Juvenile mortality and sibling replacement: a kin selection approach

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Abstract

Mortality generally is higher around birth and then progressively declines through the juvenile stage. In species where offspring depend upon their parents during maturation, a factor behind this mortality decline could be sibling replacement: offspring sacrifice their survival to benefit future or present siblings as early as possible in order to minimize losses in parental investment. Here, we propose a kin-selection model of sibling replacement. Theoretical analysis of the model and its application to demographic data of mammals suggest that sibling replacement consistently generates a selective incentive for increasing juvenile mortality at early ages when this mortality increment is the result of positive selection for juvenile altruism within the nuclear family. The model highlights how sibling replacement goes beyond optimal allocation of parental resources into dependents and can provoke greater mortality closer to birth also in response to a more favorable ratio of actors to recipients of altruism among siblings.

Keywords: age, altruism, demography, juvenile mortality, mammals, parental care, sibling replacement

Lay Summary

Parental care is costly. From an evolutionary perspective, investment into suboptimal offspring may yield a smaller return than investment into other existing offspring or into the production of new ones. Reasoning about this, evolutionary biologist William D. Hamilton hypothesized that if suboptimal offspring were altruistic toward their family, they would initiate their own death as early as possible to minimize parental losses and maximize the fitness of family members. This form of altruism toward kin would eventually produce a tendency towards higher mortality at early juvenile ages, an observation consistent with demographic data for species with parental care. The present work may be the first translation of Hamilton's hypothesis into a formal kin-selection model. The model confirms Hamilton's intuition that, if offspring are altruistic, the force of selection against juvenile mortality is attenuated at early juvenile ages.

Introduction

A conspicuous trait of many mammalian life histories is a postnatal decline of mortality that generally halts before or around reproductive maturity (Caughley, 1966; Sibly et al., 1997). Demographic data for species taxonomically distant from mammals, like rotifers and fishes, have shown that this pattern of mortality may be quite common in the tree of life (Bois et al., 2019; Emlen, 1970; Levitis, 2011). Levitis (2011) reviewed different, and possibly complementary, reasons behind this age-related drop in juvenile mortality. For example, the drop could be a statistical artifact due to heterogeneity in quality at birth. As low-quality individuals in a newborn cohort succumb earlier to death, the share of higher-quality individuals in the same cohort increases with time

and, as a result, the average cohort mortality can decline (Vaupel & Yashin, 1985). In addition, individual size, which typically increases during the developmental phase leading to reproductive maturity, may lend protection against environmental hazards and, therefore, lower mortality as a by-product (Munch & Mangel, 2006).

However, there are also arguments that natural selection could contribute to an explanation for the shape of juvenile mortality (Levitis, 2011). Hamilton (1966, pp. 38–42) put forth the hypothesis that, in species where offspring depend on their parents after birth, selection could modulate offspring mortality via sibling replacement. This roughly is the conversion of resources freed from the death of an offspring either into the production of new

offspring or into better provision for those already existing. In both cases, the earlier the death of a dependent offspring, the more limited the consequent loss in cumulative parental investment. Selection against age-specific mortality may then be less strong the earlier the juvenile age under consideration.

Hamilton (1966, p. 39) suggested that kin selection theory, which he pioneered (Hamilton, 1964a,b), would be a convenient framework to approach this problem once the offspring death is interpreted as a form of altruism toward parents or siblings. However, possibly because in his work on kin selection Hamilton avoided "confronting the extra mathematical difficulties of overlapping generations" (Hamilton, 1996, p. 88), he did not present a mathematical model of sibling replacement. The work of Lee (2003) has been considered a possible formal model of this hypothesis (Rogers, 2003). Lee built a group-selection model where offspring depend on, and thus subtract resources from, both parental and non-parental adults within their group. Consequently, the more the ratio of dependent juveniles to mature individuals increases, the more the economy of the group and, therefore, its growth and fitness shrink. Greater sensitivity of this ratio to early juvenile survival is one of the factors determining lesser selection against early juvenile mortality in this model. However, Lee's 2003 analysis did not include family structure, nor did it explicitly deal with kin relationships (Bourke, 2007; Levitis, 2011; Rogers, 2003), thereby deviating from Hamilton's original hypothesis.

To the best of our knowledge, the only explicit attempt to formalize Hamilton's hypothesis of sibling replacement has been Netz (2022). This model presupposes that a parent brings a single offspring through maturation at a time before reproducing again. Selection for offspring survival then increases with the age of the dependent offspring to compensate for the increasing cost of delayed parental fecundity. A natural scope of this model is embryonal and post-natal mortality for species with single-offspring gestations. In this respect, we should note that fetal mortality in humans may be declining from conception (Holman & Wood, 2001; Levitis, 2011). However, Netz's model neither follows up Hamilton's suggestion of taking a kin-selection perspective nor includes potential complications due to multiple dependent siblings to the same parent.

The aim of the present work is to contribute to our evolutionary understanding of juvenile mortality by proposing a model of sibling replacement that captures the essence of Hamilton's hypothesis. To build and analyze our model, we use kin-selection theory for structured populations (Lehmann & Rousset, 2014; Taylor & Frank , 1996; Taylor et al., 2007; Rousset, 2004), a theory that builds on Hamilton's original work. In particular, we adopt the approach to this theory by Taylor and Frank (1996), as detailed in their Examples 4A and B. The model we propose reveals the age-specific force of selection on the survival of altruistic juveniles who depend on their mother. Analysis of the model gives insights into the pattern of this force at different juvenile ages.

Methods

Demography

We consider a very large resident population. Individuals are asexual haploids and we refer to them as females. Females in the model are reproductively mature from age β onwards. An adult of age $k \geq \beta$ at time t survives with probability p_k to time $t + 1$ (when the adult will be of age $k + 1$) and is expected to have f_k new offspring of age 1 (first observed at time $t + 1$) with $f_k = 0$ for $k < \beta$ and $f_k > 0$ for $k \geq \beta$. Throughout the text, we shall consider

1 as the age of new recruits. Our modeling framework, however, can be flexibly interpreted so that 1 is age at conception and the juvenile dependency period includes gestation.

