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Interim Report

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Unexpected patterns of plastic energy allocation in stochastic environments

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Unexpected patterns of plastic energy allocation in stochastic environments

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1 **ABSTRACT**

2

3 When environmental conditions vary stochastically, individuals accrue fitness benefits by exhib-
4 iting phenotypic plasticity. Such benefits may be counterbalanced by costs of plasticity that
5 increase with the exhibited degree of plasticity. Here we introduce and analyze a general dy-
6 namic-programming model describing an individual's optimal energy allocation in a stochastic
7 environment. After maturation, individuals decide repeatedly how to allocate incoming energy
8 between reproduction and maintenance. We investigate the optimal fraction of energy invested
9 into reproduction and the resultant degree of plasticity in dependence on the variability and pre-
10 dictability of the environment. Our analyses reveal unexpected patterns of optimal energy
11 allocation. In environments with very low energy availability, all energy is allocated to reproduc-
12 tion, although this implies that individuals will not survive after reproduction. Above a certain
13 threshold of energy availability, the optimal reproductive investment rapidly decreases to a
14 minimum, and even vanishes entirely when the environment is highly variable. With further im-
15 provement of energy availability, optimal reproductive investment gradually increases again,
16 until almost all energy is allocated to reproduction. Costs of plasticity affect this allocation pat-
17 tern only quantitatively. Our results show that optimal reproductive investment does not increase
18 monotonically with growing energy availability and that small changes in energy availability can
19 lead to major variations in optimal energy allocation. Our results help to unify two apparently
20 opposing predictions from life-history theory, that organisms should increase reproductive in-
21 vestment both with improved environmental conditions and when conditions deteriorate
22 ('terminal investment').

23 INTRODUCTION

24
25 Phenotypic plasticity is the ability of a genotype to produce alternative phenotypes in different
26 environments. Organisms can benefit from such an ability to adjust their phenotype to a range of
27 environmental conditions (e.g., Lively 1986, Schlichting 1986, Kaitala 1991, Travis 1994, Dorn
28 et al. 2000), especially if environments are heterogeneous in space or time (e.g., Clark and Har-
29 vell 1992, Gabriel and Lynch 1992, Gomulkiewicz and Kirkpatrick 1992, Houston and
30 McNamara 1992, Ernande and Dieckmann 2004, Lind and Johansson 2007). The evolution of
31 phenotypic plasticity requires that plastic individuals have a higher fitness than non-plastic indi-
32 viduals, with fitness defined as an average over all possible environments an individual may
33 encounter (Releya 2002b). Because of this averaging, the frequency distribution according to
34 which environments are encountered influences how much trait values resulting from evolution-
35 arily optimal plasticity in a given environment differ from trait values that would be
36 evolutionarily optimal if that environment were the only encountered. Naturally, a better match is
37 expected in environments that are encountered frequently and that provide high energy levels,
38 compared to rare and/or poor environments (Zhivotovsky et al. 1996, Ernande and Dieckmann
39 2004).

40
41 In stochastically fluctuating environments, the evolutionarily optimal degree of plasticity will
42 typically depend on statistical characteristics of the environmental stochasticity (Kaitala 1991,
43 Gabriel and Lynch 1992), suggesting that being highly plastic is not always a superior strategy.
44 Phenotypic plasticity should be reduced or absent when conditions are constant (Levins 1968,
45 Via and Lande 1985) or when costs associated with plasticity are high (De Witt 1998, Van
46 Tienderen 1991). Theoretical studies showed that evolutionarily optimal reaction norms for the

47 phenotypic plasticity of life-history traits result from a balance between perfect adaptation and
48 the avoidance of costs originating from the effort of maintaining plasticity (Van Tienderen 1991,
49 Ernande and Dieckmann 2004).

50
51 Plasticity in reproductive investment strategies appears to depend strongly on the degree of envi-
52 ronmental heterogeneity. Several empirical studies (e.g., Kaitala 1991, Ellers and van Alphen
53 1997) have shown that in a variable environment, reduced survival prospects caused by a sudden
54 reduction in energy availability may lead to decreased reproductive investment, in favor of a
55 higher allocation of energy to maintenance and survival. On the other hand, there is empirical
56 evidence that reduced energy availability and the ensuing loss of survival probability favor a high
57 allocation to reproduction as a form of ‘terminal investment’ (e.g., Stelzer 2001). As yet, a theo-
58 retical framework is lacking that reconciles these two opposing predictions of life-history theory.
59 Moreover, it has not yet been explored systematically how important characteristics of stochastic
60 environments, namely their variability and predictability in time, influence the evolution of phe-
61 notypic plasticity in reproductive investment strategies.

62
63 Here we introduce a conceptual model to investigate the influence of stochastic environments (i)
64 on energy allocation to reproduction and (ii) on the degree of phenotypic plasticity in reproduc-
65 tive investment. In our model, the amount of energy available in the environment varies with
66 time, and the model organisms can repeatedly adjust their energy allocation. Using dynamic pro-
67 gramming, we investigate the evolutionarily optimal reaction norm for energy invested into
68 reproduction vs. maintenance during an organism’s lifetime when energy availability varies sto-
69 chastically. We analyze how this reaction norm and the implied degree of phenotypic plasticity

70 depend on environmental variability and predictability, and extend our model to investigate how
71 costs of plasticity affect optimal energy allocation.

72

73 **MODEL DESCRIPTION**

74

75 We consider an individual at a specific moment in time after it has reached maturation. Growth is
76 assumed to be determinate and hence no energy is allocated to growth after maturation. We
77 model the life history from the age at maturation onwards. The age a is a discrete variable with
78 values $a = 0, 1, 2, \dots, T$, with $a = 0$ referring to the age at maturation. At each age a , the individ-
79 ual has access to a certain amount of energy $e \geq 0$ available in the environment, which
80 characterizes the current state of the environment. The individual's allocation of available energy
81 to reproduction vs. maintenance may plastically depend on e . For each age a , the reaction norm
82 $f(a, e)$, with $0 \leq f \leq 1$, describes how the fraction of energy allocated to reproduction varies
83 with the energy e currently available in the individual's environment. As we will show later, the
84 evolutionarily optimal allocation reaction norm f is independent of age a . In line with this re-
85 sult and to keep notation simple, we do not make all arguments explicit but write $f(e)$ when
86 referring to $f(a, e)$.

87

88 The energy e_{net} available for allocation (which could be lower than the energy e available in the
89 environment owing to costs of plasticity; see equation (5) below) is split between reproduction,
90 $e_r(a)$, and maintenance, $e_m(a)$,

91

$$92 \quad e_{\text{net}}(a) = e_r(a) + e_m(a), \tag{1}$$

93

94 with the reaction norm $f(e)$ specifying the split,

95

$$96 \quad e_r(a) = f(e) \cdot e_{\text{net}}, \quad (2a)$$

$$97 \quad e_m(a) = (1 - f(e)) \cdot e_{\text{net}}. \quad (2b)$$

98

99 Survival increases monotonically with maintenance energy. We thus assume that the dependence
100 on e_m of the survival probability at age a is of Holling type II,

101

$$102 \quad S(a, e_m) = \frac{e_m(a)}{e_m(a) + e_{1/2}}, \quad (3)$$

103

104 where $e_{1/2}$ is the energy allocation at which survival probability reaches $\frac{1}{2}$. The smaller $e_{1/2}$, the
105 steeper is the initial increase of survival probability with e_m .

106

107 As we investigate energy allocation in stochastically fluctuating environments, the energy avail-
108 ability e is a random variable. We construct a stochastic process to describe how energy
109 availability varies over time. This process depends on two environmental characteristics, envi-
110 ronmental variability λ and predictability τ , which we will vary independently in our analysis
111 below (Fig. 1). Appendix A details the definition of this stochastic process and describes how the
112 two environmental parameters λ and τ emerge from this definition.

