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Risk Attitudes in a Changing Environment:

An Evolutionary Model of the Fourfold Pattern of Risk Preferences

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Abstract

A striking feature of human decision making is the fourfold pattern of risk attitudes, involving risk-averse behaviour in situations of unlikely losses and likely gains, but risk-seeking behaviour 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 behavioural ecology, we build an evolutionary model of risk-sensitive behaviour, to investigate whether particular types of environmental conditions could favour 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 behaviour 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

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Background

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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 characterised (von Neumann & Morgenstern, 1944; Mangel & Clark, 1988; Houston & McNamara, 1999; Sutton & Barto, 1998; Dall, 2010). Interestingly, 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), summarised in Table 1. When the non-zero 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

77 seen when individuals play the lottery and overvalue long-shot gambles (Golec & Tamarkin, 1998)
78 but are also willing to pay insurance premiums, behaviour that expected utility theory does not readily
79 explain (Friedman & Savage, 1948). Markowitz (1952) uncovered a similar fourfold pattern based on
80 the magnitudes (rather than the probabilities) of the outcomes, arguing that individuals are risk averse
81 for gambles involving large gains or small losses and risk seeking for gambles involving small gains
82 or large losses (Scholten & Read, 2014). Thus, attitudes towards risk appear to be strongly dependent
83 on the probabilities and amounts involved.

84

85 Numerous descriptive and mechanistic models have been put forward to account for the fourfold
86 pattern, including security-potential/aspiration theory (Lopes & Oden, 1999), the transfer of attention
87 exchange model (Birnbaum, 2008), the priority heuristic (Brandstätter, Gigerenzer & Hertwig, 2006,
88 Katsikopoulos & Gigerenzer, 2008), stochastic expected utility theory (Blavatsky, 2007), decisions
89 by sampling (Stewart, Chater & Brown, 2006) and ordinary Bayesian decision making (Fennell &
90 Baddeley, 2012). These are all descriptive explanations, in that they assume a particular decision-
91 making process in order to reproduce empirical observations. A prominent example is prospect theory
92 (Kahneman & Tversky, 1979; Tversky & Kahneman, 1992), a descriptive model of decision making
93 that purports to capture many of the systematic divergences that humans make from expected utility
94 theory (EUT). To account for the fourfold pattern, prospect theory invokes a probability weighting
95 function for decisions, such that individuals are assumed to overweight low-probability events
96 (behaving *as if* the probability is greater than it actually is) and underweight highly likely events
97 (behaving *as if* the probability is less than it actually is). The distorted probabilities and hypothetical
98 value functions are used to improve the predictive power of the model, with no consideration of why
99 it might be beneficial to make decisions in this way.

100

101 Our approach here is very different. We make no *a priori* assumptions about the utility and
102 probability weighting functions used in decision making. Instead, we take a normative perspective and
103 ask whether the fourfold pattern of risk preferences can be understood in adaptive terms. Specifically,
104 we seek to identify conditions under which the fourfold pattern may enhance fitness, where fitness is

105 the expected lifetime reproductive success of the decision maker. To do so, we build an evolutionary
106 model that links behaviour directly to reproductive success.

107

108 Our model is based on risk-sensitive foraging theory, which was developed by behavioural ecologists
109 as an explanatory framework for how animals should choose optimally between risky foraging
110 options (Stephens, 1981; Real & Caraco, 1986; McNamara & Houston, 1992; Kacelnik & Bateson,
111 1996; Houston & McNamara, 1999; Kacelnik & El Mouden, 2013). Recently there have been several
112 attempts to use this framework to provide an evolutionary account of human risk preferences and
113 other patterns described by prospect theory. For example, McDermott, Fowler & Smirnov (2008)
114 attempted to explain risk aversion in gains and risk seeking in losses (the first row of Table 1) using
115 risk-sensitive foraging theory, and claimed that this pattern of risk attitudes is ecologically rational
116 (*sensu* Goldstein & Gigerenzer, 2002). Similar claims have been made by Aktipis & Kurzban (2004)
117 and Mishra and colleagues (Mishra & Fiddick 2012; Mishra, Gregson & Lalumière, 2012; Mishra
118 2014). However, these claims are based on an incorrect characterisation of fitness and therefore fail to
119 explain observed risk preferences (Houston, Fawcett, Mallpress & McNamara, 2014).

120

121 Here we identify a scenario in which the fourfold pattern is in fact rational, in that it arises from a
122 strategy that maximises the expected lifetime reproductive success of the decision maker.

123 Specifically, this is the case when environmental conditions change stochastically over time, affecting
124 the options available to the decision maker, and the pattern of change shows autocorrelation (see
125 definition below). Because of this autocorrelation, the options available to the decision maker and/or
126 the outcomes of its choices provide information about the likely conditions in the near future (Fawcett
127 *et al.*, 2014), which can affect the consequences of risk-based choice. We demonstrate this principle
128 by modelling an individual foraging in an environment in which its background rate of energetic gain
129 (or loss) changes stochastically over time. We explore various patterns of environmental change and
130 identify conditions under which we might expect a fourfold pattern of risk attitudes to evolve. Our
131 study represents an important advance over previous evolutionary approaches to decision making
132 under risk (e.g. McDermott *et al.* 2008) in that it provides a logical account of choice based on

133 expected lifetime reproductive success (Houston *et al.*, 2014) and addresses the reversal of risk
 134 preferences at very low probabilities, capturing the key features of the fourfold pattern.

135

136 **The Model**

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

145

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

153

$$154 \quad \mathbf{D} = \begin{matrix} & \begin{matrix} d_j = -8 & d_j = -2 & d_j = +2 & d_j = +8 \end{matrix} \\ \begin{matrix} d_i = -8 \\ d_i = -2 \\ d_i = +2 \\ d_i = +8 \end{matrix} & \begin{bmatrix} 1-3E & E & E & E \\ E & 1-3E & E & E \\ E & E & 1-3E & E \\ E & E & E & 1-3E \end{bmatrix} \end{matrix} \quad (1)$$

155

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

157

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

165

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

172

173 If the forager's reserves ever reach 0, it dies, has a reproductive value of 0 and can no longer gain or
174 lose reserves. In addition there is a fixed background probability of mortality per time step, m_B , which
175 is independent of energetic reserves. Background mortality is not necessary for the effects we observe
176 but is known to affect optimal risk sensitivity (e.g. McNamara, Merad & Houston, 1991), so we also
177 explore the consequences of changing this parameter. We assume that the forager can only reproduce
178 (and hence gain units of reproductive value) if it builds up sufficient reserves. If the forager's
179 energetic reserves ever reach (or overshoot) some upper threshold L , it reproduces and is awarded an
180 immediate fitness pay-off of Z reproductive units, but loses an amount of energetic reserves c (where
181 $c \geq \max(d)$). The forager's life then continues at this new reserve level and it can reproduce again if it
182 crosses the reproductive threshold again. Reproduction in the form of this pay-off Z upon reaching the
183 upper threshold is the only means by which fitness is gained in the model and the forager continues
184 accruing units of reproductive value in this way until it dies.

185

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

193

194 **Risk Preference**

195 The expected risk preference of the forager can be determined for any situation (i.e. for any
196 combination of x and d) by offering it a hypothetical gamble: a one-off stochastic option that can be
197 chosen as an alternative to the background deterministic rate of energetic gain (d). The change in
198 reproductive value as a result of accepting this option can be computed and compared to that
199 experienced under the background rate. We assume that the forager is sensitive to differences in
200 reproductive value, i.e. that it has evolved to maximise the expected total quantity of offspring
201 produced in its lifetime. Therefore, if there is a difference between the background and alternative
202 options in terms of reproductive value, we expect the forager to choose the one that yields the higher
203 reproductive value.

204

205 We assume that the gamble offered is related to the current environmental state d . Specifically, the
206 alternative option is a probabilistic gain or loss, R , with probability $p = d/R$ and therefore has the same
207 expected energetic value as the current background deterministic change in reserves d (since $d = pR$).
208 Thus, large gains and losses are assumed to be less likely than small gains and losses, as is known to
209 be the case for gambles faced by humans in a wide variety of real-world contexts (Pleskac & Hertwig,
210 2014). $U_S(x, d, R)$ represents the expected reproductive value associated with this stochastic option for
211 an individual in state (x, d) , i.e. the average result of a change in reserves of size R with probability p

212 and zero change in reserves with probability $(1 - p)$. See equation A6 in Appendix A for an
 213 explanation of how we compute this.

214

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

217

$$218 \quad \Psi(x, d, R) = U_S(x, d, R) - U_D(x, d). \quad (2)$$

219

220 Equation 2 essentially represents the expected benefit, in terms of reproductive value, from gambling.

221 When $\Psi > 0$, the forager is expected to be risk seeking, as its change in reproductive value from

222 choosing the risky (stochastic) option is greater than that from choosing the fixed (deterministic)

223 option. Conversely, when $\Psi < 0$, the reproductive value from choosing the fixed option is greater than

224 that from choosing the risky option and therefore we should expect to see risk-averse behaviour.

225

226

Results

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

228 unless stated otherwise.

229

230 Figure 1a shows the predicted risk preference, in terms of the benefit of selecting the risky option over

231 the fixed option (Ψ), for an individual with intermediate reserves ($x = 50$) in each of the four

232 environmental states in a moderately autocorrelated environment ($E = 0.05$), with varying sizes of the

233 stochastic gain/loss (R). Preference values above zero indicate risk-seeking behaviour, whereas those

234 below zero indicate risk aversion. Note that as R changes (movement along the horizontal axis), the

235 probability of the gain/loss (p) also changes (such that $p = d/R$).

