

Inclusive fitness forces of selection in an age-structured population

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1 **Main Manuscript for**

2

3 Inclusive fitness forces of selection in an age-structured population

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17

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21

22 **Abstract**

23 Current evolutionary theories of senescence predict that the force of selection on survival will
24 decline from maturity to zero at the age of last reproduction, and the force of selection on
25 reproduction will decline monotonically from birth. These predictions rest upon the assumption
26 that individuals within a population do not interact with one another. This assumption,
27 however, is violated in social species, where an individual's survival and/or reproduction may
28 shape the fitness of other group members. In such species, it is inclusive fitness that natural
29 selection optimises. Yet, it remains unclear how the forces of selection on survival and
30 reproduction might be modified when inclusive fitness, rather than population growth rate, is
31 considered the appropriate metric for fitness. Here, we derive inclusive fitness forces of
32 selection for hypothetical populations of social species. We show that selection on survival is
33 not always constant before maturity, and can remain above zero in post-reproductive age
34 classes, contrary to conventional models of senescence. We also show how the trajectory of
35 the force of selection on reproduction does not always decline monotonically from birth, as
36 predicted by classical theory, but instead depends on the balance of benefits to direct fitness
37 and costs to indirect fitness. Our theoretical framework provides the unique opportunity to
38 expand our understanding of senescence across social species, with important implications to
39 species with variable life histories.

40

41 **Main Text**

42 To date, there are no general theories for how senescence might evolve differently in groups
43 of social species. At the demographic level, senescence is defined as the decline in organismal
44 fitness with increasing age¹. Hamilton² provided a mathematical explanation for the seemingly
45 counter-intuitive evolution of senescence: the force of natural selection weakens with age, and
46 so detrimental alleles acting late in life can persist despite their negative effects on fitness³⁻⁶.
47 Two years prior, Hamilton^{7,8} also introduced the concept of inclusive fitness, which has had a
48 profound impact on our understanding of the evolution of social life histories⁹⁻¹¹. Inclusive
49 fitness quantifies (i) an individual's number of offspring in the absence of social effects and
50 (ii) the effects an individual has on the number of offspring produced by other individuals,
51 weighted by relatedness^{7,8}. It has not yet been fully considered from a theoretical standpoint,
52 however, how these effects an individual has on the fitness of others may alter the evolution of
53 senescence.

54

55 An age-specific force of selection describes the relative effect on fitness at different age classes
56 of a mutant allele that impacts survival or reproduction. How might the components that
57 contribute to such age-specific forces of selection differ between a solitary and a social species?
58 First, consider an individual of a solitary species. When this individual dies, it loses access to
59 any future reproduction it might have achieved. If a mutant allele arises in this population that
60 increases the risk of dying at a certain age, say x , then the force of selection that acts against
61 the allele is proportional to the expectation of residual reproduction that the individual may
62 have realised². Now, imagine instead a social species in which individuals within a group
63 influence one another's survival and reproduction, for example, through the provision of
64 alloparental care or through competition for limiting resources. For an individual, death means
65 the loss of any future reproduction, just as in the solitary case. However, in social species, an

66 individual's death may also alter the survival and reproduction of other individuals^{12,13}. For
67 instance, the death of an individual providing alloparental care may lead to a reduction in
68 breeder productivity. Alternatively, where there is competition within groups for resources, the
69 death of an individual may release resources that other group members may use for survival
70 and reproduction. If individuals within a group are related, then these effects will be under kin
71 selection. For example, an increase in mortality late in life can be adaptive if relatives stand to
72 benefit from the death of a focal individual¹⁴⁻²⁰. On the other hand, mortality may be more
73 strongly selected against if individuals can transfer beneficial resources to others²¹⁻²³. When
74 the death and reproduction of a focal individual not only impacts its own fitness, but also the
75 fitness of relatives, the force of selection acting on a mutant allele at age x must also consider
76 these complex social effects.

77

78 To incorporate social interactions into the evolutionary theory of senescence, we develop a
79 general model for quantifying age-specific inclusive fitness forces of selection in social
80 species. Here, we focus on the effects of cooperative interactions between individuals and the
81 corresponding forces of selection, but note that our model also has scope to consider other
82 scenarios, such as cases of harm (see **Discussion**). Using an infinite island framework to
83 describe a resident social population^{16,20,24-34}, we explore the fate of a mutant allele that alters
84 (i) survival rate from age x to age $x + 1$ and (ii) reproduction at age x . We derive inclusive
85 fitness forces of selection acting on these mutant alleles, which indicate how the efficacy of
86 natural selection changes with age with respect to socio-demographic parameters. After
87 deriving general analytical results, we explore the applicability of our framework to different
88 social settings by providing numerical solutions for two examples of social structures: (i) the
89 grandmother hypothesis: post-reproductive individuals aiding juvenile survival and (ii)

90 cooperative breeding: juveniles aiding reproduction by adults. We conclude by discussing the
91 implications and possible extensions for our model.

92

93 **Results**

94 **Model**

95 We consider a population divided into an infinite number of patches, and model the population
96 dynamics of a focal patch. This infinite island approach^{16,20,24-34} allows kin selection to be
97 modelled while also considering the effects of demography, which is appropriate for
98 considering an age-structured population in which individuals have effects on one another's
99 fitness. Each patch, which could also be conceptualised as a territory, contains discrete groups
100 of exactly N individuals that are, for simplicity, haploid and asexual. We also assume that
101 patches produce a large number of offspring in each breeding season so that no position on any
102 patch is vacant at the start of each breeding season (*i.e.* a density-dependent stationary
103 population). Offspring that establish on to a patch are designated age 1 and can survive until
104 some maximum age, ω , at which point they die. Time proceeds in a series of discrete breeding
105 seasons, during which individuals have a probability of surviving to the next breeding season,
106 $p(x)$, and a rate of reproduction, $b(x)$, that may vary with age, and can be described by a
107 population matrix model (A). Individuals may receive contributions to their survival and
108 reproduction from the other $N - 1$ individuals on their patch, and may themselves contribute
109 to the survival and reproduction of the $N - 1$ conspecifics on the patch.

110

111 Fundamental to this model is the concept of ‘transfers’. Biologically, transfers represent the
112 help or harm to other individual's fitness components: survival and reproduction. Transfers
113 occur in the currency of genetic offspring equivalents, the same currency as survival and
114 reproduction. Here, we assume that the transfers an individual makes to others is a function of

115 the ages of both the actor and recipient (Fig. 1). We display transfers between individuals as
116 T_{yz}^x : if $y = 1$, this represents an individual in age class x 's social effect on the reproduction of
117 age class z , while $y = z + 1$ would represent an individual in age class x 's social effect on the
118 survival of age class z .

119

120 To quantify the inclusive fitness contributions of a focal individual of age x , a series of key
121 considerations must be made. Specifically, we must (i) exclude the fraction of the class- y
122 offspring of a focal class- x individual that are born or survive as a consequence of the social
123 environment (the help or harm of other individuals), and (ii) augment the total production of
124 class- y offspring from all other age classes, including other individuals in age class x , that are
125 born or survive due to the social contributions of a focal class- x individual. These latter
126 offspring contributions are weighted by the coefficient of relatedness between an individual of
127 age class x and the class- y offspring of the recipient class^{7,8}. For example, a focal individual
128 aged x survives with probability $p(x)$ and has a rate of reproduction $b(x)$. A fraction of these
129 rates of survival and reproduction may be due to social interactions. These fractions are
130 excluded from the inclusive fitness of the focal individual, leaving $\dot{p}(x)$ and $\dot{b}(x)$, with dot
131 notation representing the effect of a focal individual's own genotype on its own survival or rate
132 of reproduction, *i.e.* direct fitness. Of the $\dot{b}(x)$ offspring produced due to the genotype of an
133 individual aged x , a proportion d disperse, and a proportion $1 - d$ remain at their natal patch.
134 A fraction c of the dispersing offspring die, representing a cost of dispersal. Surviving,
135 dispersed offspring are evenly distributed among all sites, regardless of distance, and compete
136 (fair lottery) for sites freed by adults that die in the current breeding season. Asymmetric
137 competition is assumed so that juveniles do not displace resident adults, and die if they do not
138 gain a breeding position on a patch. Offspring of a focal individual aged x face a probability

139 of establishment $g(x)$ onto their natal patch, and \bar{g} on a different, random patch in the
 140 population.

