

Caring for parents: an evolutionary rationale

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21 **Abstract:** The evolutionary roots of human moral behavior are a key precondition to
22 understand human nature. Here we investigate whether a biological version of Fifth
23 Commandment ("Honor your father and your mother, that your days may be long"),
24 respected in different variants across cultures, can spread through Darwinian competition.
25 We show by a novel demographic model that a corresponding Fifth Rule ("During your
26 reproductive period, give away from your resources to your post-fertile parents") will
27 spread even if the cost of support to post-fertile grandmothers considerably decreases the
28 demographic parameters of fertile parents but radically increases the survival rate of
29 grandchildren. Teaching vital cultural content is likely to have been critical for the value of
30 grandparental service. Selection on such behavior may have produced an innate moral
31 tendency to honor parents even in situations, such as experienced today, when the
32 quantitative conditions would not necessarily favor the maintenance of this trait.

33

34 **Keywords:** 5th commandment, intra-familial resource transfer, kin demography,
35 menopause, grandmother, grandchild

36

37

38 1. Background

39 Darwin [1] already raised the possibility that moral has evolutionary origin. There are
40 several models rooted in evolutionary theory that shed light on some basic moral issue [2-5].
41 In contrast, we start with a moral commandment, and investigate whether a phenotype
42 corresponding to this moral commandment wins in a Darwinian struggle for existence or not,
43 similar to an investigation of the conditions under which spiteful behavior will die out [6].
44 Here we investigate the cultural norm that promotes the help of the parents (we discuss the
45 issue of grandfathers later). We refer to this norm as the Fifth commandment (see
46 Supplementary Information, see *SI*). This norm has obvious links to biology, and variants of
47 it can also be found in various cultures ranging from the East to the West (*SI*). There is
48 widespread evidence not just for the existence of such norm but for the actual support as well.
49 The form of this support can vary across cultures (emotional, instrumental, financial, etc.)
50 and might be a function of other factors, such as the health of the elderly parents, but this
51 kind of help is readily observed across different cultures [7-11]. Investigating the dynamics
52 of such norm can shed light on the evolutionary roots of religion also [12].

53

54 In the course of standard human life history infants grow to become parents who age
55 into being grandparents. Thus, longevities permitting, respect and help to parents turn out to
56 be targeted to the grandparents of one's children. This truism has important consequences for
57 the possible spread of such a behavioral trait. Behaviors can be inherited, which can be the
58 result of either genetic or cultural transmission. This inheritance assumption immediately

59 implies that if the support to grandparents spreads by Darwinian selection, then that ensures
60 longer life for the parents as their children inherit their behavior. Similarly to classical
61 evolutionary game theory, we will not consider the genetic background of the behavior [13].
62 An adaptive phenotype will outperform its rivals on a Darwinian selection time scale, where
63 Darwinian fitness is the average growth rate of a phenotype.

64

65 The establishment of a post-fertile period is critical for our case. Several hypotheses
66 deal with the origin of the menopause.

67 Shanley and Kirkwood [14] investigate two alternative theories that might explain the
68 origin of menopause. The first one can be called as the “altriciality” hypothesis that observes
69 that maternal mortality is increasing with age. It implies a trade-off between rearing existing,
70 still altricial children and giving birth to a new one. The second one is the mother hypothesis.
71 The mother hypothesis states that the post-fertile grandmother helps her fertile daughter [15].
72 They found that neither of these ideas alone is sufficient to explain the evolution of
73 menopause under a realistic range of life-history parameters; however, a combined model
74 can explain it [14, 16]. Their conclusion is corroborated by other studies both with regard to
75 altriciality [17] as well as to kin-selection [18].

76 According to the grandmother hypothesis [19-24] the advantage of the post-fertile
77 stage is that grandmothers increase the survival of their grandchildren [20, 24, 25]. increasing
78 either the survival rate or the fecundity of the latter [26, 27]. A third hypothesis is the
79 “embodied capital model”, which emphasizes that the inter-generational transfer of skill,
80 knowledge and social ability needs time, and both grandmothers and grandfathers could help

81 the “training” of their grandchildren [28]. The attained skills and knowledge during
82 childhood can increase the survival rate and fecundity for the whole adult life period of the
83 grandchildren; see Figure 1.a-c for a comparison of these alternatives. These three hypotheses
84 do not necessary exclude each other since the care for pre-fertile individuals includes
85 breastfeeding, transport, feeding and protection as well as affection and education [25, 29,
86 30].

87 All these hypotheses are aimed at explaining the evolutionary advantage of the long
88 post-fertile life period of *Homo sapiens*. However, none of them assumes a transfer of
89 resources from the parents to the grandparents, thus none of them investigates the trade-off
90 situation between parental reproduction or survival and the support to grandparents. The
91 central question is this: Will support to post-fertile grandmothers spread even if there is a
92 trade-off between this support and either the fecundity or the survival rate of fertile parents?
93

94 Chu & Lee [3] investigated the evolution of intergenerational transfer (IT) from
95 parents to grandparents in the framework of a cooperative game and they already pointed out
96 that “filial piety” can evolve by division of labor. Fertile female transfers some energy to her
97 mother, enabling the latter to redirect her efforts from inefficient foraging to grandchildren
98 care. During this time the fertile female is free from caring and she can go to forage with
99 higher efficiency than her mother. In other words, this model describes a synergistic situation
100 where everyone does the task she is the most efficient in. But the authors do not consider the
101 trade-off we wish to investigate (see Figure 1.d).

102

103 We strongly concur with the statement that “Even to demonstrate, for example, that post
104 reproductive women result in a reduction in grandchild mortality *does not establish that*
105 *menopause is adaptive unless it can be demonstrated that overall fitness is actually*
106 *enhanced.*” [16] (pp. 27, their emphasis). In establishing the selective advantage of care for
107 grandmothers we consider the effect of overall fitness of the family.

108

109 Since in our problem pre-fertile, fertile and post-fertile individuals live together in a
110 family, we have to consider a kin demographic selection model [3, 31, 32], in which the
111 survival and the fecundity parameters depend on the costs and benefits of intra-familial
112 supports. After setting up the model we investigate whether the Fifth Rule (as a biological
113 distillation of the Fifth Commandment; see *Materials and Methods*) wins in a Darwinian
114 struggle for existence. Finally, we discuss our results.