236

237 Our model predicts risk-seeking behaviour under very bad ($d = -8$) and moderately good ($d = +2$)

238 conditions and risk aversion under very good ($d = +8$) and moderately bad ($d = -2$) conditions. For an

239 equivalent magnitude of potential gains or losses, this corresponds to a tendency to accept gambles for
240 low-probability gains and high-probability losses, but to decline gambles for high-probability gains
241 and low-probability losses. For example, considering a potential gain or loss of $R = \pm 30$ (see black
242 arrows on Figure 1a), the probability of this outcome under extreme conditions ($d = \pm 8$) is 0.267; the
243 forager should accept the gamble in very bad conditions ($d = -8$) but refuse it in very good conditions
244 ($d = +8$). Under moderate conditions ($d = \pm 2$) the probability drops to 0.067, and the preferences
245 reverse: the forager should refuse the gamble in moderately bad conditions ($d = -2$) but accept it in
246 moderately good conditions ($d = +2$). This predicted pattern of risk attitudes corresponds to the
247 fourfold pattern laid out by Tversky and Kahneman (1992).

248

249 The predicted risk preferences also fit well with the fourfold pattern identified by Markowitz (1952),
250 according to which individuals are risk seeking for small potential gains and large potential losses, but
251 risk averse for large potential gains and small potential losses. Note that the potential gain or loss (R)
252 from the gamble is bigger under extreme conditions ($d = \pm 8$) than it is under moderate conditions ($d =$
253 ± 2), given a fixed probability (p) of that outcome (see white arrows on Figure 1a). Taking $p = 0.2$, for
254 example, the amount at stake in the gamble is $R = \pm 40$ under extreme conditions; the forager should
255 accept the gamble in very bad conditions ($d = -8$) but refuse it in very good conditions ($d = +8$).
256 Under moderate conditions ($d = \pm 2$) the amount at stake drops to $R = \pm 10$, and the preferences
257 reverse: the forager should refuse the gamble in moderately bad conditions ($d = -2$) but accept it in
258 moderately good conditions ($d = +2$).

259

260 The strength of the risk preferences predicted are strongly dependent on the forager's reserve level
261 (Figure 1b). Nevertheless, the fourfold pattern holds over a fairly broad range of reserves (see Figure
262 1b) except for reserve levels close to the upper ($x = L$) or lower ($x = 0$) boundary, where the
263 opportunity to reproduce or the threat of starvation is imminent and taking the gamble may result in
264 the forager hitting that boundary. Whether it is better to be risk seeking or risk averse is determined by
265 the curvature of the reproductive value functions (shown in Figure B1, Appendix B). When $d = +8$
266 and $d = -2$, the value functions are concave (i.e. decreasing in slope) over most of the range of reserve

267 levels, which implies a preference for fixed over variable outcomes, i.e. risk aversion. In contrast,
268 when $d = +2$ and $d = -8$, the value functions are convex (i.e. increasing in slope) over most of the
269 range of reserve levels, which implies a preference for variable over fixed outcomes, i.e. risk-seeking
270 behaviour (see Houston *et al.*, 2014).

271

272 Positive temporal autocorrelation is the critical feature driving this pattern of risk preferences. In an
273 autocorrelated world, the gamble offered to the forager reflects the conditions it is likely to experience
274 in the near future, which affects whether it should accept or decline the gamble. The fourfold pattern
275 begins to break down as autocorrelation becomes weak. For $E > 0.1$ the current environmental state is
276 only weakly predictive of the future environmental state, and as E approaches 0.25 (zero
277 autocorrelation) the shapes of the value functions become essentially equivalent (see Figure B3,
278 Appendix B), so the fourfold pattern disappears (Figure 2). At the opposite extreme, when $E < 0.0002$
279 it is highly unlikely that the environmental state will switch in the near future. Individuals in bad
280 environmental conditions are then very likely to die before conditions improve, whereas those in good
281 conditions are likely to reproduce many times before conditions worsen. In this scenario, risk
282 preferences in a one-off gamble have little effect on reproductive success. Between these extremes of
283 very weak or very strong autocorrelation, the fourfold pattern holds for a wide range of transition
284 probabilities (Figure 3).

285

286 Given a suitable level of positive autocorrelation ($0.0002 < E < 0.1$), the fourfold pattern is robust to
287 changes in the other parameter values (see final column of Table 2). For example, the same pattern of
288 risk preferences is observed when the loss of energetic reserves at reproduction, c , is increased from
289 10 to 70 energetic units (results not shown). Raising background mortality increases the preference for
290 risk across all environmental states (see Figure B6, Appendix B), but the fourfold pattern is preserved
291 until background mortality exceeds 1 in 1000 per time step (with other parameters kept at their default
292 values). As the best and worst environmental states become more extreme, the risk preferences
293 diverge (Figure B7, Appendix B), strengthening the fourfold pattern. Provided that the d values for
294 the four environmental states remain symmetric around zero, those values can be modified

295 extensively before the pattern is lost. For example, a similar fourfold pattern is observed when the
296 environmental states are $d = [-9, -8, +8, +9]$, $d = [-2, -1, +1, +2]$ or $d = [-9, -1, +1, +9]$, although
297 the range of parameter space over which the pattern holds may vary (see Figures B4 and B5,
298 Appendix B). Thus, an individual in environmental state $d = -8$ has a preference for risk when $d = -8$
299 is the worst possible state to be in, but prefers the fixed option when there is a worse state of $d = -9$.
300 This demonstrates that the pattern is fairly insensitive to the magnitude of the background gains and
301 losses, but instead depends on whether there are better or worse states that the environment may
302 switch to in the future.

303

304 We have focussed on a situation in which transitions to all other environmental states are equally
305 likely (i.e. α_{ij} is constant for all $j \neq i$), but the fourfold pattern extends to other patterns of change as
306 long as the transition matrix is centrosymmetric (i.e. the probabilities of moving inwards towards the
307 intermediate states or outwards towards more extreme states are symmetric about the centre). For
308 example, when transitions can only occur between adjacent environmental states (between -8 and -2 ,
309 between -2 and $+2$ and between $+2$ and $+8$), we observe similar effects (Figures B8 and B9,
310 Appendix B). The fourfold pattern is less prevalent when the switching rate is asymmetric across
311 positive and negative environmental states. The pattern is still observed in some situations in which
312 the values of the environmental states (d) are asymmetric but the mean change in energetic reserves
313 across the four states is zero (e.g. $d = [-7 -3 +1 +9]$ and $d = [-8 -2 +4 +6]$), but it typically
314 disappears when the mean change deviates significantly from zero (e.g. $d = [-8 -2 +7 +8]$ and $d = [-8$
315 $-7 +2 +8]$). A similar effect is seen when mean metabolic noise deviates significantly from zero;
316 negative values of μ favour risk seeking in all environmental states, whereas positive values favour
317 risk aversion in all environmental states. In general, ubiquitous risk seeking is observed across all
318 environmental states when the long-term average change in energy reserves is negative, and universal
319 risk aversion is observed when it is positive. Thus even when the forager is in a very good
320 environmental state (e.g. $d = +8$), if it faces a net energetic loss in the long term (i.e. averaging across
321 all states), it should be risk seeking according to our model.

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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 behaviour is adaptive at low reserves whereas risk-averse behaviour 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 scenario, selection can favour 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 & 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 favourable 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 maximise 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

350 are increasing but at a slower rate than in the best environmental state (+8), and when a switch occurs
351 it is more likely that conditions will worsen (probability $2E$) than improve (probability E). The forager
352 therefore needs to take a risk to maximise its chances of reaching the reproductive threshold before
353 conditions change. Conversely, in the moderately bad environmental state (-2 in our default setup),
354 the forager's reserves are decreasing but at a slower rate than in the worst environmental state (-8),
355 and when a switch occurs it is more likely that conditions will improve (probability $2E$) than worsen
356 (probability E). In this situation the forager should avoid taking risks because it can typically afford
357 the smaller deterministic losses (-2) until a switch occurs, before starvation becomes a serious threat.

358

359 Our evolutionary approach to explaining decision making under risk is novel for two reasons. First, in
360 contrast to previous evolutionary approaches, we have determined optimal risk preferences using a
361 rigorous and consistent method based on the concept of reproductive value, which is well established
362 in behavioural ecology (Houston & McNamara, 1999). We made no assumptions about the shape of
363 the value functions – instead, these emerged from the background environment in the model – nor did
364 we assume that subjective estimates of probabilities are biased in any way. This is a powerful feature
365 of our model – a very simple environment that changes stochastically over time can generate complex
366 patterns of risk preferences without the need for specific assumptions about the mechanisms of
367 choice. Second, our work highlights the importance of temporal autocorrelation in the evolution of
368 risk preferences. Most (if not all) environments in the real world, including those in which ancestral
369 humans evolved, show some degree of spatiotemporal heterogeneity and autocorrelation (Halley,
370 1996), so it is reasonable to suggest that these features had some influence on the evolution of our
371 attitudes to risk. By recognising the importance of autocorrelation, evolutionary theory has already
372 provided possible explanations for a number of common cognitive biases that pervade the
373 psychological literature, including contrast effects, optimism and pessimism and violations of
374 regularity (Fawcett *et al.*, 2014). Here we are suggesting that the fourfold pattern of risk preferences
375 may also represent an adaptive response to temporally autocorrelated environments, in which the
376 options available to the decision maker, and the outcomes of its choices, are indicative of future
377 conditions.