141

142 In a population with social interactions between patch members, we can populate a matrix (\mathbf{W})
 143 with the inclusive fitness (genetic offspring) contributions of individuals in age class x to
 144 individuals in age class y (w_{yx}):

145

$$146 \quad w_{yx} = \begin{cases} \dot{p}(x) + T_{x+1,x}^x, & \text{if } y = x + 1 \\ \dot{F}(x), & \text{if } y = 1 \\ 0 \text{ OR } T_{yz}^x \text{ if } y = z + 1 \end{cases},$$

147 [1]

148 where

$$149 \quad \dot{p}(x) = p(x) - \sum_z T_{x+1,x}^z$$

150 [2]

151 and

$$152 \quad \dot{b}(x) = b(x) - \sum_z T_{1,x}^z$$

153 [3]

154 and

$$155 \quad \dot{F}(x) = \dot{b}(x) + \sum_z T_{1,z}^x [(1-d)g(x) + (1-c)d\bar{g}] .$$

156 [4]

157

158 The proportions of the survival and reproduction of a focal individual aged x that are due to
 159 the genotypes of other individuals are represented in the summation terms on the right-hand
 160 side of [2] (survival) and [3] (reproduction) (where $0 \leq \sum_z t_{x+1,x}^z < p(x)$, and $0 \leq \sum_z t_{1,x}^z <$

161 $b(x)$). Importantly, these proportions are distributed to other age classes, thus ensuring that no
162 offspring is ‘double counted’^{35,36}. A focal individual of age x may also contribute to the
163 survival and reproduction of others, accumulating indirect fitness through the transfer of
164 genetic offspring. Contributions to survival are captured as $T_{y,z}^x$ (where $y = z + 1$, and $y \neq$
165 1), and reproduction as $T_{1,z}^x$ (summed across age classes to equal $\sum_z T_{1,z}^x$). The magnitude of
166 these contributions will depend on i) the expected number of individuals in the recipient age
167 class, ii) the fraction of the total contribution of all age classes combined to the survival or
168 reproduction of the recipient age class individuals that is due to a focal individual aged x , and
169 iii) the relatedness between a focal individual aged x and an individual in the recipient age
170 class (see **Supplementary Information**). This approach to modelling social interactions
171 assumes that there are fractions of survival and fecundity of each age class that are due to the
172 social environment (which could equal zero), and that these fractions are distributed to other
173 individuals across age classes. If there are no explicit social interactions between multiple
174 individuals on a patch, equation [2] simplifies to a population with limited dispersal and Ronce
175 & Promislow’s²⁰ kin competition selection gradients can be computed. With full dispersal (no
176 offspring stay at the patch in which they’re born) and no social interactions, equation [1]
177 simplifies to Hamilton’s panmictic population, and his forces of selection can be computed².

178

179 **An inclusive fitness force of selection**

180 To compute forces of selection, we are ultimately concerned with a hypothetical mutation that
181 alters survival rate or rate of reproduction at age x . The derivative of the growth rate of the
182 mutant population, λ , with respect to the phenotypic effect of the mutation, δ , gives an indicator
183 of the force of selection acting on the mutant allele^{2,20,37,38}. We consider mutations of weak
184 effects (small δ) and first-order effects of selection³⁹. Using this ‘sensitivity’ approach for an

185 age-structured population^{20,37,38,40-42}, the force of selection acting on a mutant allele can be
 186 written as:

187

$$188 \quad S = \frac{d\lambda}{d\delta_{\delta=0}} = \sum_x \sum_y \frac{f_x v_y}{\mathbf{f} \cdot \mathbf{v}} \frac{dw_{yx}}{d\delta_{\delta=0}}$$

189 [5]

190 where \mathbf{f} and \mathbf{v} are the vector of asymptotic frequencies and the vector of inclusive reproductive
 191 values for the different age classes in the resident population. The term f_x denotes the
 192 asymptotic frequency of age class x , and \mathbf{f} is the dominant right eigenvector of the demographic
 193 projection matrix (\mathbf{A}). In this model, the term v_x represents the inclusive reproductive value of
 194 age class x , and is instead derived from an inclusive fitness matrix (\mathbf{W}) that decomposes the
 195 demographic projection matrix into inclusive fitness contributions between age classes.
 196 Therefore, \mathbf{v} is the dominant left eigenvector of \mathbf{W} . Thus, the growth rate of the mutant
 197 population, λ , represents an inclusive fitness growth rate of the allele. Finally, the term w_{yx}
 198 represents the class y offspring of a class x individual (genetic offspring equivalents).
 199 Therefore, dw_{yx} represents the difference in the contribution of an individual age x to
 200 individuals aged y in the mutant population compared to the resident population. Overall, the
 201 sign of S predicts the direction of selection on the mutant allele with respect to the resident
 202 population wild type allele, whilst the magnitude of S conveys information about the force of
 203 selection^{2,20}.

204

205 **The inclusive fitness force of selection on survival**

206 A mutant allele that alters the survival rate between age x and $x + 1$ changes inclusive fitness
 207 contributions between age class according to the following (see **Methods**):

$$dw_{yx} = \begin{cases} d\dot{p}(x), & \text{if } y = x + 1 \\ -d\dot{p}(x)[\dot{h}(x) + \dot{k}(x)\hat{r}(x)], & \text{if } y = 1 \\ 0, & \text{otherwise} \end{cases}$$

209 [6]

210 where $\dot{h}(x)$ is the proportion of offspring after dispersal at the local patch that are the direct
 211 and indirect contributions of a focal individual aged x , $\dot{k}(x)$ is the proportion of offspring that
 212 are born due to the genotypes of other individuals on the patch, and $\hat{r}(x)$ is the relatedness of
 213 an individual aged x to the offspring of other patch mates (see **Methods**). As we assume
 214 mortality occurs between breeding seasons, a focal individual's contributions to the survival
 215 and reproduction of other age classes are only affected at $x + 1$, not in the current breeding
 216 season.

217

218 Let $S_p(x)$ be the component of the force of selection due the effect of a mutant allele on the
 219 survival rate between age x and $x + 1$. Using equations [5] and [6], in a stationary population
 220 with limited dispersal and social interactions between individuals, this can be written as:

221

$$S_p(x) = \frac{d\dot{p}(x)}{d\delta} \frac{f_x(v_{x+1} - [\dot{h}(x) + \dot{k}(x)\hat{r}(x)]v_1)}{\mathbf{f} \cdot \mathbf{v}}$$

223 [7]

224

225 Equation [7] shows that the overall direction of the force of selection acting on a mutant allele
 226 that affects the survival rate between age x and $x + 1$ is a balance of two forces: the inclusive
 227 reproductive value at age $x + 1$ vs the reproductive value of offspring (displaced by the
 228 survival of the focal individual) that have varying relatedness to the focal individual aged x .

229 The term $\mathbf{f} \cdot \mathbf{v}$ acts to scale the forces of selection in terms of generation time^{2,20}.

230

231 **The inclusive fitness force of selection on reproduction**

232 A mutant allele that alters reproduction at age x changes inclusive fitness contributions
 233 between age class according to the following (see **Methods** and **Supplementary**
 234 **Information**):

235

$$236 \quad dw_{yx} = \begin{cases} 0, & \text{if } y = x + 1 \\ db(x)[(1-d)g(x)[(1-h(x)) - i(x) - k(x)\hat{r}(x)] + (1-c)d\bar{g}], & \text{if } y = 1 \\ 0, & \text{otherwise} \end{cases}$$

237 **[8]**

238

239 Then, let $S_m(x)$ be the component of the force of selection due the effect of a mutant allele on
 240 reproduction at age x . Using **[5]** and **[8]**, in a stationary population with limited dispersal and
 241 social interactions between individuals, this can be written as:

242

$$243 \quad S_m(x) = \frac{d\dot{b}(x)}{d\delta} \frac{f_x v_1}{\mathbf{f} \cdot \mathbf{v}} [(1-d)g(x)[(1-h(x)) - i(x) - k(x)\hat{r}(x)] + (1-c)d\bar{g}].$$

244 **[9]**

245

246 where

247

$$248 \quad i(x) = \frac{\sum_z T_{1,z}^x (1-d)}{b(x)(1-d) + (N-1)\bar{b}(1-d) + N\bar{b}(1-c)d}$$

249 **[10]**

250 is the fraction of all offspring at the local patch after dispersal that exist due to indirect effects
 251 of the genotype of a focal individual aged x . Equation **[9]** shows that the overall force of
 252 selection acting on a mutant allele that affects the rate of reproduction at age x is also comprised
 253 of two components: (i) the effect of the allele on the probability of establishment of different

254 types of offspring onto the local patch and (ii) the effect of the allele on the dispersing offspring
 255 that are part of the direct fitness of the focal individual aged x . Selection for effect (ii) will
 256 always be positive; however, selection for effect (i) will depend on the relative weights each
 257 class of offspring contributes to the overall effect. In this model, an increase in direct
 258 reproduction is, all else being equal, beneficial for the direct fitness of a focal individual, but
 259 detrimental to the indirect fitness of the focal individual.