115

116 **2. Results**

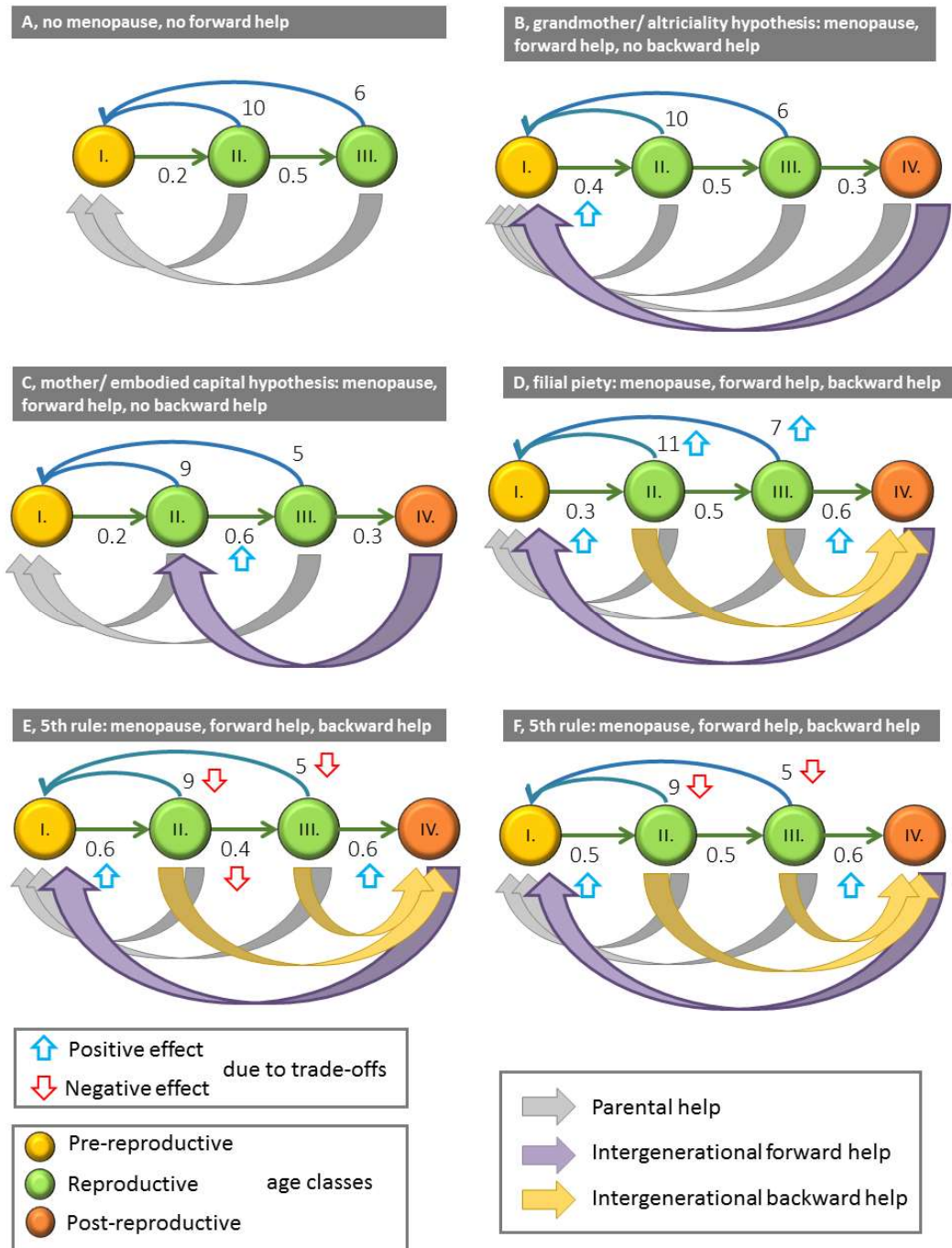
117 We consider a Leslie matrix model (see *Materials and Methods*). What is the effect
118 of the Fifth Rule on the entries of the above Leslie matrix? For the simplest mathematical
119 formulation we assume that the cost of supporting grandmothers does not depend on the age
120 class of either parents or grandmothers. Let $y \in [0,1]$ be the cost spent on grandparent support.
121 If grandmothers help in child care, the survival rates of children ω_i increase with y , and based
122 on the grandmother and the mother hypotheses, ω_j decreases and α_j increases with

123 increasing y , where $\omega_i(y)$ ($i=1, \dots, k$) denote the survival rates of children, $\omega_j(y)$ and $\alpha_j(y)$
124 ($j=k+1, \dots, K$) are the survival rate and fecundity of fertile parents, respectively.

125

126 Since there is a difference in intra-familial support between families, the Leslie
127 matrices of different family types are different. What kind of intra-familial support ensures
128 the highest long-term growth rate for the family? For sake of simplicity we denote help from
129 the grandmothers to children as “forward help” and help from the parents to the grandparents
130 as “backward help”. (See Fig.1 for comparison of the different models.) Under well-known
131 conditions (fulfilled in our case), the unique positive eigenvalue of Leslie-matrix is the long-
132 term growth rate of the family, thus we consider this eigenvalue as fitness [33, 34]. Formally,
133 the fitness $\lambda(y)$ is the unique positive eigenvalue of the y -dependent Leslie matrix (see
134 *Materials and Methods*), hence, other things being equal, families helping grandmothers are
135 competitively superior to those without this behavior.

136



137

138 **Figure 1.** Schematic representation of the different theories. Grey arrows denote parental

139 help; purple arrows denote forward help from the grandmothers to the grandchild, finally

140 yellow arrows denote backward transfer of resources from the parents to the grandparents.
141 Upward blue and downward red arrows denote positive and negative effects from trade-offs
142 respectively. (a) Standard life-history model, no menopause, no forward help and no
143 backward help; (b) grandmother (purple arrow from VI to I)/ altriciality (grey arrow from
144 VI to I) hypothesis: menopause evolved, no backward help from parents to grandmothers;
145 (c) mother and/or embodied capital hypothesis: menopause evolved, no backward help
146 from parents to grandmothers; (d) filial piety: menopause evolved, synergistic division of
147 labor with backward help from parents to grandmothers, no trade-offs; (e) Fifth rule:
148 menopause evolved, backward help from parents to grandmothers, three-way trade-off for
149 the parents between survival, fecundity and helping the grandmothers; (f) Fifth Rule:
150 menopause evolved, backward help from parents to grandmothers, two-way trade-off for
151 the parents between fecundity and helping the grandmothers.