378

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

390

391 Our model predicts that risk preferences should depend not just on the environmental conditions, but
392 also on the decision maker's current reserve level. In effect, the forager's current reserve level
393 represents a reference point, modulated by current environmental conditions, from which to assess
394 potential gains or losses. This implies that if our explanation is relevant to human decisions involving
395 money, an individual's risk preference should depend on their current level of wealth (and not just on
396 the range of options presented). We therefore make the prediction that people's risk-based choice
397 patterns should covary with their current socio-economic status. These kinds of data are seldom
398 published in decision-making experiments, but, intriguingly, a growing body of evidence suggests that
399 both current wealth and physiological state may affect risk preference. In the financial literature, for
400 example, initial wealth may influence an individual investor's level of risk aversion (Bosch-
401 Domènech & Silvestre, 2006; Guiso & Paiella, 2010). Metabolic state (specifically hunger levels) has
402 also been shown to have a significant effect on risk preference for monetary gambles, with satiation
403 leading to greater risk aversion (Symmonds, Emmanuel, Drew, Batterham & Dolan, 2010), despite
404 the differing currencies of energy and money.

405

406 The risk preferences predicted by our model also exhibit the property of path dependence, which is a
407 hallmark of prospect theory (Kahneman & Tversky, 1979) and related theories of human decision
408 making. According to this view, decision makers are more concerned with changes in their state than
409 the final state they end up in; that is, ‘the carriers of utility are gains and losses—changes of wealth
410 rather than states of wealth’ (Kahneman, 2003). In our model, the reproductive value of a forager
411 whose reserves are currently at $x = 50$ differs depending on how their reserves changed to get to that
412 state, because this reflects the conditions they are likely to experience in the near future. The
413 trajectory of the forager’s reserves is therefore linked to its reproductive value, which influences
414 subsequent risk-taking behaviour. For example, comparing the lines for $d = -8$ and $d = +8$ in Figure
415 1a, we can see that a forager who previously had energy reserves of $x = 58$ and then lost 8 units
416 should be risk seeking (assuming the environmental state persists at $d = -8$), whereas one whose
417 reserves increased 8 units from $x = 42$ should be risk averse (assuming the environmental state
418 persists at $d = +8$). Thus, providing there is sufficient autocorrelation, attitudes towards risk should be
419 dependent not only on current energy reserves, but also on how energy reserves have changed to get
420 to their current level.

421

422 Although we have identified a potential explanation for the fourfold pattern, we make no special
423 claims that this is necessarily the correct explanation for why humans show such attitudes to risk. As
424 with all scientific studies, there are some limitations. Most notably, the risk preferences elicited in our
425 model are relatively weak; the slopes of the reproductive value functions (Figures B1 and B2,
426 Appendix B) at moderate reserve levels show only a very slight curvature. We deliberately focussed
427 on choices between options with equal expected value (identical means) but different variances, since
428 then the risk preference can be clearly inferred from the reproductive value associated with each
429 option (whereas a substantial difference in expected value generally leads to a preference for the
430 option with the higher expected value). The scenario we have studied therefore may not be able to
431 account for the stronger risk aversion sometimes observed in humans (e.g. paying large premiums and
432 sacrificing considerably more favourable potential gains to avoid risk). Rabin’s (2000) analysis
433 suggests that risk attitudes across different scales exhibited in humans cannot be explained solely by

434 the shape of the value function. Despite this being the primary explanation for risk sensitivity in both
435 economics and behavioural ecology, some authors have noted that there may be a utility of gambling
436 (or certainty) that falls outside this framework (Fishburn, 1980; Diecidue, Schmidt & Wakker, 2004).
437 The possible evolutionary reasons for this have not yet been explored.

438

439 Although the fourfold pattern is associated with human decision making, the risk preferences
440 identified by our model should apply to many other animals adapted to fluctuating environments.
441 Experiments investigating analogous phenomena in non-human animals may therefore prove fruitful.
442 Risk-based preferences have been explored in a variety of species (Kacelnik & El Mouden, 2013) and
443 many of the phenomena originally discussed by Kahneman and Tversky have been observed using
444 token economies in capuchin monkeys (Chen, Lakshminarayanan & Santos 2006; Lakshminarayanan,
445 Chen & Santos, 2011). However, the extensive training necessary for many experiments on non-
446 human animals may make it difficult to assess preferences for gambles with unlikely outcomes. This
447 is because experiments which involve low-value, repeated decisions (rather than occasional or once-
448 in-a-lifetime, high-value decisions) and decisions in which values were learnt from experience (rather
449 than being described) can differ radically in their results (Hertwig & Erev, 2009). For example, using
450 50/50 gambles where the distribution of outcomes is experienced through sampling, Ludvig and
451 colleagues found risk seeking for gains and risk aversion for losses (Ludvig & Spetch, 2011; Ludvig,
452 Madan & Spetch, 2014), which is the opposite pattern to that found for decisions based on description
453 according to prospect theory (Kahneman & Tversky, 1979). Our model does not readily account for
454 this phenomenon. Note, however, that in the learning phase in these experiments, the order of trial
455 types was randomised (Ludvig & Spetch, 2011; Ludvig *et al.*, 2014), and thus there was no temporal
456 autocorrelation. It would be interesting to conduct similar experiments but with options persisting
457 over multiple trials, to see whether the same pattern of risk preferences emerges. More work on risk
458 sensitivity is needed, both theoretically and empirically, to address the realistic kinds of decisions
459 under uncertainty made in a non-stationary world.

460

461

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- 572

573 **FIGURES**

574

575 **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

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

582 **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 ii–iv)
μ	Mean metabolic noise	0	$\mu \approx 0$
σ	Standard deviation 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	$m_B < 0.001$

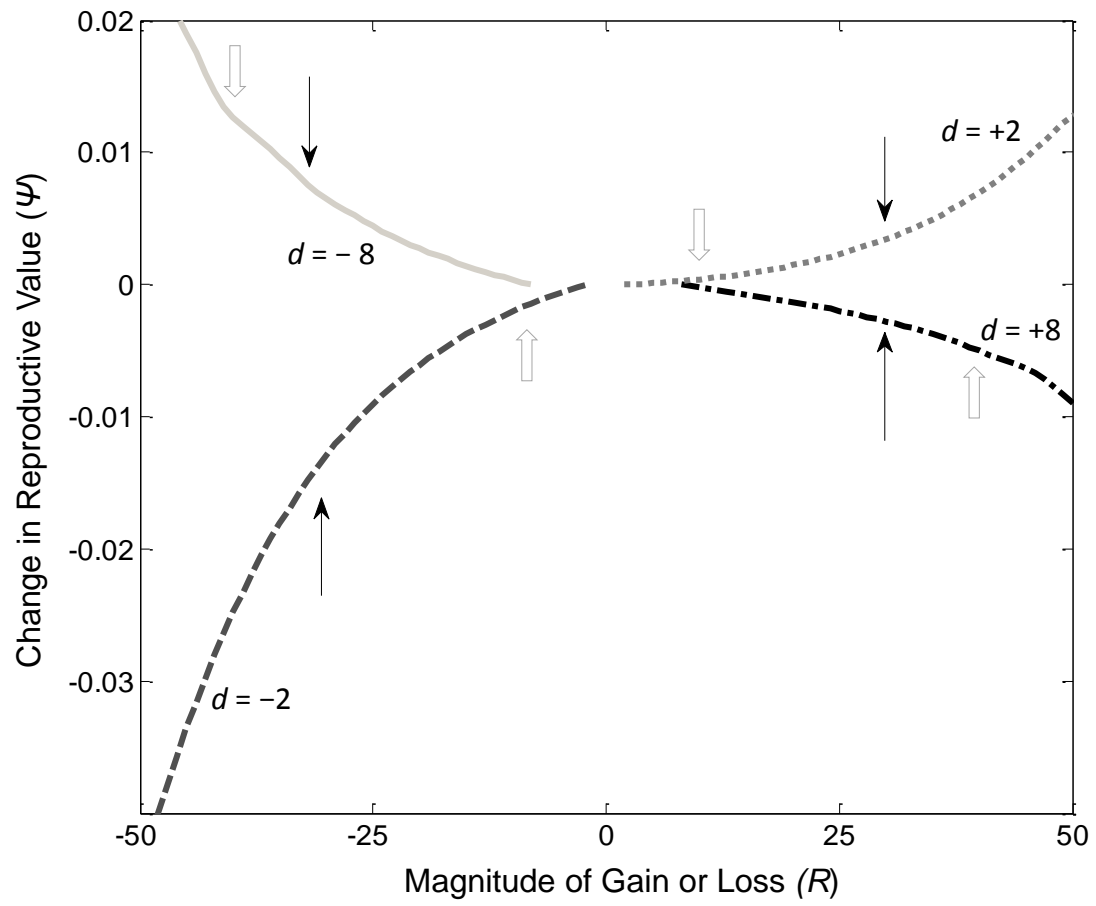
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584

