

Caring for parents: an evolutionary rationale

Supplementary Information

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22 **Supplementary Discussion**

23 **Cultural analogues of the Fifth Commandment**

24 Cultural norms that promote the help of the parents are widespread in both western and eastern
25 culture. The Fifth Commandment (of the Hebrew and protestant Bible, the Fourth one,
26 according to the catholic numbering) states: "*Honor your father and your mother, that your
27 days may be long in the land that the LORD your God is giving you.*" (Exodus 20:12)

28 From the interpretations of this commandment by the western churches we recall the following:
29 Sefer Ha-chinukh (mitzva 33) elaborates: "*A person should realize that his father and mother
30 are the cause of his existence in this world; therefore it is appropriate that he render them all
31 the honor and do them all the service he can*". St. Thomas Aquinas wrote: "*Since we receive
32 nourishment from our parents in our childhood, we must support them in their old age.*" Martin
33 Luther said: "*For he who knows how to regard them in his heart will not allow them to suffer
34 want or hunger, but will place them above him and at his side, and will share with them
35 whatever he has and possesses*" (Luther, M. p. 29).

36 We also note that in China, to take care of elderly parents is also a moral rule: e.g. Confucius
37 declared: "*In serving his parents, a filial son reveres them in daily life; he makes them happy
38 while he nourishes them; he takes anxious care of them in sickness ...*" (26)

39 Based on the above, we introduce the so-called Fifth Rule, which is a translation of the Fifth
40 Commandment into biological terms and is inherent in the above interpretations: "During your
41 reproductive period, give away from your resources to your post-fertile parents."

42

43 **Supplementary Methods**

44 In the following we investigate a biological model for intra-familial help, give some general
45 results on it, and finally, we investigate the simplest model with numerical examples.

46

47 **1. The survival at the carrying capacity**

48 Here we propose a strictly Darwinian reasoning to see that the long-term growth rate is
49 maximized by natural selection: the number of offspring, in general, is much higher than the
50 carrying capacity, so only a part of the offspring and adults will survive. Let us consider random
51 survival, assuming that the survival probabilities of individuals do not depend on phenotypes
52 (in our case intergenerational help) and on the age of individuals. (Observe that this assumption
53 gives some advantage to the families in which the intergenerational help is less.)

54 Now let us consider two phenotypes A and B with respective long-term growth rates (i.e.
55 positive eigenvalues of the corresponding Leslie matrices) $\lambda_A, \lambda_B > 1$ with $\lambda_A > \lambda_B$. To see the
56 asymptotic frequency of phenotype B, we suppose that phenotypes A and B start from
57 respective initial densities $x(0)$ and $z(0)$. According to the original Darwinian view, we need
58 some density dependent selection to keep the total density of these two phenotypes at the
59 carrying capacity. Since in the considered selection situation there is no interaction between the
60 phenotypes and we assume that the phenotypes differ only in the demographic parameters, thus
61 we can suppose there is a uniform survival process, i.e. the survival rate corresponding to the
62 carrying capacity is the same for all individuals. Now the question arises which phenotype will
63 win in the struggle for existence on the long selection time scale?

64 Let us suppose that phenotypes A and B develop according to Leslie models having the
65 respective population vectors $x(t)$, $z(t)$, and matrices L_A , L_B , total densities

66 $\|x(t)\| = \sum_i x_i(t)$, $\|z(t)\| = \sum_i z_i(t)$. Then the relative frequency of phenotype B tends to zero, as

67 it is shown below:

68 Indeed, let us suppose that the subpopulations start from initial states $x(0)$ and $z(0)$,

69 respectively, and the time unit is chosen in such a way that in unit time the total density of the

70 system always exceeds the carrying capacity K , in particular

71
$$\|L_A x(0)\| + \|L_B z(0)\| > K. \quad (\text{SI } 2)$$

72 Now, by the selection the total density of the system is reduced to K proportionally:

73
$$x(1) = \frac{K}{\|L_A x(0)\| + \|L_B z(0)\|} L_A x(0), \quad (\text{SI } 3)$$

74
$$z(1) = \frac{K}{\|L_A x(0)\| + \|L_B z(0)\|} L_B z(0). \quad (\text{SI } 4)$$

75 Indeed, obviously $\|x(1)\| + \|z(1)\| = K$.

76 We emphasize that in this model we consider the “intrinsic” survival (described by the Leslie

77 matrices) and the survival under selection independently. However, this model can be formally

78 considered as a particular Leslie-type model depending on the total density of the system, where

79 each demographic parameter in the Leslie matrices L_A and L_B is multiplied by

80
$$\frac{K}{\|L_A x(0)\| + \|L_B z(0)\|}.$$

81 Similarly, for all $t = 1, 2, 3, \dots$ we get our kin demographic selection model for two different

82 phenotypes:

83
$$\begin{aligned} x(t+1) &= \frac{K}{\|L_A x(t)\| + \|L_B z(t)\|} L_A x(t) \\ z(t+1) &= \frac{K}{\|L_A x(t)\| + \|L_B z(t)\|} L_B z(t) \end{aligned} \quad (\text{SI } 5)$$

84

85 Now, for the proportion of phenotype B we obtain

$$86 \quad \frac{\|z(t)\|}{\|x(t)\| + \|z(t)\|} = \frac{1}{\frac{\|x(t)\|}{\|z(t)\|} + 1}. \quad (\text{SI } 6)$$

87 Here

$$88 \quad \frac{\|x(t)\|}{\|z(t)\|} = \left(\frac{\lambda_A}{\lambda_B} \right)^t \frac{\lambda_A^t}{\lambda_B^t}. \quad (\text{SI } 7)$$

89 Since we can suppose that in both phenotypes the last two fecundities are positive, so the

90 Perron-Frobenius theorem (see e.g. 28) implies that both $\frac{\|x(t)\|}{\lambda_A^t}$ and $\frac{\|z(t)\|}{\lambda_B^t}$ tend to finite

91 positive limits as $t \rightarrow \infty$. In fact, the Leslie matrices can be cut at the last fertile age class, apply

92 the Perron-Frobenius theorem to these matrices, and then the convergence can be extended to

93 the post fertile age groups by simple survival. Therefore, $\lim_{t \rightarrow \infty} \frac{\|x(t)\|}{\|z(t)\|} = \infty$, implying

$$94 \quad \lim_{t \rightarrow \infty} \frac{\|z(t)\|}{\|x(t)\| + \|z(t)\|} = 0. \quad (\text{SI } 8)$$

95 Thus if $\lambda_A > \lambda_B$, then the relative frequency of phenotype B tends to zero as t tends to infinity.

96 Observe that in our model, the fecundity of a phenotype is determined by a phenotype-

97 dependent Leslie matrix, and the survival rates corresponding to the carrying capacity of

98 different phenotypes are the same, so the long-term growth rate of a phenotype determines the

99 fitness.

