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7   Risk Attitudes in a Changing Environment:

8   An Evolutionary Model of the Fourfold Pattern of Risk Preferences

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26

27   Abstract

28   A striking feature of human decision making is the fourfold pattern of risk attitudes, involving risk-

29   averse behaviour in situations of unlikely losses and likely gains, but risk-seeking behaviour in

30   response to likely losses and unlikely gains. Current theories to explain this pattern assume particular

31   psychological processes to reproduce empirical observations, but do not address whether it is adaptive

32   for the decision maker to respond to risk in this way. Here, drawing on insights from behavioural

33   ecology, we build an evolutionary model of risk-sensitive behaviour, to investigate whether particular

34   types of environmental conditions could favour a fourfold pattern of risk attitudes. We consider an

35   individual foraging in a changing environment, where energy is needed to prevent starvation and build

36   up reserves for reproduction. The outcome, in terms of reproductive value (a rigorous measure of

37   evolutionary success), of a one-off choice between a risky and a safe gain, or between a risky and a

38   safe loss, determines the risk-sensitive behaviour we should expect to see in this environment. Our

39   results show that the fourfold pattern of risk attitudes may be adaptive in an environment in which

40   conditions vary stochastically but are autocorrelated in time. In such an environment the current

41   options provide information about the likely environmental conditions in the future, which affect the

42   optimal pattern of risk sensitivity. Our model predicts that risk preferences should be both path

43   dependent and affected by the decision maker's current state.

44

45   *Keywords:* risk proneness, risk aversion, cumulative prospect theory, reproductive success,

46   temporal autocorrelation

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Risk Attitudes in a Changing Environment:

An Evolutionary Model of the Fourfold Pattern of Risk Preferences

53

Background

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 (Blavatskyy, 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 $x = 0,1,2,\ldots$). 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 α_{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
$$\mathbf{D} = \begin{array}{c} \\ d_i = -8 \\ d_i = -2 \\ d_i = +2 \\ d_i = +8 \end{array} \begin{array}{cccc} d_j = -8 & d_j = -2 & d_j = +2 & d_j = +8 \\ \begin{bmatrix} 1-3E & E & E & E \\ E & 1-3E & E & E \\ E & E & 1-3E & E \\ E & E & E & 1-3E \end{bmatrix} \end{array} \tag{1}$$

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                        $$\Psi(x,d,R) = U_S(x,d,R) - U_D(x,d).$$ (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 $R = \pm30$ (see black

242   arrows on Figure 1a), the probability of this outcome under extreme conditions ($d = \pm8$) 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 ($d = \pm2$) 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 ($d = \pm8$) than it is under moderate conditions ($d =

253   \pm2$), 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 $R = \pm40$ 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 ($d = \pm2$) the amount at stake drops to $R = \pm10$, 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.

322

Discussion

323

324   Previous attempts to explain human risk preferences from an evolutionary perspective (e.g. Aktipis &

325   Kurzban, 2004; McDermott et al., 2008) have claimed that risk-seeking behaviour is adaptive at low

326   reserves whereas risk-averse behaviour is adaptive at high reserves. Our model demonstrates that in a

327   stochastic foraging environment in which conditions are autocorrelated over time, risk preferences

328   may be much more complex. Using a rigorous evolutionary approach based on reproductive value, we

329   have shown that optimal risk preferences can be strongly influenced by the options currently

330   available, because these provide information about the likely future conditions and hence the need to

331   take risks (see Fawcett *et al.* 2014). Under this scenario, selection can favour a fourfold pattern of risk

332   preferences. Our evolutionary model predicts a preference for fair gambles over certainty for unlikely

333   gains and likely losses, but an aversion to gambling for likely gains and unlikely losses, as described

334   by Tversky & Kahneman (1992). It also predicts the stake-dependent fourfold pattern described by

335   Markowitz (1952), namely risk aversion for gambles involving large gains or small losses and risk

336   seeking for gambles involving small gains or large losses. To the best of our knowledge, our model

337   provides the first functional (adaptive) explanation for both of these reported patterns of decision

338   making.

339

340   To understand why the fourfold pattern is adaptive in our model, it is important to consider how

341   environmental conditions now and in the near future affect the probabilities of reaching the

342   reproductive threshold and avoiding the starvation boundary. When environmental conditions are very

343   good (+8 in our default setup), the forager shows risk aversion. Here the forager is in the most

344   favourable situation and is likely to reach the reproductive threshold before conditions change,

345   without having to take risks. Under very bad environmental conditions (−8 in our default setup), in

346   contrast, the forager should be risk seeking. This is the environmental state most likely to deplete the

347   forager's reserves to the starvation boundary; to maximise its chances of surviving until conditions

348   improve, it typically pays the forager to gamble. For the intermediate states, however, the preferences

349   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

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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	$m_B < 0.001$