113

114 Our aim is to find the evolutionarily optimal allocation reaction norm $f(e)$ that maximizes an
115 individual's lifetime reproductive success. For this purpose, we use the technique of dynamic

116 programming. Dynamic programming is a backward iteration approach for optimizing an inter-
 117 dependent sequence of decisions (Houston and McNamara 1999, Clark and Mangel 2000). As the
 118 fitness benefits of immediate reproduction will usually depend on how an individual chooses to
 119 reproduce in the future, it is natural to work backwards in time when searching for optimal allo-
 120 cation strategies. Dynamic programming is a deterministic procedure that allows us to identify
 121 the evolutionarily optimal allocation reaction norm, for each age a before some terminal age T
 122 and for a given combination of model parameters. For each possible energy availability e , we
 123 find the optimal allocation strategy at age a by choosing f so that the reproductive success from
 124 age a onwards, $R(a, e)$, is maximized. The dynamic-programming equation specifies $R(a, e)$,

$$125$$

$$126 \quad R(a, e) = f(e) \cdot e + S(a, (1 - f(e)) \cdot e) \cdot E(R(a + 1, e)). \quad (4)$$

127

128 We thus see that $R(a, e)$ comprises two components: (i) current reproductive success at age a , as
 129 determined by the energy allocated to reproduction at age a , $f(e) \cdot e$, and (ii) expected future
 130 reproductive success $E(R(a + 1, e))$ from age $a + 1$ onwards, weighted by the survival probability
 131 $S(a, (1 - f(e)) \cdot e)$ from age a to age $a + 1$. The expected future reproductive success is a func-
 132 tion of future energy availabilities and future allocation decisions. The dynamic-programming
 133 equation thus is recursive and can best be solved backward in time: starting at a chosen final age
 134 $a = T$, reproductive success $R(a, e)$ is maximized iteratively for younger and younger ages until
 135 $a = 0$ is reached. Determining in this manner the optimal values of f for all energy availabilities
 136 e yields the optimal allocation reaction norm $f(e)$ that maximizes lifetime reproductive success.
 137 A more detailed description of the dynamic programming technique is provided in Appendix B.

138

139 Our evolutionary allocation model contains three parameters: the variability λ of the environ-
 140 mental dynamics, the autocorrelation time τ of the environmental dynamics, and the energy
 141 level $e_{1/2}$ at which survival probability reaches $1/2$. Below we will systematically analyze how the
 142 evolutionarily optimal allocation reaction norm $f(e)$ and the implied degree of plasticity depend
 143 on these parameters. We define the degree of plasticity of a reaction norm f as the range
 144 $f_{\max} - f_{\min}$ of reproductive investments across all possible environments, based on the maximum
 145 reproductive investment $f_{\max} = \max_e f(e)$ and the minimum reproductive investment
 146 $f_{\min} = \min_e f(e)$.

147
 148 As an extension of the model specified above, we consider possible costs of phenotypic plasticity
 149 $C(a, f)$. The energy available at age a , $e(a)$, is reduced by costs of phenotypic plasticity,
 150 $C(a, f)$,

151

$$152 \quad e_{\text{net}}(a) = e(a) - C(a, f), \tag{5}$$

153

154 yielding the net energy $e_{\text{net}}(a)$ at age a . We assume that maintaining plasticity may cause costs
 155 for an individual (De Witt et al. 1998) and that these costs increase with the range of trait values
 156 that can be expressed as a result of plasticity. Plasticity costs for a reaction norm $f(e)$ are de-
 157 fined as

158

$$159 \quad C(a, f) = c \cdot (f_{\max} - f_{\min})^2, \tag{6}$$

160

161 where $f_{\max} - f_{\min}$ is the degree of plasticity and c scales the plasticity costs. The more plastic an
 162 individual's energy allocation is, and hence the more reproductive allocation $f(e)$ varies across
 163 energy availabilities e , the higher are these plasticity costs. If $f(e)$ does not vary with energy
 164 availability, so that $f_{\max} = f_{\min}$, plasticity costs vanish. Constant reaction norms in our model are
 165 thus cost-free, as was also assumed in the models of Van Tienderen (1991) and Ernande and
 166 Dieckmann (2004).

167
 168 The parameter b , with $0 \leq b \leq 1$, determines how strongly plasticity costs decrease the energy
 169 allocated to reproduction and maintenance,

170
 171
$$e_r(a) = f(e) \cdot e - b \cdot C(a, f), \tag{7a}$$

172
$$e_m(a) = (1 - f(e)) \cdot e - (1 - b) \cdot C(a, f). \tag{7b}$$

173
 174 For $b = 0$ plasticity costs only affect the energy allocated to maintenance, whereas for $b = 1$ plas-
 175 ticity costs only influence the energy allocated to reproduction. For comparison, we also analyze
 176 the implications of plasticity costs being split in proportion to energy allocation, $b = f$,

177
 178
$$e_r(a) = f(e) \cdot (e - C(a, f)), \tag{8a}$$

179
$$e_m(a) = (1 - f(e)) \cdot (e - C(a, f)). \tag{8b}$$

180
 181 When costs of plasticity are included in the model, the mutual dependence between an evolution-
 182 arily optimal reaction norm f and the associated plasticity cost necessitates an additional
 183 iteration loop when solving equation (4). When we are determining the optimal f at age a , we

184 start with costs set to zero, calculate the resultant optimal f , calculate the resultant plasticity
185 costs of f , and iterate the last two steps until f and its plasticity cost converge. This ensures
186 that we have found a self-consistent solution through which energy allocation is optimized.

187
188 The evolutionary allocation model extended by costs of plasticity has two additional parameters:
189 the maximum plasticity costs c , resulting when the degree of plasticity equals 1, and the propor-
190 tion b at which plasticity costs affect reproduction as opposed to maintenance.

191 192 **RESULTS**

193
194 Our evolutionary allocation model possesses the property of strong backward convergence
195 (Houston and McNamara 1999, p. 43). This means that, in the backward iteration process of solv-
196 ing equation (4), the evolutionarily optimal reaction norms essentially do not change with age (so
197 that for all ages a of interest $|f(a+1) - f(a)|$ falls below some small threshold, such as 10^{-5}).
198 For ages a sufficiently before $a = T$, the evolutionarily optimal reaction norm f is thus not
199 only independent of the terminal reward $R(T, e)$ but also of the age a , $f(a, e) = f(e)$.

200
201 The age-independent evolutionarily optimal allocation reaction norms resulting from our model
202 do not predict reproductive investment to increase monotonically with energy availability, but
203 instead consistently show a characteristic non-monotonic shape. When energy availability is very
204 low, it is optimal to invest into reproduction alone (Fig. 2). With increasing energy availability,
205 the evolutionarily optimal reproductive investment rapidly decreases to a unique minimum (Fig.
206 2b) or may even vanish completely (Fig. 2a, 2c, 2d). When energy availability improves further,
207 reproductive investment gradually increases again, until almost all energy is allocated to repro-

208 duction. Depending on the precise shape of the evolutionarily optimal allocation reaction norm,
209 we distinguish between two classes of outcomes: (i) the optimal reproductive investment is posi-
210 tive for all energy availabilities, so the unique minimum in reproductive investment is greater
211 than zero (Fig. 2b), or (ii) the optimal reproductive investment decreases to zero over an interme-
212 diate range of energy availabilities, so reproduction is skipped within that range (Fig. 2a, 2c, 2d).
213 The four reaction norms in Fig. 2 are no more than examples and thus cannot capture all aspects
214 of the dependence of evolutionarily optimal reaction norms on environmental variability λ and
215 predictability τ . A full exploration of these effects is provided in Fig. 3, which highlights, e.g.,
216 that the dependence of the degree of plasticity on τ is not always monotonic.