100

101 2. The general results

102 Consider the general $K \times K$ Leslie matrix, where the entries depend on the cost y spent to
 103 grandparent support. Under the grandmother hypothesis, the grandmother support decreases the
 104 fecundity and survival rate of fertile parents, but increases the survival rate of the grandmother,
 105 who therefore increases the survival rate of pre-fertile grandchildren. Then the characteristic
 106 equation is

$$107 \quad \lambda^K - \alpha_{k+1}(y) \prod_{i=1}^k \omega_i(y) \lambda^{K-(k+1)} - \alpha_{k+2}(y) \prod_{i=1}^{k+1} \omega_i(y) \lambda^{K-(k+2)} - \dots - \alpha_K(y) \prod_{i=1}^{K-1} \omega_i(y) = 0, \quad (\text{SI } 9)$$

108 and its unique positive root is obtained as the root of equation

$$109 \quad q(\lambda) = \frac{\alpha_{k+1}(y) \prod_{i=1}^k \omega_i(y)}{\lambda^{k+1}} + \frac{\alpha_{k+2}(y) \prod_{i=1}^{k+1} \omega_i(y)}{\lambda^{k+2}} + \dots + \frac{\alpha_K(y) \prod_{i=1}^{K-1} \omega_i(y)}{\lambda^K} = 1. \quad (\text{SI } 10)$$

110 It is easy to see, that if any of the numerators (i.e. the average numbers of offspring produced
 111 by an individual of the corresponding age classes) in these fractions is changed to a greater one,
 112 then the curve of the 'hyperbolic' function q shifts upwards, implying that the positive solution
 113 λ_* of this equation also will be greater. Therefore, if in a population where within the families
 114 grandparents are not supported, a new type emerges which supports grandparents, and all
 115 mentioned numerators increase, then Fifth Rule as behaviour type will propagate. If all these
 116 numerators decrease then this type will die out. Those mathematical cases when some of the
 117 numerators increase, others decrease, would need further mathematical discussions.

118

119 Observe that equation $q(\lambda) = 1$ can be written as

$$120 \quad \prod_{i=1}^k \omega_i(y) \left(\frac{\alpha_{k+1}(y)}{\lambda^{k+1}} + \frac{\alpha_{k+2}(y) \omega_{k+1}(y)}{\lambda^{k+2}} + \dots + \frac{\alpha_K(y) \prod_{j=k+1}^{K-1} \omega_j(y)}{\lambda^K} \right) = 1. \quad (\text{SI } 11)$$

121 Here factor $\prod_{i=1}^k \omega_i(y)$ measures how much child care by grandmothers increases the survival
 122 of the children. Roughly speaking, factor

$$123 \quad \frac{\alpha_{k+1}(y)}{\lambda^{k+1}} + \frac{\alpha_{k+2}(y)\omega_{k+1}(y)}{\lambda^{k+2}} + \dots + \frac{\alpha_K(y) \prod_{j=k+1}^{K-1} \omega_j(y)}{\lambda^K} \quad (\text{SI } 12)$$

124 measures, in an implicit way, to what extent the support to grandparents by the fertile age class
 125 decreases their own fecundity and survival rates. In this sense, the predictions of our model are
 126 in harmony with the cost-benefit approach saying that a trait will propagate if it eventually
 127 increases the fitness.

128

129 Now the question arises how the demographic parameters may depend on y . The
 130 following assumptions are at hand: 1. The survival rate of grandparents is a saturation function
 131 of y strictly increasing at the beginning, and remains constant after. 2. Based on the grandmother
 132 hypothesis, the survival rate of grandchildren strictly increases with the survival rate of
 133 grandparents (which on its term depend on y). The grandmother hypothesis is the worst case
 134 when two trade-offs may exist. 3. The parents' fecundity entries of the Leslie matrix (
 135 $\alpha_{k+1}, \dots, \alpha_K$) are strictly decreasing functions of y . 4. The survival rates of parents ($\omega_{k+1}, \dots, \omega_K$)
 136 are strictly decreasing functions of y .

137 These assumptions allow the Fifth Rule to win or lose the struggle for existence,
 138 depending on whether the long-term growth rate of the family increases or decreases.

139

140 Under assumption 1 there is a threshold for the support to grandparents, above which
 141 the survival of grandparents does not increase, and therefore the survival of grandchildren

142 either, but the fecundity and/or the survival of fertile parents still decrease. Over this threshold,
143 the support to grandparents has no evolutionary advantage.

144

145 Finally, we remark that the above reasoning can be applied not only to the grandmother
146 hypothesis, since either the mother hypothesis or the embodied capital model alone can ensure
147 the support to grandparents. For example, if any of the above two hypotheses implies the
148 increase of at least one of the numerators in (3), while the rest of the numerators do not decrease,
149 then the dominant eigenvalue, i.e. the asymptotic growth rate will increase. Of course, if in
150 addition to the fact that the grandmother increases the survival of her grandchildren and the
151 survival and fertility of her daughter, the hypothesis of the embodied capital model also holds
152 (the grandmother also increases the adult age survival and fertility of her grandchildren), then
153 not only $\prod_{i=1}^k \omega_i(y)$ but also factor (4) can synergically increase the asymptotic growth rate of
154 the family.

155 Finally, we note that the “altriciality” hypothesis can also be handled in terms of a
156 linear model with a matrix structured differently from the Leslie matrices (since the survivals
157 of children also depend on the age of their mothers). Thus, only a generalization our model
158 could deal with the development of menopause based on altriciality. In our opinion, our Fifth
159 Rule may be derived on the bases of “altriciality” hypothesis, but in such a future model the
160 formation of multi-generation families should also be included, since “altriciality” hypothesis
161 itself does not need the convivence of several generations.

162

163 **3. Two-age-class model**

164 For a deeper insight, in this simplest case, we will calculate first when the menopause can
165 evolve, second, when the Fifth Rule is evolutionary successful, third, using numerical
166 examples we demonstrate that convex benefit and concave cost functions promote the
167 evolution of intra-familial help.

168

169 Consider the simplest case with one child age class and one fertile age class. Then the
170 Leslie matrix is

171
$$\begin{pmatrix} 0 & \alpha_0 \\ \omega_1 & 0 \end{pmatrix},$$

172 where ω_1 is the survival rate of children and α_0 is the fecundity of fertile parents. The survival
173 rate from fertile age to post-fertile age is ω_2 , and ω_3 denotes the probability that a post-fertile
174 individual still lives (without the support by a fertile individual) when child care is needed. Now
175 the fitness is $\lambda = \sqrt{\alpha_0 \omega_1}$.

176

177 **3.1 Grandmother hypothesis**

178 Now the question arises: When is the menopause adaptive? Consider the case when fertile
179 individuals do not support grandmothers. We consider the following two cases: (i) Suppose
180 that grandmothers do not help in child care, but their survival linearly reduces their own
181 fecundity, i.e. $\omega_2(s) := s$ and $\alpha(s) := \alpha_0(1-s)$, where $s \in [0,1)$ is the cost spent on survival to
182 post-fertile age (Fig. 3 depicts the situation). The fitness of the population is the long-term
183 growth rate which can be calculated from the characteristic equation of the Leslie matrix:

184 $\lambda(s) = \sqrt{\alpha_0(1-s)\omega_1}$, and the optimal strategy is not to spend on own survival to post-fertile
185 age. (ii) Suppose that grandmothers help in child care (Figure S 2.b). Let $\omega_2(s) := \bar{\omega}_2 s$, with
186 some $\bar{\omega}_2$, $\alpha(s) := \alpha_0(1-s)$ and $\omega_1(s) := \omega_1 + a_{21}P(s)$, where $s \in [0,1)$, ω_1 is a „basic“
187 survival rate, and the probability that a grandmother is alive when her help needed is
188 $P(s) := \bar{\omega}_2 \omega_3 s$, i.e. we count only the help of those grandmothers who survive to the upper
189 boundary of the third age class and do not count those who reach ‘grandmother age’ (reach
190 the third class) but die before the upper boundary of age, and a_{21} denotes the efficiency of the
191 grandmother’s grandchild care. Clearly $a_{21}\bar{\omega}_2\omega_3 < 1$ and $\omega_1(s) = \bar{\omega}_1 + a_{21}\bar{\omega}_2\omega_3 s$, thus the
192 fitness is

$$193 \quad \lambda(s) = \sqrt{\alpha_0(1-s)(\bar{\omega}_1 + a_{21}\bar{\omega}_2\omega_3 s)}, \quad (\text{SI } 13)$$

194 which is maximal at $s^* = \frac{a_{21}\bar{\omega}_2\omega_3 - \bar{\omega}_1}{2a_{21}\bar{\omega}_2\omega_3}$. Therefore, if the effect of grandchild care on the
195 grandchild’s survival is greater than his/her survival rate without this care, i.e. $a_{21}\bar{\omega}_2\omega_3 > \bar{\omega}_1$,
196 then menopause is evolutionarily successful.

197
198

199 **3.2 The Fifth Rule**

200 Now the question arises: When is Fifth Rule adaptive? It requires us to support our elderly,
201 which is possible only if the menopause has already become evolutionarily fixed, i.e. for fixed
202 $s \in [0,1)$, let $\omega_2 := \bar{\omega}_2 s$ and $\alpha := \alpha_0(1-s)$. Let $y \in [0,1]$ denote the cost spent on the survival of
203 post-fertile parents, and suppose that the negative effect of y on fecundity is linear: $\alpha(1-y)$,
204 the children survival is $\omega_1(y) := \bar{\omega}_1 + aP(y)$, where $P(y) := \omega_2(\omega_3 + by)$ and b indicates how

205 efficiently the support to post-fertile parents by fertile individuals increases post-fertile
 206 survival, so $\omega_1(y) := \bar{\omega}_1 + a\omega_2(\omega_3 + by)$ (Fig. 4 depicts the situation). Now we have to
 207 maximize the fitness which can be calculated from the characteristic equation of the Leslie
 208 matrix, it is given by the following function in y :

209
$$\lambda(y) = \sqrt{\alpha(1-y)(\bar{\omega}_1 + a\omega_2(\omega_3 + by))}, \quad (\text{SI 14})$$

210 which attains its maximum at $y^* = \frac{a\omega_2(b - \omega_3) - \bar{\omega}_1}{2ab\omega_2}$. The latter is positive if

211 $a\omega_2(b - \omega_3) - \bar{\omega}_1 > 0$. This condition is satisfied e.g., if the efficiency of the support to post-
 212 fertile parents is sufficiently large compared to the basic post-fertile survival rate.

213

214

215 **3.3 A general multiplicative coevolution model**

216 Now we set up a model combining the model of grandmother hypothesis and the
 217 model of the Fifth Rule. Our study will be based on two biological preconditions: First, since
 218 one can help a grandmother only if she is alive, for the development of the Fifth Rule, the
 219 existence of menopause is needed. Second, if a fertile mother gave away all her resources to
 220 help the survival of her mother, her fecundity would be zero. As before, let s be the cost a
 221 fertile female spends on her own survival to post-fertile age, and y the cost a fertile female
 222 spends on the survival of post-fertile parents. Based on the first precondition, unlike the
 223 additive approach of sections 3.2 and 3.3, we express the effect of strategies s and y on the
 224 demographic parameters in multiplicative form, considering the following strategy-dependent
 225 Leslie matrix:

226
$$L(s, y) := \begin{pmatrix} 0 & \alpha_0 \alpha(s, y) \\ \bar{\omega}_1 P(s, y) & 0 \end{pmatrix}, \quad (\text{SI } 15)$$

227 where in both variables $P(s, y)$ is strictly monotonically increasing, and $\alpha(s, y)$ is strictly
 228 monotonically decreasing. Let us assume that strategies s and y act independently both on the
 229 fecundity and on the survival of children:

230
$$P(s, y) = p(s)q(y), \quad \alpha(s, y) = \beta(s)\gamma(y), \quad (\text{SI } 16)$$

231 where all one-variable functions are defined on $[0,1]$.

232 Technical conditions on the functions involved:

233 a) p, q, β, γ are twice continuously differentiable.

234 b) $p(0) = q(0) = 1, \beta(0) = \gamma(0) = 1$. We note that these technical conditions imply that
 235 $\bar{\omega}_1$ and α_0 are the demographic parameters before the appearance of the considered
 236 traits, while $\beta(1) = \gamma(1) = 0$ expresses our second precondition.

237 c) $p'(s), q'(y) > 0$ ($s, y \in [0,1]$), $\bar{\omega}_1 p(1)q(1) < 1$.

238 d) $\beta'(s), \gamma'(y) < 0$ ($s, y \in (0,1]$), $\beta'(0) = \gamma'(0) = 0$.

239 Observe that conditions c) and d) are mathematical descriptions of trade-offs.

240 e) $p''(s), q''(y), \beta''(s), \gamma''(y) < 0$ ($s, y \in (0,1)$). (This condition will guarantee strict concavity
 241 of function z near its maximum).

242

243 Now, the fitness (unique positive eigenvalue of $L(s, y)$) is

244
$$\lambda(s, y) = \sqrt{\bar{\omega}_1 \alpha_0 p(s)q(y)\beta(s)\gamma(y)} \quad (s, y \in [0,1]). \quad (\text{SI } 17)$$

245 We will show that $\lambda(s, y)$ attains a strict local maximum at an interior point of the unit square
 246 $[0,1] \times [0,1]$. Indeed, maximization of $\lambda(s, y)$ is equivalent to the maximization of

247
$$z(s, y) = \bar{\omega}_1 \alpha_0 p(s)q(y)\beta(s)\gamma(y) \quad (s, y \in [0,1]). \quad (\text{SI } 18)$$

248 The first order necessary condition for the maximum attained at an interior point is

$$249 \quad \frac{\partial}{\partial s} z(s, y) = q(y)\gamma(y)(\beta(s)p'(s) + p(s)\beta'(s)) = 0, \quad (\text{SI 19})$$

$$250 \quad \frac{\partial}{\partial y} z(s, y) = p(s)\beta(s)(\gamma(y)q'(y) + q(y)\gamma'(y)) = 0 \quad (\text{SI 20})$$

251 Since p, q, β, γ are all positive in the interval $(0,1)$, the above necessary condition is

252 equivalent to

$$253 \quad \varphi(s) := \beta(s)p'(s) + p(s)\beta'(s) = 0, \quad (\text{SI 21})$$

$$254 \quad \psi(y) = \gamma(y)q'(y) + q(y)\gamma'(y) = 0. \quad (\text{SI 22})$$

255 From conditions b), c) and d) we obtain $\varphi(0) > 0$, $\varphi(1) < 0$, hence there is an $s^* \in (0,1)$ with

256 $\varphi(s^*) = 0$. It is easy to check that conditions b), c), d) and e) also imply $\varphi'(s) < 0$, and hence φ is

257 strictly decreasing, therefore s^* is its unique zero in the interval $(0,1)$. Similar straightforward

258 checking shows that $\psi(y)$ also has a unique zero y^* in the interval $(0,1)$. Hence (s^*, y^*) is a

259 unique stationary point of function z in the interior of the unit square.