583

584

585

586   **Figure 1**

587   (a)
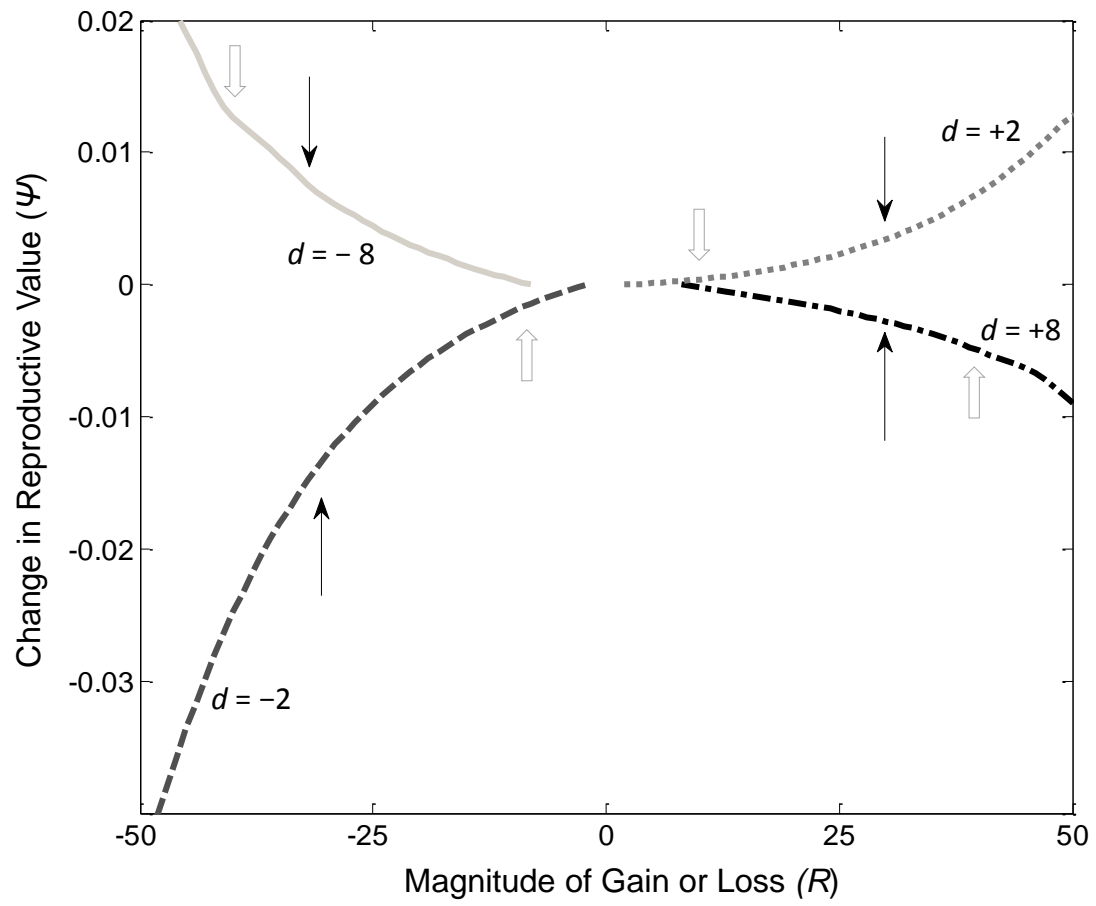
588

589

590   (b)
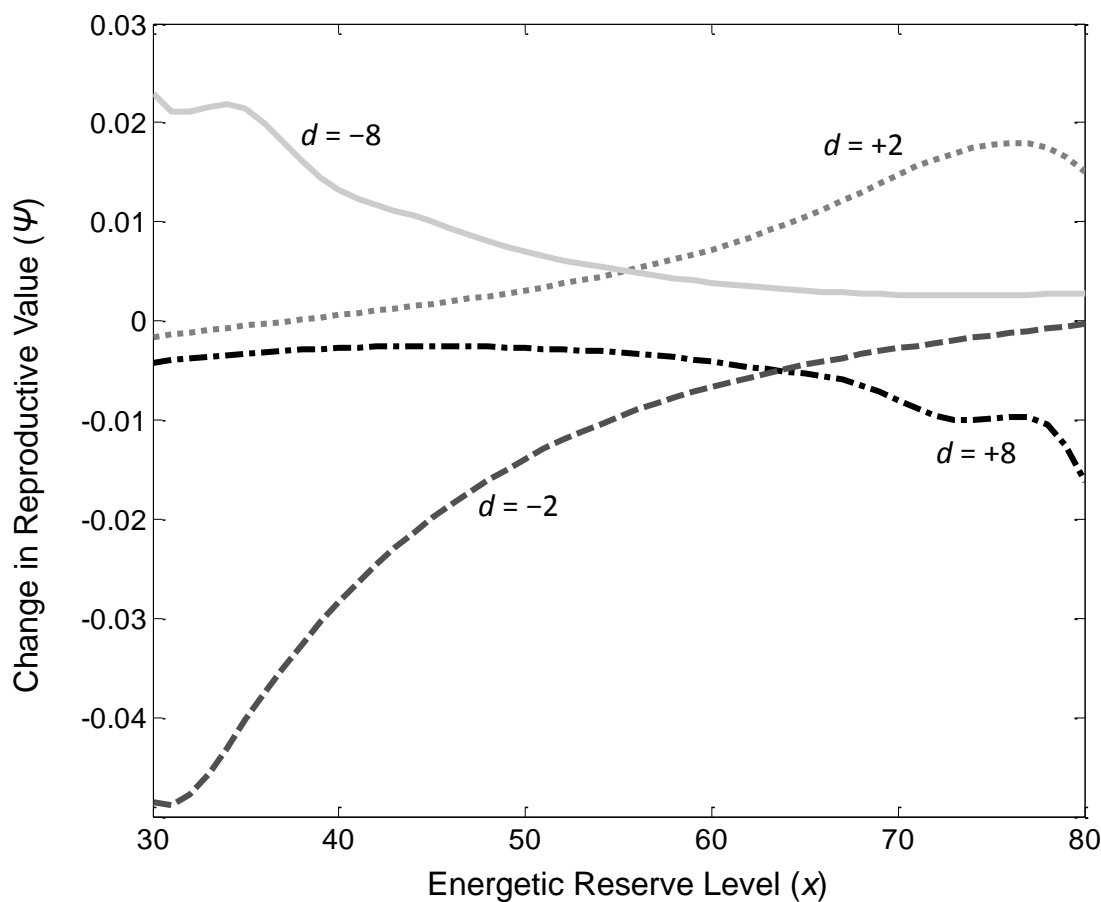
591

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 (Ψ > 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 (Ψ < 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 $R = \pm10$ (for $d = \pm2$) 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 $R = \pm30$) 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**
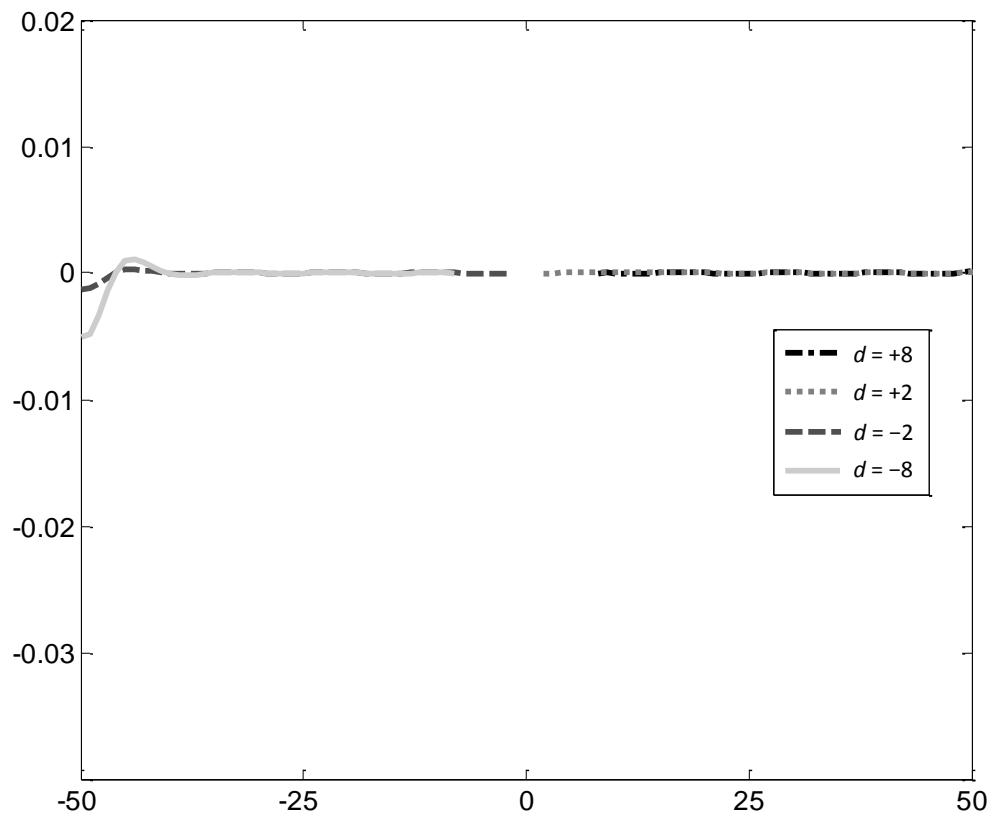
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613

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**