Each adult female takes care only of her own offspring. Offspring are independent of their mother when they are at least of age α, which is at most the age of reproductive maturity ($\alpha \leq \beta$). Before age α, juveniles fully depend on their mother and cannot survive her death. More specifically, a juvenile of age i, with $1 \leq i < \alpha$, currently depending on a mother of age $m+i$, where $m \geq \beta$ is maternal age at birth of this juvenile, survives from time t to $t+1$ with probability $p_{i,m} = s_i p_{m+i}$, where $0 < s_i < 1$ is intrinsic juvenile survival at age i while p_{m+i} is survival of the mother over the same time interval. We assume throughout that $\alpha \geq 3$ so that there can be juveniles of different ages dependent on the same mother.

Adults and independent juveniles are thus classified based on their individual age, while dependent juveniles are classified based on their individual age and on their mother's age. The population is assumed to grow by a constant factor λ per time step and to be demographically stable so that the abundance in each class represents a constant fraction of the total population. The growth rate λ corresponds to the dominant eigenvalue of the matrix model **A**, which could possibly be infinite dimensional, for the life cycle in Figure 1. In the finite dimensional case, λ is a positive, real, and simple eigenvalue of **A** (Supplementary Material, Section A.2), so that this eigenvalue has unique corresponding eigenvectors.

Modeling sibling replacement

Suppose a mutation is introduced at a very low frequency in the resident population. The mutation makes dependent juveniles altruistic. Their altruism is age-specific, as it manifests itself at a single age j during the dependency period ($1 \leq j \leq \alpha - 1$) independently of maternal age at the birth of the juvenile. We assume that altruism is a quantitative trait with a value zero in the resident population and mutant value $\delta > 0$. Weak selection is assumed so that $\delta \ll 1$. We let $C > 0$ be the cost of altruism. When acting altruistically, a mutant juvenile suffers a proportional reduction in her current survival. Juvenile survival conditional on mother's survival for a mutant actor of age j dependent on a mother of age $m+j$, for all maternal ages $m \geq \beta$, is thus $s_j(1 - \delta C)$ instead of s_j. Hence, the survival of this mutant altruist from age j to age $j + 1$ is $p_{j,m}(1-\delta C) = s_j(1-\delta C)p_{m+j}$ for all maternal ages $m \geq \beta$ at juvenile's birth. Proportional age-specific effects of mutations on survival are coherent with Hamilton's (1966) classic model of life history evolution. As for the recipient of the benefit $B > 0$ of an act of altruism, we consider two modeling alternatives: future siblings or extant siblings still dependent on the mother.

Model 1: Altruism toward future siblings

In the first modeling alternative, altruism is directed toward the mother of the actor in the form of a beneficial effect on her reproduction. Specifically, fecundity of the actor's mother when she is of age k is $f_k + \delta RB\gamma_k(j)$, where $R > 0$ is the relatedness between mother and daughter and $\gamma_k(j)$ is the number of j-aged mutant offspring (i.e., the altruists) still dependent to a female of age k. We compute $\gamma_k(j)$ using resident values for the expected number of j-aged juveniles to a mother. We treat $\gamma_k(j)$ as the number of altruistic interactions a k-aged mother of mutants receives. A scheme of this model is in Figure 2a. We previously assumed proportional effects of the mutation on survival, because this is how Hamilton (1966) envisaged age-specific mutations would act on survival. In his classic model, he also suggested that age-specific
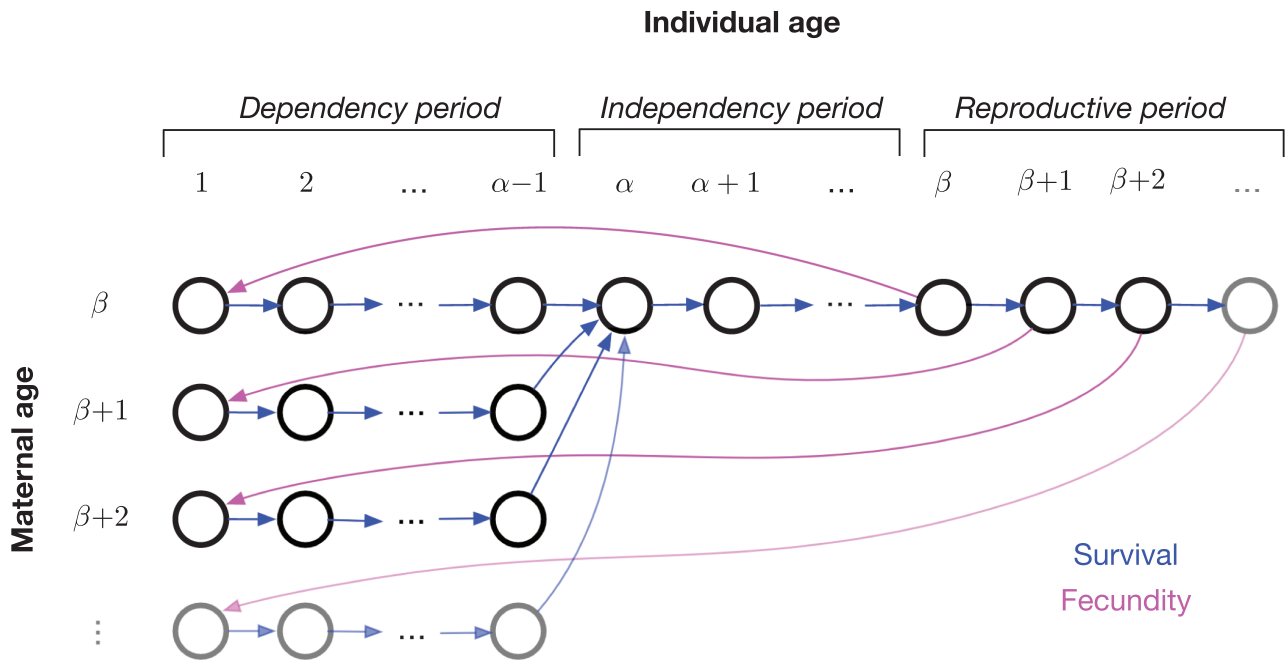
Individual age

