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Birth-order differences can drive natural selection on aging

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Abstract

Senescence—the deterioration of survival and reproductive capacity with increasing age—is generally held to be an evolutionary consequence of the declining strength of natural selection with increasing age. The diversity in rates of aging observed in nature suggests that the rate at which age-specific selection weakens is determined by species-specific ecological factors. We propose that, in iteroparous species, relationships between parental age, offspring birth order and environment may affect selection on senescence. Later-born siblings have, on average, older parents than do first-borns. Offspring born to older parents may experience different environments in terms of family support or inherited resources, factors often mediated by competition from siblings. Thus, age-specific selection on parents may change if the environment produces birth-order related gradients in reproductive success. We use an age-and-stage structured population model to investigate the impact of sibling environmental inequality on the expected evolution of senescence. We show that accelerated senescence evolves when later-born siblings are likely to experience an environment detrimental to lifetime reproduction. In general, sibling inequality is likely to be of particular importance for the evolution of senescence in species such as humans, where family interactions and resource inheritance have important roles in determining lifetime reproduction.

Keywords

Ecology; evolution; demography; inequality; inheritance; life-history

Introduction

The near ubiquity of senescence—the deterioration of survival and reproductive capacity with increasing age—is generally held to be a consequence of declining strength of natural selection with age. Weaker purifying selection at older ages allows the increase in frequency of alleles with deleterious effects at old ages, producing senescent declines in fitness.

Hamilton's classic model (1966) remains the standard framework for analyzing the strength

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of selection on genes affecting age-specific survival (and reproduction). The wide diversity in rates of aging observed in nature suggests that, while weakening selection may be universal (but see Baudisch 2005), the precise rate (and amount) at which age-specific selection weakens is determined by species-specific ecological factors. Understanding how ecological factors affect age-specific natural selection is thus essential to explaining why rates of senescence vary across the tree of life (Monaghan et al., 2008).

For example, some variation in rates of senescence can be explained by extrinsic mortality (Stearns 1992). If extrinsic adult mortality is high, for example, selection for survival and reproduction (i.e., fitness) in older adults will be weakened, promoting faster senescence. If juvenile mortality is high (through sensitivity to predation, for example) selection for survival and reproduction in adults will be stronger, leading to longer lifespan and slower reproductive senescence. Existing work on age-specific selection has allowed us to link variation in many different ecological conditions to the evolved diversity in rates of senescence (Reznick et al., 2004; Fox et al., 2011; Silvertown et al., 2001). Recently, parental-age-related variation in offspring fitness has received attention as a potentially important ecological driver of the evolution of senescence (Pavard and Branger, 2012; Käär and Jokela, 1998). Here we will focus on the question of how variation in the environment experienced by offspring, e.g., food availability, social dominance or material wealth, affects the direction and strength of selection on rates of senescence in their parents. This is a difficult problem for many reasons (Wolf and Wade, 2001), not least of which is that classical theories of aging (Hamilton, 1966; Rose et al., 2007) treat all offspring as identical.

However, selection on senescence should also depend on how the environment affects the entire life-histories of offspring produced at each parental age. If offspring produced at an old age have relatively low fitness, i.e., if their environment limits reproductive value (Goodman, 1982), parental reproduction at that age should contribute relatively less to the propagation of parental genes. Given the large empirical literature showing that offspring survival and reproduction can vary with the age of parent that produced them (Nussey et al., 2013; Gillespie et al., 2013; Hercus and Hoffmann, 2000), it is important to add these inter-generational effects into evolutionary theory. Here we show that the recognition of sibling inequality in fitness produces important changes to the mathematical structure of the theory of aging, and to its predictions for the evolution of senescence.

Although the physiological condition of older parents can matter to their offspring's survival and reproduction (Nassar and Usita, 2009), parental age can also have an impact on the environmental conditions into which an offspring is born. Offspring born to older parents may experience different environments in terms of family support (Pavard and Branger, 2012; Forbes, 2011) or inherited resources (Gibson and Gurmu, 2011; Ridley and Sutherland, 2002), factors often mediated by competition from siblings. But these effects are generally ignored in analyses of selection on senescence, despite strong empirical evidence that sibling environmental inequality can affect fitness throughout the lifetime (Gillespie et al., 2013; Gibson and Gurmu, 2011; Ridley, 2007). Work in this area has been hindered by uncertainty about how to map variation in offspring fitness to selection on parental traits (Wolf and Wade, 2001). Here we use a simplified population model to incorporate the effects of sibling environmental quality into the classical theory of aging (Coulson et al.,

2010). We assume an age-and-stage structured population (Coulson et al., 2010) where individual life-histories vary between two environments: one ‘good’ (g) and one ‘bad’ (b) for fitness. We vary the difference between environments in terms of expected amount and timing of reproduction, and the probability that newborns enter each environment. Specifically, the probability that an individual is born into the good environment varies with its number of older siblings, and therefore also with the age of its parent. This formulation captures the essential interactions between sibling environmental inequality and parental aging.