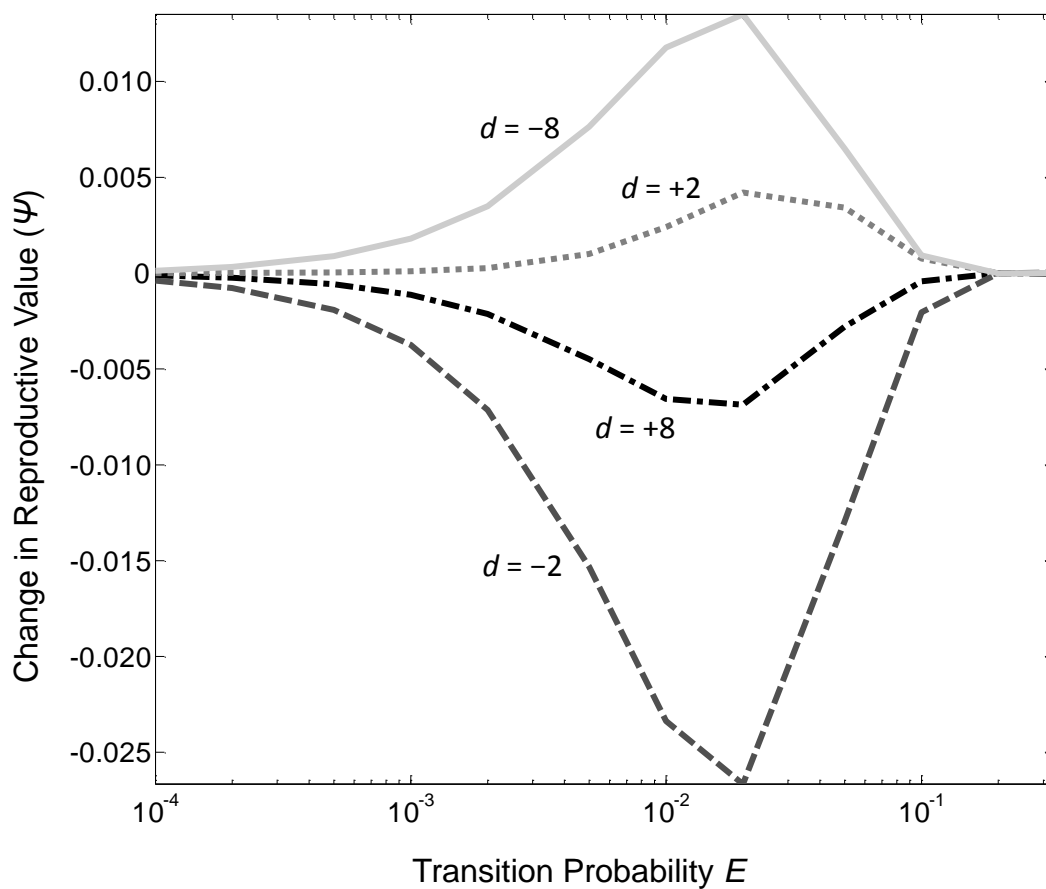
625

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

632   **Appendix A**

633   **Technical Details of the Model**

634

635   **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     $$H(y) = \frac{\exp\left(-(y-\mu)^2/2\sigma^2\right)}{\sum\limits_{y=-h}^{h}\exp\left(-(y-\mu)^2/2\sigma^2\right)}. \qquad\qquad \text{(A1)}$$

644

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

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
$$U(0, d_i, t) = 0.$$
(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. The