Figure 1. Life cycle. Juveniles up to age $\alpha - 1 \geq 2$ depend on their mother, who is aged at least $\beta \geq \alpha$. Juvenile survival from one age to the next during the dependency period is linked to survival of the mother over the same time interval. Dependent juveniles of the same age have the same intrinsic survival, yet by being born to mothers of different ages, these juveniles may have different effective survival depending on differences in maternal survival. To keep track of demographic dynamics, dependent juveniles are classified both by individual age and by maternal age at their birth. Survival and reproduction of independent juveniles and adults, instead, only depend on their own age and their classification is solely by individual age.
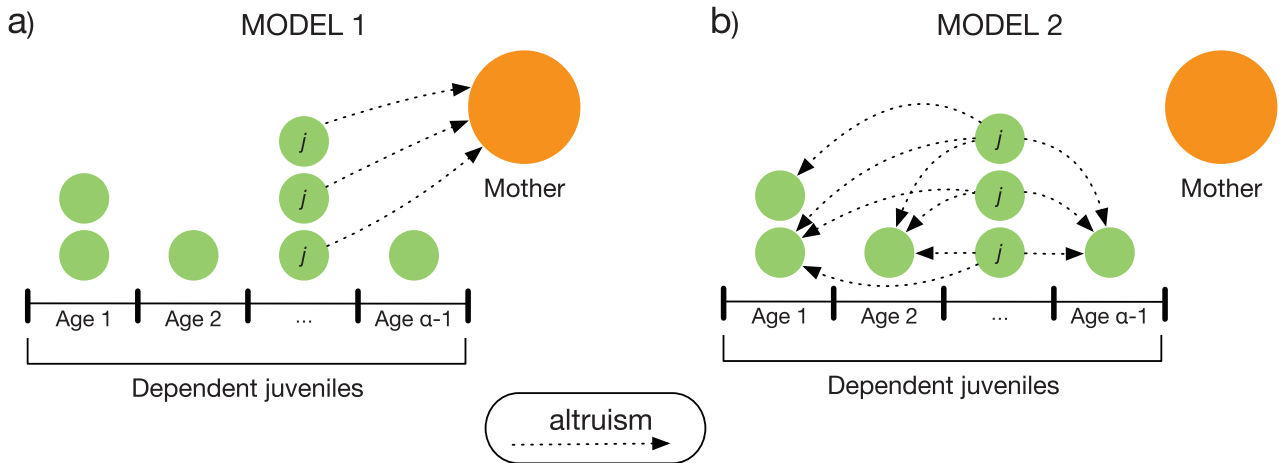

Figure 2. Altruistic interactions. Dotted arrows go from actor to recipient of altruism. Dependent juveniles of age j (for simplicity not distinguished by maternal age in this scheme) are altruistic and pay a survival cost. **a**: Model 1: Juvenile altruism toward future siblings. The benefit effectively goes to the mother's fecundity. **b**: Model 2: Juvenile altruism toward present siblings dependent on the same mother. The benefit goes to survival of recipient siblings.

mutations would have additive effects on fecundity. For coherence, in our model, we also take age-specific mutations to act additively on fecundity.

Model 2: Altruism toward current siblings

In the second modeling alternative, altruism expressed by mutant juveniles of age j is directed toward present still-dependent siblings. Recipients have a proportional increase in their intrinsic survival. Hence, a mother-dependent juvenile recipient aged $i \neq j$ with $1 \leq i \leq \alpha - 1$ survives to age $i + 1$ with probability $p_{i,m}(1 + \delta R B \theta_{i,m}(j)) = s_i(1 + \delta R B \theta_{i,m}(j))p_{m+i}$, where $R > 0$ is relatedness between any two siblings, while $\theta_{i,m}(j)$ is, for a focal i-aged

individual whose mother currently is of age $m + i$, the ratio of j-aged juveniles relative to all other offspring still dependent on the mother. Here, $\theta_{i,m}(j)$ is taken as the number of altruistic interactions an i-aged juvenile recipient, whose mother was of age m at this juvenile's birth, gets involved into. Thus, the individual chance for a mother-dependent juvenile recipient to obtain the benefit of altruism is reduced with decreasing number of altruists and increasing number of potential recipients. We compute $\theta_{i,m}(j)$ from resident values. We assume relatedness to be the same among any two juveniles dependent on the same mother so that R is an age-independent quantity. A scheme of this model is in Figure 2b.

Force of selection

Irrespective of recipient, the altruistic mutation increases mortality at a single juvenile age j. We are interested in the selective force $S(j)$ on this initially rare mutation. Therefore, we perturb the matrix model $\mathbf{A}$ by replacing, for all maternal ages $m \geq \beta$, the resident survival probability for j-aged juveniles $p_{j,m}$ with the corresponding probability $p_{j,m}(1-\delta C)$ for the mutant actor. In addition, we perturb $\mathbf{A}$ to account for the effect of altruism on recipients. In the case of altruism toward future siblings, we replace fecundity f_k with recipient fecundity $f_k + \delta R B \gamma_k(j)$ for all adult ages $k \geq \beta$. In the case of altruism toward present siblings, for all maternal ages $m \geq \beta$ and for all juvenile ages $1 \leq i \leq \alpha - 1$ with $i \neq j$, we replace the survival probability $p_{i,m}$ with the corresponding probability $p_{i,m}(1 + \delta R B \theta_{i,m}(j))$ for recipients. In both cases, we obtain a new matrix $\mathbf{A}(\delta)$ that captures the dynamics of the mutant subpopulation. This new matrix has dominant eigenvalue $\lambda(\delta)$. Letting $\mathbf{w}(\delta)$ and $\mathbf{v}(\delta)$ be the right and left dominant eigenvectors of $\mathbf{A}(\delta)$, respectively, the selective force on the mutation is

$$S(j) = \left.\frac{\partial \ln \lambda}{\partial \delta}\right|_{\delta=0} = \lambda^{-1}(0)\mathbf{v}^{\top}(0)\left.\frac{\partial \mathbf{A}}{\partial \delta}\right|_{\delta=0}\mathbf{w}(0), \quad (1)$$

where $\mathbf{w}(0)$ and $\mathbf{v}(0)$ are the right and left eigenvectors, respectively, of the resident matrix model $\mathbf{A}(0) = \mathbf{A}$ and $\lambda(0) = \lambda$ is the corresponding eigenvalue (see "Demography" section). These eigenvectors are assumed normalized so that the components of $\mathbf{w}(0)$ add up to 1 and $\mathbf{v}^{\top}(0)\mathbf{w}(0) = 1$. Thus, the vector $\mathbf{w}(0)$ contains the stable class distribution, while the vector $\mathbf{v}(0)$ gives the individual reproductive value for individuals of each class.