We measure the strengths of selection on age-specific reproduction and survival by sensitivities of the population growth rate (r) (Hamilton, 1966; Caswell, 2001) to changes in age-specific reproductive and survival rates. These sensitivities determine how rapidly a new allele with deleterious effects at a given age will be purged from the population in a constant environment, with or without density dependent regulation (Metz et al., 1992). In this context, we use the relative sensitivity of r at different ages to make inferences about the expected direction and strength of selection on senescence. We interpret lower sensitivities (i.e., weaker purifying selection) at old ages relative to younger ages to give the expectation of faster senescence. This follows because mutations with negative effects at older ages will be purged more slowly than those affecting younger ages. Conversely, we interpret lower sensitivity at younger ages to imply an expectation of slower senescence. We now use this framework to ask how the age-specific strengths of selection on survival and reproduction in parents are affected by environmentally-driven differences in reproductive value between first-born and later-born offspring.

Methods

We denote matrices as bold font face upper case, e.g., $\mathbf{X}$, vectors as bold font face lower case, e.g., $\mathbf{x}$, and matrix or vector elements as italic upper and lower case respectively, e.g., X and x . All vectors are column vectors by default and we indicate the transpose by $\mathbf{T}$.

The basics of senescence

First, we review the simplest case of age-structured selection. Throughout this study we count age in 1-year intervals. Newborns enter age-class 1, during which they can also reproduce, and individuals live at most two years. Including an initial pre-reproductive age was not needed for our demonstration but our results will also apply to life histories with pre-reproductive stages. Let M_1 and M_2 be the rates of reproduction at ages 1 and 2, and S the probability of survival from age 1 to 2. Let T be the average age at reproduction. Such a population can be described by the age-structured projection equation

$$\begin{bmatrix} n_1 \\ n_2 \end{bmatrix}_{t+1} = \begin{bmatrix} M_1 & M_2 \\ S & 0 \end{bmatrix} \cdot \begin{bmatrix} n_1 \\ n_2 \end{bmatrix}_t \quad (1)$$

The intrinsic rate of population growth (r) is given by the log of the dominant eigenvalue of the projection matrix. The stable age-structure of the population and the reproductive value

vector are given by the corresponding eigenvectors $\mathbf{u}$ and $\mathbf{v}$. The sensitivity of population growth to the rate of reproduction at age 1 (M_1) is

$$\frac{\partial r}{\partial M_1} = \frac{1}{T} \quad (2)$$

and the sensitivity of population growth to M_2 is

$$\frac{\partial r}{\partial M_2} = \frac{e^{-r} S}{T}. \quad (3)$$

The sensitivity of population growth to the rate of reproduction at age 2 (M_2) must always be less than the sensitivity of population growth to earlier reproduction M_1 because the probability of survival from age 1 to 2 (S) is less than 1. A similar result applies to survival senescence, such that

$$\frac{\partial r}{\partial S} = \frac{e^{-r} M_2}{T}. \quad (4)$$

Thus, we have rediscovered the classic results of Hamilton (1966), that in a population structured by age only, the sensitivity of population growth to both survival and reproduction always decreases with age after reproductive maturity, making reproductive and survival senescence both inevitable. The absolute rate of senescence is determined by the shape of the age structure, and is beyond the scope of this paper.

Our model

Now consider a population where survival and reproductive rates vary by age, by stage and by environment. Newborns are age 1, and maximum lifespan is still two years. Reproduction can occur at age 1 or age 2, and at most one offspring is produced each year. Each individual thus occupies one of two parity stages, determined by whether or not it has already reproduced. Note that the binary age-structure means first-borns can be born to parents of either age, but second-borns always have older parents.

New individuals are born into one of two environments defined by different effects on reproductive timing and amount. We set the timing and amount of lifetime reproduction (which together equal fitness) to be earlier and higher in the ‘good’ (g) environment than in the ‘bad’ (b) environment. We investigate the expected evolution of senescence in this system by varying three parameters: the probability (W) of being born into the ‘good’ environment; the degree of difference (x) between the two environments; and a modifier (y) that makes W a function of parental parity (i.e., W will be different for first-borns and second-borns). We will index survival and reproduction parameters by the scheme

$M_{\text{age, environment}}^{\text{parity}}$. To simplify our notation, we index individuals at age 1 by age but not parity.