585

586 **Figure 1**

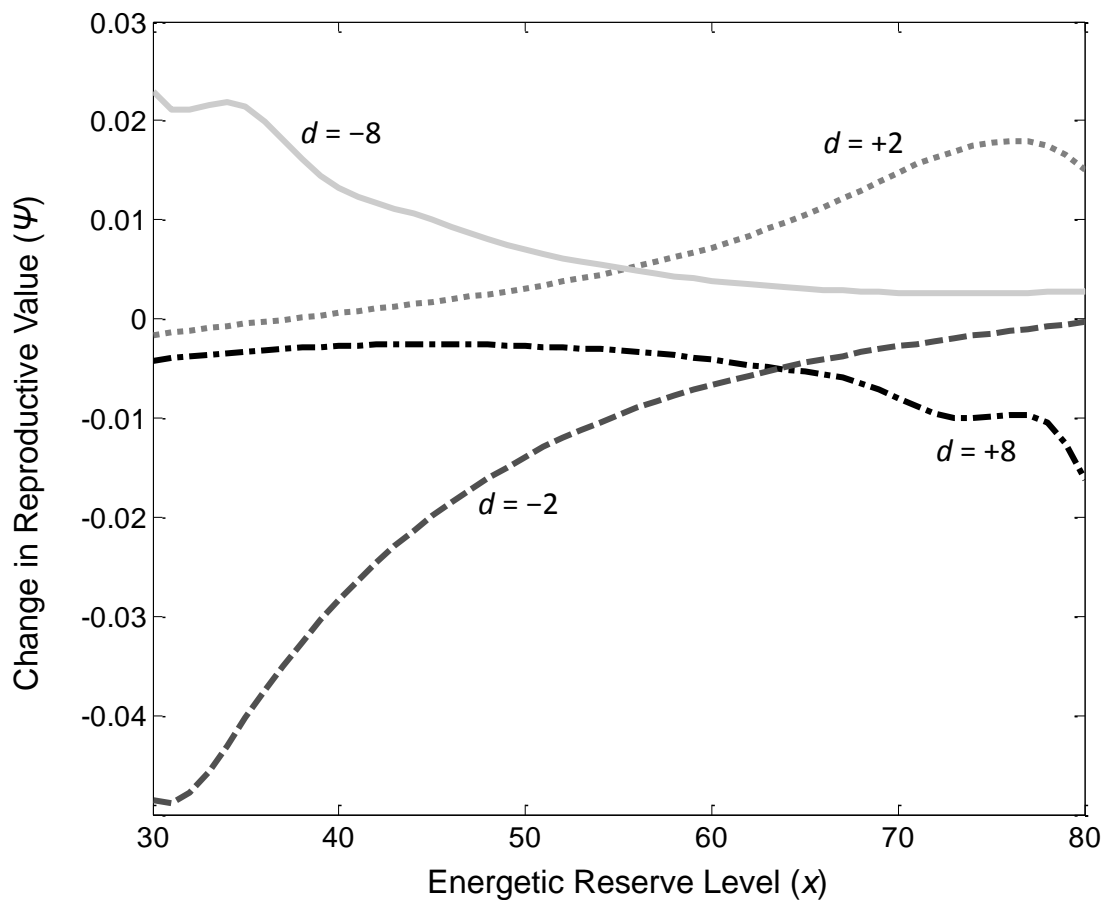
587 (a)



588

589

590 (b)



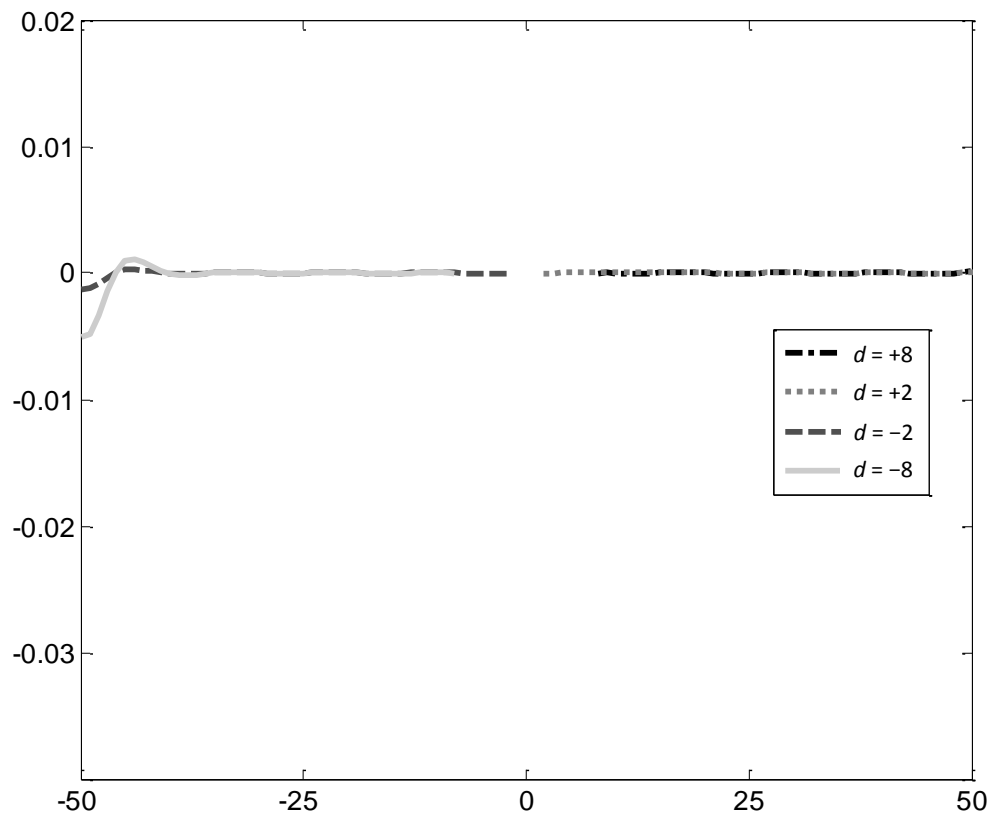
591

592 **Figure 1. (a)** The change in reproductive value (Ψ) from taking a one-off stochastic option instead of
 593 the current background deterministic option d under very good ($d = +8$), moderately good ($d = +2$),
 594 moderately bad ($d = -2$) and very bad ($d = -8$) environmental conditions, for a forager with
 595 intermediate reserves ($x = 50$) in an environment showing moderate positive autocorrelation ($E =$
 596 0.05). Each point on a given line represents a different gamble opportunity (differing in magnitude, R ,
 597 and probability, p , of the outcome). Moving along the line away from 0 increases $|R|$ and decreases p
 598 (holding the expected value equivalent to d). Points above 0 on the vertical axis ($\Psi > 0$) represent a
 599 preference for risk (greater reproductive value associated with taking the stochastic option over the
 600 deterministic option), whereas points below 0 ($\Psi < 0$) represent an aversion to risk. See Table 2 for
 601 parameter values. The black arrows on this figure indicate gambles offering a potential gain or loss of
 602 $R = \pm 30$ with a probability of either $p = 0.267$ (for $d = \pm 8$) or $p = 0.067$ (for $d = \pm 2$). The white arrows

603 indicate gambles offering a potential gain or loss of either $R = \pm 10$ (for $d = \pm 2$) or $R = \pm 40$ (for $d =$
604 ± 8) with a probability of $p = 0.2$.

605 **(b)** The change in reproductive value (Ψ) from taking a one-off stochastic option (with a potential
606 gain or loss of $R = \pm 30$) instead of the current background deterministic option d under very good ($d =$
607 $+8$), moderately good ($d = +2$), moderately bad ($d = -2$) and very bad ($d = -8$) environmental
608 conditions, for varying levels of energy reserves in an environment showing moderate positive
609 autocorrelation ($E=0.05$).