260

261 **Applications of the model**

262 Equations [7] and [9] provide general solutions for age-specific inclusive fitness forces of
 263 selection on individual survival and reproduction in group structured populations. To visualise
 264 the results, we consider two hypothetical populations of iteroparous individuals with social
 265 interactions (Fig. 2, Fig. 3). For each, we consider background demography described by age-
 266 specific vital rates, $p(x)$ and $b(x)$. We parameterise mortality risk at age x using the Siler
 267 model⁴³:

$$268 \quad \mu(x) = \alpha_1 e^{-\beta_1 x} + \alpha_2 e^{\beta_2 x} \quad [11]$$

270 The probability of survival at age x , $p(x)$, is therefore equal to $e^{-\mu(x)}$. The probability of
 271 survival to age x ($l(x)$) is then $l(x) = \prod_1^{x-1} p(x)$, with $l(1) = 1$. As we assume all patches
 272 have no breeding positions available at the start of each breeding seasons (*i.e.*, a density-
 273 dependent stationary population), we can calculate the asymptotic frequency (f_x) of each age
 274 class as

$$275 \quad f_x = \frac{l(x)}{\sum_y l(y)}. \quad [12]$$

277 We then parameterise individual rate of reproduction at age x as:

278

$$279 \quad b(x) = \begin{cases} 0, & \text{if } x < \varepsilon \\ (x - \varepsilon)e^{-\varphi(x-\varepsilon)}, & \text{if } x \geq \varepsilon \\ 0, & \text{if } x > \kappa \end{cases}$$

280

[13]

281 where ε designates the age of reproductive maturity, κ represents an age at which reproduction
282 ceases, and φ modulates the shape of reproduction across age classes.

283

284 Fig. 2A and Fig. 3A illustrate the life cycles of the two hypothetical social populations. Fig. 2A
285 considers a population with post-reproductive individuals providing care for juveniles, as seen
286 in humans⁴⁴, orcas⁴⁵, and Asian elephants⁴⁶. Fig. 3A considers a population with juvenile
287 individuals providing help to the reproduction adult breeders, as is found in many
288 cooperatively-breeding species⁴⁷. Fig. 2B and Fig. 3B display the modelled survivorship and
289 reproduction as a function of individual age. We then apply our methodology (see **Model**) to
290 partition these vital rates into inclusive fitness contributions between age classes and compute
291 a fitness matrix (**W**) with elements described in [1]. Fig. 2C and Fig. 3C show the forces of
292 selection acting on survival and reproduction at age x in these hypothetical social populations
293 according to equations [7] and [9].

294

295 We show that the force of selection acting on survival in social populations is not necessarily
296 constant before maturity, as predicted by classical theory². The exact pattern depends on
297 whether pre-reproductive individuals gain indirect fitness through transfers or not. When
298 juveniles do not engage in helping behaviour, the force of selection increases in the juvenile
299 period as relatedness to newborn offspring decreases with increasing juvenile age (Fig. 2C;
300 Fig. 2D). This decline in local relatedness facilitates a more ‘selfish’ force of selection on
301 survival throughout the juvenile period. On the other hand, when juveniles provide help to

302 adult reproduction, the force of selection on survival generally decreased from the age at which
303 indirect fitness was first accrued (Fig. 3C; Extended Data Fig. 3), rather than the age of first
304 reproduction. In both examples, the force of selection on survival then declines throughout
305 adulthood as future inclusive reproductive value declines and the relatedness to newborn
306 offspring increases. When post-reproductive adults continue to accrue indirect fitness, the force
307 of selection on survival can remain above zero in post-reproductive age classes (Fig. 2C;
308 Extended Data Fig. 1). The magnitude of the force of selection is greater in post-reproductive
309 age classes when juvenile dispersal is lower (and so there is higher local relatedness) and the
310 magnitude of help provided by post-reproductive individuals is higher (Extended Data Fig.1).
311 In general, the force of selection on survival will always have a positive component until the
312 final age at which inclusive fitness is accrued, rather than necessarily the age of last
313 reproduction. At this age, when future survival is no longer possible, the first term on the
314 numerator of Equation [7] is zero, and so, if there is some level of local relatedness (*i.e.* $\hat{r}(x) >$
315 0), selection will favour increased mortality as it will benefit the establishment of related
316 juveniles.

317

318 In populations with relatively long lifespans, the force of selection on reproduction was weaker
319 than the force of selection on survival. The force of selection acting on reproduction at age x
320 generally declined from birth, as predicted by Hamilton's model², but not always (Extended
321 Data Fig. 4), and the decline was more rapid when the rate of dispersal was lower (Extended
322 Data Fig. 2). This more rapid decline is likely due to the greater inclusive fitness costs of
323 increasing personal reproduction when local relatedness is higher. The force of selection on
324 reproduction in early life is also weaker when post-reproductive adults have a more significant
325 impact on juvenile survival. In all iterations of the model (Fig. 3C; Extended Data Fig. 3), there

326 was a slight increase in the force of selection acting on reproduction in the final age class, when
327 the force of selection on rate of survival becomes negative.

328

329 When considering the evolution of demographic senescence, evolutionary biologists use
330 population growth rate, r , as the measure of fitness⁴⁸ (but see⁴⁹). The magnitude of the change
331 in population growth rate due to an age-specific change in survival and/or reproduction
332 generally declines with age (but see⁵⁰ for other indicators of the force of selection), and this
333 decline facilitates the evolution of senescence². However, for social species, it is crucial to
334 consider explicitly the inclusive fitness of individuals as the quantity that natural selection
335 seeks to maximise¹⁰. Indeed, the change in inclusive fitness due to an age-specific change in
336 individual survival and/or reproduction must consider the combined effect on all individuals
337 that are affected by the change²⁴. Here, we show that, in an age-structured model for patch-
338 structured social populations, considering the inclusive fitness effects of an allele significantly
339 alters the form of the forces of selection acting on age-specific survival rate and rate of
340 reproduction.

341

342 Our framework provides several key insights into the force of selection acting on survival and
343 reproduction in social species. First, the force of selection acting on the survival rate of that
344 age class is the product of future inclusive reproductive value (IRV), rather than conventional
345 reproduction value (RV⁴⁸), and the asymptotic frequency (stationary age distribution) of that
346 age class. Since IRV remains above zero after reproduction ceases, if post-reproductive adults
347 continue to accrue indirect fitness benefits, selection on survival of post-reproductive age-
348 classes does not necessarily go to zero as in Hamilton's model². Importantly, this finding
349 provides a formal inclusive fitness framework for the 'grandmother hypothesis'^{51,52}, supporting
350 work that has suggested indirect fitness benefits are essential to sustained post-reproductive

351 lifespan^{23,31}. In our framework, the force of selection on survival of social species will remain
352 non-zero until there is no future IRV. At this point, if there is some local relatedness, the force
353 of selection on increased survival will be negative. Combined with an increase in the force of
354 selection on reproduction at a ‘final age class’, a kin-selected terminal investment strategy, in
355 which it pays to invest heavily in reproduction at the expense of survival to maximise the
356 establishment of kin, may be favoured¹⁹.

357

358 The incorporation of age-specific indirect fitness into the evolutionary theory of senescence
359 means that selection on survival before maturity is not necessarily constant (Fig. 2C; Fig. 3C).
360 This difference occurs because of the balance between the future IRV of the individual and the
361 IRV of newborns displaced by increased survival. If relatedness to other individuals declines
362 throughout the juvenile period as a focal individual ages, and the focal individuals own IRV
363 increases as they approach maturity, the balance in Equation [7] is weighed more heavily
364 towards the first term, and the force of selection on increased survival will increase. On the
365 other hand, in populations where juveniles help and accrue indirect fitness, the force of
366 selection on survival will decline from the age at which indirect fitness is first gained. This
367 result implies that, in species with pre-reproductive help, senescence should start from the age
368 at which inclusive fitness is first gained, rather than the age of first reproduction, as in
369 conventional models^{2,20}.

370

371 An inclusive fitness force of selection acting on reproduction depends on the costs and benefits
372 associated with increasing personal reproduction. In our framework, selection for increased
373 reproduction will always have a positive component due to the increased probability of an
374 offspring (whether philopatric or dispersive) establishing on to a patch. However, the
375 subsequent decrease in probability of other locally produced offspring establishing on to the

376 patch reduces the magnitude of the force of selection acting on reproduction. This result may
377 be especially important for groups experiencing strong competition over resources¹². For
378 example, a negligible force of selection on reproduction may favour reproductive restraint by
379 some individuals within cooperatively-breeding groups, when access to reproduction is limited
380 and inclusive fitness costs of increasing personal reproduction would be substantial³².