217
218 As the degree of plasticity is determined by the range $f_{\max} - f_{\min}$ of reproductive investments
219 across all possible energy availabilities that an individual may encounter, and since for all evolu-
220 tionarily optimal allocation reaction norms the maximum expressed reproductive investment was
221 found to be 1, the degree of plasticity resulting from an optimal reaction norm is $1 - f_{\min}$, and
222 thus determined by the minimal value f_{\min} . We can thus focus on f_{\min} for characterizing how the
223 evolutionarily optimal degree of plasticity depends on model parameters in general, and on the
224 statistical characteristics of environmental stochasticity in particular. Each point in the three-
225 dimensional parameter space in Fig. 3b represents a combination of the three parameters $e_{1/2}$
226 (energy required for 50% survival), τ (environmental predictability), and λ (environmental
227 variability). The surfaces in the figure divide this parameter space into five ranges with different
228 degrees of phenotypic plasticity being exhibited by the optimal reaction norms resulting for each
229 parameter combination. In the range above the surface for $f_{\min} = 0$, optimal reaction norms pos-
230 sess an intermediate region of skipped reproduction, while below this surface optimal

231 reproductive investment is always positive (Fig. 3a, b). The three surfaces for $f_{\min} = 0, 0.25,$ and
232 0.5 continuously rise for increasing environmental predictability τ . Surprisingly, the surface for
233 $f_{\min} = 0.75$ first drops with increasing environmental predictability, but eventually rises again,
234 although only very slowly, as predictability is further increased. Thus, as environmental predict-
235 ability τ is enhanced, the evolutionarily optimal degree of plasticity drops when environmental
236 variability λ is high, but rises when environmental variability is low. Also the parameter $e_{1/2}$
237 affects plasticity. We recall that, when $e_{1/2}$ is low, little energy is needed to ensure survival. The
238 shown surfaces first slightly drop with decreasing $e_{1/2}$, but when $e_{1/2}$ becomes small, the drop
239 first becomes steeper and then the behavior changes entirely: the surfaces suddenly curve up-
240 wards and thereby indicate how the optimal degree of plasticity rapidly decreases as $e_{1/2}$
241 approaches 0 (Fig. 3b). Since survival becomes assured when $e_{1/2}$ approaches 0, it is intuitive
242 that reproductive investment increases. The evolutionarily optimal allocation reaction norms thus
243 approach $f(e)=1$ for all energy availabilities e . As a result, the range of parameter combina-
244 tions below each of the shown surfaces expands. Of all three parameters, environmental
245 variability λ , which determines the amplitude of stochastic fluctuations in energy availability,
246 has the strongest influence on the evolutionarily optimal degree of plasticity and thus on the
247 shapes of the corresponding reaction norms. When λ is increased, the minimum f_{\min} of the op-
248 timal reaction norm lowers. For each combination of τ and $e_{1/2}$, one value of λ exists for which
249 the minimum f_{\min} of the optimal reaction norm reaches zero. Increasing λ beyond that value,
250 thus broadening and flattening the distribution of energy availabilities, enlarges the intermediate
251 range of energy availability for which reproduction is skipped (Fig. 4).

252

253 Costs of phenotypic plasticity influence evolutionarily optimal energy allocation patterns only
254 quantitatively. As expected, the minimum of the optimal reaction norm rises with increasing
255 magnitude of plasticity costs c , so that the degree of plasticity decreases (Fig. 5a, b). Analysis of
256 the effect of increased plasticity costs in interaction with the other parameters reveals that the
257 qualitative dependence of optimal reaction norms on the parameters λ and τ is not altered for
258 different values of c . As can be expected, the region in parameter space in which plasticity is
259 maximal shrinks with increasing c (Fig. 5b): the more costly it is to be plastic, the lower is the
260 evolutionarily optimal degree of plasticity. The line of combinations (τ, λ) separating reaction
261 norms with maximum plasticity from those with less plasticity does not change shape, but only
262 moves towards larger values of λ (and, equivalently, smaller values of τ) as plasticity costs in-
263 crease. Less plastic strategies thus become optimal under a wider range of conditions, occurring
264 for higher environmental variability and lower environmental predictability (Fig. 5b).

265
266 Also the parameter b , which determines the relative extent by which plasticity costs reduce the
267 energy available for reproduction, affects the optimal reaction norms only quantitatively. When
268 b is decreased, the surface of combinations $(e_{1/2}, \tau, \lambda)$ separating reaction norms with maximum
269 plasticity from those with less plasticity hardly changes shape, but only moves towards smaller
270 values of λ (Fig. 6). Decreasing b causes the minimum of the optimal reaction norms to de-
271 crease, and hence plasticity to increase. We obtained qualitatively similar results (not shown)
272 when assuming that costs affect maintenance and reproductive energy in proportion to energy
273 allocation, so that $b = f$.

274
275 We tested the influence of a mortality component that cannot be diminished by higher energy al-
276 location e_m to maintenance, by investigating survival functions $S = \alpha e_m / (e_m + e_{1/2})$ that reach

277 their asymptotes at some maximal survival value α , with $0 < \alpha < 1$, instead of at $\alpha = 1$ as in
278 equation (3). Including this additional mortality component again does not change evolutionarily
279 optimal reaction norms qualitatively, but only leads to a rise of their minimum f_{\min} (results not
280 shown). Since the potential for future reproduction diminishes when α is lowered, it is intuitive
281 that evolution responds by an increase in immediate reproduction.

282
283 Reproductive investment f in our model varies between 0 and 1, and evolution fixes it at 1 for
284 very low energy availability. We tested the influence of physiological limits that restrict the frac-
285 tion f of the available energy e that can be invested into reproduction, by introducing an upper
286 limit f_l , with $0 < f_l < 1$, for reproductive investment f , so that evolution had to respect the con-
287 straint $f \leq f_l$. Once again, this does not alter the U-shape of the evolutionarily optimal allocation
288 reaction norm, but only prevents f from increasing all the way up to 1 for very low or very high
289 energy availability e . As a result, f equals f_l for energy availabilities close to 0, decreases to a
290 minimum as e grows, and then rises again up to f_l for increasing e . In other words, reproduc-
291 tive investment is as high as the physiological limit allows for low and high energy availability,
292 whereas it drops to a minimum in between.

293

294 **DISCUSSION**

295

296 We have investigated how evolutionarily optimal reproductive investment depends on the pre-
297 dictability and variability of energy availability in stochastic environments. Our model shows that
298 at certain energy levels a slight change in energy availability must be expected to cause a major
299 change in optimal energy allocation. Investment into reproduction alone is optimal when energy

300 availability is low: mortality due to starvation is then likely, and options for future reproduction
301 are virtually non-existent. When energy availability is intermediate, the probability of future re-
302 productive success becomes high enough to outweigh the benefits of immediate reproduction.
303 Reproductive investment is then drastically reduced and reaches a unique intermediate minimum,
304 or reproduction is even skipped altogether. When energy availability is high, a high reproductive
305 investment occurs even in very variable environments.

306
307 Skipped reproduction is frequently observed in nature (in fish: Bull and Shine 1979, Rideout et
308 al. 2005, Engelhard and Heino 2006, Jørgensen 2006a, b; in amphibians: Bull and Shine 1979,
309 Harris and Ludwig 2004; in reptiles: Bull and Shine 1979, Brown and Weatherhead 2004; in
310 birds: Illera and Diaz 2006). Poor individual condition or poor environmental quality are thought
311 of as the main causes for skipped reproduction (Bull and Shine 1979, Dutil 1986, Rideout et al.
312 2005), which is expected to occur when future reproductive success outweighs the benefits of
313 immediate reproduction (Engelhard and Heino 2005, Jørgensen 2006a). However, to our knowl-
314 edge no previously analyzed life-history model has predicted the occurrence of skipped
315 reproduction only for intermediate environmental qualities, with high reproductive investment
316 being optimal at both ends of a gradient of environmental quality.

317
318 Interestingly, previous life-history theory made two apparently contradictory predictions about
319 optimal reproductive investment in stochastic environments. Theoretical studies concluded that
320 worsened environmental conditions favor *decreased* reproductive investment per reproductive
321 event (Erikstad 1998). This is supported by empirical evidence (Kaitala 1991, Ellers and van Al-
322 phen 1997) and agrees with the right-hand side of the evolutionarily optimal allocation reaction
323 norm resulting from our model. On the other hand, it has been hypothesized that when survival is

324 suddenly reduced because of worsened environmental conditions, reproductive investment should
325 be *increased* as a form of ‘terminal investment’ (Gadgil and Bossert 1970, Michod 1979). Also
326 this prediction is supported by empirical results (Stelzer 2001) and agrees with the left-hand side
327 of the evolutionarily optimal allocation reaction norm resulting from our model. While so far
328 these two predictions were regarded as separate phenomena, our results suggest that they may
329 apply to different ranges of energy availability and thus are, in fact, part of the same reaction
330 norm. Our model results hence help reconcile these apparently contradictory previous life-history
331 predictions.