152

153 ***Grandmother hypothesis***

154 Consider the case when fertile individuals do not support grandmothers (see Figure
155 1.e for a general depiction of the idea). We consider the following two cases (see *Materials*
156 *and Methods*): (i) If grandmothers do not help in child care, but their survival linearly reduces
157 their own fecundity, then the optimal strategy is not to spend on own survival to post-fertile
158 age. (ii) If grandmothers help in child care then the menopause is evolutionarily successful
159 if the effect of grandchild care ($a_{21}\bar{\omega}_2\omega_3$) on the grandchild's survival ($\bar{\omega}_1$) is greater than
160 his/her survival rate without this care, i.e. $a_{21}\bar{\omega}_2\omega_3 > \bar{\omega}_1$ (see Table 1 for notation, $\bar{\omega}_*$ denotes
161 averages). Summing up, the grandmother hypothesis concerns the way a female of

162 reproductive age allocates her resource between own survival and fecundity. Note that we
163 have adopted the hypothesis that the cost spent on living to the post-fertile age reduces
164 fecundity. Without this trade-off, living to the post-fertile age is a neutral property in the first
165 case, and a benefit in the second case.

166

167 **Table 1.** Notation of the model.

Life-history parameters
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)
Benefit-parameters
a_{21} : efficacy of the grandparent's help on the survival of the offspring
b : effectiveness of backward help, the maximum efficacy of the parents help on the grandparent's survival

168

169

170 ***The Fifth Rule***

171 The fifth rule requires us to support our elderly (see Figure 1.f for a general depiction
172 of the idea), which may occur when the menopause has already become evolutionarily fixed
173 (see *Materials and Methods*). We show (SI) that the Fifth Rule (backward help) evolves
174 when $a_{21}\omega_2(b - \omega_3) > \bar{\omega}_1$. This condition is satisfied if, for example, the efficiency of the

175 support to post-fertile parents is sufficiently large compared to the basic post-fertile survival
176 rate (if the latter is high than grandmothers would be around even if not helped).

177 Of course, the coevolution of two traits: long life in menopause and an effective Fifth
178 Rule is also possible. The analytical study presented in *Materials and Methods* is based on
179 two conditions. First, the development of the Fifth Rule is conditional on the existence of the
180 menopause, since one can help a grandmother only if she is alive. (Based on this
181 conditionality, in the *Materials and Methods* we suppose that traits s and y determine both
182 the increase of the grandmother's survival probability and the decrease of fecundity in
183 multiplicative form.) Consequently, the rarity of an effective Fifth rule is hardly surprising.
184 Second, if a fertile mother were to give away all her resources to help the survival of her
185 mother, her fecundity drops to zero. In the *Materials and Methods*, in terms of a fitness
186 landscape, we show that, if the fitness $\lambda(s, y)$ has a global strict maximum point (s^*, y^*) (e.g.
187 in our case if $\lambda(s, y)$ is strictly concave), then there exists a unique evolutionarily optimal
188 behavior (s^*, y^*) , hence the species evolves into this state.

189 The Fifth Rule will spread if the cost of support to post-fertile grandmothers decreases
190 slightly the demographic parameters of fertile parents, but sufficiently increases the survival
191 rate of grandchildren. However, in general, there is a threshold over which support to
192 grandmothers has no evolutionary advantage. If the cost of support to post-fertile
193 grandmothers only decreases the demographic parameters of the family, but it offers no
194 increase in the survival rate of the grandchildren, then the Fifth Rule has no evolutionary
195 advantage. The mother hypothesis and “embodied capital model” should imply that
196 grandmothers increase the survival rate of their children and that of grandchildren during

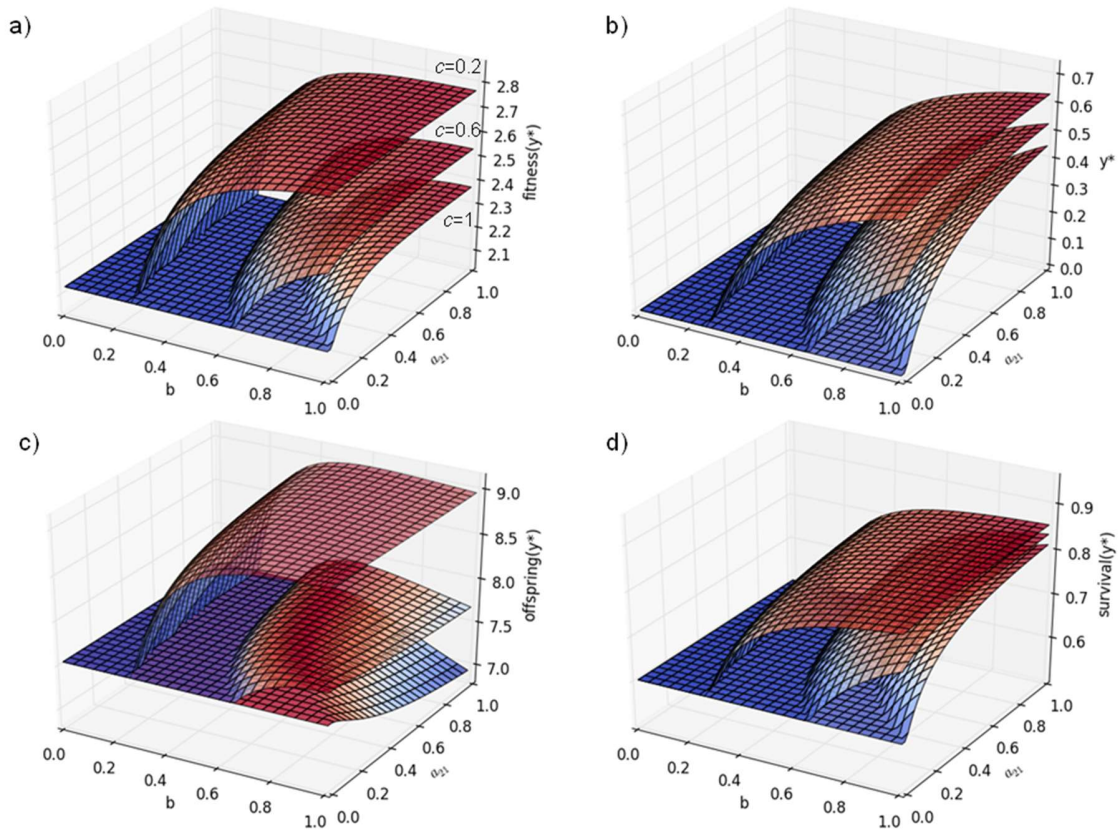
197 their lives. Thus, if these ideas also work in human evolution then it is even “easier” for the
198 Fifth Rule to evolve (see *Materials and Methods*).