381

382 **Discussion**

383 Our framework builds on previous work that has made significant ground in incorporating
384 social effects into the evolutionary theory of senescence. Lee's²³ model showed that the force
385 of selection acting on age-specific mortality can be modified by intergenerational transfers of
386 resources. However, kin selection did not enter the formal model as no explicit spatial
387 structured was considered. Here, by explicitly considering a patch structured population with
388 dispersal, we allow for variation in relatedness and thus a larger breadth of possible kin
389 selection effects to be considered. Ronce & Promislow²⁰ derived analytical solutions that
390 provided the baseline framework for the model here, showing that the force of selection on
391 increased survival includes a negative component driven by the displacement of offspring from
392 establishing on the local patch. This term is similar to the negative term in [7]; however, our
393 framework also explicitly considers the impact of survival on the establishment of other locally
394 produced offspring. By only considering single individuals on a patch, social interactions in
395 Ronce & Promislow's model were limited to kin competition between parent and offspring
396 over residency on the patch. Here, by including multiple individuals on the patch, we can also
397 incorporate social effects into the form of the force of selection on reproduction ([10]). Finally,
398 Moorad & Nussey⁵³ took a quantitative genetics approach to add indirect genetic effects,
399 explicitly considering maternal effect senescence, but modelled no explicit demography. A

400 combination of explicit demography, as modelled here, and quantitative genetics could prove
401 a major future step.

402

403 The framework we present here provides a base to expand our understanding of senescence
404 across social species. For example, previous work has found mixed evidence for extended
405 lifespan in cooperative breeders⁵⁴⁻⁵⁷, and some evidence for differences in rates of senescence
406 between cooperative and non-cooperative breeders⁵⁸. Previous theory suggests that it is longer
407 life and overlapping generations that initially favour cooperation²⁶, but also that a delayed age
408 of first reproduction as a result of queuing for reproduction might be a self-reinforcing
409 mechanism for extended lifespan in cooperative breeders⁵⁹. However, multiple other facets of
410 the demography of cooperative breeding systems, including the process of group formation⁶⁰,
411 the structure of dominance hierarchies⁶¹ and levels of reproductive skew⁶² all have the potential
412 to play a role in determining lifespan and rates of senescence. All have the potential to
413 contribute to the shape of the age class asymptotic frequency and inclusive reproductive value
414 distributions that, as we have shown here, underpin inclusive fitness forces of selection. Our
415 model provides a framework to stimulate further theoretical work for how these features of
416 cooperative breeding systems may impact the evolution of lifespan and senescence.

417

418 Here, we focused on how cooperative interactions between members of a group can alter age-
419 specific inclusive fitness forces of selection. However, in many groups, competitive
420 interactions over limited resources are also rife. In our model, transfers between age classes
421 reflect the net effect of the presence of an individual in one age class on the survival and
422 reproduction of an individual in another age class. If the net effect is negative, then the genetic
423 offspring transfer is also negative. For example, consider again the social system illustrated in
424 Figure 2. Instead of post-reproductive individuals having a positive effect of the survival of

425 juveniles, let us instead imagine a scenario in which the presence of post-reproductive
426 individuals is harmful to the survival of juveniles. An allele that increases the rate of survival
427 in such post-reproductive individuals will be selected against due to the inclusive fitness costs
428 imposed from the negative effects on related juvenile individuals, potentially hastening the
429 evolution of more rapid senescence. Finally, in our model, we only considered indirect fitness
430 returns from social interactions. In many cooperative breeding systems, however, direct fitness
431 returns from social interactions can be the main driver for alloparental care⁴⁷. Some form of
432 direct fitness benefits could be incorporated into the model by delaying the age at which returns
433 from social interactions are realised, as hypothesised by group augmentation theory⁶³.

434

435 In summary, recent research has focused on the potential for social interactions to drive
436 variation in senescence across species^{1,64}. The model we present here shows that when
437 inclusive fitness consequences of increasing individual survival or reproduction are considered,
438 age-specific forces of selection can vary markedly from previous asocial models. Our results
439 thus support the hypothesis that sociality can shape patterns of senescence in nature. Further
440 theoretical, empirical and comparative studies are now needed to determine the amount of
441 variation in senescence patterns that can be explained by social modes of life.

442

443 **Methods**

444

445 **Appendix A: Relatedness**

446

447 In order to quantify indirect genetic contributions, it is essential to consider the relatedness between different age
 448 classes of individuals in the population. The relatedness of a focal individual aged x to other individuals on the
 449 patch, including themselves, can then be described as:

450

451

$$r(x) = \frac{1}{N} + \frac{N-1}{N} \hat{r}(x) .$$

452

[A1]

453

454 Then, let r_{yx} denote the probability that an allele sampled randomly from a given locus in an individual aged x is
 455 identical by descent (IBD) to an allele sampled randomly from the same locus in an individual aged y ^{26,27,32,34,65,66}.

456 The term $\hat{r}(x)$ represents the average relatedness of a breeding individual aged x to another random breeder on
 457 the same patch^{26,27}, which is equivalent to the mean relatedness of a focal individual aged x across all age classes
 458 ($\hat{r}(x) = \overline{r_{yx}}$). Given the assumption of haploid genetics and asexuality, $\hat{r}(x)$ is therefore also the relatedness of a
 459 focal individual aged x to the offspring of the other individuals on the patch. Under the assumption of infinite
 460 patches, any immigrants arriving at the focal patch will not have any relatives when they arrive, and the relatedness
 461 of individuals on the patch of any age to these immigrants is equal to 0.

462

463 Let us define $h(x)$ as the proportion of offspring after dispersal at the local patch that are the offspring (not
 464 partitioned into inclusive fitness contributions) of a focal individual aged x :

465

466

$$h(x) = \frac{b(x)(1-d)}{b(x)(1-d) + (N-1)\bar{b}(1-d) + N\bar{b}d(1-c)}$$

467

[A2]

468

469 where \bar{b} represents the average rate of reproduction. For simplicity, we assume no demographic stochasticity
 470 within patches (see **Discussion**). Then, let $k(x)$ define the proportion of offspring after dispersal at the local patch
 471 that are the demographic offspring of other individuals on the patch besides the focal individual aged x :

472

473

$$k(x) = \frac{(N-1)\bar{b}(1-d)}{b(x)(1-d) + (N-1)\bar{b}(1-d) + N\bar{b}d(1-c)}$$

474

[A3]

475

476 Using equations [A2] and [A3], we can describe the relatedness between an individual aged x to a different
 477 individual on the patch aged y as a function of both individual's ages:

478

479

$$r_{yx} = \begin{cases} h(x-y) + k(x-y)\hat{r}(x-y), & y < x \\ (1-d)^2[\bar{h}^2 + (1-\bar{h}^2)\hat{r}(1)], & y = x \\ h(y-x) + k(y-x)\hat{r}(1), & y > x \end{cases} .$$

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[A4]

First, consider the case when the individual of age x is older than the individual of age y (top row of [A4]). The individual aged y was born $x - y$ breeding seasons ago, when the individual aged x was $x - y$ years old. At age $x - y$, the proportion of offspring at the local patch after dispersal that are the offspring of an individual aged $x - y$ is defined as $h(x - y)$. Therefore, with probability $h(x - y)$, the individual aged y is the offspring of the individual aged x from $x - y$ breeding seasons ago, and thus the relatedness between the two individuals is one. Then, let $k(x - y)$ define the proportion of offspring at the local patch after dispersal $x - y$ breeding seasons ago that were the offspring of other individuals on the patch. With probability $k(x - y)$, therefore, the individual aged y was born to another individual on the patch. Therefore, the relatedness of the individual aged x to the individual aged y is equal to the relatedness of an individual aged $x - y$ to a random offspring born locally to the patch, which is equal to the relatedness of an individual aged $x - y$ to another random individual on the patch ($\hat{r}(x - y)$). The remaining proportion of offspring at the patch after dispersal $x - y$ breeding seasons ago ($1 - h(x - y) - k(x - y)$) were from elsewhere in the population and thus relatedness is 0.

Second, consider the case when both individuals are the same age (second row of [A4]). The probability that both are local to the patch is $(1 - d)^2$. If both individuals are born locally, we then have to consider the probability that both individuals were born to the same mother, and thus are siblings related by 1. If the average proportion across age classes of offspring that are born to an individual is \bar{h} , then the probability that two offspring born x breeding seasons ago were born to the same mother is equal to \bar{h}^2 . One minus \bar{h}^2 is then the probability that these two locally born offspring x breeding seasons ago were born to different mothers, in which case the relatedness of an individual aged x to a same aged individual is equal to the relatedness of an individual to a random member of the patch at age 1 when the focal individual established onto the patch ($\hat{r}(1)$). The final scenario (bottom row of [A4]) considers the case when the individual aged y is older than the individual aged x . In this case the logic is the opposite to the case when the individual aged x is older than the individual aged y .