332
333 Why have U-shaped reaction norms for optimal reproductive investment in stochastic environ-
334 ments not been detected in earlier studies? In contrast to most previous theoretical studies, our
335 analysis describes reproductive investment by a reaction norm, and thus as a function of energy
336 availability. Early studies instead compared the fitness of fixed reproductive strategies in variable
337 and constant environments (Murphy 1968, Schaffer 1974) and found that increased environ-
338 mental variability leads to a decrease in the optimal reproductive investment per reproductive
339 event. Both of these models did not allow for plasticity in reproductive investment, but only con-
340 sidered fixed reproductive strategies. The models by Gadgil and Bossert (1970) and Michod
341 (1979) of iteroparous life histories considered variations in reproductive investment at different
342 ages, but again did not allow for plasticity in reproductive investment at any specific age. Gurney
343 and Middleton (1996) demonstrated in a population model that mixed investment in both repro-
344 duction and growth can become a superior strategy in highly variable environments as opposed to
345 investment into growth followed by a switch to reproduction at a certain time in an individual’s
346 life. They also did not allow for plasticity in allocation strategies nor did they derive reaction
347 norms. More recently, Benton and Grant (1999) studied a matrix population model of optimal

348 resource allocation that included density dependence and stochastic fluctuations in survival and
349 fecundity. They demonstrated through numerical simulations that as environmental variability
350 increases, the resultant change in the evolutionarily stable reproductive investment on average
351 also increases, which qualitatively agrees with our findings. Also in this study, no reaction norms
352 were considered. To our knowledge, Erikstad et al. (1998) is the only preceding theoretical study
353 that analyzed the reaction norm of optimal reproductive investment for a range of environmental
354 conditions in a stochastic environment. They reported that optimal reproductive investment in-
355 creases monotonically with improving environmental conditions. Erikstad et al. designed their
356 model to describe long-lived bird species with a fixed clutch size. Below a certain threshold of
357 environmental quality, they defined current reproduction to be zero, as the available energy
358 would not suffice for producing a clutch. Hence, while their findings agree with the right-hand
359 side of the U-shaped evolutionarily optimal allocation reaction norm found in our study, their
360 model did not allow detecting the left-hand side of this reaction norm, as reproduction at very low
361 energy levels was prevented *a priori*.

362

363 An experimental study on rotifers illustrated nicely that a single organism can exhibit both of the
364 effects predicted above when exposed to a full spectrum of food concentrations, from very low to
365 *ad libitum* (Stelzer 2001). Reproductive investment of rotifers, measured as energy flow into the
366 ovary during an egg-laying interval, was highest at very low food concentrations and decreased
367 when food availability was improved. High reproductive investment at low food concentrations
368 was often followed by immediate death after reproduction. When food concentration was im-
369 proved further, however, the reproductive rate of individuals increased, with more offspring
370 being produced per time unit. This translates into in a high reproductive investment when food
371 availability was high. Both of these observations are thus in agreement with our predictions.

372
373 Costs of phenotypic plasticity have been predicted to impede the evolution of phenotypic plastic-
374 ity (e.g., Via and Lande 1985, Gomulkiewicz and Kirkpatrick 1992, Scheiner 1993, De Witt et. al
375 1998, Ernande and Dieckmann 2004, Pigliucci 2005). A number of experimental studies identi-
376 fied costs of plasticity in different taxa and traits, including plasticity in behavioral,
377 morphological, and life-history traits in amphibian larvae (Releya 2002a) and freshwater snails
378 (DeWitt 1998) as a response to predators; plasticity in morphological traits in response to light
379 cues and resources in plants (Dorn et al. 2000, Van Kleunen 2000, Weinig et al. 2006, Dechaine
380 et al. 2007); and plasticity in flowering time in response to temperature (Stinchcombe et al.
381 2004). Each of these studies established support for the existence of costs of plasticity, at least for
382 some of the traits investigated. Still, the frequency of studies in which plasticity costs have been
383 detected is low relative to the total number of tests, and, even when detected, the magnitude of
384 such costs often turns out to be small, rendering general conclusions about the importance of
385 plasticity costs difficult. It has been suggested that plasticity costs have not often been detected
386 unequivocally because of the employed experimental setups and the genetic background of the
387 studied genotypes (Agrawal 2001, Weinig 2006). In particular, most studies testing for plasticity
388 costs sampled genotypes from natural populations, even though genotypes with high plasticity
389 costs, which may have been present initially, might subsequently have been removed during pro-
390 tracted evolution by natural selection (Weinig 2006).

391
392 Bearing in mind that the more general importance of plasticity costs is still unclear, we first re-
393 ported our main results in the absence of any such costs and then demonstrated the robustness of
394 these results in an extended model in which plasticity costs were taken into account. As expected,
395 our extended results show that when plasticity is costly, a reduced degree of plasticity is optimal.

396 Surprisingly, however, our extended results reveal that evolutionarily optimal allocation reaction
397 norms were not qualitatively altered by plasticity costs. High plasticity costs just moved the op-
398 timal reaction norm toward the cost-free flat reaction norm, in agreement with previous findings
399 by Van Tienderen (1991) and Ernande and Dieckmann (2004).

400
401 It may be worth highlighting that we modeled costs of phenotypic plasticity as ‘maintenance
402 costs’ *sensu* DeWitt et al. (1998), and also that our definition of plasticity costs includes costs of
403 acquiring information about the environment. Since we focus on the phenotypic expression of
404 plasticity and do not study the underlying genetic architecture, we do not address the conse-
405 quences of potential genetic costs of, or constraints on, plasticity originating from linkages or
406 epistasis between loci underlying plasticity and loci affecting other fitness-relevant traits (DeWitt
407 et al. 1998). We tested the robustness of our results against using another cost function, based on
408 the variance of reaction norms (Ernande and Dieckmann 2004), without finding any qualitative
409 departures from the predictions presented above (results not shown). This confirms that our re-
410 sults on the influence of plasticity costs are qualitatively robust and do not depend on a particular
411 form of the underlying cost function.

412
413 Our model allows us to vary how strongly costs of plasticity reduce the energy available for
414 maintenance as opposed to that available for reproduction. When plasticity costs mainly reduce
415 maintenance energy, the evolutionarily optimal degree of plasticity is enhanced by limiting re-
416 productive investment when energy availability is low, so as to ensure survival.

417
418 Various model approaches have been employed to explore the conditions favoring the evolution
419 of phenotypic plasticity (e.g., Via and Lande 1985, Van Tienderen 1991, Gomulkiewicz and

420 Kirkpatrick 1992, Moran 1992, Ernande and Dieckmann 2004). Our results agree with findings
421 based on optimality models and quantitative genetics models in that plastic strategies are always
422 superior to fixed strategies in variable environments (e.g., Clark and Harvell 1992, Scheiner
423 1993). In contrast to earlier models (e.g., Moran 1992, Houston and McNamara 1992), we ana-
424 lyzed the gradual degree of plasticity, rather than just considering its presence or absence: a
425 unique property of our model is that we considered both environmental quality and the pheno-
426 typic response to the environment, in terms of reproductive investment, as continuous variables.
427 This allowed us to demonstrate how minor changes in environmental quality can imply major
428 changes in the evolutionarily optimal reproductive investment.

429
430 Some assumptions underlying our model might limit the generality of our results. We derived the
431 evolutionarily optimal allocation reaction norms as evolutionary endpoints in stochastic environ-
432 ments with different statistical characteristics. At these endpoints, the selection pressures on
433 energy allocation vanish. Such optima are of course unlikely to be exactly tracked by natural
434 populations, for three reasons. First, as with any evolutionary endpoint, selection pressures di-
435 minish as the endpoint is approached, so that evolution close to the endpoint becomes
436 increasingly slow. Second, ecological systems are changing continuously, so that their statistical
437 characteristics, even in terms of features as general as environmental variability and predictabil-
438 ity, might change faster than adaptation can occur. However, when evolutionary rates are not too
439 slow and changes in the statistical characteristics of the stochastic environment are not too fast,
440 we can expect evolution by natural selection to take populations close to the identified endpoints.
441 Third, as already mentioned above, we assume that evolving populations do not run out of ge-
442 netic variance as they respond to the existing selection pressures on energy allocation.