260 Now, for a second order sufficient condition for the maximum of function z , we calculate its

261 Hessian:

262

$$263 \quad H(s, y) = \begin{pmatrix} q(y)\gamma(y)(\beta(s)p''(s) + 2p'(s)\beta'(s) + p(s)\beta''(s)) & (\beta(s)p'(s) + p(s)\beta'(s))(\gamma(y)q'(y) + q(y)\gamma'(y)) \\ (\beta(s)p'(s) + p(s)\beta'(s))(\gamma(y)q'(y) + q(y)\gamma'(y)) & p(s)\beta(s)(\gamma(y)q''(y) + 2q'(y)\gamma'(y) + q(y)\gamma''(y)) \end{pmatrix},$$

$$264 \quad (\text{SI 23})$$

265 Observe that from $\varphi(s^*) = 0$ and $\psi(y^*) = 0$, we obtain

$$266 \quad H(s^*, y^*) = \begin{pmatrix} q(y^*)\gamma(y^*)(\beta(s^*)p''(s^*) + 2p'(s^*)\beta'(s^*) + p(s^*)\beta''(s^*)) & 0 \\ 0 & p(s^*)\beta(s^*)(\gamma(y^*)q''(y^*) + 2q'(y^*)\gamma'(y^*) + q(y^*)\gamma''(y^*)) \end{pmatrix}$$

267 From conditions a)-e), we easily get

$$268 \quad q(y^*)\gamma(y^*)(\beta(s^*)p''(s^*) + 2p'(s^*)\beta'(s^*) + p(s^*)\beta''(s^*)) < 0 \quad (\text{SI 24})$$

269
$$p(s^*)\beta(s^*)(\gamma(y^*)q''(y^*) + 2q'(y^*)\gamma'(y^*) + q(y^*)\gamma''(y^*)) < 0, \quad (\text{SI } 25)$$

270 imply $\text{tr}H(s^*, y^*) < 0$ and $\det H(s^*, y^*) > 0$, i.e. $H(s^*, y^*)$ is negative definite. Therefore (s^*, y^*)
271 is a strict local maximum point. Since (s^*, y^*) is the unique stationary point, it is also a strict
272 global maximum point in the interior of the unit square.

273 Finally, we note that, if Hessian $H(s, y)$ is negative definite in the interior of the unit
274 square, then function λ is globally strictly concave, and therefore (s^*, y^*) is a global
275 maximum point of λ . In the terminology of fitness landscapes, in the sense of any reasonable
276 strategy dynamics the species will evolve into the evolutionarily optimal behavior (s^*, y^*) .

277

278 **3.4 Numerical Examples**

279 In this section, by numerical study, we illustrate the effect of different (linear, convex and
280 concave) trade-offs on the level of the optimal backward help (y^*). We calculated the
281 maximal long-term growth rate (fitness) of various populations as a function of y from the
282 characteristic equation of the corresponding Leslie matrix. The value of y that gives the
283 highest long-term growth rate termed as the optimal backward help (y^*). We also calculated
284 the number of offspring and the offspring survival given the optimal y^* . We investigated the
285 effects of different cost-benefit parameters on the evolvability of backward help (y). Life-
286 history parameters are based on the figures from Mace [1]. It is possible to generate all the
287 possible combinations of cost-benefit trade-offs by setting the appropriate cost, benefit
288 parameters to zero (c, d, h). Also, convex or concave cost-benefit functions can be achieved
289 by setting the appropriate parameters (c, d, h) to smaller or to greater than one (see Table S1
290 for a summary of parameters). We used the following general Leslie matrix (see Fig. 5 for a
291 schematic description):

292

293
$$\left(\begin{array}{c} 0 \\ \bar{\omega}_1 + a_{21}\omega_2(1-y)^d(\omega_3 + b(1-(1-y)^h)) \end{array} \alpha(1-y)^c + a_{12}\omega_2(1-y)^d(\omega_3 + b(1-(1-y)^h)) \right)$$

294

295

296

297

<p>Life-history parameters</p> <p>α: Number of offspring ω_1: survival of the first age class (offspring) ω_2: survival of the first reproductive class (parents) ω_3: survival of the non-reproductive class (grandparents)</p> <p>Benefit-parameters</p> <p>a_{12}: efficacy of the granny's help on the fecundity of the parent a_{21}: efficacy of the granny's help on the survival of the offspring b: effectiveness of IT, the maximum efficacy of the parents help on the grandparent's survival h: efficacy of the parents help (steepness)</p> <p>Cost parameters</p> <p>c: cost of helping grannies on the fecundity of the parent (steepness) d: cost of helping grannies on the survival of the parent (steepness)</p>
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299

300 Four possible combinations exist in terms of the benefit functions: (i) $a_{12}, a_{21} > 0$; (ii)
 301 $a_{12} > 0, a_{21} = 0$, (iii) $a_{12} = 0, a_{21} > 0$; and (iv) $a_{12}, a_{21} = 0$. In the first case, grandmothers give
 302 benefits for both the number of offspring and for the survival of them, in the second case they
 303 give benefit only for the number of offspring; in the third case they only give benefit for the
 304 survival of the offspring and finally, in the last case, they do not provide any benefit. This last
 305 case is not interesting for us, thus it will not be investigated any further.

306 In the same way, four possible combinations exist in terms of the cost functions: (i) $c,$
 307 $d > 0$; (ii) $c > 0, d = 0$, (iii) $c = 0, d > 0$; and (iv) $c, d = 0$. In the first case helping
 308 grandmothers imposes a cost on both the parents' reproductive output and on the parents'
 309 survival, in the second case only on the number of offspring, in the third only on the survival
 310 of the parent, and finally, in the last case it imposes no cost at all. Just as before, this last case

311 is not interesting for us, thus it will not be investigated any further. See Table S2 for
 312 investigated parameter combinations.

313

314 **Table S2.** The investigated parameter combinations (see Figures S1-S7 for the corresponding
 315 results).

	Grandparental help	Shape of the cost function	Shape of the benefit function	Figure:
1.	$a_{12}, a_{21} > 0$	$d = 1$	$h = 1$	S1
2.		$d = 1$	$h = 2$	S2
3.		$d = 0.5$	$h = 2$	S3
4.	$a_{12} = 0, a_{21} > 0$	$d = 1$	$h = 1$	S4
5.		$d = 0.5$	$h = 2$	S5
6.	$a_{12} > 0, a_{21} = 0$	$d = 1$	$h = 1$	S6
7.		$d = 0.5$	$h = 2$	S7

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317 **3.5 Illustrative numerical examples: results**

318 IT evolves the most readily when the grandparental help increases both the survival of
 319 the offspring and the number of offspring (Figure S1-S3). Linear cost and benefit functions do
 320 not favour the evolution of IT (Figs. S1, S4, S6, $d=1, h=1$); conversely, convex benefit and
 321 concave cost functions promote the evolution of IT (Fig. S2, S3, S5, S7, $d=0.5, h=2$). It is
 322 possible to find cost parameters (c, d) where IT evolves even if the efficacy parental transfer
 323 and grandparental help (a_{21} and b respectively) is low (Figs. S2, S3). Conversely, it is possible

324 to find (high) a_{21} , b parameters where IT evolves even if it imposes a high cost on the survival
325 of the parents or on the number of offspring (d and c , respectively, see Figs. S1, S2).