To calculate $\hat{r}(x)$, the average relatedness of an individual aged x to another individual on the patch, we need to calculate the average relatedness of individuals aged x to all other age classes. Using each possible relatedness between age classes ([A4]), we can do this by weighting each age class specific relatedness term by the asymptotic frequencies of the relevant age classes:

$$\hat{r}(x) = \left(\sum_{y < x} f_y [(h(x - y) + k(x - y)\hat{r}(x - y))] \right) + f_x (1 - d)^2 (\bar{h}^2 + (1 - \bar{h}^2)\hat{r}(1)) + \left(\sum_{y = x+1}^{y = \omega} f_y [h(y - x) + k(y - x)\hat{r}(1)] \right)$$

[A5]

515 **Deriving $\hat{r}(1)$**

516

517 To find a general solution for $\hat{r}(1)$, which is the relatedness of an individual aged 1 to another random breeder on
 518 the patch, let us consider a case of a population with 3 age classes ($\omega = 3$). Using the logic that $x = 1$ is the first
 519 age class and therefore y cannot be younger than x , $\hat{r}(1)$ with 3 age classes becomes:

520

$$521 \quad \hat{r}(1) = f_1(1-d)^2[\bar{h}^2 + \hat{r}(1)(1-\bar{h}^2)] + \sum_{y=2}^3 f_y[h(y-x) + k(y-x)]\hat{r}(1)$$

522 **[A6]**

523 Expanding the summation term, this becomes:

524

$$525 \quad \hat{r}(1) = f_1(1-d)^2[\bar{h}^2 + \hat{r}(1)(1-\bar{h}^2)] + f_2[h(1) + k(1)\hat{r}(1)] + f_3[h(2) + k(2)\hat{r}(1)]$$

526

527 **[A7]**

528 Expanding out each term, this becomes:

529

$$530 \quad \hat{r}(1) = f_1(1-d)^2\bar{h}^2 + f_1(1-d)^2\hat{r}(1)(1-\bar{h}^2) + f_2 h(1) + f_2 k(1)\hat{r}(1) + f_3 h(2) + f_3 k(2)\hat{r}(1)$$

531

532 **[A8]**

533 Factoring on the RHS by $\hat{r}(1)$, this becomes:

534

$$535 \quad \hat{r}(1) = \hat{r}(1)[f_1(1-d)^2(1-\bar{h}^2) + f_2 k(1) + f_3 k(2)] + f_1(1-d)^2\bar{h}^2 + f_2 h(1) + f_3 h(2)$$

536

537 **[A9]**

538

539 Re-arranging, and factoring on the LHS by $\hat{r}(1)$ this becomes:

540

$$541 \quad \hat{r}(1) \left[1 - [f_1(1-d)^2(1-\bar{h}^2) + f_2 k(1) + f_3 k(2)] \right] = f_1(1-d)^2\bar{h}^2 + f_2 h(1) + f_3 h(2)$$

542

543 **[A10]**

544

545 Dividing both sides by $\left[1 - [f_1(1-d)^2(1-\bar{h}^2) + f_2 k(1) + f_3 k(2)] \right]$, this becomes:

546

547

$$548 \quad \hat{r}(1) = \frac{f_1(1-d)^2\bar{h}^2 + f_2 h(1) + f_3 h(2)}{1 - [f_1(1-d)^2(1-\bar{h}^2) + f_2 k(1) + f_3 k(2)]}$$

549

550 **[A11]**

551 Finally, to generalise for all possible number of age classes, we can re-write **[A11]** as

552

553

$$\hat{r}(1) = \frac{f_1(1-d)^2\bar{h}^2 + \sum_{y=2}^{\omega} f_y h(y-1)}{1 - [f_1(1-d)^2(1-\bar{h}^2) + \sum_{y=2}^{\omega} f_y k(y-1)]}$$

554

555

[A12]

556

Once we have $\hat{r}(1)$, $\hat{r}(x)$ for all other age classes can be solved recursively.

557

558 **Appendix B: Analytical Solutions**

559

560 **The effect of a mutant allele that alters age-specific survival in a social population**

561

562 Let us first consider how, in a resident population with limited dispersal and social interactions, a mutant allele
 563 that affects survival at age x will alter the number of class- y offspring of a focal individual aged x . First, the most
 564 obvious effect of this allele is to change the individual's probability of survival to the next breeding season, which
 565 is $d\dot{p}(x)$. A change in survival will also alter the contributions a focal individual aged x makes to the offspring
 566 class, w_{1x} . For example, if the mutant allele increases survival at age x , then there is a greater chance the focal
 567 individual survives to age $x + 1$, and this subsequently reduces the probability that an offspring at the focal patch
 568 after dispersal will establish onto the patch before the next breeding season. Four classes of offspring will exist at
 569 the focal patch after dispersal: 1) the offspring of a focal individual aged x , 2) the offspring of other individuals
 570 on the patch that exist due to the genotype of a focal individual aged x , 3) the offspring of other individuals on
 571 the patch that don't owe their existence to the genotype of a focal individual aged x , and 4) offspring from
 572 elsewhere in the population. As we are interested in the inclusive fitness effect of the mutant allele, we must
 573 consider the fates of all the offspring that are impacted by the effect of the allele²⁴.

574

575 We can consider the first two sets of offspring together and ask how a change in survival at age x alters the direct
 576 and indirect production of offspring of a focal age x individual (working showed below).

577

578
$$\frac{dw_{1x}(1,2)}{d\dot{p}(x)} = \dot{F}(x)[(1-d)g(x) + (1-c)d\bar{g}] - \dot{F}(x)[(1-d)g'(x) + (1-c)d\bar{g}]$$

579

[B1]

580 with $g'(x)$ displaying that the effect of the allele is to alter the probability that the direct and indirect offspring of
 581 the individual aged x establish on to the patch. **[B1]** can be worked through and simplified as:

582

583
$$\frac{dw_{1x}(1,2)}{d\dot{p}(x)} = \dot{F}(x)(1-d)g(x) + \dot{F}(x)(1-c)d\bar{g} - \dot{F}(x)(1-d)g'(x) - \dot{F}(x)(1-c)d\bar{g}$$

584

585
$$= \dot{F}(x)(1-d)g(x) - \dot{F}(x)(1-d)g'(x)$$

586

587
$$= \dot{F}(x)(1-d)[g(x) - g'(x)]$$

588

589
$$= \dot{F}(x)(1-d) \left[\frac{1-p(x) + (N-1)(1-\bar{p})}{b(x)(1-d) + (N-1)\bar{b}(1-d) + N\bar{b}(1-c)d} \right.$$

 590
$$\left. - \frac{1-p'(x) + (N-1)(1-\bar{p})}{b(x)(1-d) + (N-1)\bar{b}(1-d) + N\bar{b}(1-c)d} \right]$$

591

592
$$= \dot{F}(x)(1-d) \left[\frac{-d\dot{p}(x)}{b(x)(1-d) + (N-1)\bar{b}(1-d) + N\bar{b}(1-c)d} \right]$$

593

$$594 \quad = -d\dot{p}(x) \left[\frac{\dot{F}(x)(1-d)}{b(x)(1-d) + (N-1)\bar{b}(1-d) + N\bar{b}(1-c)d} \right]$$

595

596 Finally, let $\dot{h}(x) = \frac{\dot{F}(x)(1-d)}{b(x)(1-d) + (N-1)\bar{b}(1-d) + N\bar{b}(1-c)d}$ be defined as the proportion of offspring at the focal patch
 597 after dispersal that are born due the genotype of a focal individual aged x . Note, $\dot{h}(x)$ is different from $h(x)$ (see
 598 **Methods Appendix A**), as $h(x)$ does not partition the offspring with respect to inclusive fitness contributions.
 599 The relatedness of the indirect offspring has already been discounted in the calculation of $\dot{F}(x)$, and the relatedness
 600 of a focal individual to its own offspring is 1, so we can re-write **[B1]** as

601

$$602 \quad \frac{dw_{1x}(1,2)}{dp(x)} = -d\dot{p}(x)\dot{h}(x) \quad \text{[B2]}$$

603

604
 605 Let us now consider the third set of offspring and ask how a change in survival of a focal individual at age x
 606 impacts the offspring of other individuals on the patch that don't owe their existence to the genotype of a focal
 607 individual aged x . In the resident population, this contribution is 0. However, an increase in survival of an
 608 individual aged x , for example, will reduce the likelihood that any of these offspring that do not disperse will
 609 establish onto the patch before the next breeding season. We can write the average number of offspring of all
 610 other individuals on the patch, in the presence of a focal individual aged x , that will establish onto the local patch
 611 as