We specify that the environment affects the probability of reproduction at age 1 only, such that

$$\begin{aligned} M_{1,g} &= M_1(1+x), \\ M_{1,b} &= M_1(1-x). \end{aligned}$$

Thus, the parameter x ($-1 \leq x \leq 1$) determines the difference in both reproductive level and timing between the ‘good’ and ‘bad’ environments. This is the driver of the environmental difference in offspring reproductive value.

We specify that the probability that an offspring is born into the ‘good’ environment varies only by the parental parity at its birth, i.e., its birth-order, such that

$$\begin{aligned} W^0 &= W(1+y), \\ W^1 &= W(1-y). \end{aligned}$$

Thus, the parameter y ($-1 \leq y \leq 1$) determines how first-born and second-born offspring are distributed between environments.

We define population growth by the simplified projection equation:

$$\begin{bmatrix} n_{1,g}^0 \\ n_{1,b}^0 \\ n_2^0 \\ n_2^1 \end{bmatrix}_{t+1} = \begin{bmatrix} M_{1,g}W^0 & M_{1,b}W^0 & M_2W^0 & M_2W^1 \\ M_{1,g}(1-W^0) & M_{1,b}(1-W^0) & M_2(1-W^0) & M_2(1-W^1) \\ S(1-M_{1,g}) & S(1-M_{1,b}) & 0 & 0 \\ SM_{1,g} & SM_{1,b} & 0 & 0 \end{bmatrix} \cdot \begin{bmatrix} n_{1,g}^0 \\ n_{1,b}^0 \\ n_2^0 \\ n_2^1 \end{bmatrix}_t \quad (5)$$

Figure 1 shows the corresponding 4-stage life-cycle. Note that the projection matrix in (5) is of the form

$$\begin{bmatrix} \mathbf{F}_1 & \mathbf{F}_2 \\ \mathbf{P} & 0 \end{bmatrix},$$

where reproduction at age 1 is described by the submatrix $\mathbf{F}_1$, reproduction at age 2 by the submatrix $\mathbf{F}_2$, and survival from age 1 to 2 by the submatrix $\mathbf{P}$.

When x is positive, the good environment produces higher reproduction at age 1 than the bad environment. Thus, offspring born into the good environment will have higher reproductive value. When y is positive, first-born offspring are more likely than second-born offspring to enter the good environment. These effects are opposite when the parameters are negative. To test the effects of varying the environment between first- and second-born offspring, we held x constant at 0.25 and varied y over its full range.

Note that here environment does not affect reproduction at age 2. We use values of $W = 0.5$ and $S = 0.65$. We allow M_1 and M_2 to vary independently between 0.5 and 1.0. In the Supporting Information, we show in general how the parameters x and y affect the strengths of selection on S , M_1 and M_2 .

For all parameter combinations, we arrive at age- and stage-specific selection strengths by standard lower-level vital-rate sensitivity analysis (Caswell 2001, Morris and Doak 2004).

Results

First, we note that increasing the environmental advantage of first-born offspring always increases the overall rate of population growth because on average individuals reproduce more and earlier in their lifetimes (Fig. 2). However, we will see that an environmental advantage of first-borns can have strong effects on age-specific selection strengths in the parental generation.

We now examine the strengths of selection on the probability of survival from age 1 to 2 (S), and the rate of reproduction at ages 1 and 2 (M_1 and M_2 ; see Supporting Information for details). In our analysis, age structure and reproductive value differ according to the birth environment.

Survival Senescence

The strength of selection on survival from age 1 to 2 is

$$\frac{\partial r}{\partial S} = \frac{e^{-r} M_2}{T} [\bar{v}_1 + W y (v_{1,g} - v_{1,b}) \{1 - 2M_1 [1 + x (u_{1,g} - u_{1,b})]\}]. \quad (6)$$

Here we keep track of the difference between the reproductive values at birth, $v_{1,g}$ and $v_{1,b}$, and similarly between the proportion of newborns, $u_{1,g}$ and $u_{1,b}$. The first term in (6) is Hamilton's (Hamilton, 1966) original result. The new second term (in square brackets) accounts for the effects of sibling environmental inequality. Figure 3 shows that when first-born offspring are more likely than second-born offspring to enter the good environment ($y > 0$), the probability of survival to the next age is subject to weaker selection, leading to the expected evolution of lower survival. Under these conditions, (6) also shows that selection weakens further with increased reproduction at age 1, because this means more newborns will have older siblings, and so be disadvantaged. The result is that we expect faster survival senescence, i.e., the evolution of a lower probability of survival from age 1 to 2.