443

444 Our approach assumes that the evolutionarily optimal allocation reaction norm is independent of
445 density. While density would influence resource abundance, and thus energy availability, it
446 should not alter an individual's allocation decisions at a given energy level. Likewise, even
447 though density-dependent competition could change environmental variability and predictability,
448 these effects can be accounted for in our model as it treats environmental variability and predict-
449 ability as parameters. What our model does not capture is frequency-dependent selection. If, for
450 example, environmental variability and predictability become dependent on the reaction norm
451 currently prevalent in the population, an environmental feedback is created that precludes the use
452 of any optimality model.

453
454 Another critical assumption underlying our analysis is that the modeled organisms are 'income
455 breeders' that can acquire energy for reproduction and maintenance only during the current re-
456 productive period and that must thus spend all such energy during the current season (Stearns
457 1992, Jönsson 1997). This may explain why we found full investment into reproduction close to
458 starvation. An interesting extension of the framework presented here would be to investigate how
459 allocation decisions are affected by the possibility of energy storage between seasons, which is a
460 widespread strategy helping individuals to cope with temporarily poor environmental conditions
461 (e.g., Rogers 1987, Rogers and Smith 1993, Kooi and Troost 2006). Even though the possibility
462 of energy storage will affect evolutionarily optimal allocation reaction norms, it should be borne
463 in mind that there usually exists a fundamental asymmetry between investments into reproduction
464 and maintenance. When energy availability is high, many organisms can increase their reproduc-
465 tive success by investing more energy into reproduction by increasing, within physiological
466 limits, their reproductive frequency, their clutch size, and their investment into each individual
467 offspring. By contrast, all investments into maintenance cannot push the probability of survival

468 above 1. This asymmetry is captured by the saturating survival function in our model and serves
469 as a conceptual cornerstone for understanding elevated investment into reproduction at high en-
470 ergy availability.

471
472 We conclude that stochastic environments can cause unexpected patterns of plastic energy alloca-
473 tion, with evolutionarily optimal reproductive investment not necessarily just increasing or
474 decreasing monotonically with energy availability. The U-shaped allocation reaction norms pre-
475 dicted here imply maximal reproductive investment at the extreme ends of environmental quality
476 and minimal reproductive investment for intermediate conditions. We find that the transitions be-
477 tween these three outcomes are quite sharp: consequently, evolutionarily optimal reproductive
478 investment in stochastic environments can be very sensitive to small changes in energy availabil-
479 ity.

480

481 **APPENDIX A**

482 **Definition of stochastically fluctuating environments**

483

484 A time series of environmental states $\{e_1, e_2, e_3, \dots, e_T\}$ is a realization of a stochastic process de-
485 scribing varying energy availability (Fig. 1), with the individual states applying at ages
486 $a = 1, 2, \dots, T$ of the model organism. Considering all possible realizations, we obtain the fre-
487 quency distribution of e at each age a . Thus, for defining the stochastic process we need to
488 make assumptions about the distribution of e at each age a .

489

490 In nature, the abundance of organisms and resources often follows a lognormal distribution
491 (Limpert et al. 2001), owing to the central limit theorem for multiplicative stochastic variables.

492 We thus assume that energy availability e is lognormally distributed with mean μ and variance
493 σ^2 , which implies that the logarithm of e is normally distributed, with mean μ_N and variance
494 σ_N^2 . In line with this, we assume environmental dynamics to follow a multiplicative autoregres-
495 sive process of order 1, AR(1), which means that energy availability at a given age depends on
496 two factors, the energy availability at the previous age and a noise term. Consequently, energy
497 availability at age $a+1$, e_{a+1} , is given by the product of energy availability at the previous age a ,
498 e_a , and an age-specific noise term ε_a , which is the source of randomness,

$$499$$

$$500 \quad e_{a+1} = e_a^\varphi \cdot \varepsilon_a, \quad (9)$$

501

502 with $\varphi \geq 0$. The parameter φ describes how much e_a influences e_{a+1} . When $\varphi = 0$, subsequent
503 environmental states are not correlated, and e_{a+1} is independent of e_a and thus fully determined
504 by the error term ε_a . Since correlations between ages are thus captured by φ , ε_a can be assumed
505 to be uncorrelated between ages. Since e_a and e_{a+1} are lognormally distributed, the noise term
506 ε_a must also follow a lognormal distribution. The logarithm of ε_a is thus a normally distributed
507 white-noise process, with mean $\mu_{\varepsilon,N}$ and variance $\sigma_{\varepsilon,N}^2$. This white noise serves as the source of
508 randomness for the environmental fluctuations in our model. We assume this stochastic process
509 to be stationary, which means that the mean and variance of e_a are independent of a , which in
510 turn implies $\mu_{\varepsilon,N} = 0$. Taking the logarithm of equation (4) and subsequently taking variances,
511 this results in $\sigma_{\varepsilon,N}^2 = \sigma_N^2 \cdot (1 - \varphi^2)$, which implies $\varphi < 1$. The variance σ_N^2 of the logarithm of e

512 and the parameter φ thus determine the variance $\sigma_{\varepsilon,N}^2$ of the noise term. Since $\mu_{\varepsilon,N} = 0$ and
 513 $\sigma_{\varepsilon,N}^2$ are independent of age a , the noise process is stationary, $\varepsilon_a = \varepsilon$.

514
 515 The autocorrelation time τ of the stochastic environmental dynamics of e measures the duration
 516 over which the correlation between successive energy availabilities decreases to $1/e \approx 36.8\%$
 517 (with $e \approx 2.718$ denoting Euler's number); τ is given by

$$519 \quad \tau = -\frac{1}{\ln \varphi}. \quad (10a)$$

520
 521 We use τ as a convenient measure of environmental predictability. To reduce the number of pa-
 522 rameters needed for describing the environmental dynamics, and since we can choose the unit for
 523 e freely, we set the geometric mean of e to 1, which is equivalent to $\mu_N = 0$; we thus measure
 524 energy availability relative to its geometric mean. With this we obtain $\sigma^2 = (e^{\sigma_N^2} - 1) \cdot e^{\sigma_N^2}$ and
 525 $\mu = e^{\sigma_N^2/2}$ for the mean and variance of the lognormal distribution of e . We use the coefficient of
 526 variation,

$$528 \quad \lambda = \frac{\sigma}{\mu} = e^{\sigma_N - \sigma_N^2/2} \sqrt{e^{\sigma_N^2} - 1}, \quad (10b)$$

529
 530 for quantifying environmental variability. Using the two parameters λ and τ for characterizing
 531 the fluctuating environment allows us to independently vary the variability and predictability of
 532 fluctuating energy availability (Fig. 1).

534 **APPENDIX B**

535 **Determination of evolutionarily optimal reaction norms through dynamic programming**

536

537 Evolutionarily optimal reaction norms in our model are computed by applying the technique of
 538 dynamic programming. For this purpose, we need to discretize the energy scale to obtain a vector
 539 of n discrete energy states e_i , $i=1,2,\dots,n$. For each of these, we find the optimal allocation
 540 strategy at age a by choosing f so that the reproductive success from age a onwards, $R(a,e_i)$,
 541 is maximized. The recursive dynamic-programming equation is

542

543
$$R(a,e_i) = \operatorname{argmax}_{f(e_i)} \left[f(e_i) \cdot e_i + S(a, (1-f(e_i)) \cdot e_i) \cdot \sum_{j=1}^n p(e_j | e_i) R(a+1, e_j) \right], \quad (11)$$

544

545 where the transition probability $p(e_j | e_i)$ determines the likelihood of the transition from energy
 546 state e_i at age a to state e_j at age $a+1$. These transition probabilities follow directly from the
 547 definition of the autoregressive process,

548

549
$$p(e_j | e_i) = p(e_j = e_i^\varphi \cdot \varepsilon | e_i) = p(\varepsilon = e_i^{-\varphi} \cdot e_j) = \frac{e^{-\frac{1}{2} \log^2 \varepsilon / \sigma_{\varepsilon,N}^2}}{\sqrt{2\pi \varepsilon \sigma_{\varepsilon,N}}}, \quad (12)$$

550

551 and can be assembled in a $n \times n$ matrix P with elements $P_{ij} = p(e_j | e_i)$, $i, j = 1, 2, \dots, n$. (The last
 552 step above follows from the fact that $\varepsilon = e_i^{-\varphi} \cdot e_j$ is lognormally distributed, and it is accurate
 553 when n is large.) Starting with $R(T, e_j)$ at age $a = T$, equation (11) is solved iteratively for
 554 younger and younger ages until $a = 0$ is reached. At each age and for each energy state e_i , $f(e_i)$

555 is chosen so as to maximize the expression in square brackets (this is the meaning of the argmax
556 function). The set of numbers $f(e_i)$, $i=1,2,\dots,n$, resulting at $a=0$ then describes the evolu-
557 tionarily optimal allocation reaction norm.

