risks because it can typically afford the smaller deterministic losses (-2) until a switch occurs, before starvation becomes a serious threat.

Our evolutionary approach to explaining decision making under risk is novel for two reasons. First, in contrast to previous evolutionary approaches, we have determined optimal risk preferences using a rigorous and consistent method based on the concept of reproductive value, which is well established in behavioral ecology (Houston & McNamara, 1999). We made no assumptions about the shape of the value functions—instead, these emerged from the background environment in the model—nor did we assume that subjective estimates of probabilities are biased in any way. This is a powerful feature of our model—a very simple environment that changes stochastically over time can generate complex patterns of risk preferences without the need for specific assumptions about the mechanisms of choice. Second, our work highlights the importance of temporal autocorrelation in the evolution of risk preferences. Most (if not all) environments in the real world, including those in which ancestral humans evolved, show some degree of spatiotemporal heterogeneity and autocorrelation (Halley, 1996), so it is reasonable to suggest that these features had some influence on the evolution of our attitudes to risk. By recognizing the importance of autocorrelation, evolutionary theory has already provided possible explanations for a number of common cognitive biases that pervade the psychological literature, including contrast effects, optimism and pessimism, and violations of regularity (Fawcett et al., 2014). Here we are suggesting that the fourfold pattern of risk preferences may also represent an adaptive response to temporally autocorrelated environments, in which the options available to the decision maker, and the outcomes of its choices, are indicative of future conditions.

According to our model, risk taking should depend on the pattern of environmental change to which the decision maker is adapted, and in particular how long it expects current conditions to continue. This does not necessarily imply, however, that the risk preferences measured in experiments on human decision making will be sensitive to information regarding the degree of autocorrelation between choices and the extent to which current options predict options available in the future. Rather, our interpretation is that natural selection has favored certain attitudes to risk that regulate, in a fairly automatic or subconscious way, the tendency for people to accept gambles as a function of their current situation. Clearly, the type of environment we have modeled differs markedly from the typical set-up in studies of human decision making; our basic argument is that, in such studies, people may be acting on the basis of evolved predispositions that are adapted to natural environments with a richer temporal structure.

Our model predicts that risk preferences should depend not just on the environmental conditions, but also on the decision maker's current reserve level. In effect, the forager's current reserve level represents a reference point, modulated by current environmental conditions, from which to assess potential gains or losses. This implies that if our explanation is relevant to human decisions involving money, an individual's risk preference should depend on their current level of wealth (and not just on the range of options presented). Therefore, we make the prediction that people's risk-

based choice patterns should covary with their current socioeconomic status. These kinds of data are seldom published in decision-making experiments, but, intriguingly, a growing body of evidence suggests that both current wealth and physiological state may affect risk preference. In the financial literature, for example, initial wealth may influence an individual investor's level of risk aversion (Bosch-Domènech & Silvestre, 2006; Guiso & Paiella, 2010). Metabolic state (specifically hunger levels) has also been shown to have a significant effect on risk preference for monetary gambles, with satiation leading to greater risk aversion (Symmonds, Emmanuel, Drew, Batterham, & Dolan, 2010), despite the differing currencies of energy and money.

The risk preferences predicted by our model also exhibit the property of path dependence, which is a hallmark of prospect theory (Kahneman & Tversky, 1979) and related theories of human decision making. According to this view, decision makers are more concerned with changes in their state than the final state they end up in; that is, "the carriers of utility are gains and losses—changes of wealth rather than states of wealth" (Kahneman, 2003). In our model, the reproductive value of a forager whose reserves are currently at $x = 50$ differs depending on how their reserves changed to get to that state, because this reflects the conditions they are likely to experience in the near future. The trajectory of the forager's reserves is therefore linked to its reproductive value, which influences subsequent risk-taking behavior. For example, comparing the lines for $d = -8$ and $d = 8$ in Figure 1a, we can see that a forager who previously had energy reserves of $x = 58$ and then lost 8 units should be risk seeking (assuming the environmental state persists at $d = -8$), whereas one whose reserves increased 8 units from $x = 42$ should be risk averse (assuming the environmental state persists at $d = 8$). Thus, providing there is sufficient autocorrelation, attitudes toward risk should be dependent not only on current energy reserves, but also on how energy reserves have changed to get to their current level.