The derivative in (Equation 1) tells us how the fitness of mutants changes, as compared to residents, in response to the deviation mutants exhibit in their behavior (Taylor & Frank, 1996; Taylor et al., 2007). In particular, the product $\delta S(j)$ approximates the difference $\ln \lambda(\delta) - \ln \lambda(0)$ for small δ.

Supposing $S(j)$ to be positive and looking at its magnitude at different juvenile ages j of altruism, we ask: If selection favors this altruism-induced age-specific increase in mortality, is there any tendency to favor it earlier than later? We emphasize that we do not ask why a form of altruism is selected for in the first place and what the circumstances are that favor it. Our question is about the relative strength of positive selection for juvenile altruism at different ages. Note that this question is logically posterior to selection for this altruism. Specifically, we are interested in the exact extent to which age-specific altruism of juveniles toward extant or future siblings is selected for depending on its age of expression assuming positive selection for altruism throughout. However, we use Box 1 to separately give conditions under which selection favors juvenile altruism of either form.

Box 1. Conditions for positive selection on juvenile altruism

Selection favors altruism at juvenile age j during the period of dependency on the mother when the gradient $S(j)$ in Equation (1) is positive. Here, we give conditions under which $S(j) > 0$ for each model in Figure 2 (Supplementary Material, Sections A.3.2 and A.4.2). Using techniques from elasticity analysis (Bienvenu & Legendre, 2015; Giaimo and Traulsen, 2021, 2023), we express these conditions in two

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different ways, one of which emphasizes how positive selection on altruism depends on how the cost-to-benefit ratio of altruism compares to the product between relatedness and the weighted average over maternal ages of the number of altruistic interactions per recipient. The conditions we give involve the generation time (T) and growth rate (λ) of the resident life cycle, the stable resident fraction ($w_{i,m}$), and reproductive value ($v_{i,m}$) of dependent juveniles of individual age $i = 1, \ldots, \alpha - 1$ and maternal age $m \geq \beta$, the stable fraction (w_m) of resident mothers of age $m \geq \beta$, and the elasticity $\epsilon_\lambda(f_m) = (f_m/\lambda)(\partial\lambda/\partial f_m)$ of λ to resident fecundity f_m at age $m \geq \beta$. When juvenile altruism is toward future siblings, we have $S(j) > 0$ when

$$\frac{C}{B} < RT\lambda^{-1}\sum_{m=\beta}^{\infty}\gamma_m(j)v_{1,m}w_m = R\frac{\sum_{m=\beta}^{\infty}(\gamma_m(j)/f_m)\epsilon_\lambda(f_m)}{\sum_{m=\beta}^{\infty}\epsilon_\lambda(f_m)},$$

where $\gamma_m(j)/f_m$ is the number of j-aged offspring dependent to a mother of age m relative to her current fecundity. When juvenile altruism is toward present still-dependent siblings, we have $S(j) > 0$ when

$$\frac{C}{B} < RT\lambda^{-1}\sum_{m=\beta}^{\infty}\sum_{\substack{i=1 \\ i \neq j}}^{\alpha-1}\theta_{i,m}(j)v_{i+1,m}w_{i,m}p_{i,m}$$

$$= R\frac{\sum_{m=\beta}^{\infty}\left(\sum_{\substack{i=1 \\ i \neq j}}^{\alpha-1}\theta_{i,m}(j)\right)\epsilon_\lambda(f_m)}{\sum_{m=\beta}^{\infty}\epsilon_\lambda(f_m)},$$

where $\theta_{i,m}(j)$ is the ratio of j-aged juveniles relative to all other offspring dependent on the $(m+i)$-aged mother of an i-aged dependent juvenile. This juvenile survives to the next time step with probability $p_{i,m}$. The right-hand side of the above inequalities is the potential for altruism, as defined by Gardner (2010), in each model.

Life histories for numerical exploration

To numerically explore the model, we constructed life histories with adult survival following a Weibull-like function with shape parameter η (> 1 increasing mortality with age, < 1 decreasing mortality with age, $= 1$ constant mortality with age). Intrinsic survival for dependent juveniles was set constant with their age. We regarded this as the most natural backdrop against which to compute and compare selective forces at different ages. Maximum age was set as the last age at which at least 1% of an adult cohort is still alive. The number of ages of juvenile dependency was set equal to 1/4 of the number of adult ages. At the end of the dependency period, juveniles directly transitioned into adulthood without any intermediate period of juvenile independence ($\alpha = \beta$). For fecundity, we explored different trajectories with the most realistic being fecundity as a cubic function of adult age in a strong analogy with a Brass model, which fits well mammalian data (Gage, 2001). But we also considered fecundity to linearly increase, linearly decrease, exponentially increase, or exponentially decrease with adult age. By scaling fecundities uniformly with respect to age, constructed life histories were set at ecological equilibrium with a dominant eigenvalue of the corresponding matrix model equal to 1. More information about

the construction of these life histories is in the Supplementary Material (Section C).

Parametrization with data

Demographic data for mammals typically include information about survival and fecundity based on individual age and not on maternal age at birth. Our model instead treats juvenile survival during the dependency period as specific to both individual age and maternal age at birth. It can then be problematic to use age-only demographic data to parametrize our model because the data provide a single value of survival for each juvenile age while the model requires as many values of survival as there are maternal ages for each juvenile age during the dependency period. Hence, we may end up dealing with many "free parameters." To gain insights from existing demographic data while overcoming this potential problem, we simplify our model into one where the effect of maternal age is implicitly present even if the demographic classification of all individuals is by their age only. The simplification consists in setting juvenile survival during the dependency period to $p_k = s_k \bar{r}_k$, with $1 \leq k \leq \alpha - 1$, where s_k is intrinsic survival and $\bar{r}_k$ is the average survival of mothers of juveniles of age k. In this way, we only need to estimate up to $\alpha - 1$ additional parameters, that is, the s_k, from the data (Supplementary Material, Section B), as opposed to up to $(\alpha - 1)\zeta$ additional parameters, that is, the $s_{k,m}$, which would be needed for ζ maternal ages in the full model. Please note that, in our model, maternal ages must exceed juvenile ages during dependency, for otherwise no juvenile would survive to maturity. Since we expect adults to reproduce and bring to maturity one or more offspring, maternal ages will exceed, sometimes considerably, juvenile ages during dependency. This fact makes the simplified model considerably more parsimonious than the full model when it comes to parametrization with data. Roughly, the number of additional parameters required by the simplified model is linear in the number of juvenile ages, while the number of additional parameters required by the full model is quadratic, at a minimum, in the number of juvenile ages.