558

559 It is important to understand that this $f(e)$ is potentially very different from the function $f'(e)$
560 we would obtain by optimizing energy allocation separately for each energy state e_i when assum-
561 ing the absence of stochastic fluctuations in energy availability. While $f(e)$ describes the
562 expected endpoint of evolution by natural selection in a single population exposed to a fluctuat-
563 ing environment, $f'(e)$ would describe the collection of evolutionary endpoints in many
564 completely separated populations, each exposed to a constant environment with a specific energy
565 availability e . The formal reason for this biologically crucial distinction is that for evolution in
566 stochastically fluctuating environments energy states are coupled by the considered stochastic
567 environmental process, with this coupling being reflected in equation (11) by the sum across all
568 possible energy states. More specifically, the evolutionarily optimal energy allocation $f(e_i)$ at
569 age a and energy state e_i not only depends on (i) how likely it is that the individual will survive
570 until $a+1$, $S(a, (1-f(e_i)) \cdot e_i)$, but also on (ii) how likely energy state e_j is encountered at age
571 $a+1$, $p(e_j | e_i)$, and on (iii) how valuable that encounter will be in terms of future reproductive
572 success, $R(a+1, e_j)$.

573

574 We choose a terminal age T that is so large that virtually no survival from age $a=0$ until age
575 $a=T$ is possible. Hence the terminal reward $R(T, e)$, denoting the vector of reproductive suc-
576 cess for all energy states e_i from age T onwards, has no effect on results at ages of interest (for

577 which survival from age $a=0$ is non-negligible), and can thus be assumed to vanish,
578 $R(T, e) = 0$. At the terminal age, future reproductive success is obviously maximized by allocat-
579 ing all available energy to reproduction, $f(e_i) = 1$ for all e_i at age T .

580

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582

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590

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705 **FIGURE LEGENDS**

706

707 **Figure 1.** Stochastic fluctuations in energy availability in four environments with different vari-
708 ability and predictability. The average amplitude of the time series increases with environmental
709 variability λ , while its average frequency decreases with environmental predictability τ . Dotted
710 lines show the resultant 95%-confidence intervals for energy availability. Environmental variabil-
711 ity λ is larger in the bottom row than in the top row, while environmental predictability τ is
712 larger in the right column than in the left column: (a) $\lambda = 5$, $\tau = 1$; (b) $\lambda = 5$, $\tau = 10$; (c) $\lambda = 50$,
713 $\tau = 1$; (d) $\lambda = 50$, $\tau = 10$. Note that horizontal axes are scaled logarithmically.

714

715 **Figure 2.** Evolutionarily optimal allocation reaction norms, describing the dependence of the op-
716 timal reproductive investment f on energy availability e , in four environments with different
717 variability and predictability (Fig. 1). Dotted lines show the resultant 95%-confidence intervals
718 for energy availability. Dashed curves show the survival probabilities resulting from the pre-
719 sented reaction norm at different energy availabilities. Environmental variability λ is larger in
720 the bottom row than in the top row, while environmental predictability τ is larger in the right
721 column than in the left column: (a) $\lambda = 10$, $\tau = 20$; (b) $\lambda = 10$, $\tau = 50$; (c) $\lambda = 50$, $\tau = 20$; (d)
722 $\lambda = 50$, $\tau = 50$. Note that horizontal axes are scaled logarithmically. Other parameters: $e_{1/2} = 5$.

723

724 **Figure 3.** Classification of evolutionarily optimal allocation reaction norms. (a) Examples of re-
725 action norms $f(e)$ with minima at $f = 0, 0.25, 0.5$, or 0.75 . (b) Surfaces of parameter
726 combinations $(e_{1/2}, \tau, \lambda)$ resulting in optimal reaction norms with these minima. Plasticity thus
727 increases from bottom to top.

728

729 **Figure 4.** Effects on evolutionarily optimal allocation reaction norms of environmental variabil-
730 ity. Optimal reaction norms $f(e)$ are shown for different levels of environmental variability λ :
731 $\lambda_1 = 1$, $\lambda_2 = 10$, $\lambda_3 = 20$, $\lambda_4 = 50$, and $\lambda_5 = 100$. Increased environmental variability leads to
732 skipped reproduction across wider ranges of energy availability (grey bars). Other parameters:
733 $e_{1/2} = 5$ and $\tau = 50$.

734
735 **Figure 5.** Effects on evolutionarily optimal allocation reaction norms of the scale c of plasticity
736 costs. (a) Optimal reaction norms for different values of c , with $\tau = 50$ and $\lambda = 10$. Increased
737 plasticity costs reduce the optimal degree of plasticity. (b) Lines of parameter combinations
738 (τ, λ) resulting in optimal reaction norms with a minimum $f = 0$ for different values of c :
739 $c = 0, 10, 100$, and 1000 are indicated by growing line widths. Other parameters: $e_{1/2} = 5$ and
740 $b = 1$.

741
742 **Figure 6.** Effects on evolutionarily optimal allocation reaction norms of the proportion b at
743 which plasticity costs affect reproduction as opposed to maintenance. Surfaces of parameter
744 combinations $(e_{1/2}, \tau, \lambda)$ resulting in optimal reaction norms with a minimum at $f = 0$ for differ-
745 ent values of b : $b = 0$ (white), $b = 0.5$ (light grey), and $b = 1$ (dark grey). Increased allocations
746 of plasticity costs to reproduction reduce the optimal degree of plasticity. Other parameters:
747 $c = 1$.