Although we have identified a potential explanation for the fourfold pattern, we make no special claims that this is necessarily the correct explanation for why humans show such attitudes to risk. As with all scientific studies, there are some limitations. Most notably, the risk preferences elicited in our model are relatively weak; the slopes of the reproductive value functions (Figure B1 and B2, Appendix B) at moderate reserve levels show only a very slight curvature. We deliberately focused on choices between options with equal expected value (identical means) but different variances, since then the risk preference can be clearly inferred from the reproductive value associated with each option (whereas a substantial difference in expected value generally leads to a preference for the option with the higher expected value). Therefore, the scenario we have studied may not be able to account for the stronger risk aversion sometimes observed in humans (e.g., paying large premiums and sacrificing considerably more favorable potential gains to avoid risk). Rabin's (2000) analysis suggests that risk attitudes across different scales exhibited in humans cannot be explained solely by the shape of the value function. Despite this being the primary explanation for risk sensitivity in both economics and behavioral ecology, some authors have noted that there may be a utility of gambling (or certainty) that falls outside this framework (Diecidue, Schmidt, & Wakker, 2004; Fishburn, 1980). The possible evolutionary reasons for this have not yet been explored.

Although the fourfold pattern is associated with human decision making, the risk preferences identified by our model should apply

to many other animals adapted to fluctuating environments. Experiments investigating analogous phenomena in nonhuman animals may therefore prove fruitful. Risk-based preferences have been explored in a variety of species (Kacelnik & El Mouden, 2013) and many of the phenomena originally discussed by Kahneman and Tversky have been observed using token economies in capuchin monkeys (Chen, Lakshminarayanan, & Santos, 2006; Lakshminarayanan, Chen, & Santos, 2011). However, the extensive training necessary for many experiments on nonhuman animals may make it difficult to assess preferences for gambles with unlikely outcomes. This is because experiments that involve low-value, repeated decisions (rather than occasional or once-in-a-lifetime, high-value decisions) and decisions in which values were learnt from experience (rather than being described) can differ radically in their results (Hertwig & Erev, 2009). For example, using 50/50 gambles where the distribution of outcomes is experienced through sampling, Ludvig and colleagues found risk seeking for gains and risk aversion for losses (Ludvig, Madan & Spetch, 2014; Ludvig & Spetch, 2011), which is the opposite pattern to that found for decisions based on description according to prospect theory (Kahneman & Tversky, 1979). Our model does not readily account for this phenomenon. Note, however, that in the learning phase in these experiments, the order of trial types was randomized (Ludvig et al., 2014; Ludvig & Spetch, 2011), and thus, there was no temporal autocorrelation. It would be interesting to conduct similar experiments but with options persisting over multiple trials, to see whether the same pattern of risk preferences emerges. More work on risk sensitivity is needed, both theoretically and empirically, to address the realistic kinds of decisions under uncertainty made in a nonstationary world.

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(Appendices follow)

Appendix A

Technical Details of the Model

Metabolic Noise

In addition to the background gain or loss of energy, d , which is set by the current environmental state, we assume a small gain or loss, y , in each time step that is independent of the environmental state or the forager's behavior (so the overall change in reserves in one time step is $d + y$). This could be because of a variable metabolic expenditure or unspecified gains and losses from other sources not considered. y takes integer values between $-h$ and h , drawn from a truncated pseudonormal distribution with mean μ and $SD \sigma$ and then renormalized so that the cumulative distribution function sums to 1. The probability of a particular value of y is thus:

$$H(y) = \frac{\exp(-(y - \mu)^2/2\sigma^2)}{\sum_{y=-h}^h \exp(-(y - \mu)^2/2\sigma^2)} \quad (\text{A1})$$

Value Calculations

We calculate the value of being in each state (i.e., each combination of x and d) at any time by using a technique similar to stochastic dynamic programming (Bellman, 1957; Houston & McNamara, 1999; Mangel & Clark, 1988), with the exception that the individual being modeled does not have a choice at each time step. We can calculate the value of being in a particular state at time t by summing up the values of being in every possible state at time $t + 1$, weighted by the likelihood of ending up in those states. The values we use represent reproductive value (i.e., the forager's expected future number of offspring before death). For all reserve levels excluding the lower ($x = 0$) and upper ($x = L$) boundaries, the reproductive value U at time t is

$$U(x, d_i, t) = \sum_{y=-h}^h \left(H(y) \times \sum_{j=1}^k \alpha_{ij} \times U(x + d_i + y, d_j, t + 1) \right) \times (1 - m_B) \quad \text{for } 0 < x < L \quad (\text{A2})$$

There is a $1 - m_B$ chance that the forager survives until the next time step. Given this, it gains d_i units of energy plus some metabolic noise y and the environmental state changes to d_j with probability α_{ij} .

$$U_S(x, d_i, R) = \left[\sum_{y=-h}^h \left(H(y) \times \sum_{j=1}^k \alpha_{ij} \times U(x + R + y, d_j) \right) \times (1 - m_B) \times p \right] + \left[\sum_{y=-h}^h \left(H(y) \times \sum_{j=1}^k \alpha_{ij} \times U(x + 0 + y, d_j) \right) \times (1 - m_B) \times (1 - p) \right] \quad (\text{A6})$$

where $p = d_i/R$. The derivation follows the same logic as A2.