610

611 **Figure 2**

612

613

614

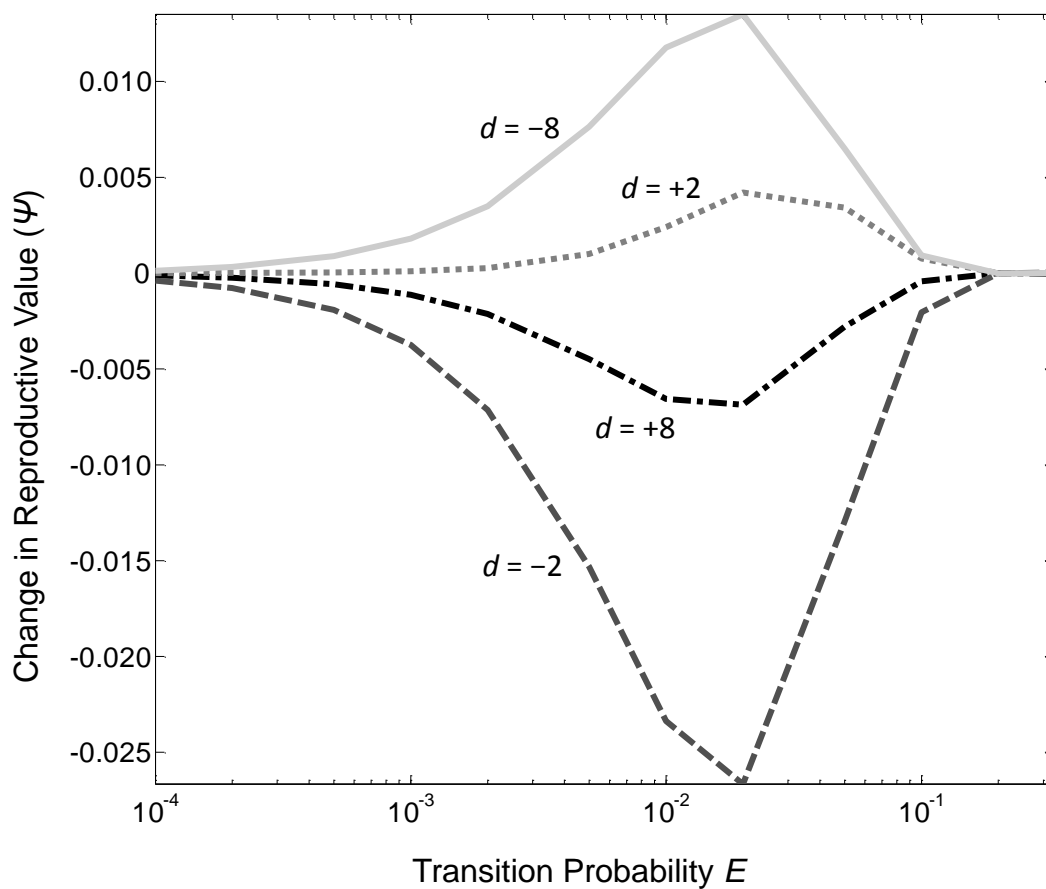
615 **Figure 2.** The change in reproductive value (Ψ) from taking a one-off stochastic option instead of the
616 current background deterministic option d under very good ($d = +8$), moderately good ($d = +2$),
617 moderately bad ($d = -2$) and very bad ($d = -8$) environmental conditions, for a forager with
618 intermediate reserves ($x = 50$) in an environment showing zero autocorrelation ($E = 0.25$). See Figure
619 1 for more details.

620

621

622

623

624 **Figure 3**

625

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

631

Appendix A

Technical Details of the Model

632

633

634

Metabolic Noise

636 In addition to the background gain or loss of energy, d , which is set by the current environmental
 637 state, we assume a small gain or loss, y , in each time step that is independent of the environmental
 638 state or the forager's behaviour (so the overall change in reserves in one time step is $d + y$). This could
 639 be due to a variable metabolic expenditure or unspecified gains and losses from other sources not
 640 considered. y takes integer values between $-h$ and h , drawn from a truncated pseudo-normal
 641 distribution with mean μ and standard deviation σ and then renormalized so that the cumulative
 642 distribution function sums to 1. The probability of a particular value of y is thus

643

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

644

Value Calculations

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

654

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

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

657

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

659
$$U(0, d_i, t) = 0. \quad (\text{A3})$$

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

661
$$U(x, d_i, t) = \left(Z + \sum_{y=-h}^h \left(H(y) \times \sum_{j=1}^k \alpha_{ij} \times U(x - c + y, d_j, t + 1) \right) \right) \times (1 - m_B) \quad \text{for } x \geq L \quad (\text{A4})$$

662 Again there is a $1 - m_B$ chance that the forager survives the time step. Given this, it produces Z 663 offspring and its reserves decrease by c , which represents the energetic cost of reproduction. The664 forager also experiences metabolic noise y and the environmental state changes from d_i to d_j with665 probability α_{ij} .

666

667 We do not assume any fixed time horizon, but the forager will eventually die at some point (either

668 from the background mortality m_B or long run of bad conditions) and so total lifetime reproductive

669 success is finite. To calculate this, we iterate backwards through time using equations A2–A4.

670 Initially, when there are relatively few time steps before the end of the modelled period, the forager's

671 reproductive value (as a function of its energy reserves and the environmental state) depends on how

672 much time is left. However, as we continue iterating backwards, the probability of reaching this end

673 point becomes vanishingly small and the reproductive value converges to a stable value $U_D(x, d_i)$ that

674 is independent of time:

675
$$U_D(x, d_i) = \lim_{t \rightarrow -\infty} U(x, d_i, t). \quad (\text{A5})$$

676 These calculations result in a look-up table that lays out the reproductive value for every possible

677 combination of x and d .

678

679 $U_S(x, d_i, R)$ represents the expected reproductive value associated with the stochastic (risky) option, i.e.680 a change in reserves R with probability p and a change of 0 with probability $1 - p$, where $p = d_i/R$. The

681 forager's initial state is (x, d_i) . As before, the forager experiences metabolic noise y and the
 682 environmental state variable changes to d_j with the same transition probabilities:

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

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

685

686

Appendix B

687

Supplementary Figures

688

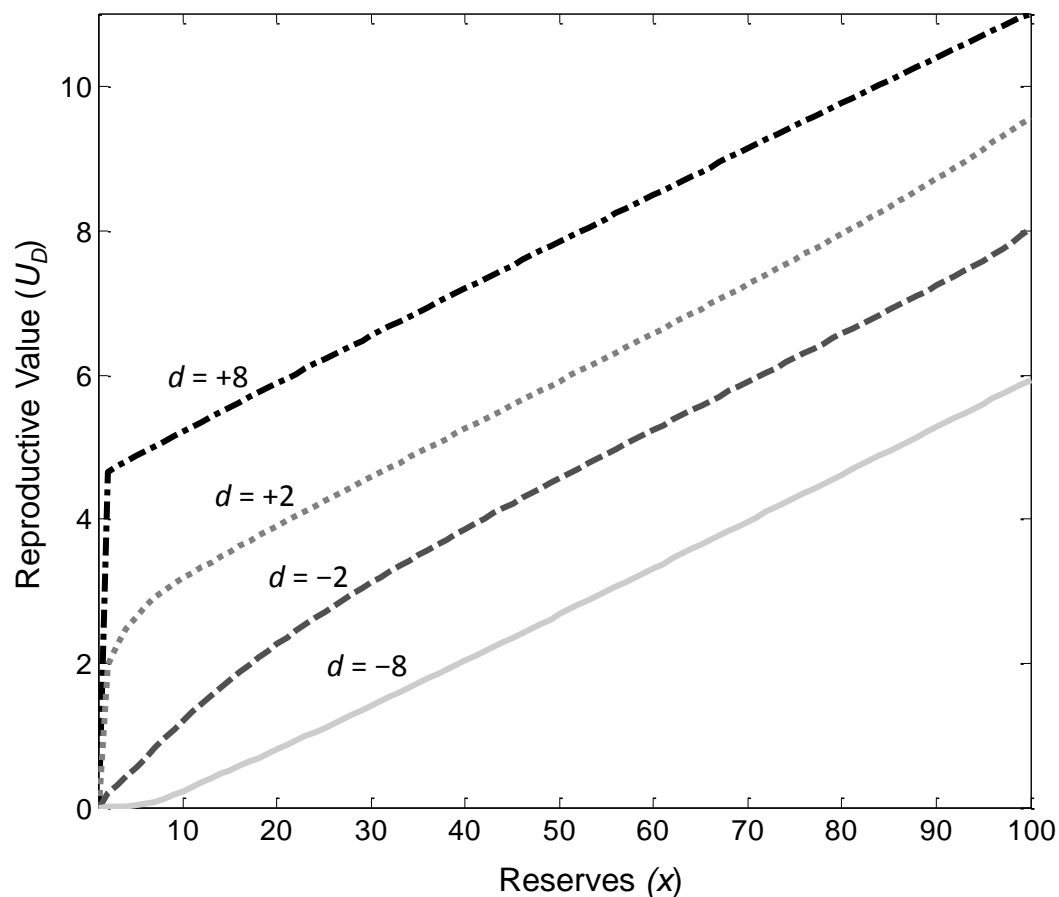
689 (i) Additional Results for Default Setup

690 Relating to Figure 1 in the main text, the corresponding value functions and second derivatives of the

691 value functions are displayed below.