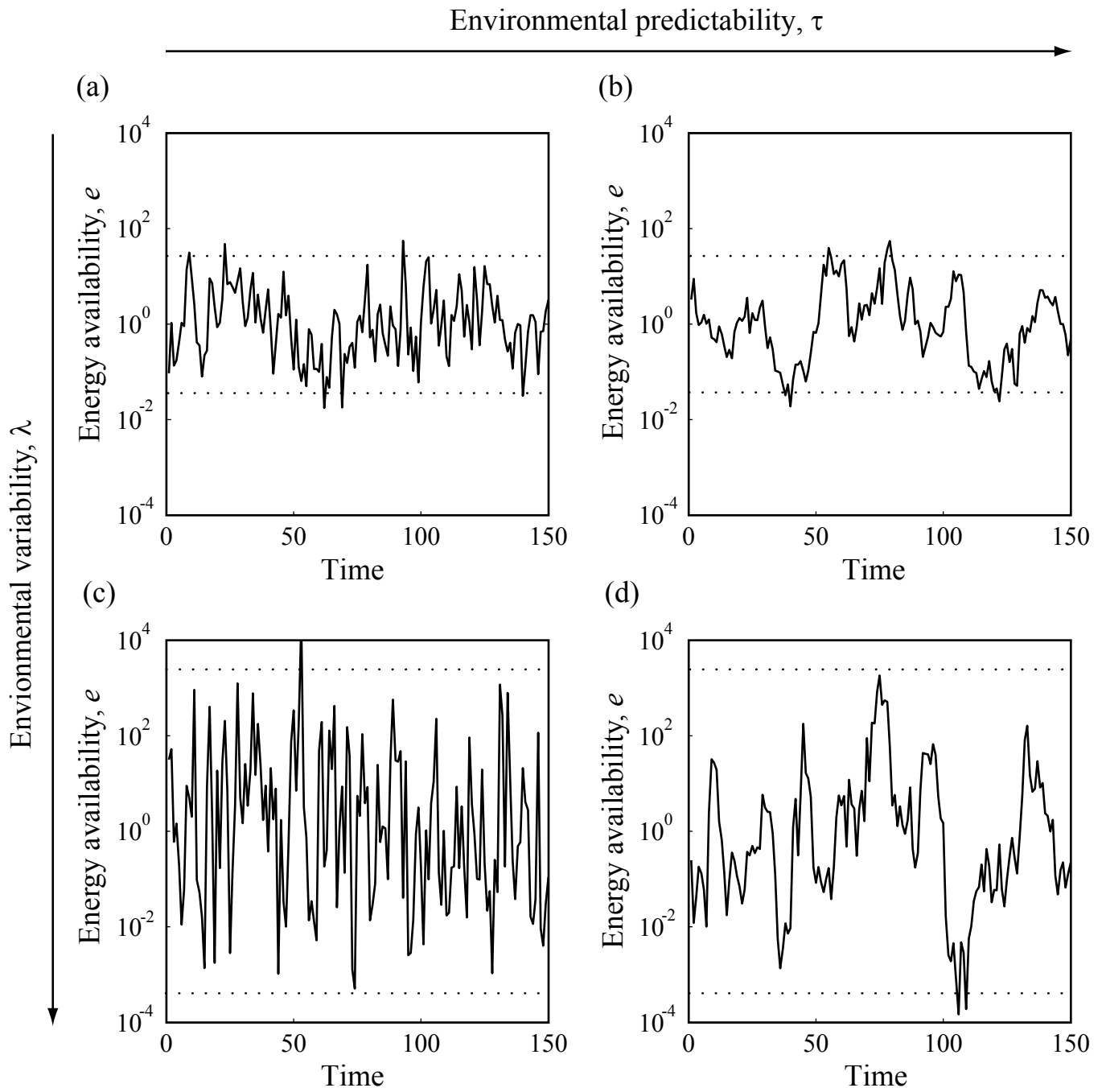


Figure 1.

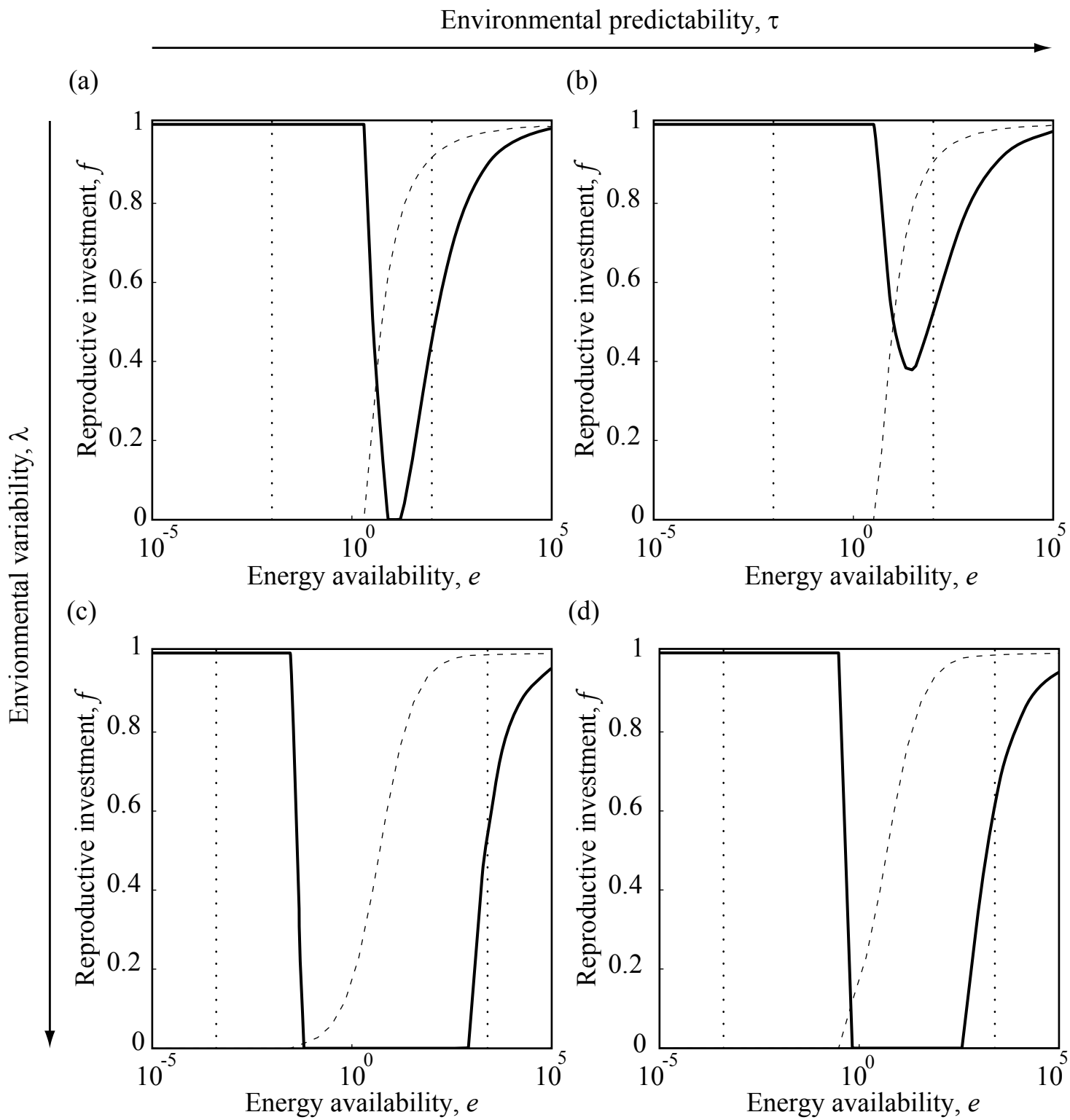


Figure 2.

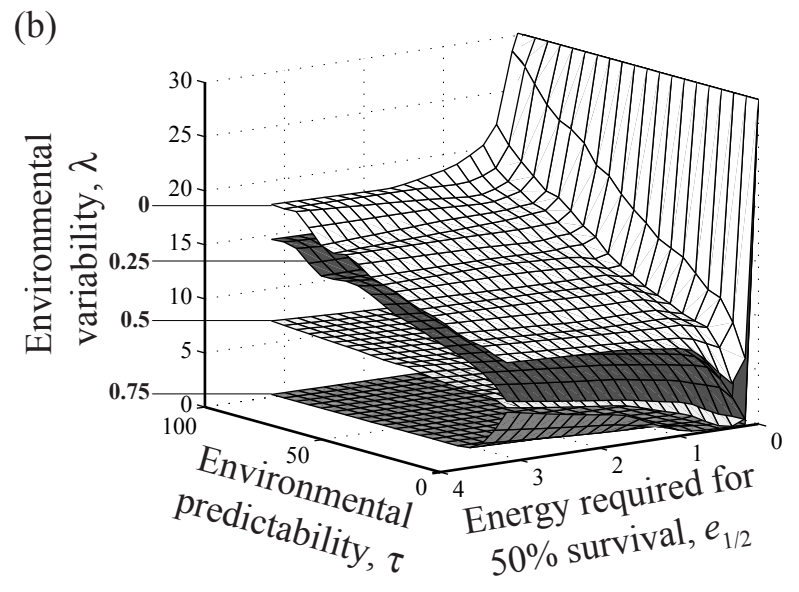
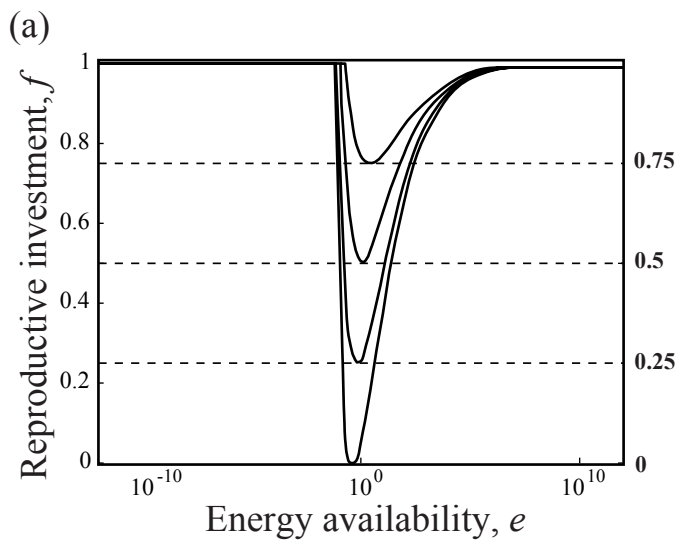


Figure 3.