612

$$613 \quad (N-1)\bar{F}(1-d)g(x) \quad \text{[B3]}$$

614
 615 The effect of a mutant allele that alters the survival of a focal individual aged x on this expected number of
 616 offspring can then be written as

617

$$618 \quad \frac{dw_{1x}(3)}{d\dot{p}(x)} = (N-1)\bar{F}(1-d)g(x) - (N-1)\bar{F}(1-d)g'(x) \quad \text{[B4]}$$

619

620
 621 **[B4]** can then be worked through and simplified as

622

$$623 \quad \frac{dw_{1x}(3)}{d\dot{p}(x)} = (N-1)\bar{F}(1-d)[g(x) - g'(x)]$$

$$624$$

$$625 \quad = (N-1)\bar{F}(1-d) \left[\frac{1-p(x) + (N-1)(1-\bar{p})}{b(x)(1-d) + (N-1)\bar{b}(1-d) + N\bar{b}(1-c)d} \right.$$

$$626 \quad \left. - \frac{1-p'(x) + (N-1)(1-\bar{p})}{b(x)(1-d) + (N-1)\bar{b}(1-d) + N\bar{b}(1-c)d} \right]$$

627

628
$$= (N - 1)\bar{F}(1 - d) \left[\frac{-d\dot{p}(x)}{b(x)(1 - d) + (N - 1)\bar{b}(1 - d) + N\bar{b}(1 - c)d} \right]$$

629

630
$$= -d\dot{p}(x) \left[\frac{(N - 1)\bar{F}(1 - d)}{b(x)(1 - d) + (N - 1)\bar{b}(1 - d) + N\bar{b}(1 - c)d} \right]$$

631

632 Similar to the logic above, let $\dot{k}(x) = \frac{(N-1)\bar{F}(1-d)}{b(x)(1-d)+(N-1)\bar{b}(1-d)+N\bar{b}(1-c)d}$ be defined as the proportion of offspring at

633 the focal patch after dispersal that are average direct and indirect offspring of all other individuals bar the focal

634 individual aged x . These offspring are related to the focal individual by $\hat{r}(x)$ and so the above becomes

635

636
$$\frac{dw_{1x}(3)}{d\dot{p}(x)} = -d\dot{p}(x)\dot{k}(x)\hat{r}(x)$$

637

[B5]

638 Given our assumptions of an infinite population, we can assume that relatedness of any individual on a patch to

639 offspring that have dispersed from elsewhere will be equal to zero. Therefore, the relatedness of a focal individual

640 aged x to the proportion of offspring after dispersal that were not born locally on the patch is zero. Thus, there is

641 an overall balance of the effect of the mutant allele on a focal individual of age x 's production of newborns

642 weighted on one side by locally produced offspring (with varying relatedness) and on the other side by dispersed

643 offspring. The total effect of a mutant allele that alters age-specific survival on the production of offspring can

644 then be summed as

645

646
$$\frac{dw_{1x}}{d\dot{p}(x)} = -d\dot{p}(x)\dot{h}(x) - d\dot{p}(x)\dot{k}(x)r_{1x} = -d\dot{p}(x)[\dot{h}(x) + \dot{k}(x)\hat{r}(x)]$$

647

[B6]

648

649 The overall effect (dw_{yx} for all y) of a mutant allele that alters age-specific survival is then shown in [6] in the

650 main text.

651

652 **The effect of a mutant allele that alters age-specific reproduction in a social population**
653

654 Let us now consider how a mutant allele that affects reproduction at age x will alter the class- y offspring a focal
655 individual aged x in our social population. First, we assume for simplicity that a change in reproduction of a focal
656 individual aged x does not alter the individual's probability of survival to the next breeding season, or its
657 contributions to the survival of other individuals alive on the patch. These are obvious extensions for future
658 iterations of the model (see **Discussion**). We therefore limit the effects of a change in reproduction to altering the
659 contributions a focal individual aged x makes to the offspring class, w_{1x} . There are four different types of offspring
660 to consider: 1) the offspring of a focal individual aged x that exist due to its own genotype, 2) the offspring of
661 other individuals on the patch that exist due to the genotype of a focal individual aged x , 3) the offspring of other
662 individuals on the patch that don't owe their existence to the genotype of a focal individual aged x , and 4) offspring
663 from elsewhere in the population. Again, as we are interested in the inclusive fitness effect of the mutant allele,
664 we must consider the fates of all the offspring that are impacted by the effect of the allele²⁴.

665
666 The inclusive fitness effects of a mutant allele that causes a change in the direct rate of reproduction of a focal
667 individual aged x for each class of offspring can be displayed as follows:
668

$$669 \quad \frac{dw_{1x}(1)}{db(x)} = \dot{b}(x)[(1-d)g(x) + (1-c)d\bar{g}] - \dot{b}'(x)[(1-d)g'(x) + (1-c)d\bar{g}]$$

670 **[B7]**

$$672 \quad \frac{dw_{1x}(2)}{db(x)} = \sum_z T_{1,z}^x (1-d)g(x) - \sum_z T_{1,z}^x (1-d)g'(x)$$

673 **[B8]**

$$675 \quad \frac{dw_{1x}(3)}{db(x)} = (N-1)\bar{F}(1-d)g(x) - (N-1)\bar{F}(1-d)g'(x)$$

676 **[B9]**

677
678 with prime notation displaying that the explicit effects of the allele. Above, **[B7]** considers the effect of the allele
679 on the focal individual's direct production of offspring, **[B8]** the effect of the allele on the indirect offspring of
680 focal, and **[B9]** the effect on offspring born to other individuals on the patch not due to the genotype of focal, but
681 whom focal might be related to more than the population average (zero). Again, individuals that disperse from
682 elsewhere in the population to the focal patch are assumed to be related to any individual on the patch by zero,
683 and so the inclusive fitness effect of the allele with regards to the fourth class of offspring is also equal to zero.
684 Furthermore, given our assumption of infinite patches, the effect of the allele on the second and third classes of
685 offspring is limited to those offspring which do not disperse *i.e.* compete for a site at the local patch. The
686 simplification of **[B7 – B9]** follows the same logic as **[B1 – B5]**. The resulting derivations are lengthy and so are
687 available in the Supplementary Information. The overall effect of the mutant allele that causes a change in the rate
688 of reproduction of a focal individual aged x is the sum of the effects **[B7 – B9]** and can be expressed as:

689

690

$$\frac{dw_{1x}}{db(x)} = db(x)[(1-d)g(x)[(1-h(x)) - i(x) - k(x)\hat{r}(x)] + (1-c)d\bar{g}]$$

691

[B10]

692

693

The overall effect (dw_{yx} for all y) of a mutant allele that alters age-specific reproduction is then shown in **[8]** in

694

the main text.