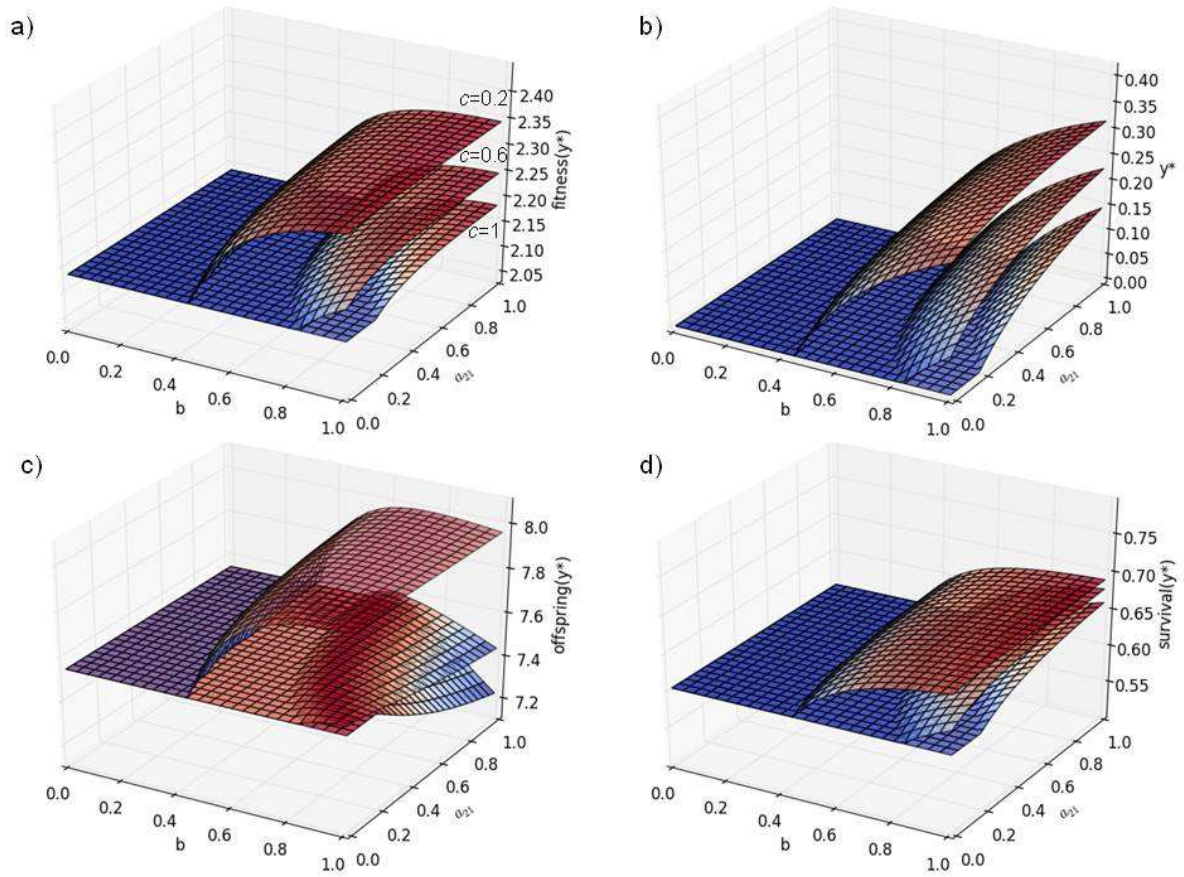
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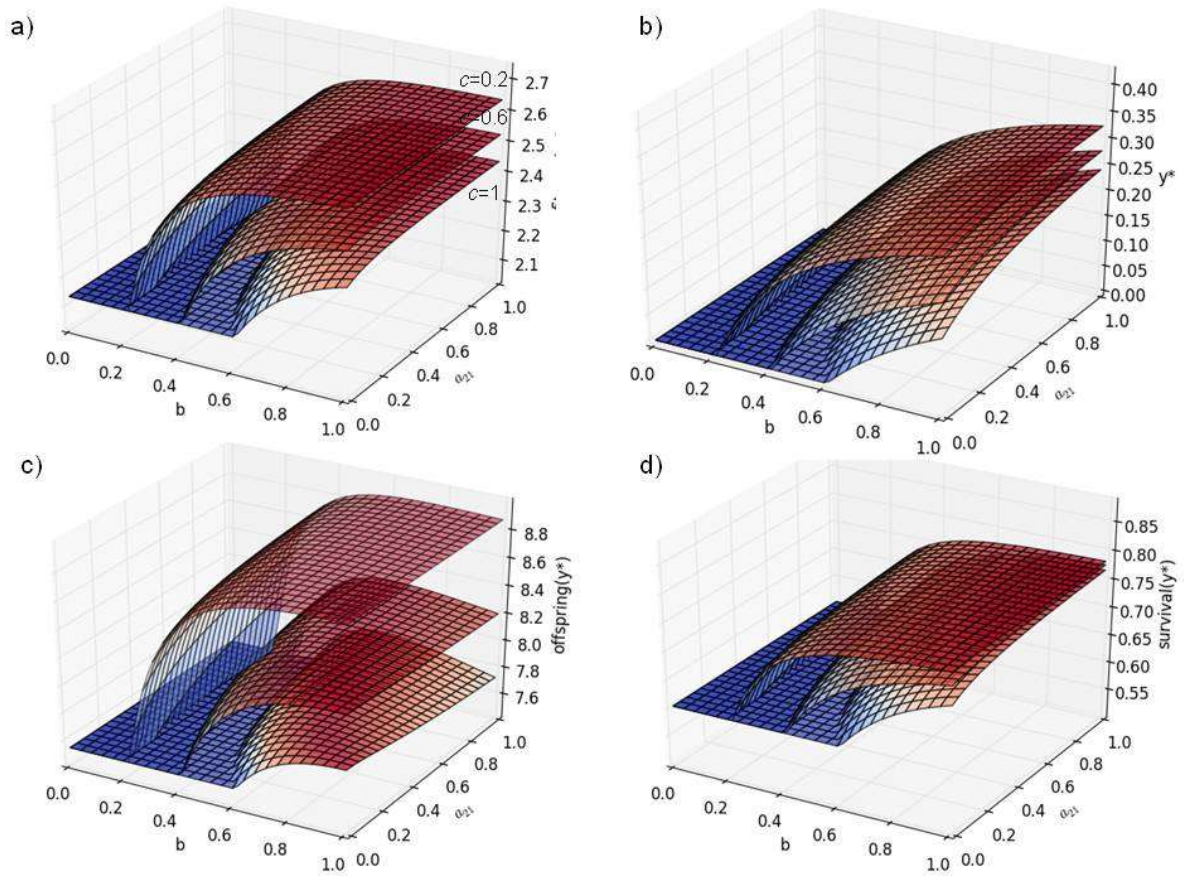
333 **Figure S1.** Numerical example for the Fifth Rule, grandmothers increase both offspring
334 survival and the number of offspring ($a_{12}, a_{21} > 0$). a) Dominant eigenvalues (fitness); b)
335 corresponding y^* value; c) offspring number as a function of y^* ; d) survival of offspring as a
336 function of y^* ; all four subfigures plotted as a function of the effectiveness of IT (b) and the
337 efficacy of the grandparental help on the survival of the offspring (a_{21}). Parameters: $\alpha_2=6$,
338 $\omega_1=0.45$, $\omega_2=0.62$, $\omega_3=0.25$, $d = 1$, $h = 1$, $c = 0.2, 0.6, 1$; $a_{12}=10$.