In this simplified model, a j-aged juvenile altruist reduces its intrinsic survival by a factor $(1 - \delta C)$ and survives with probability $p_j(1 - \delta C)$ to the next time step. For the setup of Model 1 in "Model 1: Altruism toward future siblings" section, our simplification has no further consequences. For the setup of Model 2 in "Model 2: Altruism toward current siblings" section, the simplification implies that a focal recipient aged $i \neq j$, with $1 \leq i \leq \alpha - 1$, survives to age $i+1$ with probability $p_i(1 + \delta RB\bar{\theta}_i(j))$, where $\bar{\theta}_i(j)$ is the expectation, over all possible maternal ages, of the ratio of j-aged juveniles to all other offspring still dependent on the mother of the focal recipient.

Results

Altruism toward future siblings

We first assume that the ratio of fecundity at adult age $k + 1$ to fecundity at adult age k is never smaller than the maximum intrinsic survival probability for dependent juveniles. This assumption includes the case of age-independent fecundity, which reflects the modeled demography of several species with parental care, for example, (Balme et al., 2009; Carroll et al., 2003; Chastant et al., 2014; Finkelstein et al., 2010; Hebblewhite et al., 2003; Lee et al., 2016; Wang et al., 2017). But the assumption also includes the case of negative reproductive senescence, when fecundity increases with age, and the case of moderate reproductive senescence, when fecundity declines with age at a rate not exceeding maximal intrinsic survival for dependent juveniles. Under our assumption, selection is always stronger on a mutation that induces juveniles of age j to reduce their survival in order to improve their mother's fecundity than on a similar mutation with effect at age $j + 1$ (Supplementary Material, Section A.3.3). Hence, positive selection of this form of altruism invariably has a tendency to produce higher mortality at earlier juvenile ages. The intuition behind this result is that the juvenile may die between ages j and $j+1$ before her altruism materializes, effectively diluting its benefit. A further dilution effect comes from the fact that only mothers of age at least $\beta + j$, where β is the age at first breeding, can have j-aged (altruistic) offspring. Hence, the later the altruistic act, the smaller the probability the mother will survive to obtain the corresponding benefit. We can show that the same theoretical result holds for the simplified model outlined in "Parametrization with data" section (Supplementary Material, Section A.3.4).

Next, we look at the effect of deviations from simplifying assumptions by taking two different approaches. The first approach is based on computing the selection force on altruism at each juvenile age during the dependency period for life histories parametrized by η for different patterns of fecundity (see "Life histories for numerical exploration" section) and then taking the difference in selection force between any two consecutive ages of juvenile altruism. When the sign of this difference is positive, an altruism-induced increase in mortality is favored more at juvenile age j than at juvenile age $j + 1$. When the sign is negative, such an increase is favored more at juvenile age $j + 1$ than at juvenile age j. Figure 3 shows that, for the life histories under consideration, the sign of the difference in selection force is always positive. This is evidence that, when favored by selection, juvenile altruism toward future siblings tends to generate higher mortality at earlier juvenile ages.

The second approach is based on data. We queried the COMADRE database (2023, v.4.21.8.0) for population projection matrices of mammalian species. Our focus on mammals has two main motivations. First, the virtual ubiquity of parental care and declining postnatal mortality in mammals. Second, matrix models for non-mammalian species with parental care, like birds, are often not granular enough to include more than one age class with dependent juveniles. For example, chicks of northern fulmar fledge on average 2 months after birth (Falk & Møller, 1997), yet a usual time unit for matrix models of this avian species are years (Kerbiriou et al., 2012). Of the obtained matrices for mammals, we retained those that conformed to our modeling assumptions and showed variation in fecundity (Supplementary Material, Section D.1). From each of the retained matrices, we used the simplified model outlined in "Parametrization with data" section to compute differences in selection force between any two consecutive juvenile ages of altruism. In our sample, these differences are always positive (Figure 4). This is further evidence of a tendency to increase mortality at earlier juvenile ages in response to selection for age-specific juvenile altruism toward future siblings.