For individuals that reach the lower boundary ($x = 0$), death occurs and reproductive value is zero:

$$U(0, d_i, t) = 0. \quad (\text{A3})$$

For individuals that exceed the reproduction threshold ($x \geq L$), the reproductive value is

$$U(x, d_i, t) = \left(Z + \sum_{y=-h}^h \left(H(y) \times \sum_{j=1}^k \alpha_{ij} \times U(x - c + y, d_j, t + 1) \right) \right) \times (1 - m_B) \quad \text{for } x \geq L \quad (\text{A4})$$

Again there is a $1 - m_B$ chance that the forager survives the time step. Given this, it produces Z offspring and its reserves decrease by c , which represents the energetic cost of reproduction. The forager also experiences metabolic noise y and the environmental state changes from d_i to d_j with probability α_{ij} .

We do not assume any fixed time horizon, but the forager will eventually die at some point (either from the background mortality m_B or a long run of bad conditions) and so total lifetime reproductive success is finite. To calculate this, we iterate backward through time using equations A2–A4. Initially, when there are relatively few time steps before the end of the modeled period, the forager's reproductive value (as a function of its energy reserves and the environmental state) depends on how much time is left. However, as we continue iterating backward, the probability of reaching this end point becomes vanishingly small and the reproductive value converges to a stable value $U_D(x, d_i)$ that is independent of time:

$$U_D(x, d_i) = \lim_{t \rightarrow -\infty} U(x, d_i, t). \quad (\text{A5})$$

These calculations result in a look-up table that lays out the reproductive value for every possible combination of x and d .

$U_S(x, d_i, R)$ represents the expected reproductive value associated with the stochastic (risky) option, that is, a change in reserves R with probability p and a change of 0 with probability $1 - p$, where $p = d_i/R$. The forager's initial state is (x, d_i) . As before, the forager experiences metabolic noise y and the environmental state variable changes to d_j with the same transition probabilities:

(Appendices continue)

Appendix B

Supplementary Figures

Additional Results for Default Setup

Relating to Figure 1 in the main text, the corresponding value functions and second derivatives of the value functions are displayed in Figures B1–B3.

Changes to Environmental State d

By using different sets of d values for the four environmental states, we can see that the appearance of the fourfold pattern is predominantly dependent on the relative ordering of the d values, rather than their magnitudes (Figure B4 and B5). For example, an individual in state $d = -8$ has a preference for risk when $d = -8$ is the worst possible state to be in, but chooses the safe option when there is an even worse state of $d = -9$ (compare Figure B4 below with Figure 1a from the main text).

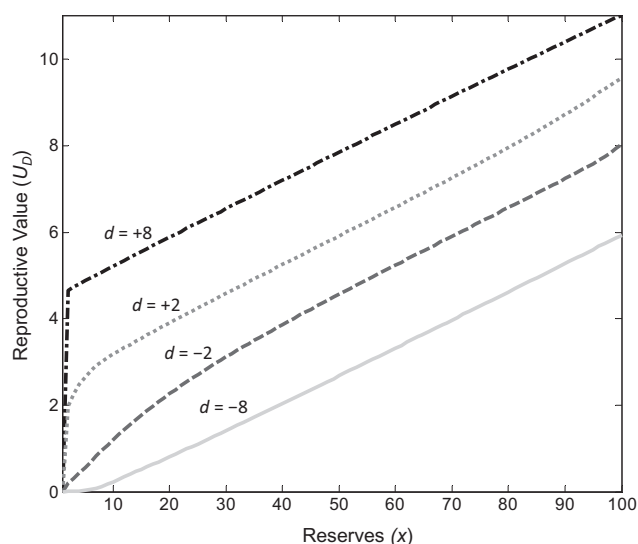


Figure B1. Reproductive value (expected future reproductive success) with respect to energy reserves for a forager in very good ($d = 8$), moderately good ($d = 2$), moderately bad ($d = -2$) or very bad ($d = -8$) environmental conditions, in an environment showing moderate positive autocorrelation ($E = 0.05$). Parameter values are the same as in Figure 1a in the main text.