692

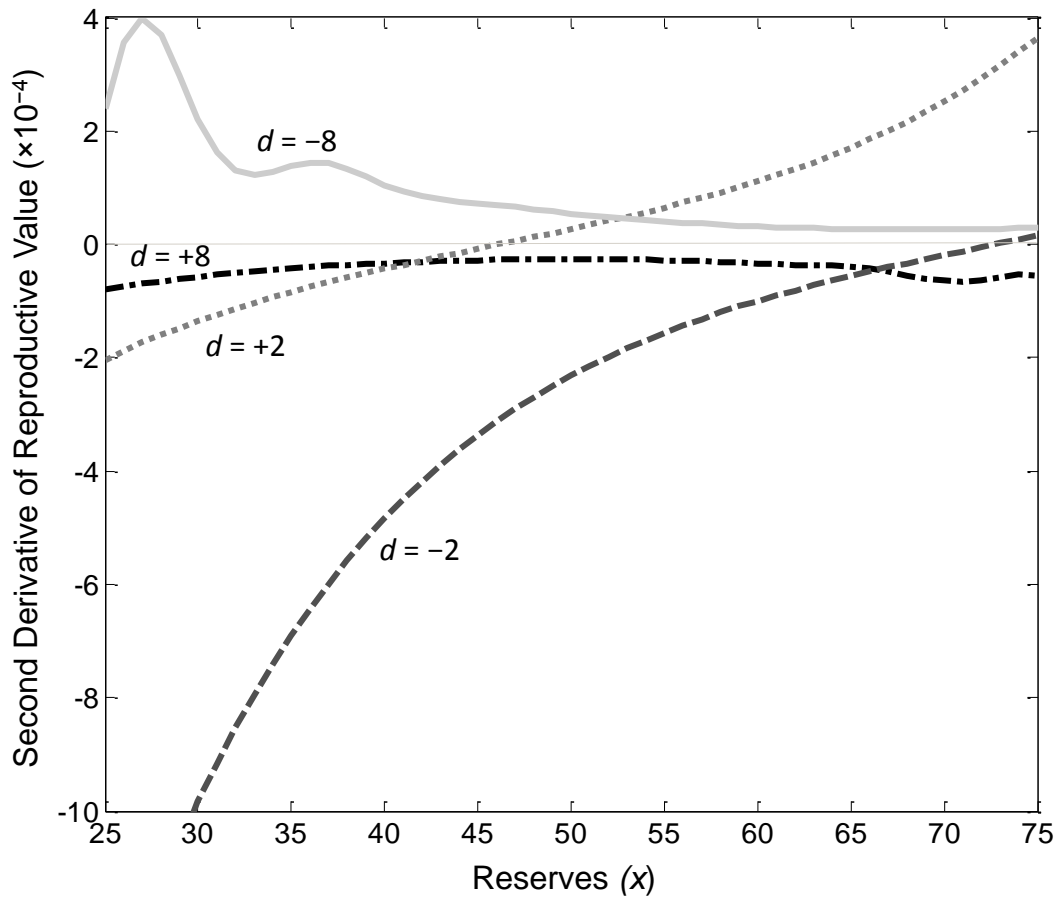
693 Figure B1



694

695 Figure B1. Reproductive value (expected future reproductive success) with respect to energy reserves

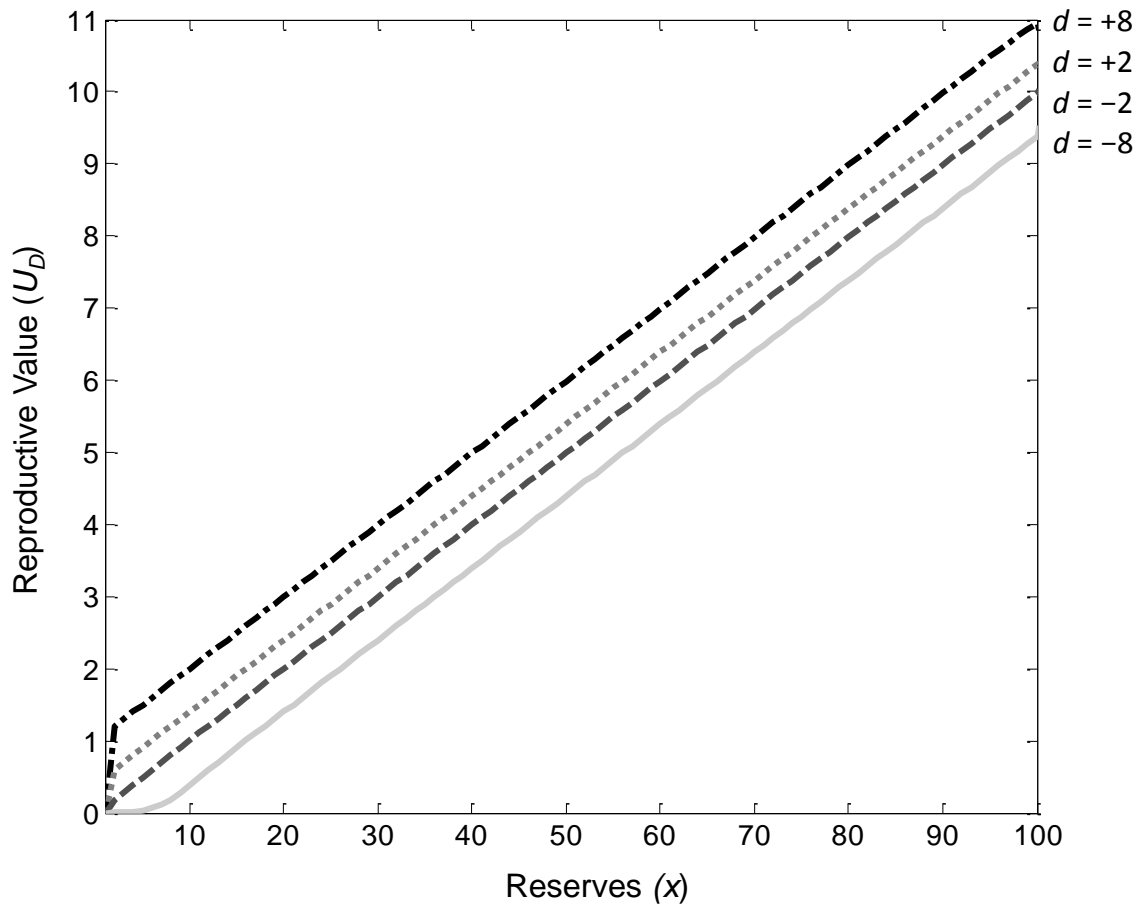
696 for a forager in very good ($d = +8$), moderately good ($d = +2$), moderately bad ($d = -2$) or very bad (d 697 $= -8$) environmental conditions, in an environment showing moderate positive autocorrelation ($E =$ 698 0.05). Parameter values are the same as in Figure 1a in the main text.

699 **Figure B2**

700

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

707

708 **Figure B3**

709

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

714

715

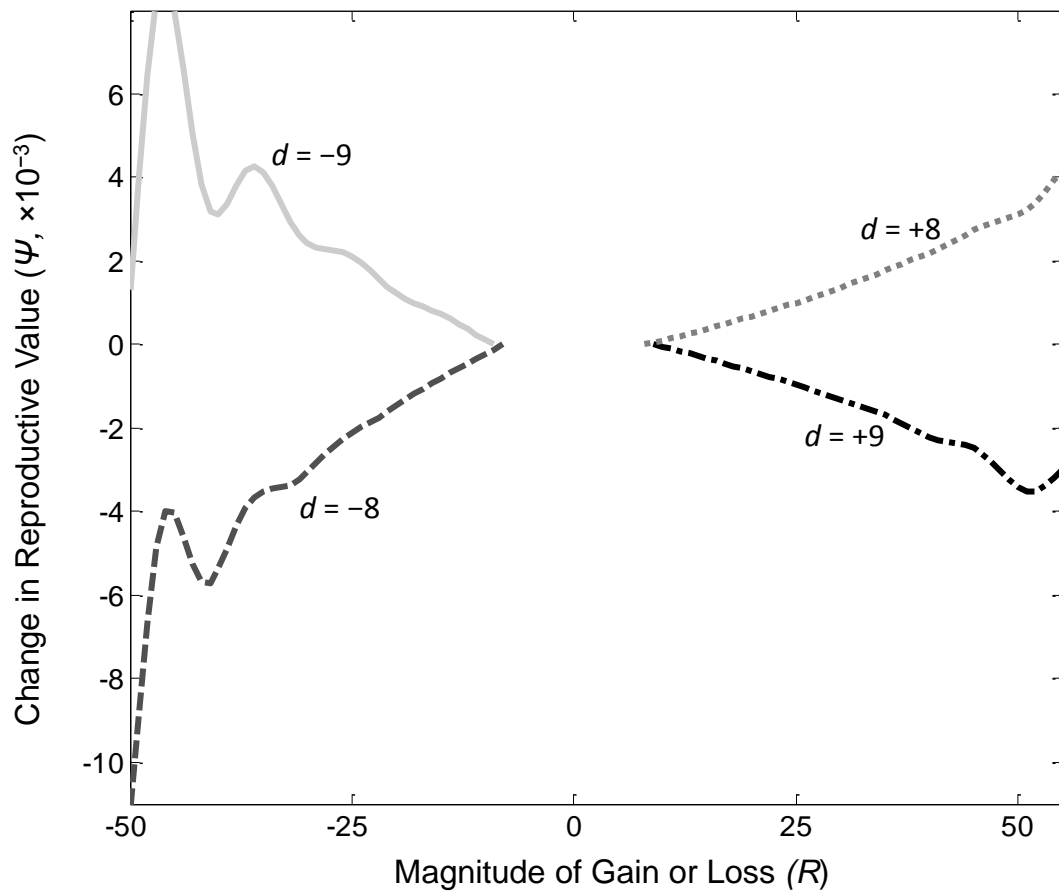
716 (ii) Changes to Environmental State d

717 By using different sets of d values for the four environmental states, we can see that the appearance of
 718 the fourfold pattern is predominantly dependent on the relative ordering of the d values, rather than
 719 their magnitudes. For example, an individual in state $d = -8$ has a preference for risk when $d = -8$ is
 720 the worst possible state to be in, but chooses the safe option when there is an even worse state of $d =$

721 -9 (compare panel B4 below with Figure 1a from the main text). All other parameter values are the
722 default values from Table 2, although the patterns of risk preference for B4 and B5 are stable over a
723 much wider parameter range.