Reproductive Senescence

The strength of selection on reproduction at age 1 is

$$\frac{\partial r}{\partial M_1} = \frac{1}{T} [\bar{v}_1 + W y (v_{1,g} - v_{1,b}) \{1 - 2e^{-r} S M_2\}]. \quad (7)$$

which, by comparison with the age-structured case (see (2)), shows that the sensitivity of population growth to M_1 is now adjusted by: 1) the relative production at age 1 of newborns that enter the good environment; 2) the probability of surviving to age 2, fertility at age 2, and the relative production at age 2 of newborns that enter the good environment.

Here we see that when first-borns are more likely to enter the good environment (y is positive), there is stronger selection on reproduction at age 1 leading to the expected evolution of greater early reproductive investment. However, this increase in selection strength is counteracted by the dependency of second-born production on reproduction at age 1. We deduce from (7) that if the net rate of reproduction at age 2 ($e^{-r}SM_2$) exceeds 0.5, and first-borns are relatively advantaged, selection strength on reproduction at age 1 decreases rather than increases as we might expect. In this case, it would be selectively advantageous to delay all first reproduction until age 2.

The strength of selection on reproduction at age 2 is

$$\frac{\partial r}{\partial M_2} = \frac{e^{-r}S}{T} [\bar{v}_1 + Wy(v_{1,g} - v_{1,b}) \{1 - 2M_1 [1 + x(u_{1,g} - u_{1,b})]\}]. \quad (8)$$

Compared to (3) this is a long expression—but as with (7) the difference from the age-structured case comes from the reproductive value-based adjustment of reproduction by the relative entrance of newborns into the good and bad environments. The result also depends on the rate of iteroparity, since if few second-borns are produced, parity has little influence on the environmental distribution of newborn offspring. When y is positive, second born offspring have a relatively lower likelihood of entering the good environment, and thus have lower than average reproductive value. The result is that as relatively more first borns enter the good environment (i.e., as y increases), the bracketed term in (8) falls in magnitude, and so the strength of selection on reproduction at age 2 weakens. The expected rate of reproductive senescence is given by the difference between the strengths of selection on reproduction (7) and (8) at ages 1 and 2 (Fig. 4). If $\frac{\partial r}{\partial M_1} - \frac{\partial r}{\partial M_2}$ is positive, we predict faster reproductive senescence, and if it is negative we predict slower reproductive senescence and a decrease in early reproduction.

$$\frac{\partial r}{\partial M_1} - \frac{\partial r}{\partial M_2} = \frac{1}{T} [\bar{v}_1(1 - e^{-r}S) + 2Wy(v_{1,g} - v_{1,b}) \{M_1[1 + x(u_{1,g} - u_{1,b})] - e^{-r}SM_2\}], \quad (9)$$

Thus, we see that when first borns are advantaged (i.e., $2Wy(v_{1,g} - v_{1,b}) > 0$), reproductive senescence should accelerate if

$$M_1 [1 + x(u_{1,g} - u_{1,b})] \geq e^{-r}SM_2. \quad (10)$$

I.e., only when the net rate of reproduction at age 1 (left-hand side) exceeds that at age 2 (right-hand side) should the evolution of reproductive senescence mirror changes in the birth-order effect on lifetime reproduction.

Age-specific selection on both reproduction and survival depends on the difference between environments in the reproductive value ($v_{1,g} - v_{1,b}$) and the proportion ($u_{1,g} - u_{1,b}$) of newborns in each environment. These factors combine to adjust the average reproductive value of newborns v_1 , by the effects of environmental difference.

Discussion

We have shown that environmental inequality among offspring has two important effects on the evolution of senescence. First, as offspring born to older parents become more likely to enter environments that constrain their lifetime reproduction, the strength of selection on old-age reproduction and survival weakens beyond the expectation under Hamilton's original model. Thus, when later-borns are disadvantaged, we expect faster reproductive and survival senescence. We also find an interaction between parental reproductive history and the nature of sibling inequality: When later-borns are disadvantaged, increased reproduction by young parents further weakens selection for reproduction and survival at old ages because this means more newborns will have older siblings, and so be disadvantaged. Conversely, if no one reproduces at age 1, all offspring born to age 2 mothers will be advantaged first-borns, and selection for old-age survival and reproduction will be strong.