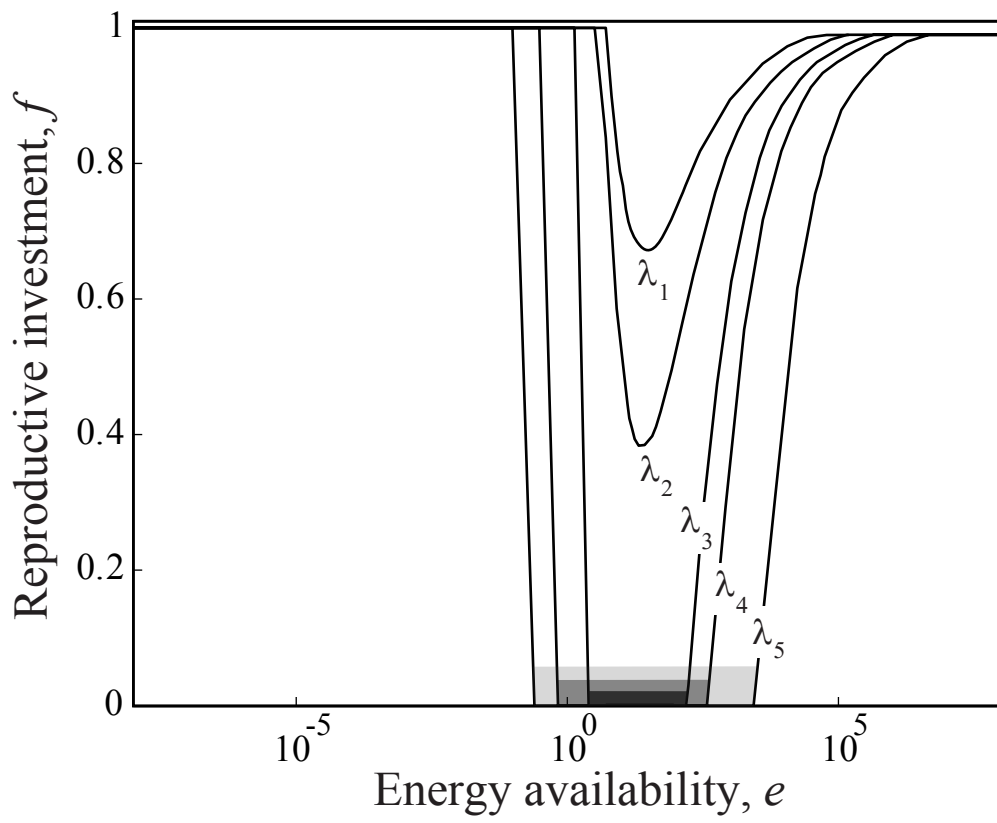


Figure 4.

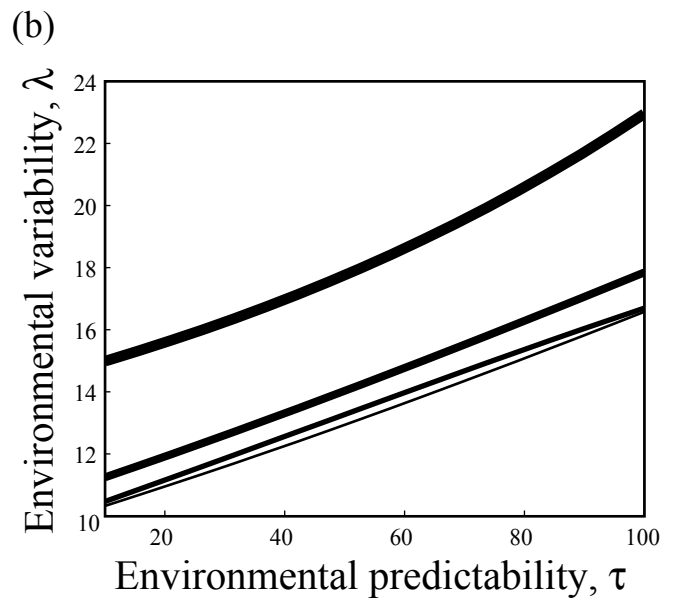
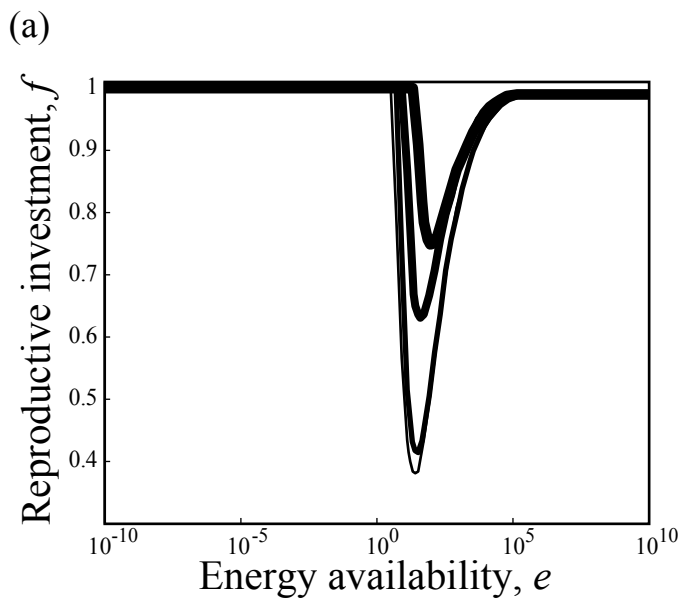


Figure 5.

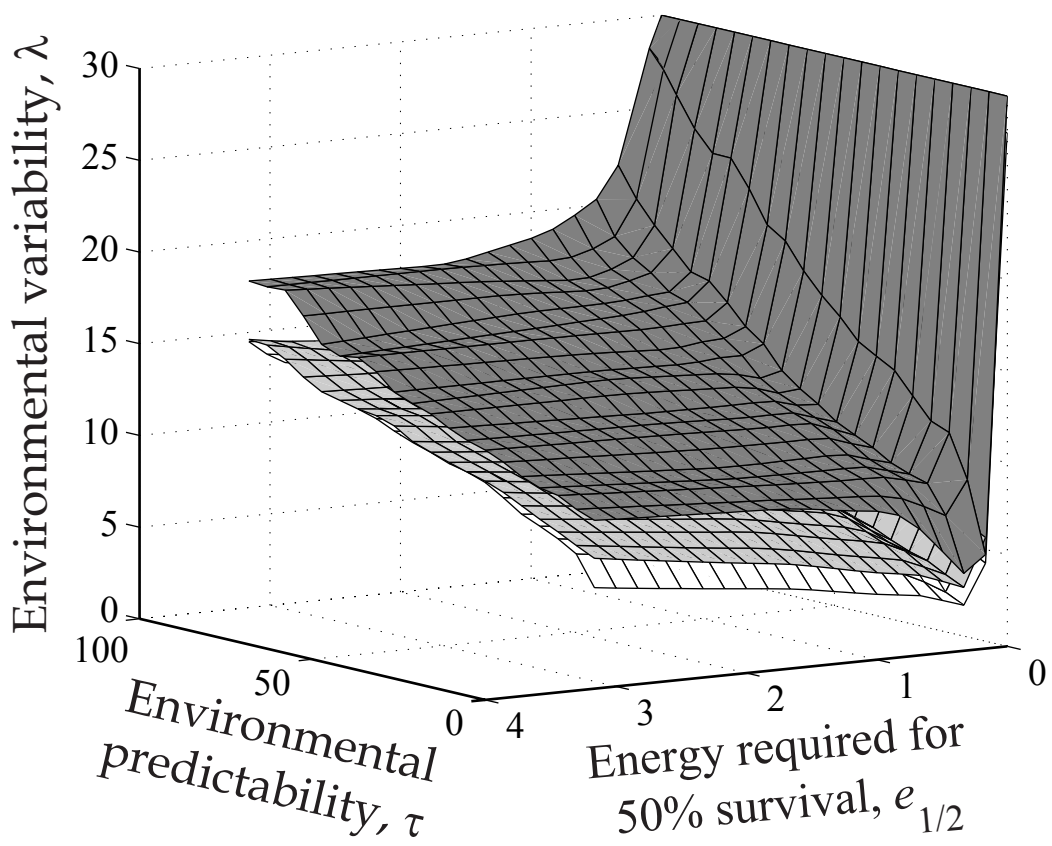


Figure 6.