724

725 **Figure B4.** Change in reproductive success when $d = [-9, -8, +8, +9]$



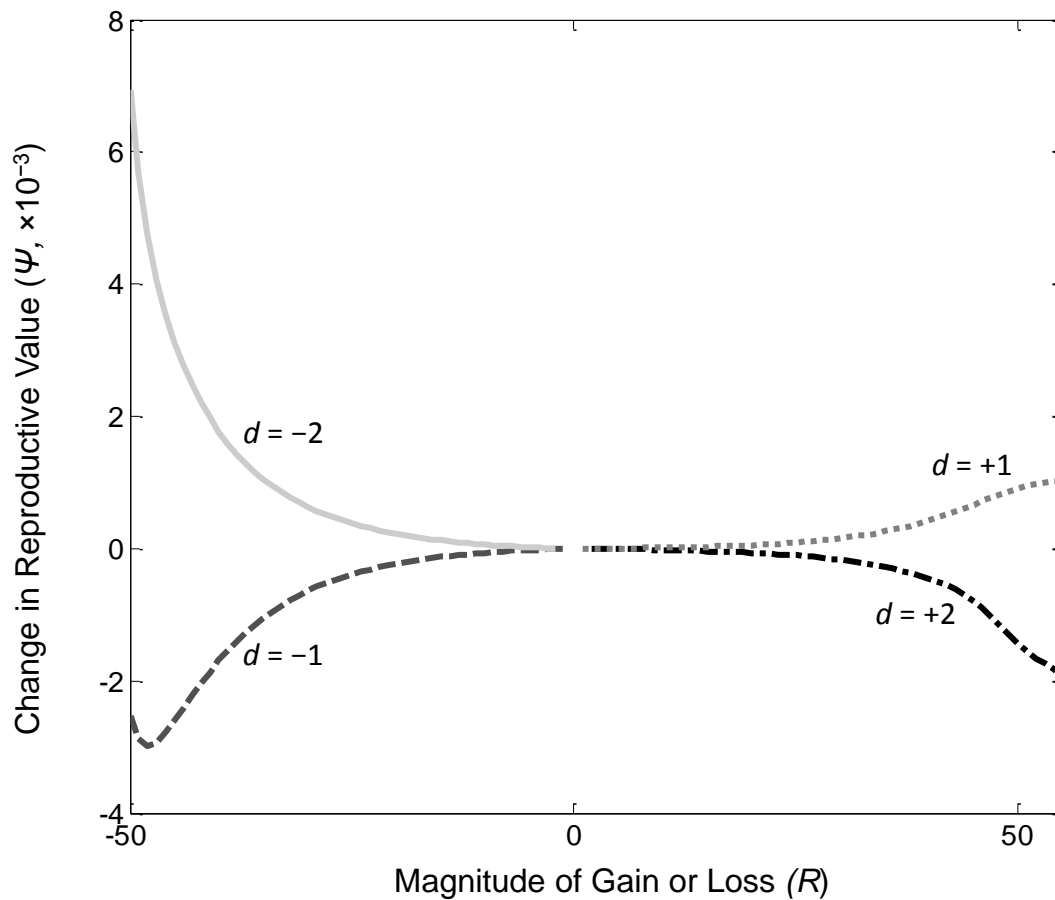
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730 **Figure B5.** Change in reproductive success when $d = [-2, -1, +1, +2]$



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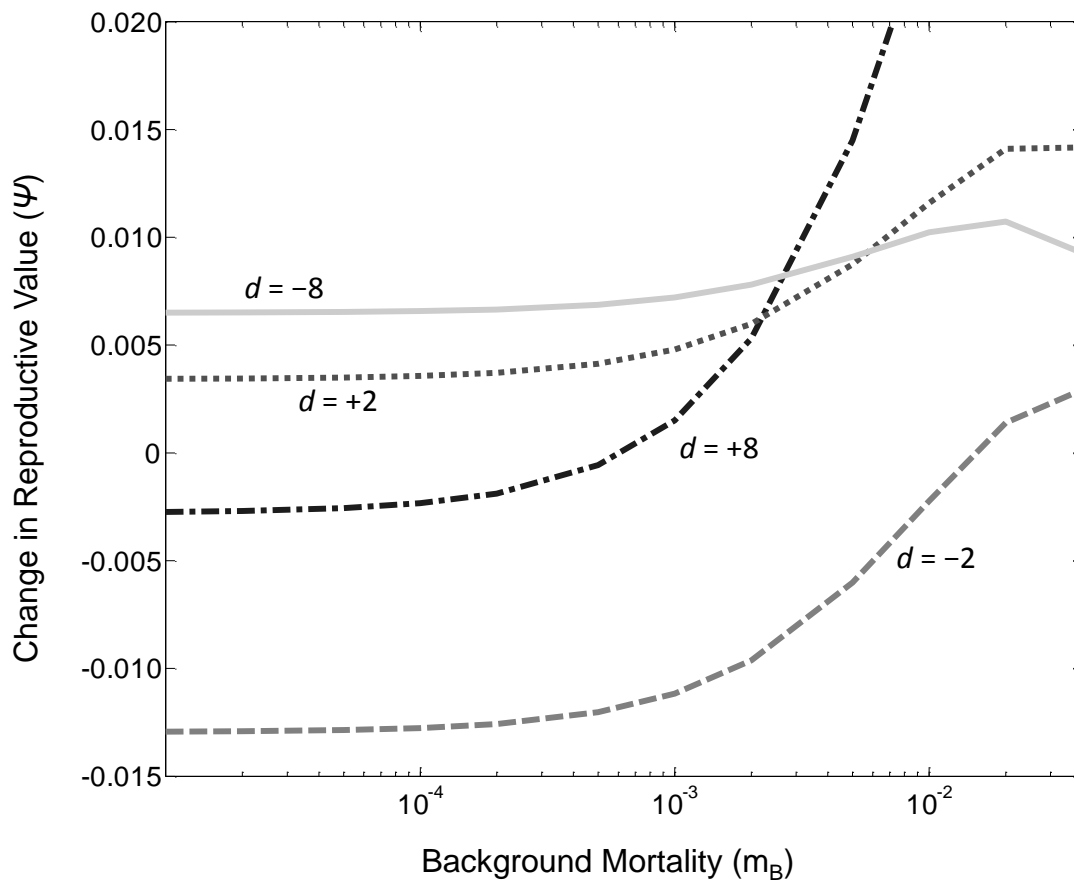
733

734 **(iii) Additional Results across Parameter Space**

735 The ‘fourfold pattern’ has been found robustly across large areas of parameter space. Besides the
 736 transition probability (Figure 3, main text), the effect is also shown across background mortalities
 737 (m_B) (Figure B6) and the size of reserve changes in extreme environments (d_1 and d_4) (Figure B7).

738 The figures below show the change in reproductive value (Ψ) from taking a one-off stochastic option
 739 (with a potential gain or loss of $R = \pm 30$) instead of the current background deterministic option d
 740 under very good (d_4), moderately good (d_3), moderately bad (d_2) and very bad (d_1) environmental
 741 conditions, for a forager with intermediate reserves ($x = 50$). All other parameters are held constant at
 742 their default values (see Table 2).

743

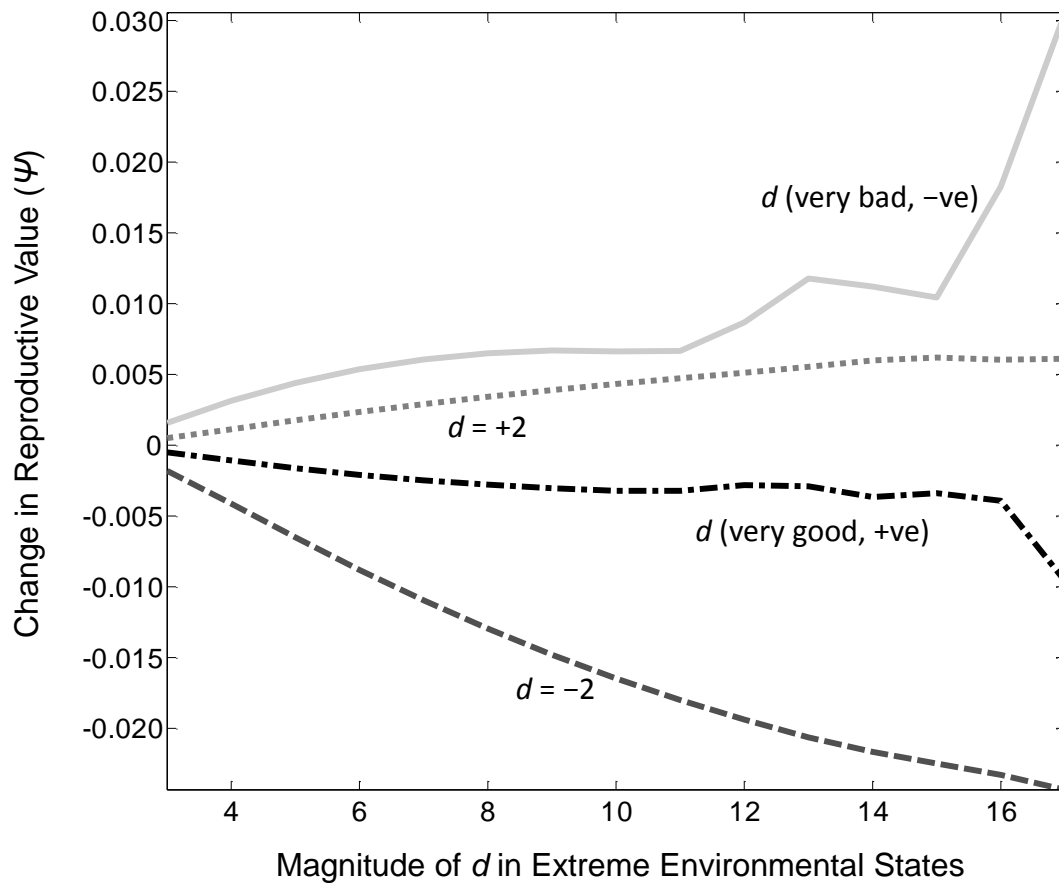
744 **Figure B6.** The effect of changing background mortality (m_B) on the change in reproductive success745 for taking the one-off stochastic option ($R = \pm 30$)