Single dependent offspring

Hamilton, in formulating his sibling replacement hypothesis, was especially attentive to juvenile mortality in humans. In natural-fertility human populations, mothers often raise several dependents of different ages simultaneously (Kramer, 2005).
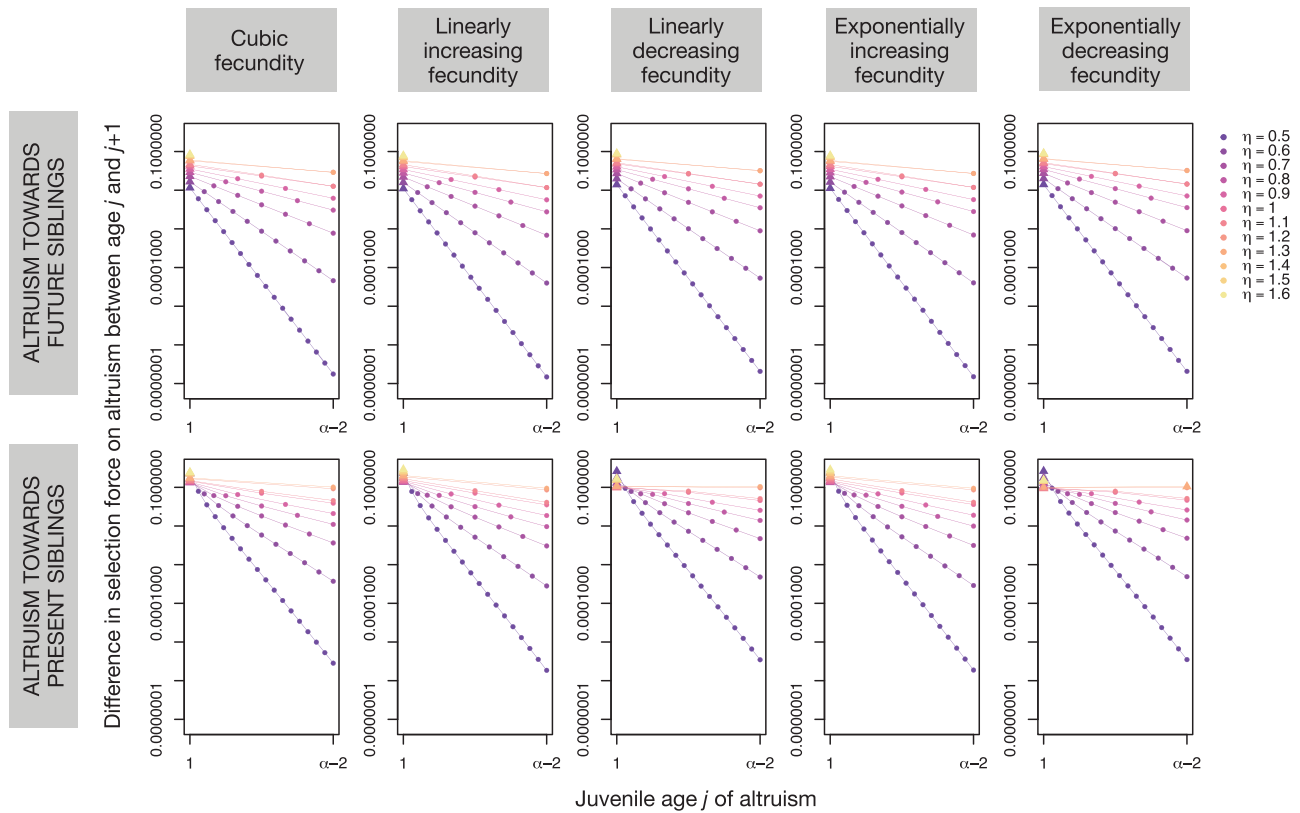
Figure 3. Differences in selection on altruism-induced juvenile mortality between an altruistic act taking place at age j and the same act taking place at age $j + 1$ for juvenile ages $j = 1, 2, \ldots, \alpha - 2$, where α is age at independence, for life histories parametrized by η ("Life histories for numerical exploration" section and Supplementary Material, Section C). Life histories with different η values can differ in the number of total ages and juvenile ages. For altruism toward future siblings (panels in the first row), the y-axis reports $\Delta_\gamma(j)$ (Supplementary Material, Equation (SM9)), which is proportional to the age-specific difference in selection. For altruism toward present siblings (panels in the second row), the y-axis reports $\Delta_\theta(j)$ (Supplementary Material, Equation (SM31)), which is proportional to the age-specific difference in selection. Triangles indicate the maximal value of the age-specific difference in selection force for each life history. Different columns correspond to different patterns of fecundity over adult age.

Human life history, however, is different from that of many primates, where mothers almost exclusively give birth to, and take care of, a single offspring at a time (Allman & Hasenstaub, 2001; Kramer, 2011; Reeder, 2003). We should then separately consider this relevant case, as our model was not specifically built to capture it.

Suppose vital rates in the population are such that the ratio of dependent juveniles to adult females is at most 1 at demographic equilibrium. Then, each adult female, on average, takes care of at most a single offspring at a time. Assuming juvenile survival, adult survival, and fecundity independent of age, regions of the parameter space of our model exist where the ratio of dependent juveniles to adult females is at most 1 (Supplementary Material, Section A.3.5). Hence, our result in the previous section for age-independent fecundity, that is, stronger selection for an altruism-induced increase in mortality as early as possible during the period of juvenile dependence, can extend to life histories with single-offspring pregnancies and parental care.

To consider deviations from simplifying assumptions, we also took a data-based approach. We looked at demographic data about non-human primates from a study (Bronikowski et al., 2016) not included in the COMADRE database. Figure 4 shows how, for these data, selection for juvenile mortality induced by altruism toward future siblings gets stronger at earlier juvenile ages in these primates.

Altruism toward present siblings

Suppose fecundity is constant with adult age and intrinsic survival of dependent juveniles is not too high. Specifically, if s_{max} is maximal intrinsic survival for dependent juveniles we should have $s_j \leq 2/3$ when $s_j < s_{max}$ and $s_j \leq s^*$ with $s^* \approx 0.755$ when $s_j = s_{max}$. Under these assumptions, there is always a stronger selection to increase mortality at juvenile age j than at age $j + 1$, when this additional mortality is the cost to pay to benefit one's present siblings and this form of altruism is under positive selection (Supplementary Material, Section A.4.3). An intuitive way of understanding this result is as follows: The fitness cost of altruism, a proportional decrease in survival, is independent of the exact age of the juvenile actor. This is because the fitness effect of any age-specific proportional change in survival at juvenile ages is independent of the exact age at which the change occurs. The fitness gain of altruism, on the other hand, depends both on recipient age and actor age. The reason is that such gain is an increasing function of the ratio of actors (i.e., altruists) to recipients among siblings dependent on the same mother. As individuals of any age may fail to survive to the next age, juveniles of age j tend to be more numerous than juveniles of age $j + 1$ within a given family when adult fecundity is constant with age. Consequently, the earlier the age of juvenile altruism, the greater the ratio of actors to recipients and so the benefit to the latter. We can show (Supplementary Material, Section A.4.4) that the same theoretical result
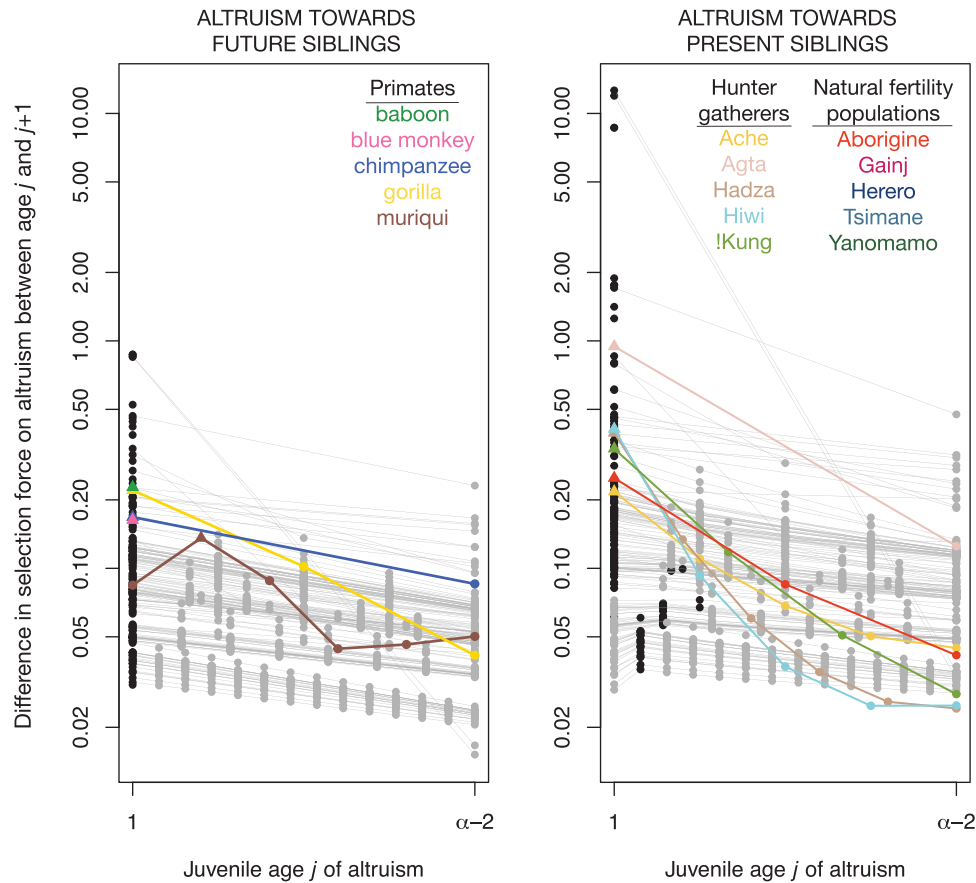
Figure 4. Differences in selection on altruism-induced juvenile mortality between an altruistic act taking place at age j and the same act taking place at age $j+1$ for juvenile ages $j = 1, 2, \ldots, \alpha-2$, where α is age at independence. These differences were computed using data from 187 projection matrices of mammalian life histories (points in gray with black signaling maximal values) from the same dataset and non-human and human primates (points in color with triangles signaling maximal values) from separate datasets. For altruism toward future siblings, the y-axis reports $\Delta_\gamma^\circ(j)$ (Supplementary Material, Equation (SM19)), which is proportional to the age-specific difference in selection. For altruism toward present siblings, the y-axis reports $\Delta_\theta^\circ(j)$ (Supplementary Material, Equation (SM61)), which is proportional to the age-specific difference in selection. In reported primate species, mothers almost exclusively take care of single offspring. In reported natural-fertility human populations, mothers can have multiple dependent offspring (Supplementary Material, Section D.3).