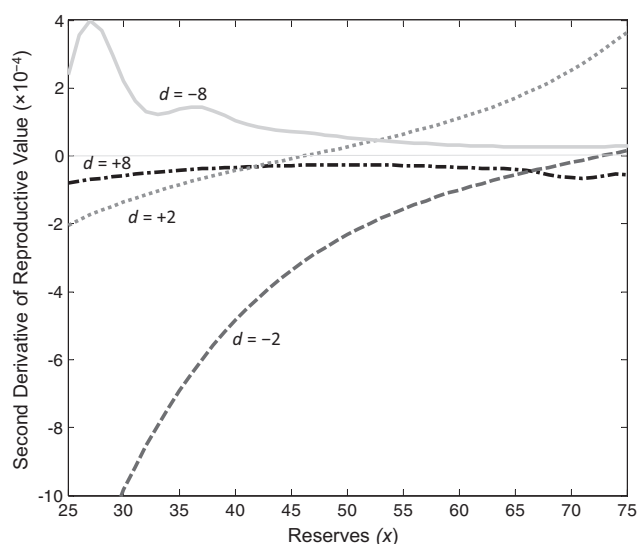


Figure B2. Second derivatives for the reproductive value functions shown in Figure B1. When the second derivative is positive (indicating a convex value function) the forager would be expected to be risk seeking (according to Jensen's inequality), whereas when the second derivative is negative (indicating a concave value function) it should be risk averse (see Houston et al., 2014). Note that these patterns closely correspond to the expected benefit (relative to the background deterministic option d) of accepting a single gamble with $R = \pm 30$, as depicted in Figure 1b in the main text.

Additional Results Across Parameter Space

The “fourfold pattern” has been found robustly across large areas of parameter space. Besides the transition probability (Figure 3, main text), the effect is also shown across background mortalities (m_B ; Figure B6) and the size of reserve changes in extreme environments (d_1 and d_4 ; Figure B7). Figures B6 and B7 show the change in reproductive value (Ψ) from taking a one-off stochastic option (with a potential gain or loss of $R = \pm 30$) instead of the current background deterministic option d under very good (d_4), moderately good (d_3), moderately bad (d_2) and very bad (d_1) environmental conditions, for a forager with intermediate reserves ($x = 50$) and all other parameters held constant at their default values (see Table 2).

(Appendices continue)

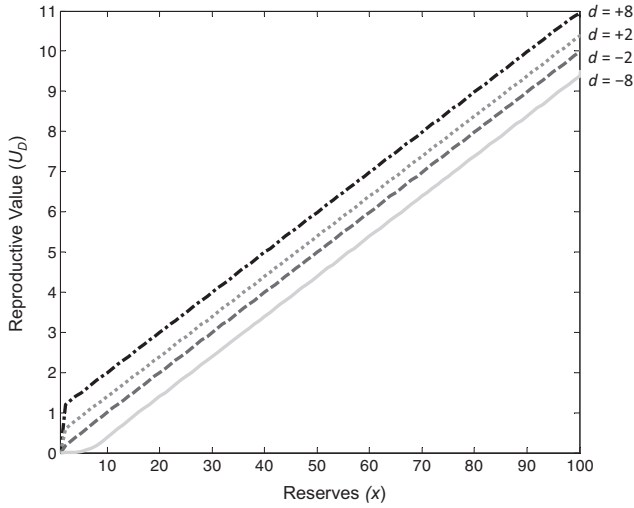


Figure B3. Reproductive value with respect to energy reserves for a forager in very good ($d = 8$), moderately good ($d = 2$), moderately bad ($d = -2$), or very bad ($d = -8$) environmental conditions, in an environment showing no autocorrelation ($E = 0.25$). Note that the value functions are parallel and show no obvious curvature.