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



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754 (iv) Modifications to the Transition Matrix

755 The same 'fourfold pattern' effects can also be observed in less homogeneous stochastic
 756 environments, where the environment only switches between adjacent states and the intermediate
 757 states (e.g. $d = +2$ or $d = -2$) are more common than the more extreme states ($d = +8$ or $d = -8$), as
 758 represented by the following transition matrix:

759

$$760 \quad \mathbf{D} = \begin{bmatrix} 1-C & C & 0 & 0 \\ B & 1-(A+B) & A & 0 \\ 0 & A & 1-(A+B) & B \\ 0 & 0 & C & 1-C \end{bmatrix}.$$

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

$$762 \quad \mathbf{D} = \begin{bmatrix} 0.8 & 0.2 & 0 & 0 \\ 0.05 & 0.85 & 0.1 & 0 \\ 0 & 0.1 & 0.85 & 0.05 \\ 0 & 0 & 0.2 & 0.8 \end{bmatrix}.$$

763 The effects of modifying the transition probability from intermediate to extreme environmental states

764 (B) in these more complex autocorrelated environments can be seen below. The default parameters are

765 $A = 0.1$ and $C = 0.2$.

766

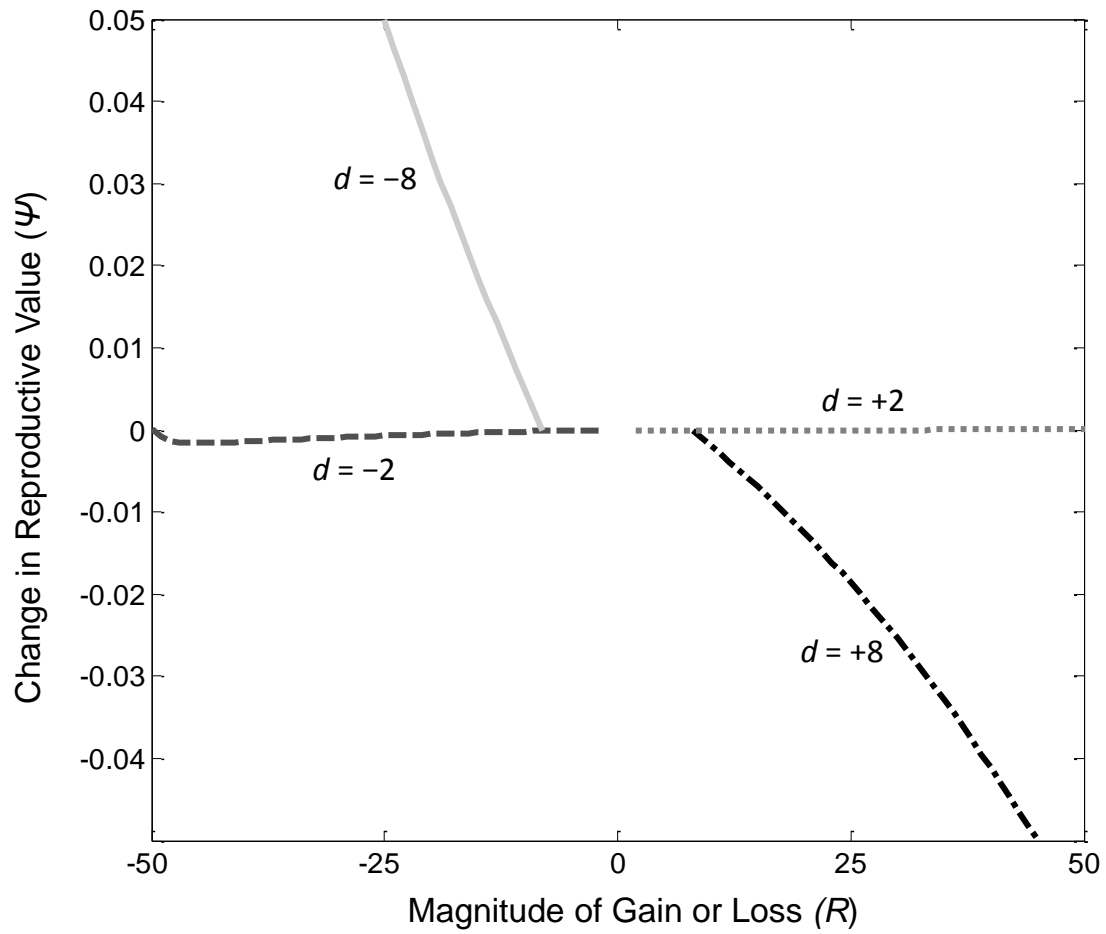
767 **Variations in transition probability from intermediate to extreme environmental states**

768 **(parameter B)**

769

770 **Figure B8.** Transition probability $B = 0.001$

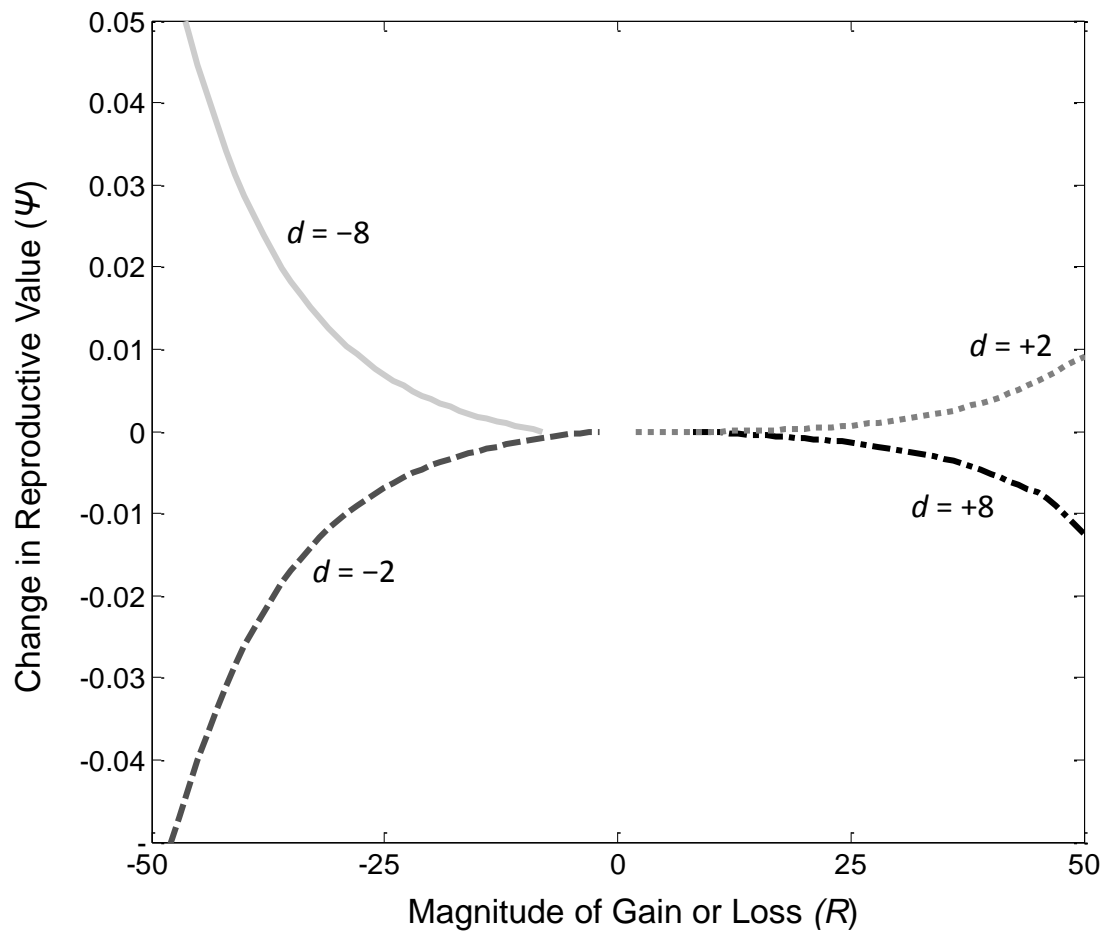
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775 **Figure B9.** Transition probability $B = 0.1$ 

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777

778 These figures show the change in reproductive value (Ψ) from taking a one-off stochastic option
 779 instead of the current background deterministic option d under very good ($d = +8$), moderately good
 780 ($d = +2$), moderately bad ($d = -2$) and very bad ($d = -8$) environmental conditions, for a forager with
 781 intermediate reserves ($x = 50$) in an environment showing positive autocorrelation but in which
 782 changes are only possible between adjacent environmental states (see modified transition matrix
 783 above). The fourfold pattern of risk preferences holds across a very large range of transition
 784 probabilities from the intermediate environmental states to the adjacent extreme environmental states,
 785 $B = 0.001$ (Figure B8) and $B = 0.1$ (Figure B9).

786