holds for the simplified model outlined in "Parametrization with data" section.

To look at the effect of deviations from simplifying assumptions, we adopt the same two approaches as in "Altruism toward future siblings" section. First, we compute the difference in selection force on altruism between any two consecutive juvenile ages for life histories parametrized by η and then look at the sign of this difference. Figure 3 shows that, for these life histories, the difference is always positive. This is evidence that, when favored by selection, juvenile altruism toward present siblings tends to generate higher mortality at earlier juvenile ages.

The second approach relies on computing the age-specific difference in selection force on altruism using the same matrix-based demographic data as in "Altruism toward future siblings" section. Results (Figure 4) show that, in our sample of mammalian species, the selection difference is always positive. This is further evidence of a tendency to increase mortality at earlier juvenile ages in response to selection for age-specific juvenile altruism toward present siblings.

As already noted in "Single dependent offspring" section, humans are special among primates because human mothers can have several dependent offspring of diverse ages (Kramer,

2005, 2011). Hence, humans represent a case worth considering separately. Figure 4 reports the difference in selection force between consecutive juvenile ages of altruism toward present siblings computed for five hunter-gatherer populations and five natural fertility populations (Supplementary Material, Section D.3). Demographic data were obtained from Davison and Gurven (2021). This figure shows that in humans, too, there is a selective tendency to increase mortality earlier during the dependency period when this increase is the cost of selected altruism toward present siblings.

Discussion

Since selection on juvenile survival is strong in virtually all species, phenomena like abortion, production of zygotes well beyond ecological capacity and parental or sibling cannibalism appear puzzling (Stearns, 1987). But the evolutionary logic behind all these phenomena could be rooted in the difficulty of combining variability in offspring quality and limitations in parental resources. Parents would select either directly, for example, via abortion or cannibalism, or indirectly, via induction of sibling competition, the best offspring from the lot to invest

upon (Kozlowski & Stearns, 1989). This logic applies both spatially when selecting from several simultaneous offspring those worth parental investment, and temporally, when regulating the residual time spent investing into an offspring before producing the next one. Aspects of the spatial dimension of this logic have been explored in models of zygote overproduction (Kozlowski & Stearns, 1989; Stearns, 1987; Stearns & Ebert, 2001), while aspects of the temporal dimension have been explored in models of reproductive compensation (Hastings, 2000; Hurst, 2022; Porcher & Lande, 2005).

Reasoning about parental control over offspring quality (Hurst, 2022; Kozlowski & Stearns, 1989), Hamilton (1966) proposed sibling replacement as a mechanism that, in species where offspring depend on their parents after birth, may contribute to explain the initially declining trend of juvenile mortality observed in these species. Our model supports Hamilton's view: selection can favor a mortality increase as early as possible during the dependency period if this mortality increase entails a sufficient benefit to siblings. By considering both the spatial (altruism toward present siblings) and the temporal (altruism toward future siblings) dimensions, our modeling of Hamilton's hypothesis gives new insights into the pattern of selective forces operating on juvenile survival. It is usual to construe his hypothesis of sibling replacement as a strategy to avoid a bigger loss by terminating early a cumulative investment and start a new, and possibly more profitable, one. However, by capturing only the temporal dimension of sibling replacement, this interpretation of the hypothesis only gives us part of the reason that selection can favor earlier juvenile mortality. Our modeling highlights how purely demographic factors can be at play in sibling replacement. When the benefit of altruism-induced juvenile mortality goes to existing siblings still depending on the same mother (spatial dimension), the effective fitness gain of recipients increases with the relative abundance of altruists. Since younger juveniles generally outnumber older juveniles within the same family when fecundity does not vary much with age, the balance between fitness losses and fitness gains of altruism is selectively more favorable when juvenile altruists are younger.

In our model, the cost-to-benefit ratio of altruism and relatedness, which are usually conspicuous in results derived from kin-selection theory (Taylor & Frank , 1996; Taylor et al., 2007), do not appear to influence our findings (Supplementary Material, Sections A.3.1 and A.3.4). But actually, both these quantities are crucial in determining whether there is positive selection in the first place for either of the two forms of juvenile altruism that we consider (Box 1).