Modifications to the Transition Matrix

The fourfold pattern can also be observed in less homogeneous stochastic environments, where the environment only switches be-

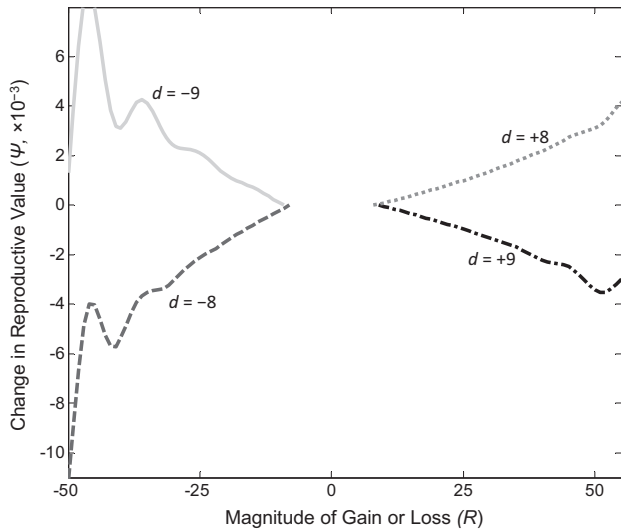


Figure B4. Change in reproductive value from taking the one-off stochastic option instead of the current background deterministic option d , when $d = [-9, -8, 8, 9]$. All other parameter values are the default values from Table 2, although the patterns of risk preference shown are stable over a much wider parameter range.

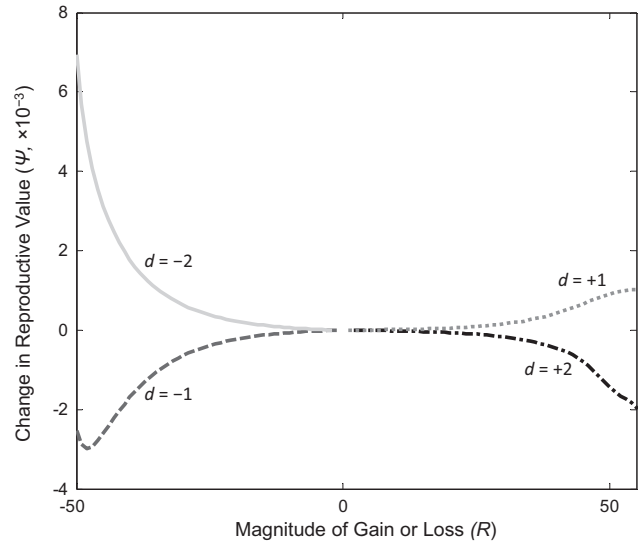


Figure B5. Change in reproductive value from taking the one-off stochastic option instead of the current background deterministic option d , when $d = [-2, -1, 1, 2]$. All other parameter values are the default values from Table 2, although the patterns of risk preference shown are stable over a much wider parameter range.

tween adjacent states and the intermediate states (e.g., $d = 2$ or $d = -2$) are more common than the more extreme states ($d = 8$ or $d = -8$), as represented by the following transition matrix:

$$D = \begin{bmatrix} 1 - C & C & 0 & 0 \\ B & 1 - (A + B) & A & 0 \\ 0 & A & 1 - (A + B) & B \\ 0 & 0 & C & 1 - C \end{bmatrix}$$

An example of an autocorrelated environment like this where the effects are strong can be seen below.

$$D = \begin{bmatrix} 0.8 & 0.2 & 0 & 0 \\ 0.05 & 0.85 & 0.1 & 0 \\ 0 & 0.1 & 0.85 & 0.05 \\ 0 & 0 & 0.2 & 0.8 \end{bmatrix}$$

The effects of modifying the transition probability from intermediate to extreme environmental states (B) in these more complex autocorrelated environments can be seen in Figures B8 and B9, with $A = 0.1$ and $C = 0.2$.

The fourfold pattern of risk preferences holds across a very large range of transition probabilities from the intermediate environmental states to the adjacent extreme environmental states, $B = 0.001$ (Figure B8) and $B = 0.1$ (Figure B9).

(Appendices continue)

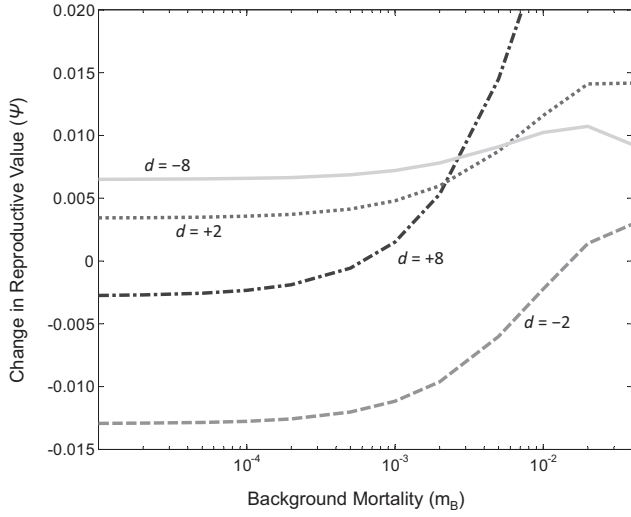


Figure B6. The effect of changing background mortality (m_B) on the change in reproductive value from taking the one-off stochastic option ($R = \pm 30$).