199

200 In order to investigate the effects of different cost-benefit parameters on the
201 evolvability of IT we have constructed a general example, which was analyzed numerically
202 (see *Materials and Methods*). Conclusions of the model are as follows: IT evolves most
203 readily when the grandparental help increases both the survival and the number of offspring
204 [20, 24, 25] (Figure 2, Figs. S1-S3). Linear cost and benefit functions do not favor the
205 evolution of IT (Figs. S1, S4, S6); conversely, convex benefit and concave cost functions
206 promote the evolution of IT (Figs. S2, S3, S5, S7). It is possible to find cost parameters (c, d)
207 where IT evolves even if the efficacy of parental transfer and grandparental help (a_{21} and b
208 respectively) is low (Figs. S2, S3). Conversely, it is possible to find (high) a_{21} , b parameters
209 where IT evolves even if it imposes a high cost on the survival of the parents or on the number
210 of offspring (d and c , respectively, see Figs. S1, S2).

211 Since we are dealing with “family issues” the natural conceptual framework is that of
212 kin selection. Our problem does not, however, readily yield to standard inclusive fitness
213 modeling, since the latter is not sensitive to demography. There are different contributions to
214 a female’s fitness from the three stages of her life-history: girl, mother and grandmother. Our
215 demographic model can account for these complications in a straightforward manner. Note
216 also that our account involves an unusual loop from parent to grandparent to grandchild. Our
217 analysis applies to grandfathers as well, provided the menopause in grandmothers constrains
218 the realized fertility of the former in a similar way.

219



220

221 **Figure 2.** Numerical example for a 2x2 Leslie matrix (see *Materials and Methods* for
222 details). (a) Maximum family long term growth rate (fitness); (b) optimal level of backward
223 help (y^*), (c) average number of offspring at y^* ; (d) offspring survival at y^* as a function b
224 (effectiveness of backward help) and a_{21} (effectiveness of forward help to offspring
225 survival). Parameters: $\alpha_2=6$, $\omega_1=0.45$, $\omega_2=0.62$, $\omega_3=0.25$, $d = 0.3$, $h = 1$, $c = 0.2, 0.6, 1$;
226 $a_{12}=10$.

227

228 **3. Conclusions**

229 We demonstrate that an essential part of Fifth Commandment (support to elderly) can confer
230 selective advantage under the right conditions; hence some kind of “evolutionary moral
231 sense” might be genetically endowed. This holds if grandparents have a positive effect on
232 the growth rate of their family. However, this is not necessarily true nowadays [35]. It is very
233 well possible that this support can be rooted in past human evolution. Darwinian success of
234 the Fifth Rule cannot completely explain the present-day Fifth Commandment. Human moral
235 rules, although rooted in Darwinian evolution, are more than what that theory supports. It
236 seems that the main difference is that moral commandments are unconditional rules, while
237 in Darwinian evolution there must be a selective condition determining whether a behavior
238 is adaptive or not.

239

240 **4. Materials and Methods**

241 4.1 Cultural analogues of the Fifth Commandment

242 Cultural norms that promote the help of the parents are widespread in both western and
243 eastern culture. The Fifth Commandment (of the Hebrew and protestant Bible, the Fourth
244 one, according to the catholic numbering) states: “*Honor your father and your mother, that*
245 *your days may be long in the land that the LORD your God is giving you.*” (Exodus 20:12)
246 From the interpretations of this commandment by the western churches we recall the
247 following: Sefer Ha-chinukh (mitzva 33) elaborates: “*A person should realize that his father*

248 *and mother are the cause of his existence in this world; therefore it is appropriate that he*
249 *render them all the honor and do them all the service he can*". St. Thomas Aquinas wrote:
250 *"Since we receive nourishment from our parents in our childhood, we must support them in*
251 *their old age."* Martin Luther said: *"For he who knows how to regard them in his heart will*
252 *not allow them to suffer want or hunger, but will place them above him and at his side, and*
253 *will share with them whatever he has and possesses"* (Luther, M. p. 29).

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

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

260

261 4.2 The model

262 Our model strictly follows the Darwinian view: the fitness is determined by the fecundity
263 and the survival rate. The fecundity of the family is determined by the intergenerational
264 help, which modifies the demographic parameters within the family. Furthermore, the
265 carrying capacity also has an effect on the survival. Thus, the survival of an individual
266 depends on the intra-familiar help, see subsection 4.3, and the survival probability
267 according to the carrying capacity, see subsection 4.4. Our model combines these two
268 factors.

269

270 4.3 The phenotype-dependent Leslie matrix

271 We consider the following age-structured model with two sub-models. The development of
 272 a family is described by the following Leslie matrix, which contains the survival and
 273 fecundity parameters of pre-fertile and fertile individuals, and all entries depend on the level
 274 of the intra-familiar (backward) help, denoted by y :

$$\begin{pmatrix}
 0 & 0 & \dots & 0 & \alpha_{k+1}(y) & \dots & \alpha_{K-1}(y) & \alpha_K(y) \\
 \omega_1(y) & 0 & \dots & 0 & 0 & \dots & 0 & 0 \\
 0 & \omega_2(y) & \dots & \dots & \dots & \dots & \dots & \dots \\
 0 & 0 & \dots & 0 & \dots & \dots & \dots & \dots \\
 \dots & \dots & \dots & \omega_k(y) & 0 & \dots & \dots & \dots \\
 \dots & \dots & \dots & 0 & \omega_{k+1}(y) & \dots & \dots & \dots \\
 \dots & \dots & \dots & \dots & 0 & \dots & 0 & \dots \\
 0 & 0 & \dots & 0 & \dots & \dots & \omega_{K-1}(y) & 0
 \end{pmatrix}, \quad (1)$$

276 where $\omega_i(y)$ ($i=1, \dots, k$) denote the survival rates of children, $\omega_j(y)$ and $\alpha_j(y)$ ($j=k+1, \dots, K$)
 277 are the survival rate and fecundity of fertile parents, respectively. Figure S11 depicts an
 278 example. The multiplication of the age-structured population vector by this Leslie matrix
 279 describes the dynamics of the family. The age classes of grandparents will be handled
 280 separately, since the development of the family depends on the survival rate of pre-fertile and
 281 the fecundity of the fertile family members. Formally, $x_l = \omega_{l-1}(y)x_{l-1}$ where $\omega_l(y)$
 282 ($l=K+1, \dots, H$) are the survival rates of the grandparents, and x_l is the number of grandparents
 283 in age class l .

284

285 4.4 The survival at the carrying capacity

286 In the framework of the Leslie model, it is widely accepted that the Darwinian fitness is the
287 long-term growth rate of the phenotype (i.e. the dominant positive eigenvalue of the Leslie
288 matrix, see 23), surprisingly, in the literature we could not find a Darwinian explanation to
289 this. Below, adapting our recent reasoning from (27), we propose a strictly Darwinian
290 reasoning to see that the long-term growth rate is maximized by natural selection: The
291 number of offspring, in general, is much higher than the carrying capacity, so only a part of
292 the offspring and adults will survive. Let us consider random survival, assuming that the
293 survival probabilities of individuals do not depend on phenotypes (in our case
294 intergenerational help) and on the age of individuals. (Observe that this assumption gives
295 some advantage to the families in which the intergenerational help is less.)