664 forager also experiences metabolic noise y and the environmental state changes from d_i to d_j with

665 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
$$U_D(x, d_i) = \lim_{t \to -\infty} U(x, d_i, t).$$
(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:

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

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

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**
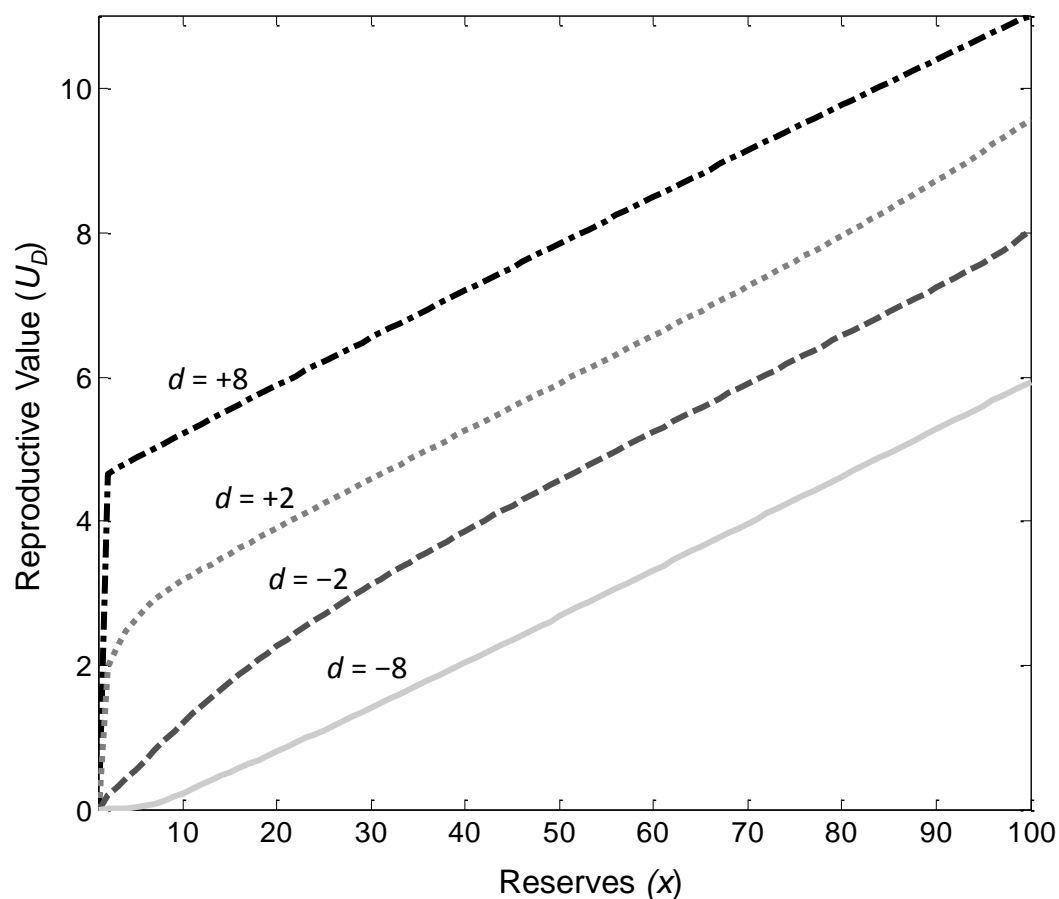
694

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**
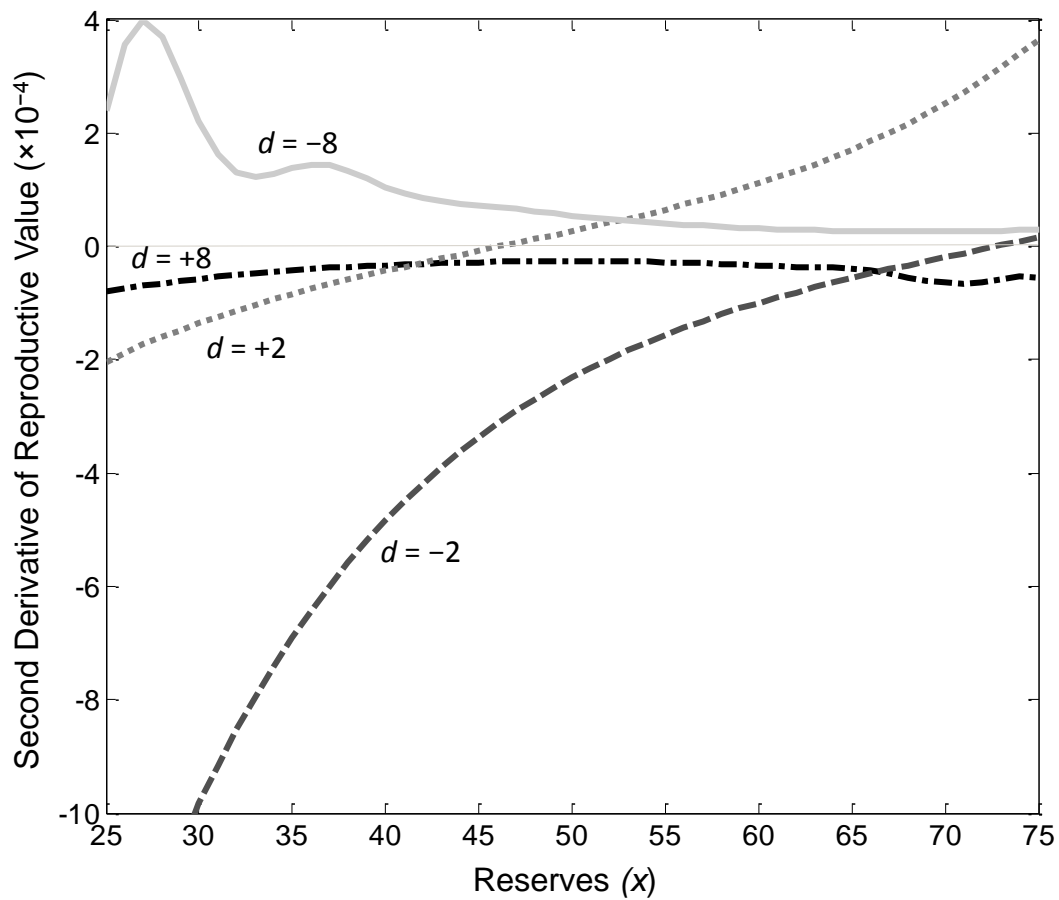
700