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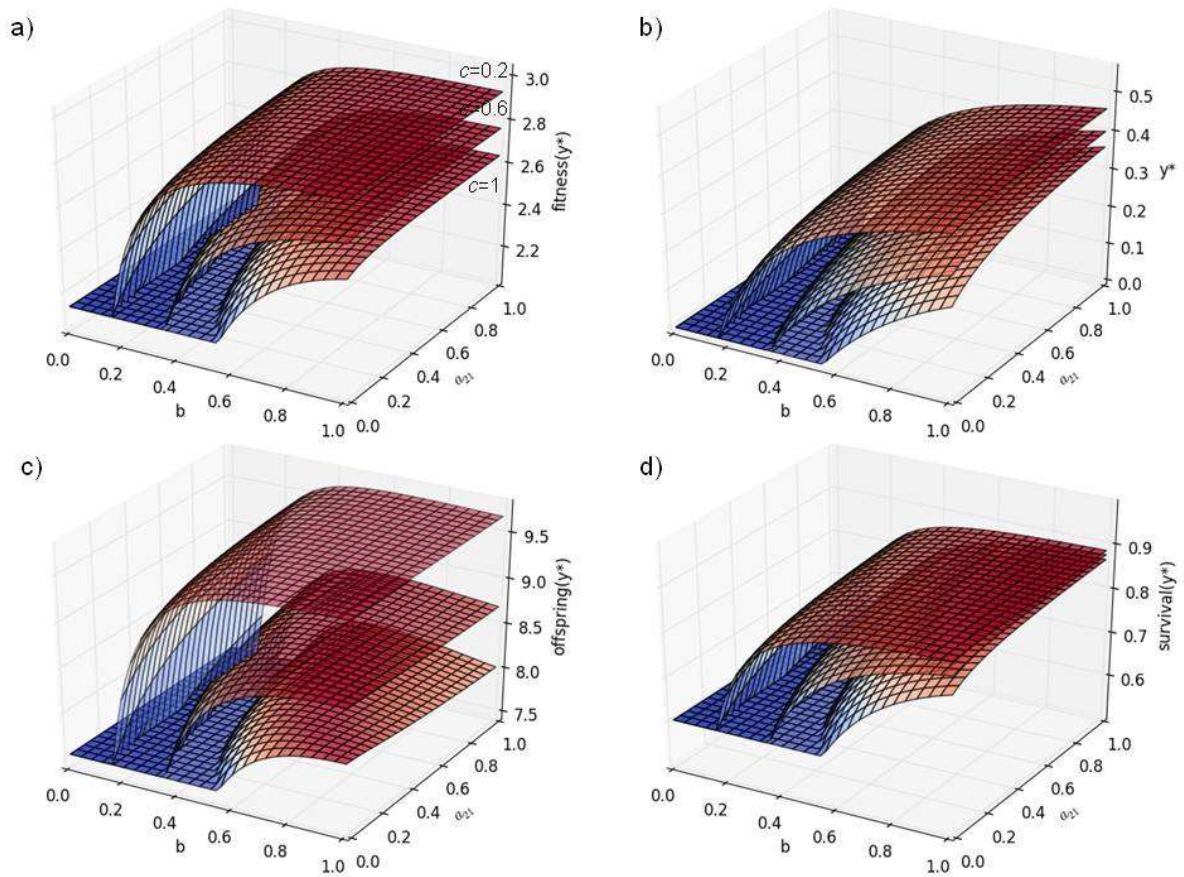
345 **Figure S2.** Numerical example for the Fifth Rule: grandmothers increase both offspring
346 survival and the number of offspring ($a_{12}, a_{21} > 0$). a) Dominant eigenvalues (fitness); b)
347 corresponding y^* value; c) offspring number as a function of y^* ; d) survival of offspring as a
348 function of y^* ; all four subfigures plotted as a function of the effectiveness of IT (b) and the
349 efficacy of the grandparental help on the survival of the offspring (a_{21}). Parameters: $\alpha_2=6$,
350 $\omega_1=0.45, \omega_2=0.62, \omega_3=0.25, d=1, h=2, c=0.2, 0.6, 1; a_{12}=10$.

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357 **Figure S3.** Numerical example for the Fifth Rule: grandmothers increase both offspring
358 survival and the number of offspring ($a_{12}, a_{21} > 0$). a) Dominant eigenvalues (fitness); b)
359 corresponding y^* value; c) offspring number as a function of y^* ; d) survival of offspring as a
360 function of y^* ; all four subfigures plotted as a function of the effectiveness of IT (b) and the
361 efficacy of the grandparental help on the survival of the offspring (a_{21}). Parameters: $\alpha_2=6$,
362 $\omega_1=0.45$, $\omega_2=0.62$, $\omega_3=0.25$, $d = 0.5$, $h = 2$, $c = 0.2, 0.6, 1$; $a_{12}=10$.