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

306 Let us suppose that phenotypes A and B develop according to Leslie models having the
307 respective population vectors $x(t)$, $z(t)$, and matrices L_A , L_B , total densities
308 $\|x(t)\| = \sum_i x_i(t)$, $\|z(t)\| = \sum_i z_i(t)$. Then the relative frequency of phenotype B tends to zero,
309 as it is shown below:

310 Indeed, let us suppose that the subpopulations start from initial states $x(0)$ and $z(0)$,
311 respectively, and the time unit is chosen in such a way that in unit time the total density of
312 the system always exceeds the carrying capacity K , in particular

$$313 \quad \|L_A x(0)\| + \|L_B z(0)\| > K. \quad (2)$$

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

$$315 \quad x(1) = \frac{K}{\|L_A x(0)\| + \|L_B z(0)\|} L_A x(0), \quad (3)$$

$$316 \quad z(1) = \frac{K}{\|L_A x(0)\| + \|L_B z(0)\|} L_B z(0). \quad (4)$$

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

318 We emphasize that in this model we consider the “intrinsic” survival (described by the Leslie
319 matrices) and the survival under selection independently. However, this model can be
320 formally considered as a particular Leslie-type model depending on the total density of the
321 system, where each demographic parameter in the Leslie matrices L_A and L_B is multiplied

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

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

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

326

327 Now, for the proportion of phenotype B we obtain

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

329 Here

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

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

332 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

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

334 apply the Perron-Frobenius theorem to these matrices, and then the convergence can be

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

336 implying

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

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

339 Observe that in our model, the fecundity of a phenotype is determined by a phenotype-
 340 dependent Leslie matrix, and the survival rates corresponding to the carrying capacity of
 341 different phenotypes are the same, so the long-term growth rate of a phenotype determines
 342 the fitness.

343

344 4.5 The general results

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

$$350 \quad \lambda^K - \alpha_{k+1}(y) \prod_{i=1}^k \omega_i(y) \lambda^{K-(k+1)} - \alpha_{k+2}(y) \prod_{i=1}^{k+1} \omega_i(y) \lambda^{K-(k+2)} - \dots - \alpha_K(y) \prod_{i=1}^{K-1} \omega_i(y) = 0, \quad (9)$$

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

$$352 \quad q(\lambda) = \frac{\alpha_{k+1}(y) \prod_{i=1}^k \omega_i(y)}{\lambda^{k+1}} + \frac{\alpha_{k+2}(y) \prod_{i=1}^{k+1} \omega_i(y)}{\lambda^{k+2}} + \dots + \frac{\alpha_K(y) \prod_{i=1}^{K-1} \omega_i(y)}{\lambda^K} = 1. \quad (10)$$

353 It is easy to see, that if any of the numerators (i.e. the average numbers of offspring produced
 354 by an individual of the corresponding age classes) in these fractions is changed to a greater
 355 one, then the curve of the 'hyperbolic' function q shifts upwards, implying that the positive
 356 solution λ_* of this equation also will be greater. Therefore, if in a population where within
 357 the families grandparents are not supported, a new type emerges which supports
 358 grandparents, and all mentioned numerators increase, then Fifth Rule as behaviour type will

359 propagate. If all these numerators decrease then this type will die out. Those mathematical
 360 cases when some of the numerators increase, others decrease, would need further
 361 mathematical discussions.

362

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

$$364 \quad \prod_{i=1}^k \omega_i(y) \left(\frac{\alpha_{k+1}(y)}{\lambda^{k+1}} + \frac{\alpha_{k+2}(y)\omega_{k+1}(y)}{\lambda^{k+2}} + \dots + \frac{\alpha_K(y) \prod_{j=k+1}^{K-1} \omega_j(y)}{\lambda^K} \right) = 1. \quad (11)$$

365 Here factor $\prod_{i=1}^k \omega_i(y)$ measures how much child care by grandmothers increases the survival

366 of the children. Roughly speaking, factor

$$367 \quad \frac{\alpha_{k+1}(y)}{\lambda^{k+1}} + \frac{\alpha_{k+2}(y)\omega_{k+1}(y)}{\lambda^{k+2}} + \dots + \frac{\alpha_K(y) \prod_{j=k+1}^{K-1} \omega_j(y)}{\lambda^K} \quad (12)$$

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

372

373 Now the question arises how the demographic parameters may depend on y . The
 374 following assumptions are at hand: 1. The survival rate of grandparents is a saturation
 375 function of y strictly increasing at the beginning, and remains constant after. 2. Based on the
 376 grandmother hypothesis, the survival rate of grandchildren strictly increases with the survival

377 rate of grandparents (which on its term depend on y). The grandmother hypothesis is the
378 worst case when two trade-offs may exist. 3. The parents' fecundity entries of the Leslie
379 matrix $(\alpha_{k+1}, \dots, \alpha_K)$ are strictly decreasing functions of y . 4. The survival rates of parents (
380 $\omega_{k+1}, \dots, \omega_K$) are strictly decreasing functions of y .

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

383

384 Under assumption 1 there is a threshold for the support to grandparents, above which
385 the survival of grandparents does not increase, and therefore the survival of grandchildren
386 either, but the fecundity and/or the survival of fertile parents still decrease. Over this
387 threshold, the support to grandparents has no evolutionary advantage.

388

389 Finally, we remark that the above reasoning can be applied not only to the
390 grandmother hypothesis, since either the mother hypothesis or the embodied capital model
391 alone can ensure the support to grandparents. For example, if any of the above two
392 hypotheses implies the increase of at least one of the numerators in (3), while the rest of the
393 numerators do not decrease, then the dominant eigenvalue, i.e. the asymptotic growth rate
394 will increase. Of course, if in addition to the fact that the grandmother increases the survival
395 of her grandchildren and the survival and fertility of her daughter, the hypothesis of the
396 embodied capital model also holds (the grandmother also increases the adult age survival and

397 fertility of her grandchildren), then not only $\prod_{i=1}^k \omega_i(y)$ but also factor (4) can synergically
398 increase the asymptotic growth rate of the family.