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**
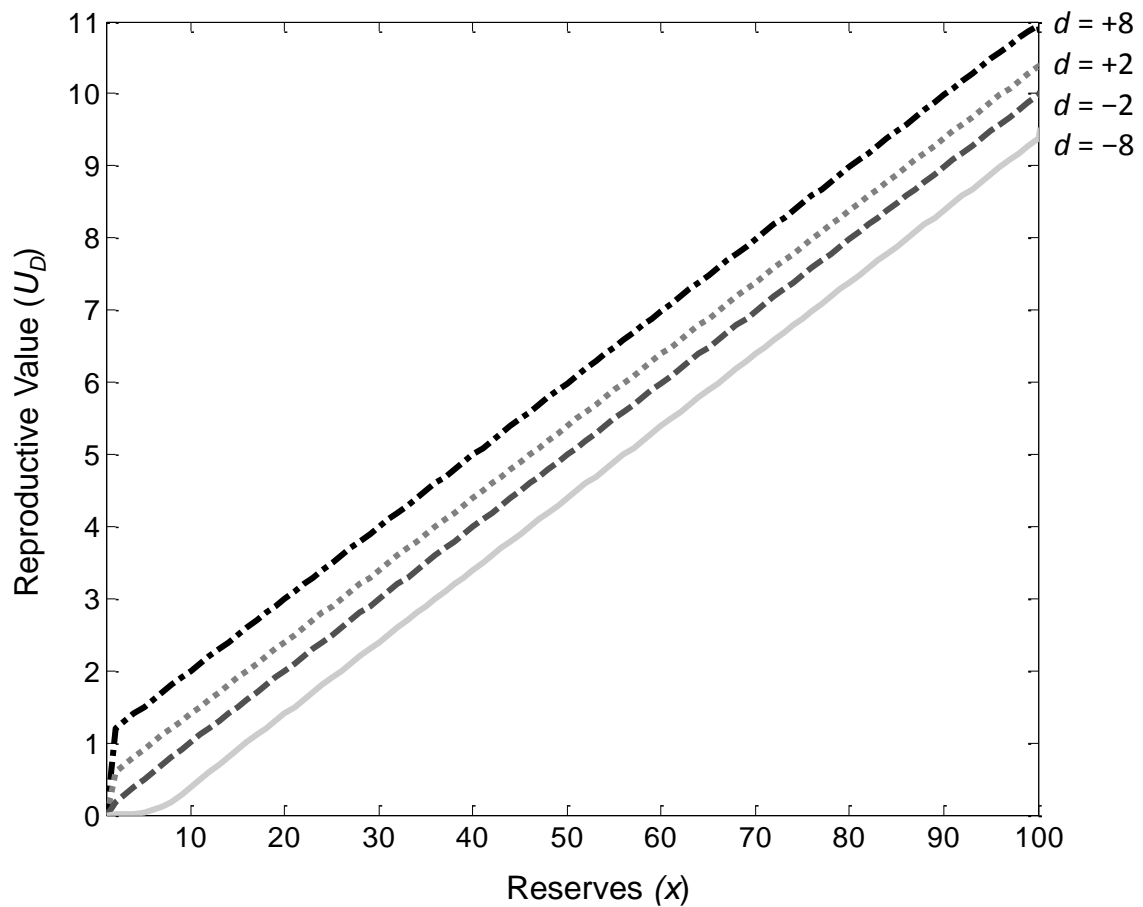
709