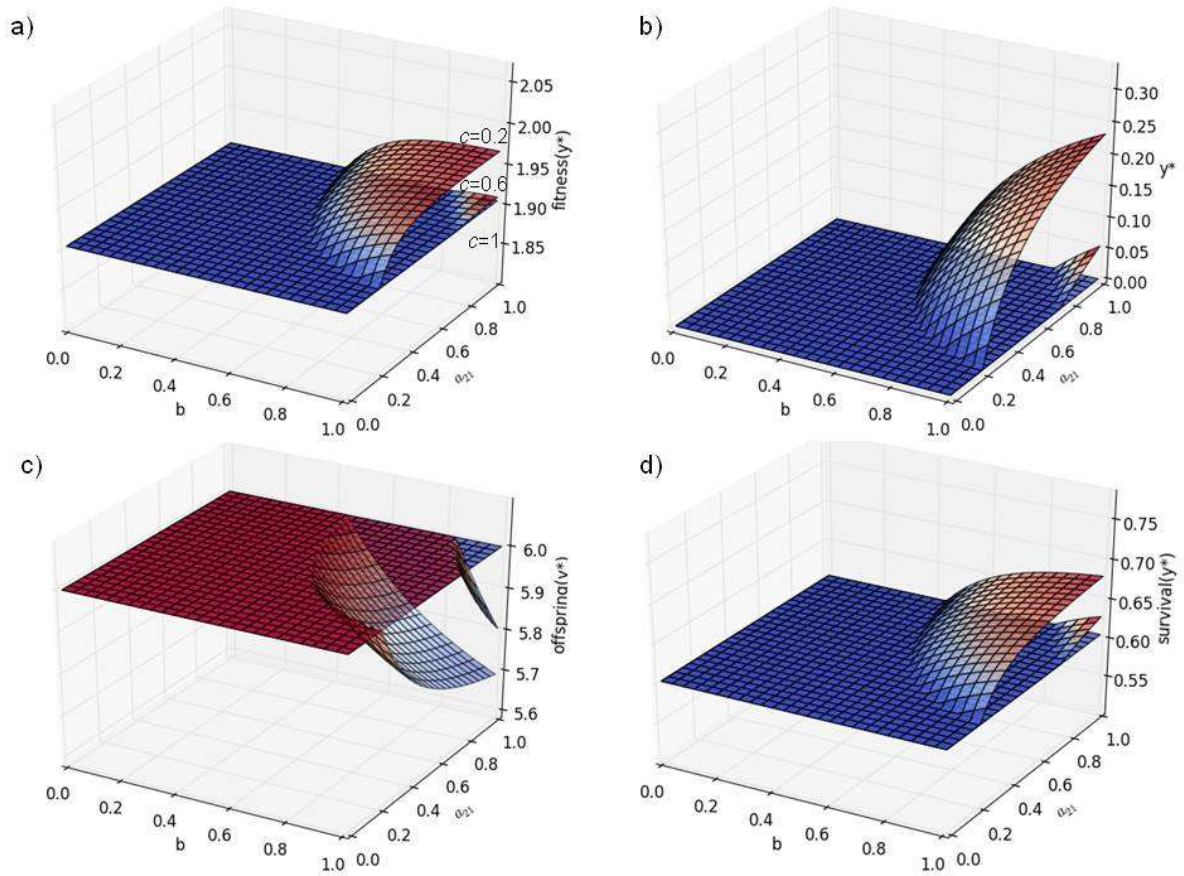
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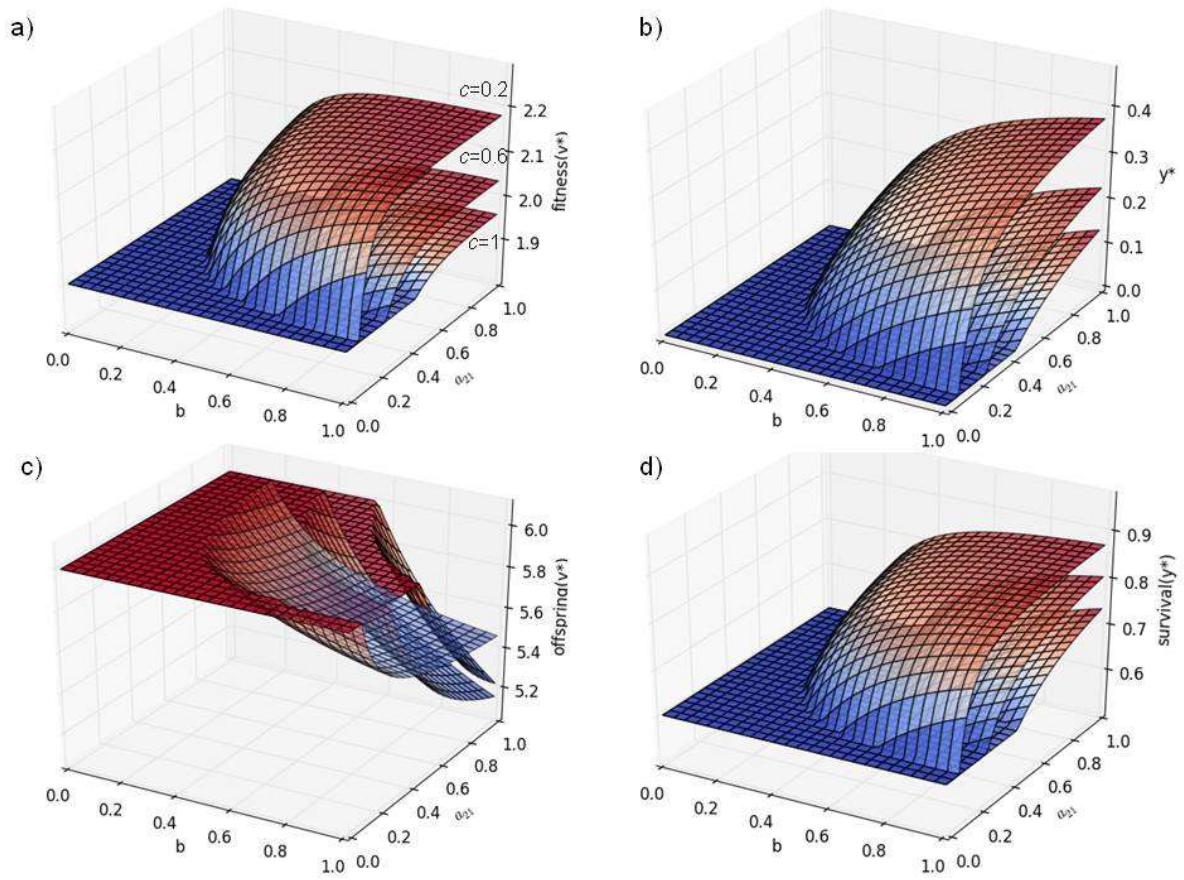
370 **Figure S4.** Numerical example for the Fifth Rule, grandmothers only increase offspring
371 survival ($a_{12}=0$, $a_{21} > 0$). a) Dominant eigenvalues (fitness); b) corresponding y^* value; c)
372 offspring number as a function of y^* ; d) survival of offspring as a function of y^* ; all four
373 subfigures plotted as a function of the effectiveness of IT (b) and the efficacy of the
374 grandparental help on the survival of the offspring (a_{21}). Parameters: $\alpha_2=6$, $\omega_1=0.45$, $\omega_2=0.62$,
375 $\omega_3=0.25$, $d=1$, $h=1$, $c=0.2, 0.6, 1$; $a_{12}=0$.

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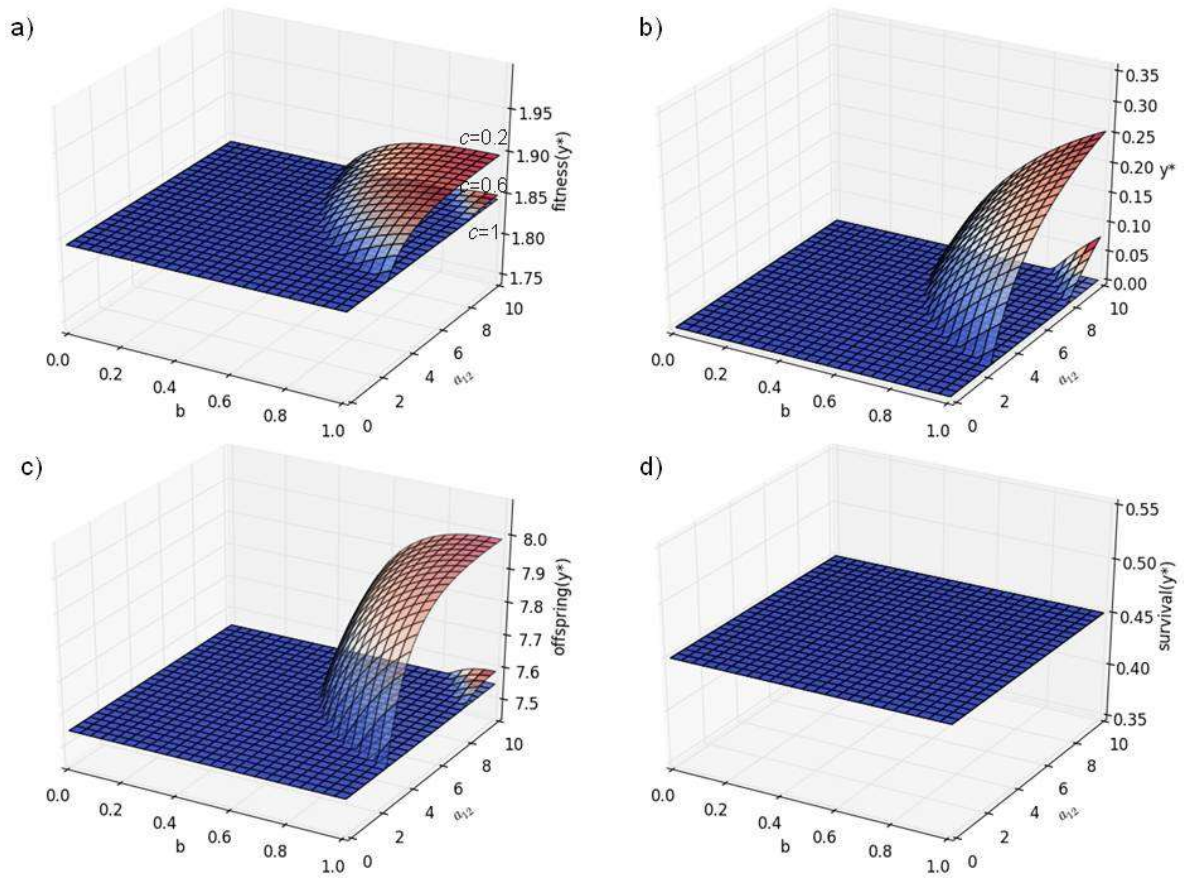