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

406

407 4.6 Two-age-class model

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

412

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

415
$$\begin{pmatrix} 0 & \alpha_0 \\ \omega_1 & 0 \end{pmatrix},$$

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

420

421 4.7 Grandmother hypothesis

422 Now the question arises: When is the menopause adaptive? Consider the case when fertile
423 individuals do not support grandmothers. We consider the following two cases: (i) Suppose
424 that grandmothers do not help in child care, but their survival linearly reduces their own
425 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
426 to post-fertile age (Figure 3.a depicts the situation). The fitness of the population is the
427 long-term growth rate which can be calculated from the characteristic equation of the Leslie
428 matrix: $\lambda(s) = \sqrt{\alpha_0(1-s)\omega_1}$, and the optimal strategy is not to spend on own survival to
429 post-fertile age. (ii) Suppose that grandmothers help in child care (Figure 3.b). Let
430 $\omega_2(s) := \bar{\omega}_2 s$, with some $\bar{\omega}_2$, $\alpha(s) := \alpha_0(1-s)$ and $\omega_1(s) := \omega_1 + a_{21}P(s)$, where $s \in [0,1)$,
431 ω_1 is a „basic” survival rate, and the probability that a grandmother is alive when her help
432 needed is $P(s) := \bar{\omega}_2 \omega_3 s$, i.e. we count only the help of those grandmothers who survive to
433 the upper boundary of the third age class and do not count those who reach ‘grandmother
434 age’ (reach the third class) but die before the upper boundary of age, and a_{21} denotes the

435 efficiency of the grandmother's grandchild care. Clearly $a_{21}\bar{\omega}_2\omega_3 < 1$ and

436 $\omega_1(s) = \bar{\omega}_1 + a_{21}\bar{\omega}_2\omega_3s$, thus the fitness is

437
$$\lambda(s) = \sqrt{\alpha_0(1-s)(\bar{\omega}_1 + a_{21}\bar{\omega}_2\omega_3s)}, \quad (13)$$

438 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

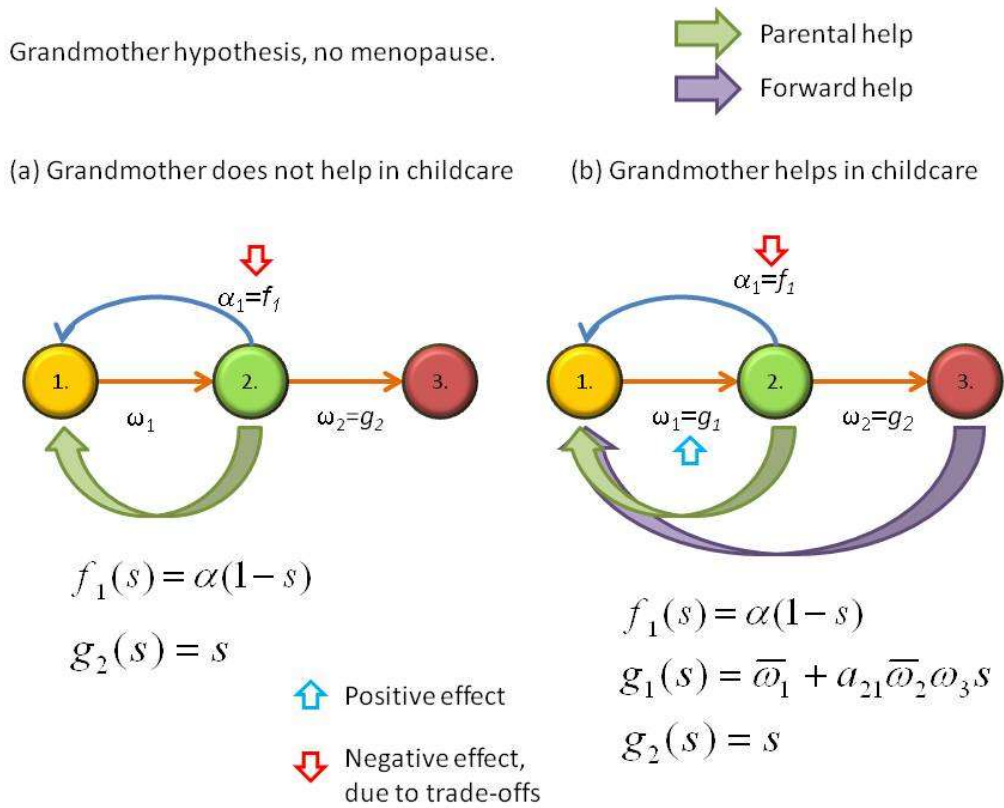
439 grandchild's survival is greater than his/her survival rate without this care, i.e. $a_{21}\bar{\omega}_2\omega_3 > \bar{\omega}_1$

440 , then menopause is evolutionarily successful.

441

442

443



444

445 **Figure 3.** Grandmother hypothesis without (a) and with (b) childcare. Green arrows denote
 446 parental help; purple arrows denote forward help from the grandparents to the grandchild.

447

448 4.8 The Fifth Rule

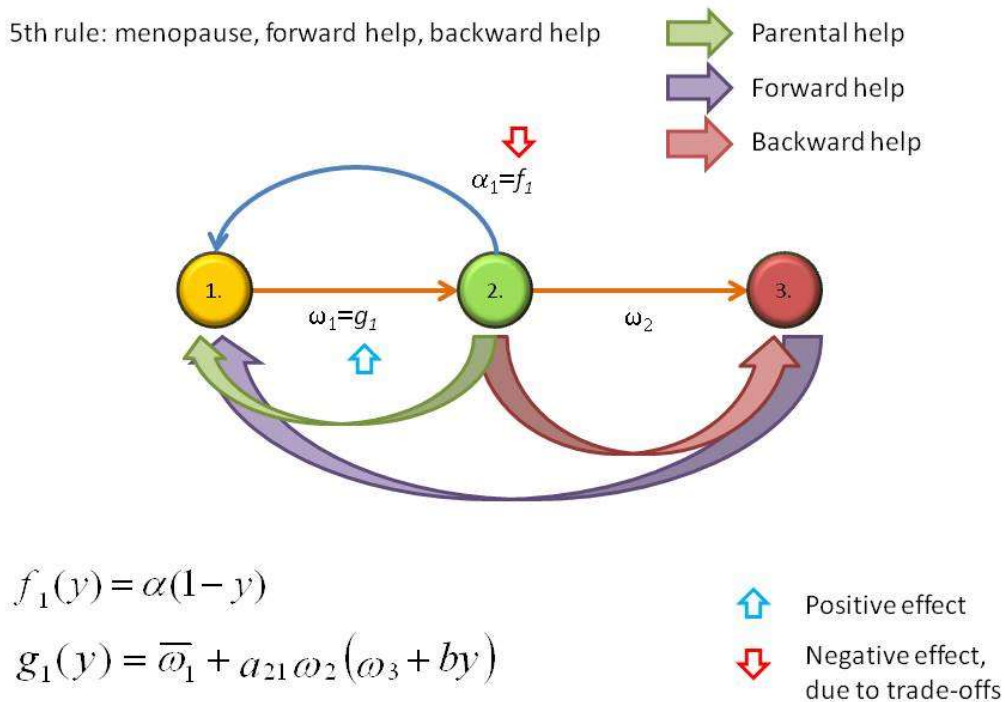
449 Now the question arises: When is Fifth Rule adaptive? It requires us to support our elderly,
 450 which is possible only if the menopause has already become evolutionarily fixed, i.e. for
 451 fixed $s \in [0,1)$, let $\omega_2 := \bar{\omega}_2 s$ and $\alpha := \alpha_0(1-s)$. Let $y \in [0,1]$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