Our results provide a clear theoretical demonstration of how environmental differences among offspring can influence the evolution of senescence, both in isolation and through interactions with parental reproductive history. Sibling inequality could affect selection on senescence across a wide range of organisms (Nussey et al., 2013), particularly in family-living species where social structure is shaped strongly by inequalities in resource transmission to offspring (Ridley and Sutherland, 2002). We suggest that sibling inequality is likely to be of particular importance for understanding the evolution of human senescence. This is because humans live in complex structured societies, in which resource holding, the transmission of resources and dispersal are closely linked (Kaplan et al., 2000; Borgerhoff Mulder et al., 2009; Rogers et al., 2011). Consequently, some form of sibling inequality was likely present across the historic continuum of ecological and economic environments (Borgerhoff Mulder and Beheim, 2011; Gibson and Gurm, 2011). For example, ancient pre-agricultural society may have been characterised by inequalities in the transmission of knowledge or social status from parents to offspring (Gurven et al., 2006). Here we have discussed ecological differences that may arise among siblings, but the definition of environment in our model can be extremely broad and could also, for example, refer to sibling differences in epigenetic factors expressed at old ages (Greer et al., 2011), or in culture (e.g., preference for family size (Anderton and Mineau, 1987)). The evolution of sex differences in senescence could also result if sibling inequality operates differently between the sexes, e.g., when sons but not daughters compete for parental resources. The generalised link between sibling inequality and aging can be exploited in analyses of population responses to environmental, social and economic change, on both ecological and evolutionary time-scales (Rees and Ellner, 2009). Future extensions of our model could include allowing reproduction to vary by parity (i.e., incorporating a pre-existing interaction between past and present reproduction), or allowing environmental inheritance to depend on parental age and environment. Such interactions can be accommodated by extending our

model and using our analytical approach, and may be especially useful in adapting our model to different empirical contexts.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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Fig. 1. Life-cycle

Here we show the life-cycle that represents our projection equation (5). Newborns enter age-class 1, during which they can reproduce, and individuals live for a maximum of two years. Individuals exist in good or bad environments but the environment only affects reproduction at age 1. Individuals progress to age 2 either with or without having reproduced at age 1. In our simplified projection equation, the environment entered by newborns depends only on parental parity at their birth.

Fig. 2. Population growth

Here we plot how changing the birth-order effect on reproduction affects: r , the intrinsic rate of population growth; R_0 , the rate of increase in number of newborns between generations, or average lifetime reproduction in a cohort of individuals; T_c , the cohort generation time, or average age of reproduction in a cohort of individuals. The relationship between these is approximately $r = \frac{\ln(R_0)}{T_c}$ (see (Steiner and Tuljapurkar, 2013)). In the points above: '1st born adv' show the new values when first-borns always and second-borns never enter the good environment; 'equality' show the case when first- and second-borns have equal chances of entering the good environment—where lifetime reproduction is earlier and higher than the bad environment; '2nd born adv' show the new values when first-borns never and second-borns always enter the good environment. Bars show the effects of varying the probability of reproduction at age 1 and 2 independently between 0.5 and 1.0.

Fig. 3. Selection on survival

How selection strength on survival from age 1 to 2 ($\frac{\partial r_s}{\partial S}$, see 6) depends on the birth-order effect on reproduction. Selection strength is given by the sensitivity of population growth to the probability of survival. This is the change in population growth caused by a unit positive change to survival. In the points above: '1st born adv' shows the new selection strength when first-borns always and second-borns never enter the good environment; 'equality' shows selection when first-and second-borns have equal chances of entering the good environment; '2nd born adv' shows the new selection strength when first-borns never and second-borns always enter the good environment. Bars show the effects of varying the probability of reproduction at age 1 and 2 independently between 0.5 and 1.0.

Fig. 4. Selection on reproduction

How the drop in selection strength on reproduction between ages 1 and 2 ($\frac{\partial r}{\partial M_1} - \frac{\partial r}{\partial M_2}$, see 9) depends on the birth-order effect on reproduction. Positive values predict faster reproductive senescence, and negative values slower reproductive senescence. In the points above: '1st born adv' show the new strengths of selection when first-borns always and second-borns never enter the good environment; 'equality' show the case when first- and second-borns have equal chances of entering the good environment; '2nd born adv' show the new strengths of selection when first-borns never and second-borns always enter the good environment. Bars show the effects of varying the probability of reproduction at age 1 and 2 independently between 0.5 and 1.0.