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 $d = [-9, -8, +8, +9]$
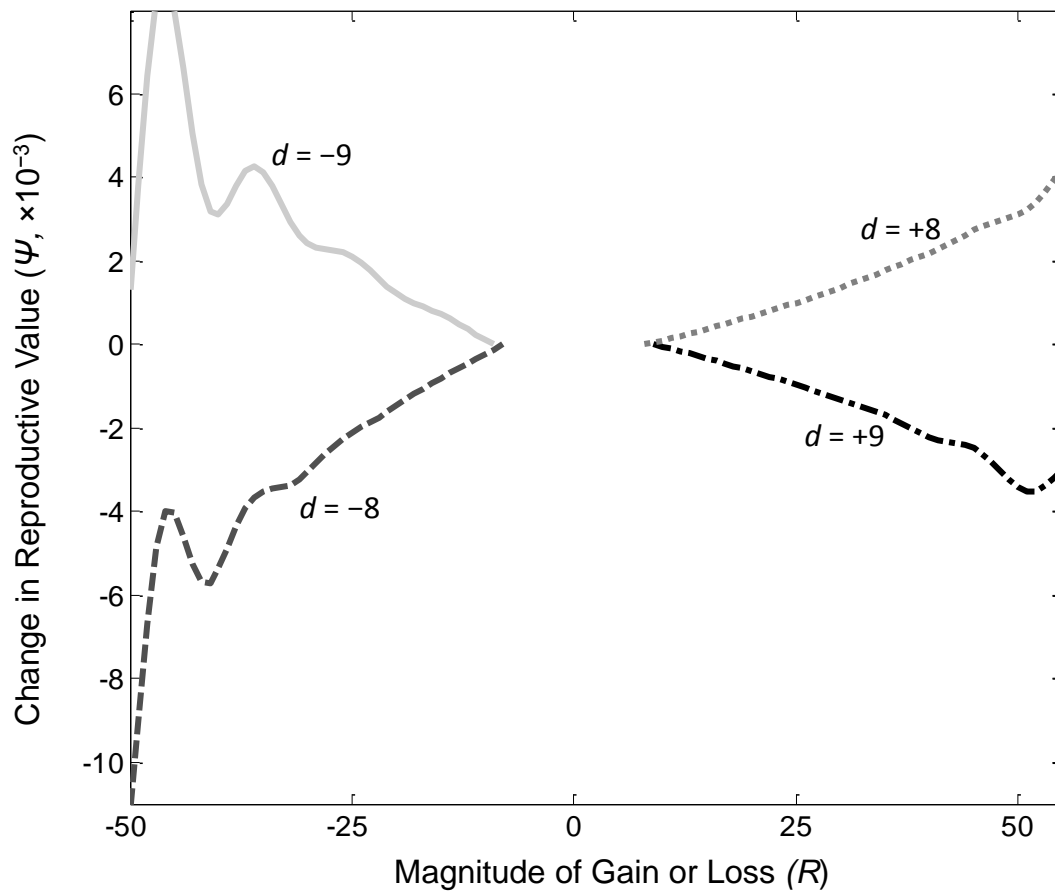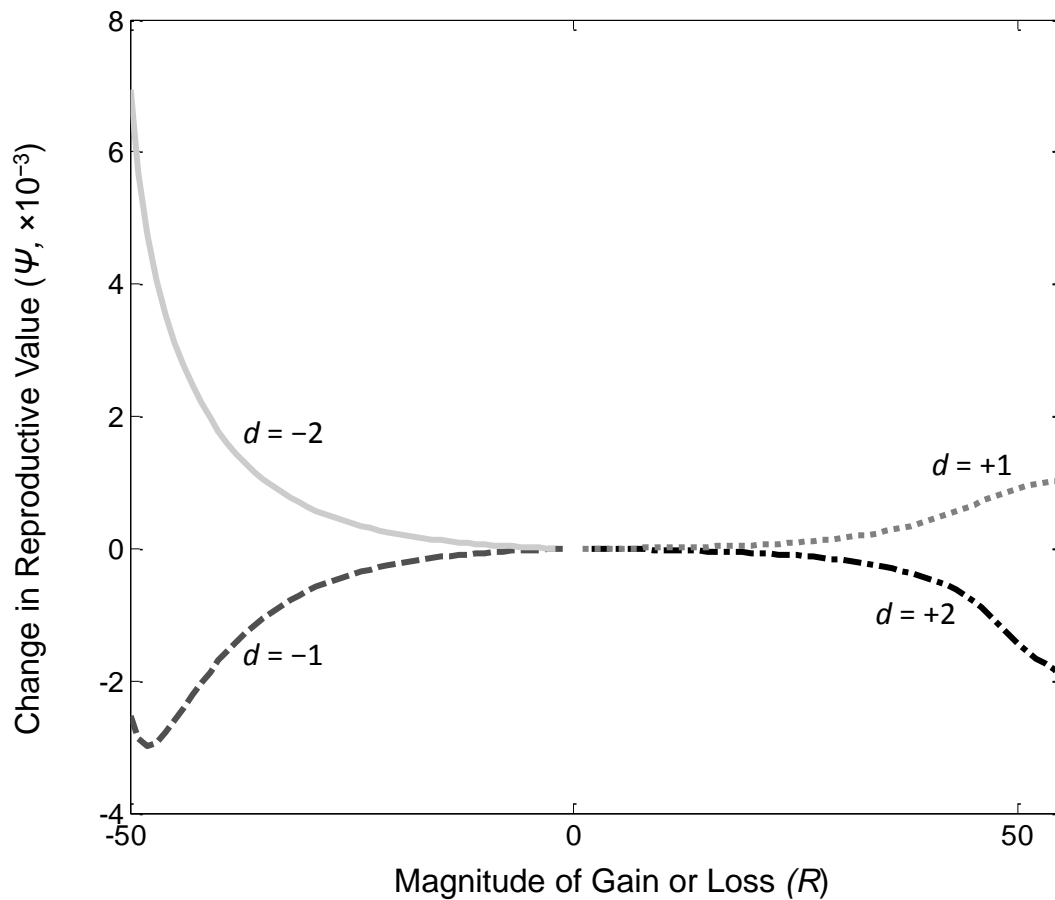