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

458
$$\lambda(y) = \sqrt{\alpha(1-y)(\bar{\omega}_1 + a\omega_2(\omega_3 + by))}, \quad (14)$$

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

460 $a\omega_2(b - \omega_3) - \bar{\omega}_1 > 0$. This condition is satisfied e.g., if the efficiency of the support to post-
 461 fertile parents is sufficiently large compared to the basic post-fertile survival rate.



462

463 **Figure 4.** The fifth rule: forward help in childcare and backward help to the grandparents.

464 Green arrows denote parental help; purple arrows denote forward help from the
465 grandparents to the grandchild, finally red arrows denote backward transfer of resources
466 from the parents to the grandparents.

467

468 4.9 A general multiplicative coevolution model

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

$$479 \quad L(s, y) := \begin{pmatrix} 0 & \alpha_0 \alpha(s, y) \\ \bar{\omega}_1 P(s, y) & 0 \end{pmatrix}, \quad (15)$$

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

$$483 \quad P(s, y) = p(s)q(y), \quad \alpha(s, y) = \beta(s)\gamma(y), \quad (16)$$

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

485 Technical conditions on the functions involved:

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

487 b) $p(0) = q(0) = 1, \beta(0) = \gamma(0) = 1$. We note that these technical conditions imply

488 that $\bar{\omega}_1$ and α_0 are the demographic parameters before the appearance of the

489 considered traits, while $\beta(1) = \gamma(1) = 0$ expresses our second precondition.

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

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

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

493 e) $p''(s), q''(y), \beta''(s), \gamma''(y) < 0$ ($s, y \in (0,1)$). (This condition will guarantee strict

494 concavity of function z near its maximum).

495

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

497
$$\lambda(s, y) = \sqrt{\bar{\omega}_1 \alpha_0 p(s)q(y)\beta(s)\gamma(y)} \quad (s, y \in [0,1]). \quad (17)$$

498 We will show that $\lambda(s, y)$ attains a strict local maximum at an interior point of the unit

499 square $[0,1] \times [0,1]$. Indeed, maximization of $\lambda(s, y)$ is equivalent to the maximization of

500
$$z(s, y) = \bar{\omega}_1 \alpha_0 p(s)q(y)\beta(s)\gamma(y) \quad (s, y \in [0,1]). \quad (18)$$

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

502
$$\frac{\partial}{\partial s} z(s, y) = q(y)\gamma(y)(\beta(s)p'(s) + p(s)\beta'(s)) = 0, \quad (19)$$

503
$$\frac{\partial}{\partial y} z(s, y) = p(s)\beta(s)(\gamma(y)q'(y) + q(y)\gamma'(y)) = 0 \quad (20)$$

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

506
$$\varphi(s) := \beta(s)p'(s) + p(s)\beta'(s) = 0, \quad (21)$$

507
$$\psi(y) = \gamma(y)q'(y) + q(y)\gamma'(y) = 0. \quad (22)$$

508 From conditions b), c) and d) we obtain $\varphi(0) > 0$, $\varphi(1) < 0$, hence there is an $s^* \in (0,1)$ with
509 $\varphi(s^*) = 0$. It is easy to check that conditions b), c), d) and e) also imply $\varphi'(s) < 0$, and hence φ
510 is strictly decreasing, therefore s^* is its unique zero in the interval $(0,1)$. Similar
511 straightforward checking shows that $\psi(y)$ also has a unique zero y^* in the interval $(0,1)$.
512 Hence (s^*, y^*) is a unique stationary point of function z in the interior of the unit square.

513 Now, for a second order sufficient condition for the maximum of function z , we calculate
514 its Hessian:

515

516
$$H(s, y) = \begin{pmatrix} q(y)\gamma(y)(\beta(s)p''(s) + 2p'(s)\beta'(s) + p(s)\beta''(s)) & (\beta(s)p'(s) + p(s)\beta'(s))(\gamma(y)q'(y) + q(y)\gamma'(y)) \\ (\beta(s)p'(s) + p(s)\beta'(s))(\gamma(y)q'(y) + q(y)\gamma'(y)) & p(s)\beta(s)(\gamma(y)q''(y) + 2q'(y)\gamma'(y) + q(y)\gamma''(y)) \end{pmatrix},$$

517
$$(23)$$

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

519
$$H(s^*, y^*) = \begin{pmatrix} q(y^*)\gamma(y^*)(\beta(s^*)p''(s^*) + 2p'(s^*)\beta'(s^*) + p(s^*)\beta''(s^*)) & 0 \\ 0 & p(s^*)\beta(s^*)(\gamma(y^*)q''(y^*) + 2q'(y^*)\gamma'(y^*) + q(y^*)\gamma''(y^*)) \end{pmatrix}$$

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

521
$$q(y^*)\gamma(y^*)(\beta(s^*)p''(s^*) + 2p'(s^*)\beta'(s^*) + p(s^*)\beta''(s^*)) < 0 \quad (24)$$

522
$$p(s^*)\beta(s^*)(\gamma(y^*)q''(y^*) + 2q'(y^*)\gamma'(y^*) + q(y^*)\gamma''(y^*)) < 0, \quad (25)$$

523 imply $\text{tr}H(s^*, y^*) < 0$ and $\det H(s^*, y^*) > 0$, i.e. $H(s^*, y^*)$ is negative definite. Therefore

524 (s^*, y^*) is a strict local maximum point. Since (s^*, y^*) is the unique stationary point, it is

525 also a strict global maximum point in the interior of the unit square.

526 Finally, we note that, if Hessian $H(s, y)$ is negative definite in the interior of the unit

527 square, then function λ is globally strictly concave, and therefore (s^*, y^*) is a global

528 maximum point of λ . In the terminology of fitness landscapes, in the sense of any

529 reasonable strategy dynamics the species will evolve into the evolutionarily optimal

530 behavior (s^*, y^*) .