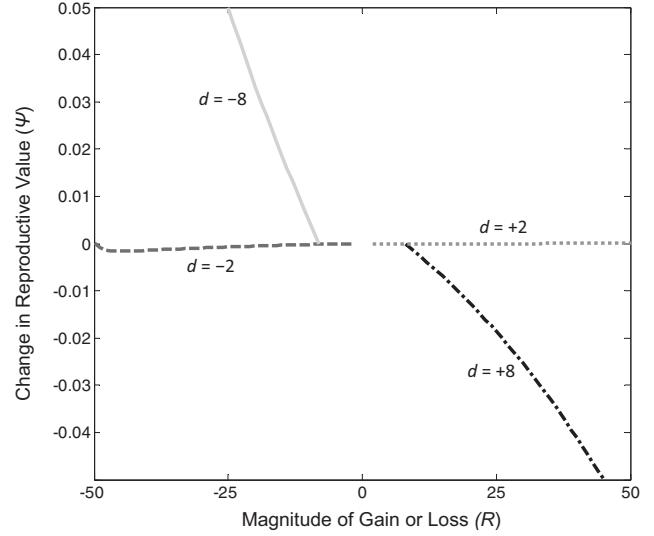


Figure B8. The change in reproductive value from taking the one-off stochastic option when transitions are only possible between adjacent environmental states. Transition probability $B = 0.001$.

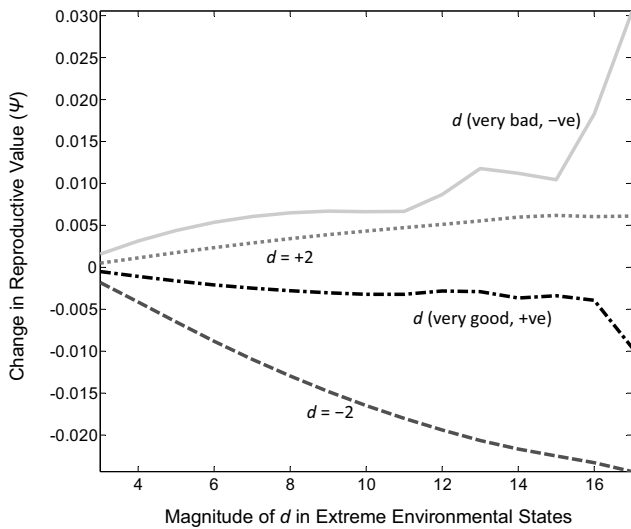


Figure B7. The effect of changing the size of reserve changes in extreme environments (d_1 and d_4) on the change in reproductive value from taking a one-off stochastic option ($R = \pm 30$).

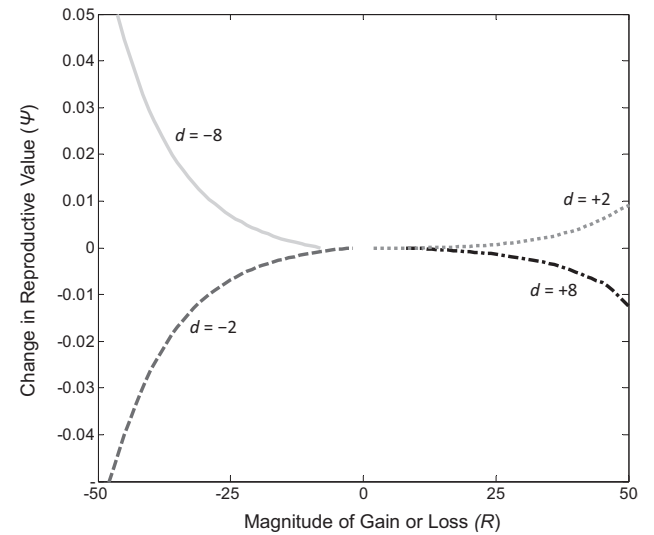


Figure B9. The change in reproductive value from taking the one-off stochastic option when transitions are only possible between adjacent environmental states. Transition probability $B = 0.1$.

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