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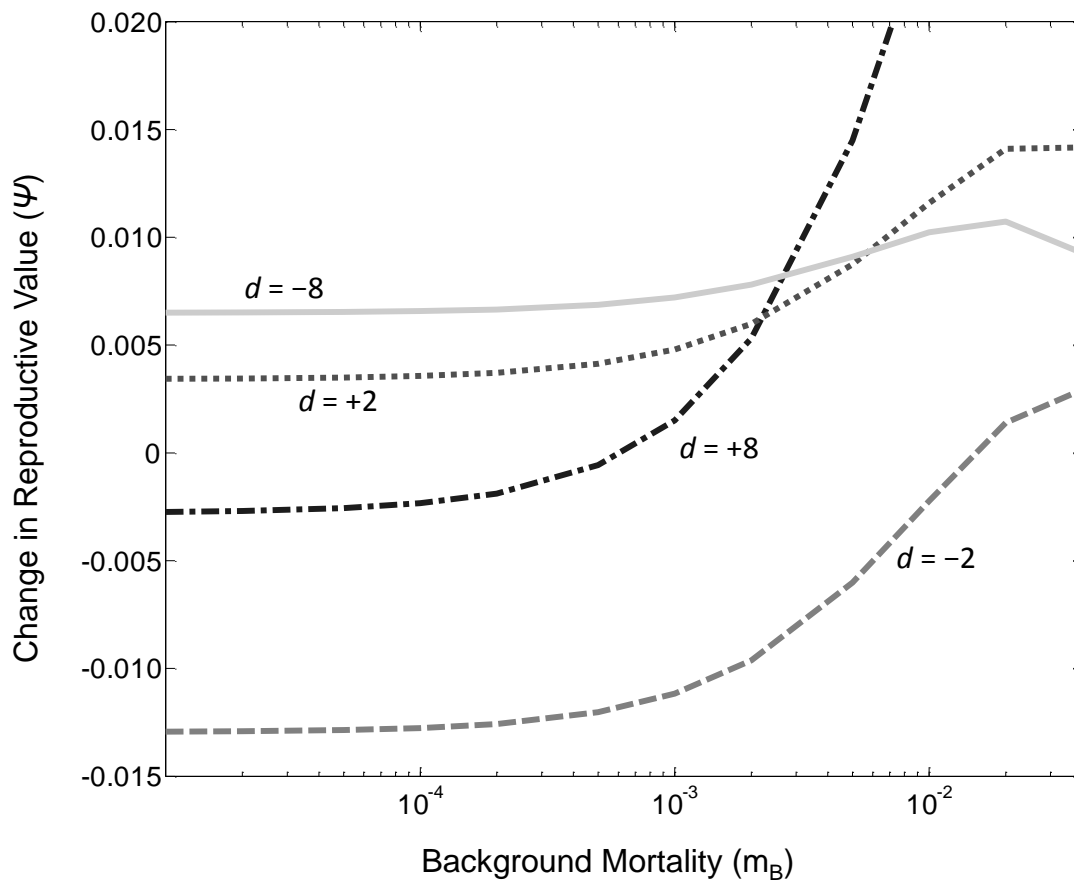730   **Figure B5**. Change in reproductive success when $d = [-2, -1, +1, +2]$

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732

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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 success

745   for taking the one-off stochastic option ($R = \pm 30$)

746

747

748

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 $R = \pm 30$)
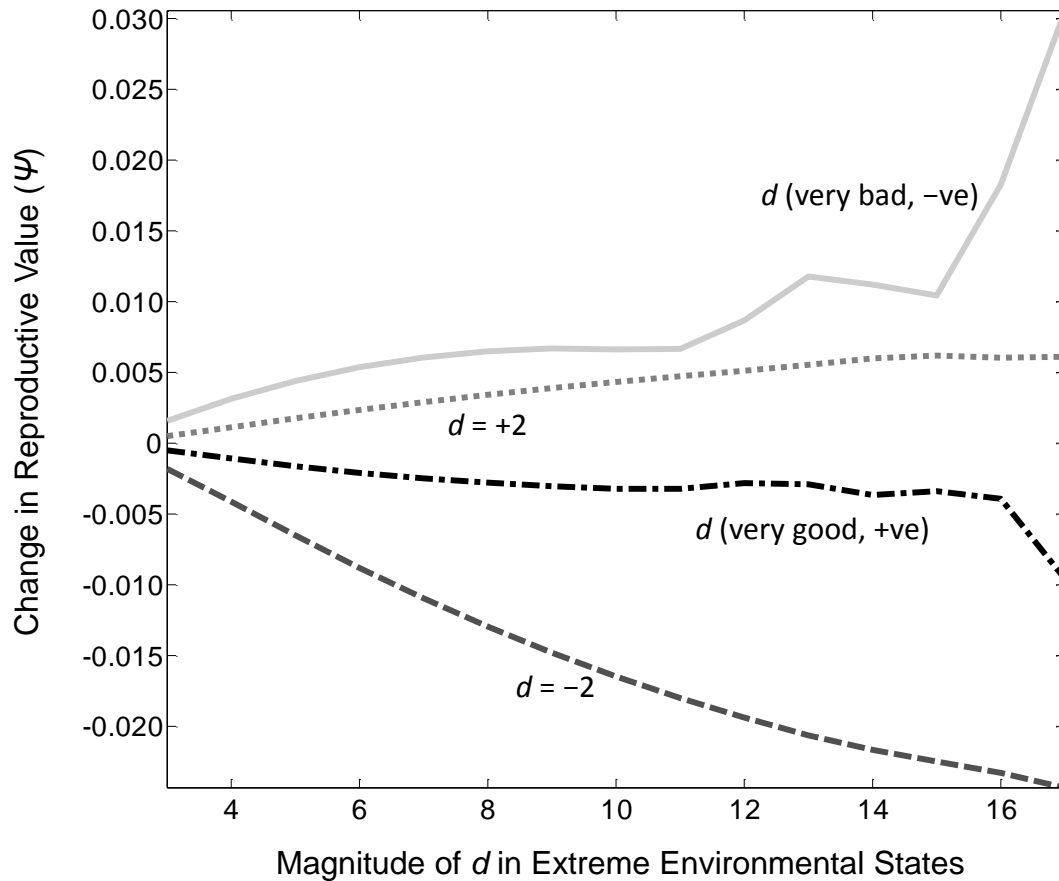
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754 **(iv)   Modifications to the Transition Matrix**