How does our work relate to the only other explicit model (Netz, 2022) of sibling replacement? Our model is more general in two ways: First, when altruistic benefits are toward future siblings, our model in "Model 1: Altruism toward future siblings" section can capture Netz's as a special case. For this to happen, it is required that the demographically stable ratio of adult females to dependent juveniles is at least 1. This ratio implies at most a single dependent offspring per adult female, which includes as a special case the assumed 1:1 ratio in Netz's model. Second, this assumption by Netz implies both that parents only have a single dependent offspring at the time and that adult fecundity does not vary with age. Hence, unlike our model, Netz's model focuses on the temporal dimension described above and does not capture the spatial dimension, where selective forces on juvenile mortality arising from the presence of multiple dependent offspring and age-dependent fecundity are at play.

A limitation of our model is that the dependency of juveniles on their mother is absolute and that this dependency ends abruptly: if the mother dies so does any dependent offspring. Yet, once the offspring becomes independent, their survival and the survival of their mother are completely unlinked. While these are convenient modeling simplifications, they fail to represent the complexity of parental care and offspring progression into maturity in several species. Offspring independence may be reached gradually, as in immature orangutans who achieve nutritional and locomotory independence earlier than ecological independence (van Adrichem et al., 2006). Dependent orphans may still survive to maturity. Also adoption is observed in primates (Anand et al., 2022; Botero, 2020; Thierry & Anderson, 1986), although orphan fitness may be reduced even multigenerationally (Zipple et al., 2020). More generally, care of offspring may be paternal and alloparental, which can compensate for the loss of maternal care (Riedmann, 1982; Wynne-Edwards, 1995). The difficulty in dealing with these complications becomes evident when we apply our model to demographic data from both human and non-human primates. Our modeling assumption that juvenile survival is a product of intrinsic juvenile survival and mother survival conveniently enables us to estimate intrinsic juvenile survival from life table data (Supplementary Material Section B). However, these estimates may occasionally return meaningless intrinsic survival probabilities exceeding the value of 1. To cope with these cases in our data-based analysis, we took the first juvenile age with estimated intrinsic survival exceeding 1 to be the age of juvenile independence. This has the consequence that the period of offspring complete dependency on the mother would not go beyond the age of about 6 years for our analysis of human data. Observations in hunter-gatherer groups, however, reveal that infancy ends around the second or third year of life with weaning and is followed by a juvenile period stretching into teen ages where children receive both maternal and non-maternal support while helping in food production and childcare (Kramer, 2011). More complex models are needed to sort out subtle selective consequences on offspring survival that may arise from different combinations of mono-, bi-, and allo-parental care and cooperative interactions within and beyond the nuclear family. A basis for this future work could be age-structured models including sociality where care for juveniles is not strictly mono- or bi-parental (Lee, 2003) and kin structure is accounted for (Lee, 2008; Rogers, 2003; Roper et al., 2023).

Our model assumes altruism to be an age-dependent social behavior. This assumption is biologically realistic (Emlen, 1970; Rodrigues, 2018; Rodrigues & Gardner, 2022). But our model assumes costs and benefits of altruism to be age independent. As for this, we note that any assumption about age-specific costs and benefits, for example increasing costs with increasing juvenile age or decreasing benefits with increasing maternal age, is at risk of hard-wiring into the model either the desired effect (stronger selection for earlier altruism-induced juvenile mortality) or its opposite. Hence, age-independent costs and benefits of juvenile altruism may be seen as a more parsimonious modeling assumption to assess the merits of sibling replacement. Furthermore, we suspect that dropping the assumption of age-independent costs and benefits can make the model analytically impenetrable. By expansion of the parameter space, application of the model to demographic data and its interpretation can also become much clumsier.

We do not explicitly model parental investment, although age-independence of costs and benefits, also in combination with their

way (additive or proportional) of impacting vital rates, can be interpreted as specifying an investment scheme by parents. Are our results robust to the explicit imposition of different schemes of parental investment? Since different schemes would correspond to different specifications of age-dependent costs and benefits, we are back to the point in the previous paragraph: imposing one scheme or the other could potentially orient the whole pattern of selective forces in descending or ascending order with juvenile age. In the uncertainty of which scheme to adopt, empirical findings offer limited guidance as they are not collectively unambiguous, with some studies finding evidence of increasing investment with offspring age and other studies finding evidence of decreasing investment with offspring age (Thünken et al., 2010, p. 69). In birds, theoretical predictions are that parents should generally increase investment in nest defence with offspring age (Andersson et al., 1980; Barash, 1975; Montgomerie & Weatherhead, 1988). Yet these predictions are inspired by demographic considerations, for example, that "the relative difference between parent and offspring in expected future survival decreases with increasing offspring age" (Andersson et al., 1980, p. 536), that are analogous to those emerging from our model. Moreover, predictions of increasing parental investment with offspring age are also based upon ideas similar to sibling replacement, for example, Barash (1975, p. 371) notes that "the amount of [parental] investment worth expending on any particular clutch would be to some degree a function of the amount already invested, and the older the egg-nestling unit, the greater parental investment it represents." Hence, while there might be schemes of parental investment that can alter our results, it would appear that a sensible choice of such scheme should obey principles similar to those that are behind the hypothesis of sibling replacement, thereby indirectly upholding the validity of this hypothesis.

Despite not including the full complexity of the offspring care system in human and non-human species, our model shows the clear presence of a selective force to increase juvenile mortality as early as possible in the presence of selected altruism performed by dependent offspring. Hence, within the original context envisaged by Hamilton of offspring dependence on their parents, we believe that our model can capture the essence of his hypothesis of sibling replacement as a plausible link between offspring altruism and declining juvenile mortality.

Supplementary material

Supplementary material is available online at *Evolution Letters*.

Data and code availability

Data used in this work were either taken from reported publicly accessible sources or from authors' of mentioned publications. Code used in this work is at DRYAD, see Giaimo and Traulsen (2024): https://doi.org/10.5061/dryad.7wm37pw1h

Author contributions

S.G. conceived and developed the project and did the analytical and computational analysis. A.T. and S.G. reviewed the analysis. S.G. wrote the manuscript with feedback from A.T.

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