695

696

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702

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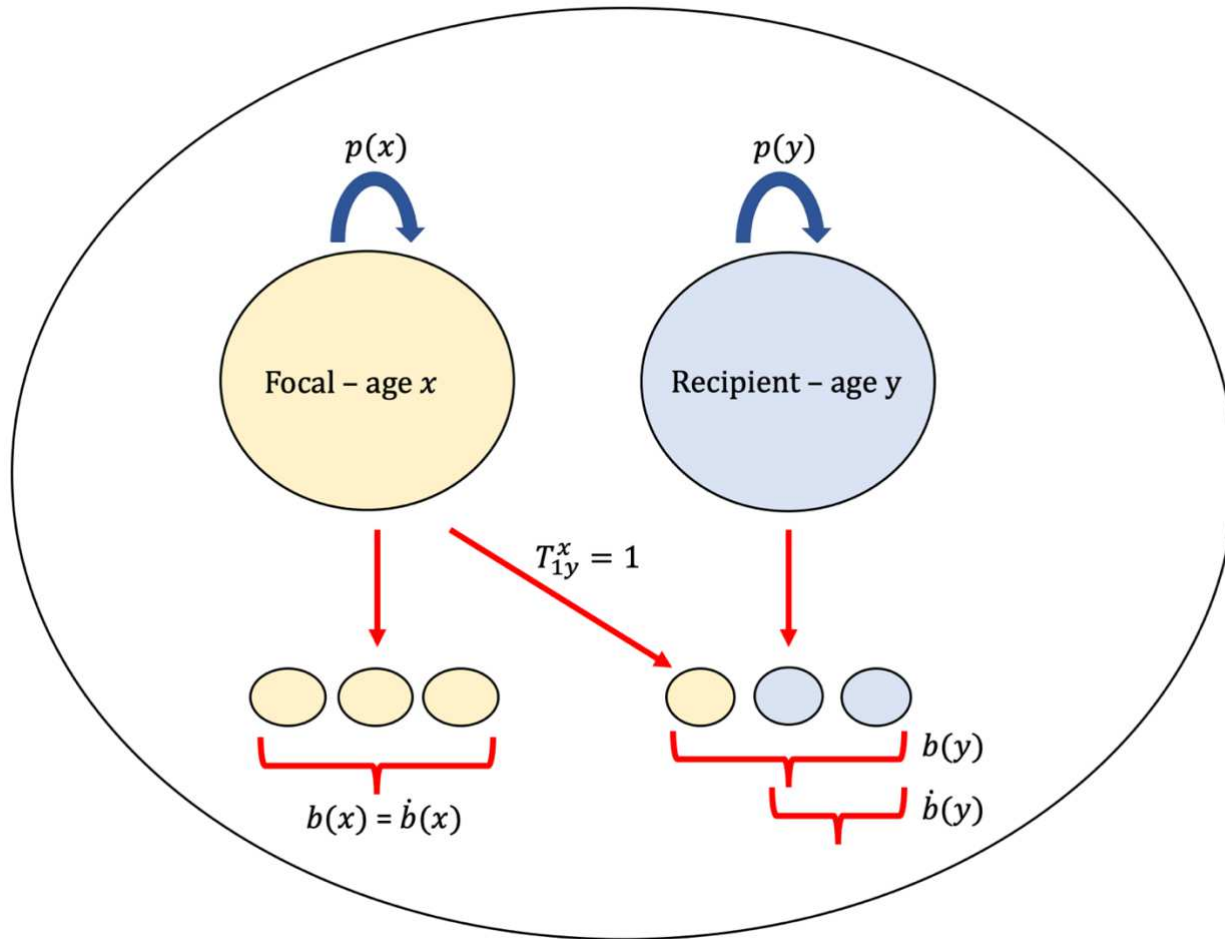
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838 **Figures**

839 **Figure 1**

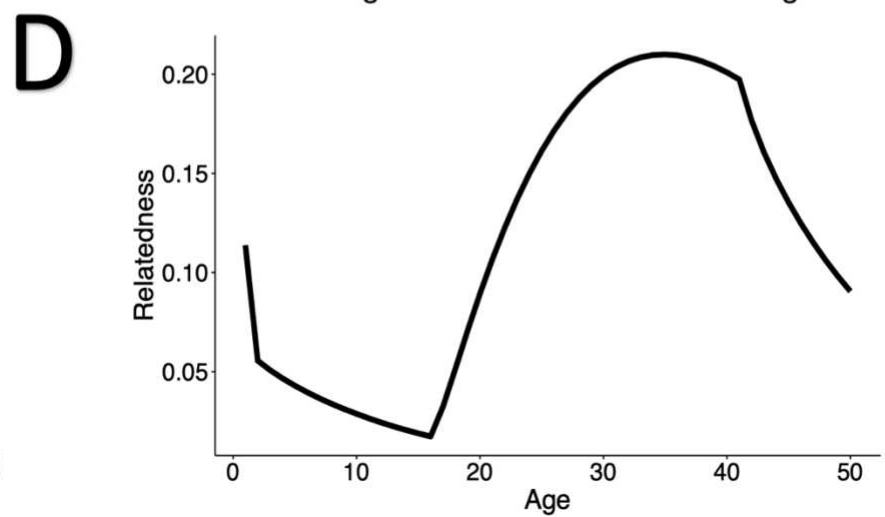
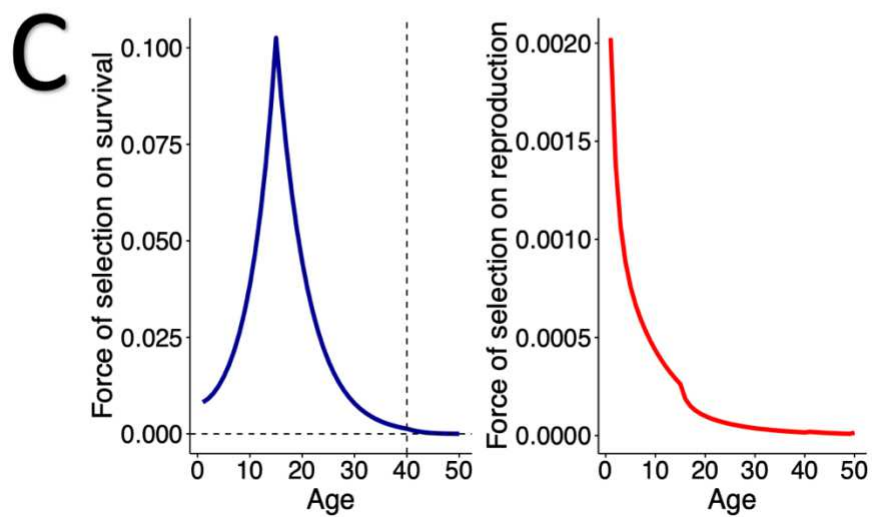
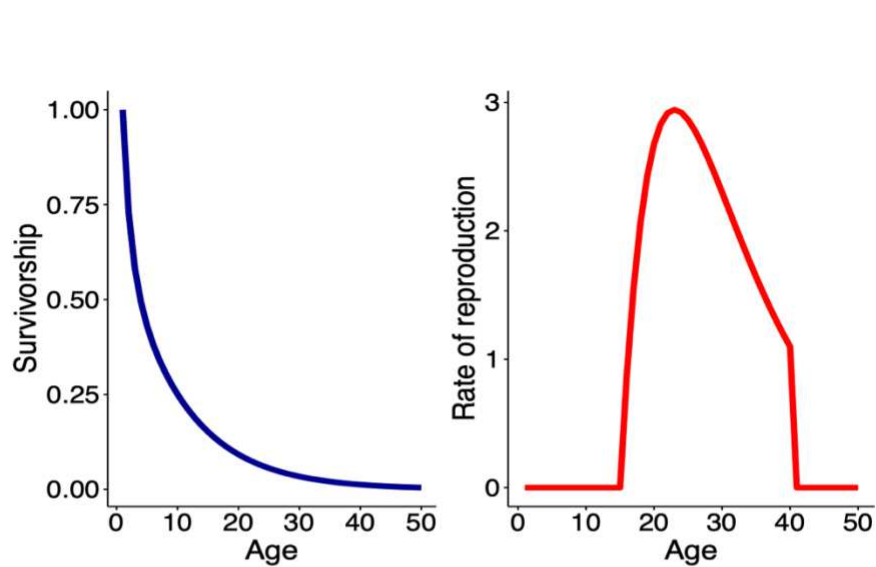
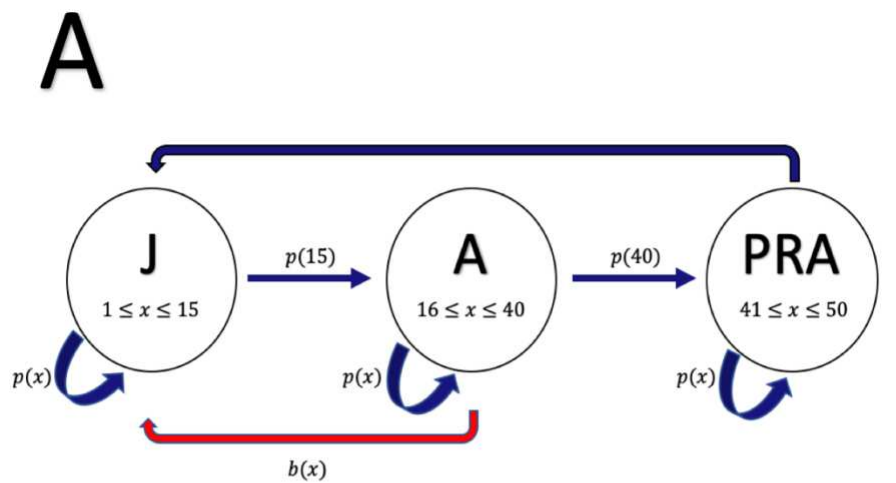
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854 **Figure 1. An example of a genetic offspring transfer between two individuals using inclusive fitness.** To illustrate transfers, we consider a
855 patch with two individuals, one of age x and the other of age y . The individual aged x has $b(x)$ offspring, survives with probability $p(x)$, and
856 receives no social transfers from other individuals in the population when aged x . We imagine a social behaviour exists whereby the individual
857 aged x contributes to the reproduction of individuals aged y . In this scenario, the individual aged y has $b(y)$ offspring in the current breeding
858 season, but one of these offspring is due to the transfer from the focal individual aged x . Following inclusive fitness logic, the offspring produced
859 due to the social behaviour of the individual aged x is stripped from the inclusive fitness of the individual aged y , leaving $\dot{b}(y)$ as their inclusive
860 fitness contribution to age class 1. The inclusive fitness contribution of the focal individual aged x to age class 1 is $\dot{b}(x) + T_{1y}^x \hat{r}(x)$, where $\hat{r}(x)$
861 represents the relatedness of an individual aged x to the offspring it helped to produce.