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

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

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

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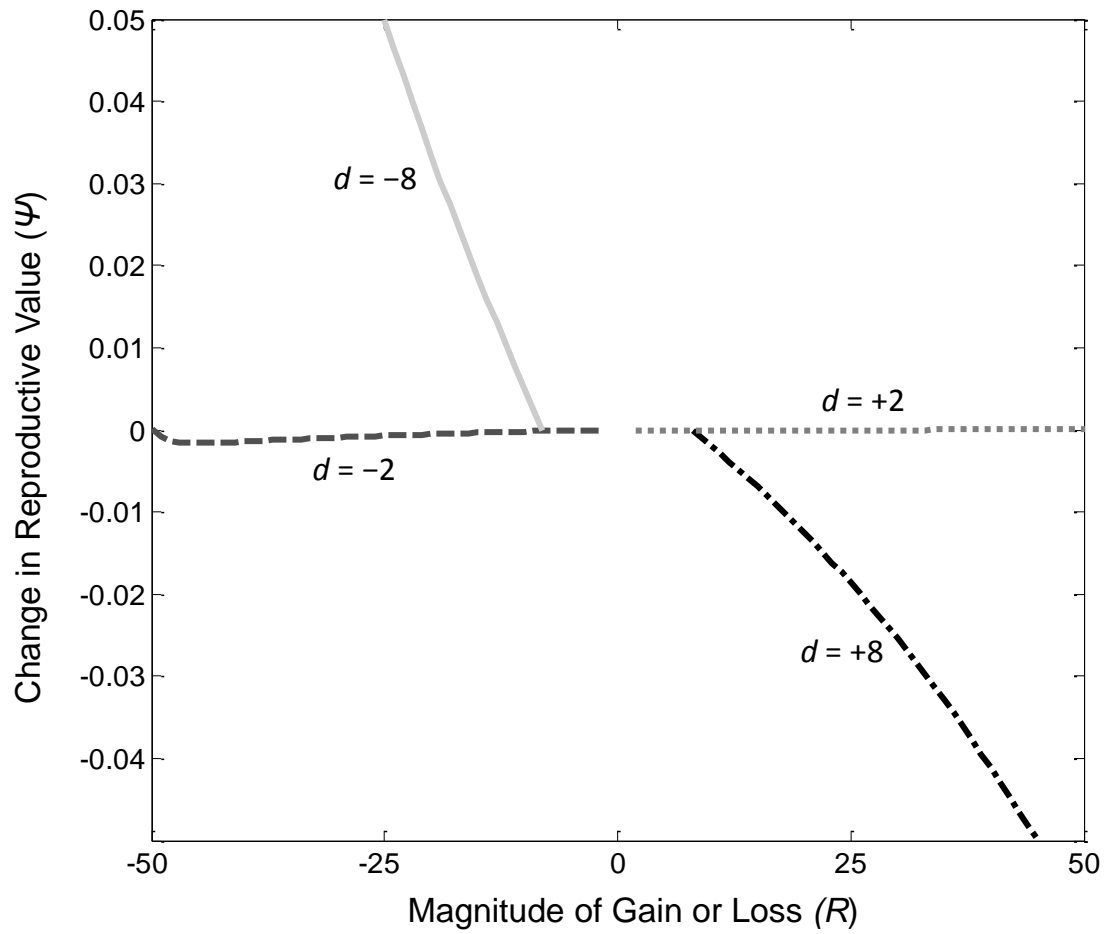
765 $A = 0.1$ and $C = 0.2$.

766

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

768 **(parameter B)**

769

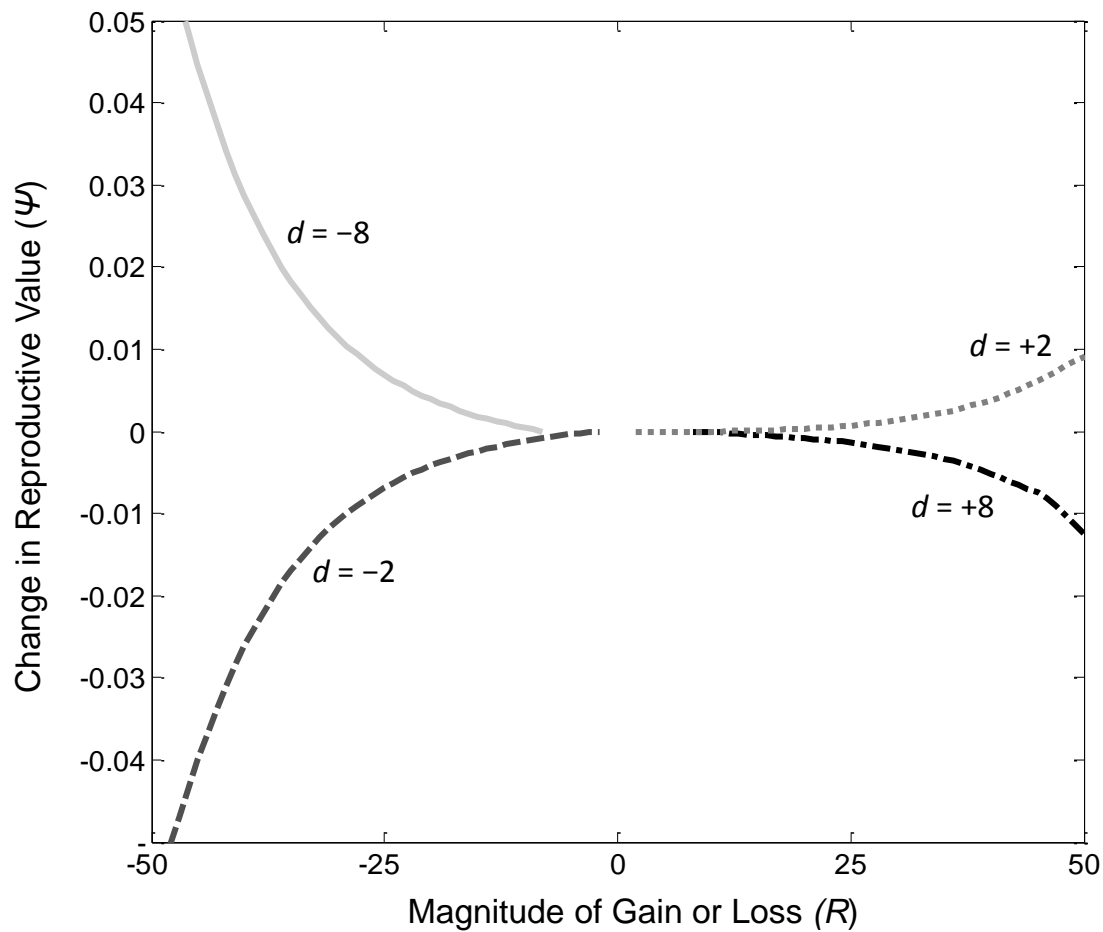770   **Figure B8**. Transition probability $B = 0.001$

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774

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

776

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