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382 **Figure S5.** Numerical example for the Fifth Rule, grandmothers only increase offspring
383 survival ($a_{12}=0$, $a_{21} > 0$). a) Dominant eigenvalues (fitness); b) corresponding y^* value; c)
384 offspring number as a function of y^* ; d) survival of offspring as a function of y^* ; all four
385 subfigures plotted as a function of the effectiveness of IT (b) and the efficacy of the
386 grandparental help on the survival of the offspring (a_{21}). Parameters: $\alpha_2=6$, $\omega_1=0.45$, $\omega_2=0.62$,
387 $\omega_3=0.25$, $d=0.5$, $h=2$, $c=0.2, 0.6, 1$; $a_{12}=0$.

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392 **Figure S6.** Numerical example for the Fifth Rule, grandmothers only increase offspring

393 number ($a_{12} > 0$, $a_{21} = 0$). a) Dominant eigenvalues (fitness); b) corresponding y^* value; c)

394 offspring number as a function of y^* ; d) survival of offspring as a function of y^* ; all four

395 subfigures plotted as a function of the effectiveness of IT (b) and the efficacy of the

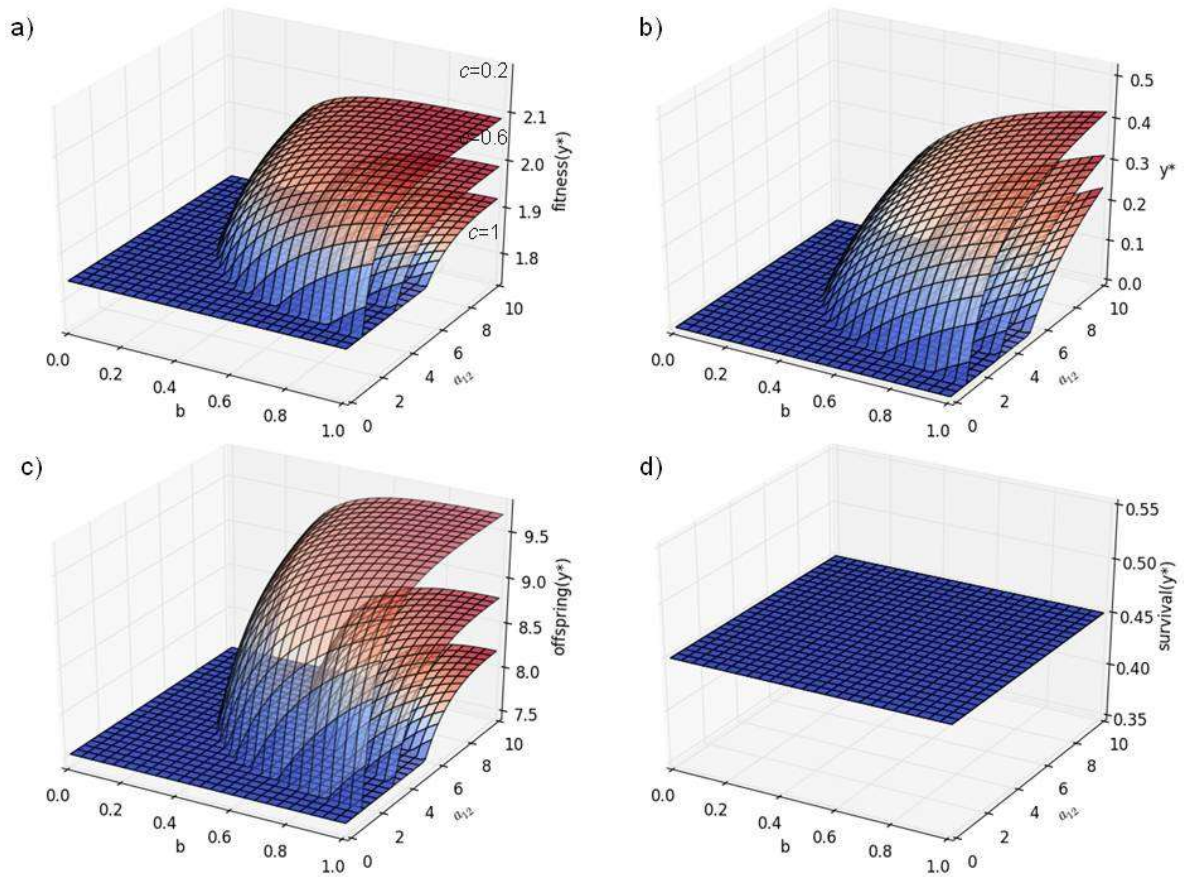
396 grandparental help on the fecundity of the parent (a_{12}). Parameters: $\alpha_2=6$, $\omega_1=0.45$, $\omega_2=0.62$,

397 $\omega_3=0.25$, $d = 1$, $h = 1$, $c = 0.2, 0.6, 1$; $a_{21} = 0$.

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404 **Figure S7.** Numerical example for the Fifth Rule, grandmothers only increase offspring

405 number ($a_{12} > 0$, $a_{21} = 0$). a) Dominant eigenvalues (fitness); b) corresponding y^* value; c)

406 offspring number as a function of y^* ; d) survival of offspring as a function of y^* ; all four

407 subfigures plotted as a function of the effectiveness of IT (b) and the efficacy of the

408 grandparental help on the fecundity of the parent (a_{12}). Parameters: $\alpha_2=6$, $\omega_1=0.45$, $\omega_2=0.62$,

409 $\omega_3=0.25$, $d = 0.5$, $h = 2$, $c = 0.2, 0.6, 1$; $a_{21} = 0$.

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412 **References**

- 413 1. Mace R: **Evolutionary ecology of human life history**. *Animal behaviour* 2000,
414 **59(1):1-10**.
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