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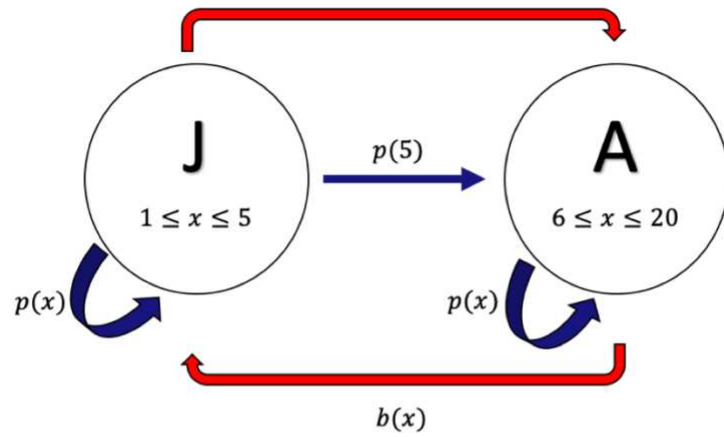
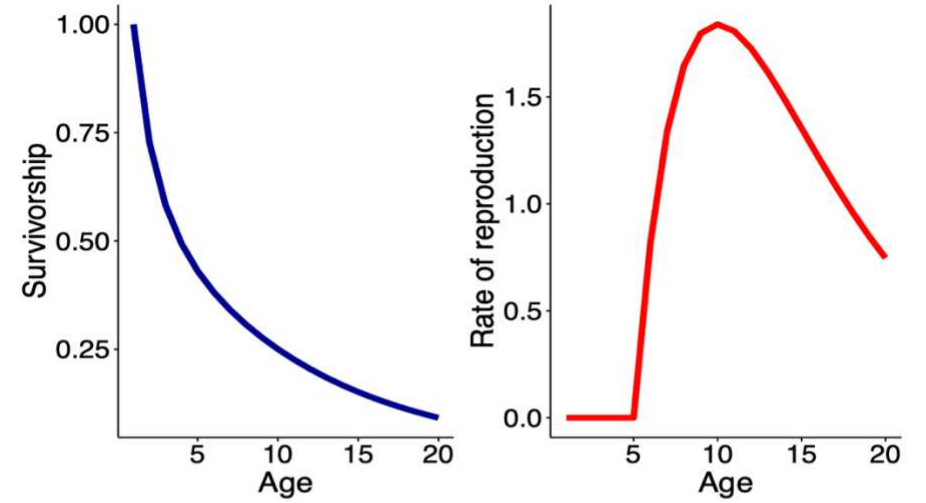
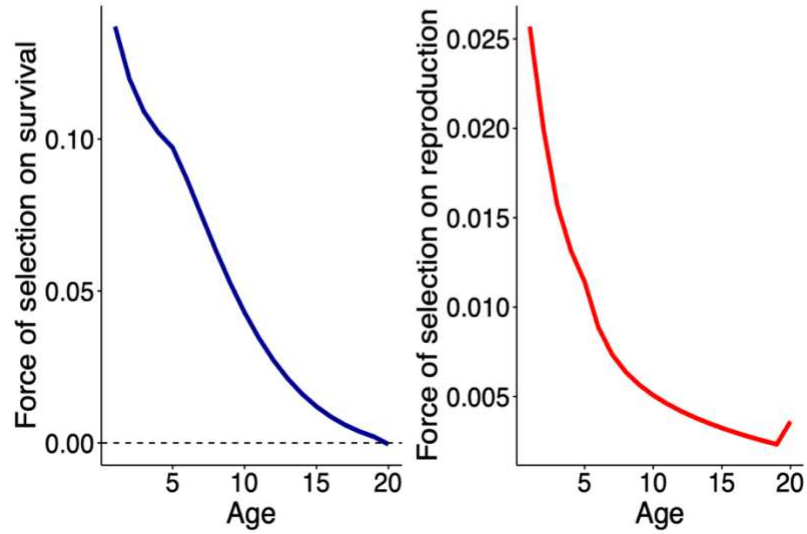
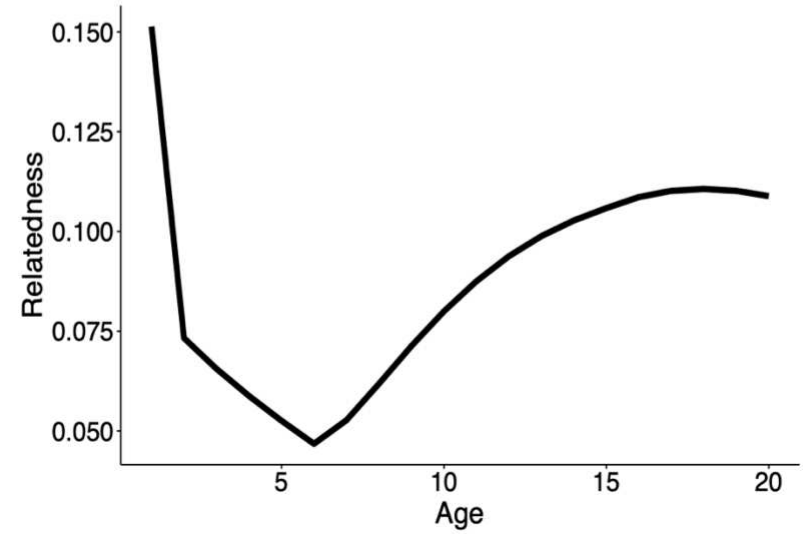
864 **Figure 2. Age specific forces of selection in a social population with post-reproductive help.** A) A hypothetical population of iteroparous
865 individuals classified into three life cycle stages: juvenile (J), reproductive adult (A), and post-reproductive adult (PRA). The red arrow from A to
866 J represents the reproduction of adult individuals, whereas the dark blue arrow from PRA to J represents the social contributions from post-
867 reproductive adults to the survival of juveniles. B) The background vital rates of survivorship and reproduction of the model social population.
868 Survival probability at age x is produced from a Siler model ([11]) with parameters: $\alpha_1 = 0.4$, $\beta_1 = 0.6$, $\alpha_2 = 0.1$, $\beta_2 = 0$ (See SOM for further
869 details). Reproduction at age x is modelled according to [13] with parameters: $\varepsilon = 15$, $\varphi = 0.125$, and $\kappa = 40$ (SOM). C) The forces of selection
870 acting on survival at age x increases during the juvenile period and then decreases but remains above zero in the post-reproductive period. The
871 force of selection acting on reproduction at age x is weaker than the force of selection acting on survival and declines from birth. Other demographic
872 parameters to produce these forces of selection were set to $c = 0$, $d = 0.5$, $N = 4$ and $\omega = 50$. (see **Model** and SOM D) The relatedness of an
873 individual aged x to another random individual on the patch declines throughout the juvenile (pre-reproductive) window, and then increases during
874 adult reproduction before declining again as reproduction ceases.

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A**B****C****D**

880 **Figure 3. Age specific forces of selection in a social population with pre-reproductive help.** A) A hypothetical population of iteroparous
881 individuals with two lifecycle stages: juvenile (J) and reproductive adult (A). The red arrow from J to A represents the social contributions from
882 juveniles to the reproduction of adults. Note that here, help is in the currency of reproduction, rather than survival (See Fig. 2A). B) The background
883 vital rates of survivorship and reproduction. Survival at age x is produced from a Siler model ([11]) with parameters: $\alpha_1 = 0.4$, $\beta_1 = 0.6$, $\alpha_2 =$
884 0.1 , $\beta_2 = 0$. Rate of reproduction at age x is modelled according to [13] with parameters: $\varepsilon = 5$, $\varphi = 0.2$, and $\kappa = 21$. C) The force of selection
885 acting on survival at age x declines from birth. The force of selection acting on reproduction at age x is weaker than the force of selection on
886 survival and also declines from birth but then increases in the final age class. Other demographic parameters to produce these forces of selection
887 were set to $c = 0$, $d = 0.5$ and $N = 4$ and $\omega = 20$. D) The relatedness of an individual aged x to another random individual on the patch declines
888 throughout the juvenile period, and then increases during adult reproduction.

Supplementary Files

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