531

532 4.10 Numerical Examples

533 In this section, by numerical study, we illustrate the effect of different (linear, convex and

534 concave) trade-offs on the level of the optimal backward help (y^*). We calculated the

535 maximal long-term growth rate (fitness) of various populations as a function of y from the

536 characteristic equation of the corresponding Leslie matrix. The value of y that gives the

537 highest long-term growth rate termed as the optimal backward help (y^*). We also calculated

538 the number of offspring and the offspring survival given the optimal y^* . We investigated

539 the effects of different cost-benefit parameters on the evolvability of backward help (y).

540 Life-history parameters are based on the figures from Mace (27). It is possible to generate

541 all the possible combinations of cost-benefit trade-offs by setting the appropriate cost,

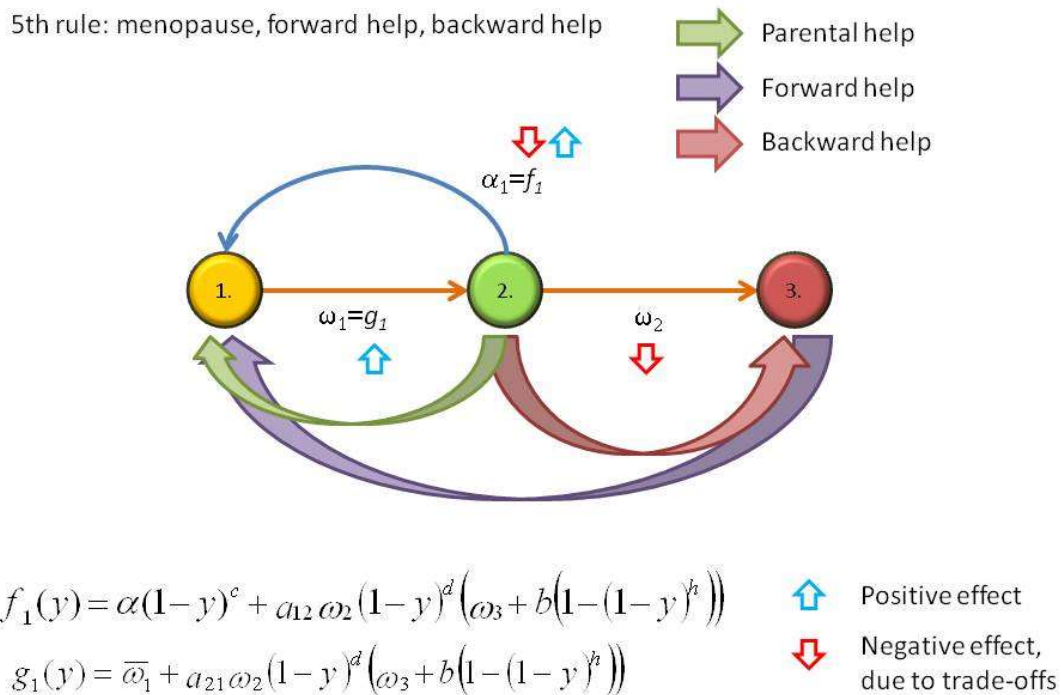
542 benefit parameters to zero (c, d, h). Also, convex or concave cost-benefit functions can be

543 achieved by setting the appropriate parameters (c , d , h) to smaller or to greater than one
 544 (see Table 2 for a summary of parameters). We used the following general Leslie matrix
 545 (see Figure 5 for a schematic description):

546

$$547 \begin{pmatrix} 0 & \alpha(1-y)^c + a_{12}\omega_2(1-y)^d(\omega_3 + b(1-(1-y)^h)) \\ \bar{\omega}_1 + a_{21}\omega_2(1-y)^d(\omega_3 + b(1-(1-y)^h)) & 0 \end{pmatrix}$$

548



549

550 **Figure 5.** Schematic description of the two-age-class general model. Green arrows denote
 551 parental help; purple arrows denote forward help from the grandparents to the grandchild,

552 finally red arrows denote backward transfer of resources from the parents to the
553 grandparents.

554

555 **Table 2.** Parameters of the model.

Life-history parameters

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)

Benefit-parameters

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)

Cost parameters

c : cost of helping grannies on the fecundity of the parent (steepness)

d : cost of helping grannies on the survival of the parent (steepness)

556

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

563 In the same way, four possible combinations exist in terms of the cost functions: (i)
 564 $c, d > 0$; (ii) $c > 0, d = 0$, (iii) $c = 0, d > 0$; and (iv) $c, d = 0$. In the first case helping
 565 grandmothers imposes a cost on both the parents' reproductive output and on the parents'
 566 survival, in the second case only on the number of offspring, in the third only on the
 567 survival of the parent, and finally, in the last case it imposes no cost at all. Just as before,
 568 this last case is not interesting for us, thus it will not be investigated any further. See Table
 569 3 for investigated parameter combinations.

570

571 **Table 3.** The investigated parameter combinations (see Figures S1-S7 for the
 572 corresponding results).

	Grandparental help	Shape of the cost function	Shape of the benefit function	Figure:
1.	$a_{12}, a_{21} > 0$	$d = 1$	$h = 1$	S4
2.		$d = 1$	$h = 2$	S5
3.		$d = 0.5$	$h = 2$	S6
4.	$a_{12} = 0, a_{21} > 0$	$d = 1$	$h = 1$	S7
5.		$d = 0.5$	$h = 2$	S8
6.	$a_{12} > 0, a_{21} = 0$	$d = 1$	$h = 1$	S9
7.		$d = 0.5$	$h = 2$	S10

573

574

575

576 4.11 Illustrative numerical examples: results

577 IT evolves the most readily when the grandparental help increases both the survival
578 of the offspring and the number of offspring (Figure S1-S3). Linear cost and benefit functions
579 do not favour the evolution of IT (Figs. S1, S4, S6, $d=1$, $h=1$); conversely, convex benefit
580 and concave cost functions promote the evolution of IT (Fig. S2, S3, S5, S7, $d=0.5$, $h=2$). It
581 is possible to find cost parameters (c , d) where IT evolves even if the efficacy parental
582 transfer and grandparental help (a_{21} and b respectively) is low (Figs. S2, S3). Conversely, it
583 is possible to find (high) a_{21} , b parameters where IT evolves even if it imposes a high cost on
584 the survival of the parents or on the number of offspring (d and c , respectively, see Figs. S1,
585 S2).
586

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588 E.S., Z.V. and S.S. helped write the article, S.S. calculated the numerical examples and made
589 the figures.

590

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601

602 **Additional information:**

603 Supplementary Materials

604

605 **Competing interests**

606 The authors declare no competing financial interests.

607

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