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Grandmothering drives the evolution of longevity in a probabilistic model

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HIGHLIGHTS

- A probabilistic agent-based model of the evolution of human post-menopausal longevity.
- Grandmothering drives the shift from great ape-like to human-like life history.
- Weak grandmothering alone can push the evolution of a post-fertile stage.
- Simulations reveal two stable life-histories with no intermediates.

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ABSTRACT

We present a mathematical model based on the Grandmother Hypothesis to simulate how human post-menopausal longevity could have evolved as ancestral grandmothers began to assist the reproductive success of younger females by provisioning grandchildren. Grandmothers' help would allow mothers to give birth to subsequent offspring sooner without risking the survival of existing offspring. Our model is an agent-based model (ABM), in which the population evolves according to probabilistic rules governing interactions among individuals. The model is formulated according to the Gillespie algorithm of determining the times to next events. Grandmother effects drive the population from an equilibrium representing a great-ape-like average adult lifespan in the lower twenties to a new equilibrium with a human-like average adult lifespan in the lower forties.

The stochasticity of the ABM allows the possible coexistence of two locally-stable equilibria, corresponding to great-ape-like and human-like lifespans. Populations with grandmothering that escape the ancestral condition then shift to human-like lifespan, but the transition takes longer than previous models (Kim et al., 2012). Our simulations are consistent with the possibility that distinctive longevity is a feature of genus *Homo* that long antedated the appearance of our species.

1. Introduction

In primates, and mammals generally, females ordinarily die while they are still fertile. Only under conditions of unusually low mortality like domestication or captivity does normal adulthood include a post-fertile period (Williams, 1957; Levitis et al., 2013). Humans are exceptional; we are the only primates with substantial fractions of females still healthy and productive beyond the fertile years (Alberts et al., 2013; Levitis et al., 2013). Although it is widely assumed that survival past menopause is a novelty of recent times, that misconception is based on erroneous inferences from life expectancy. Life expectancies are very sensitive to fertility levels, so high birth rates with attendant high infant and juvenile mortality bring down average lifespans (Coale and Demeny, 1983; Hawkes, 2004). National life expectancies rose past 50 only in the 20th century (Oeppen and Vaupel, 2002), and women's fertility approaches zero by about 45 (Coale and Trussell, 1974), but historical and ethnographic demography show a substantial fraction of post-fertile female years in populations where life expectancies are less than 40 (Hamilton, 1966; Hawkes, 2003; Voland et al., 2005; Gurven and Kaplan, 2007; Levitis et al., 2013). Hunter-gatherer women remain economically

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productive and physically strong past the childbearing years (Hawkes et al., 1989; Blurton Jones and Marlowe, 2002; Walker and Hill, 2003; Kaplan et al., 2010); and sociological demographers routinely assume economic productivity up to the age of 65 in calculating the widely used dependency ratio to characterize human populations.

Mismatch between the end of fertility and the end of economic productivity in women is well established and has prompted inquiries framed in two different ways. One asks why fertility stops early in women. This "evolution of menopause" question generally assumes an ancestor with longevity like ours, but female fertility extending decades longer. In Williams's especially influential version, he hypothesized that changes in our lineage made late births more dangerous with maternal mortalities more costly to offspring survival (Williams, 1957). Consequently, he hypothesized that females who stopped early left more descendants.

The other framework focuses on longevity, asking why we evolved slower somatic aging without a concomitant extension of female fertility, so that women usually outlive the childbearing years. This framework uses comparative data from our closest cousins the other great apes (Perelman et al., 2011), noting that oldest ages of parturition are similar in all of us (Robbins et al., 2006; Robson et al., 2006). On grounds of this similarity, and similar rates of ovarian follicle loss with age in women and our closest relative chimpanzees (Jones et al., 2007), this framework assumes we retain the ancestral pattern of female fertility decline shared by all the living hominids and it was adult lifespans that lengthened. From that perspective, the question is how selection could favor greater longevity in our lineage without an increase in the age of last birth.

Evidence of life history regularities across the primates (Charnov, 1993), and evidence from hunter-gatherers of grandmothers supplying foods that just weaned juveniles cannot acquire effectively for themselves (Hawkes et al., 1997), stimulated the Grandmother Hypothesis to answer that question. In the other great apes, and mammals generally, juveniles feed themselves after weaning when mothers move on to bear their next offspring. Even though humans depend on foods that just-weaned juveniles cannot manage, humans have shorter birth intervals than great apes because mothers have help (Hrdy, 2009). Grandmothers' subsidies for dependent juveniles can explain the evolution of distinctive features of human life history (Hawkes et al., 1998). But, as Kirkwood and Shanley (2010, p.27) noted, verbal models are not enough. There must be also, "…a quantitative demonstration that there is indeed an associated increase in fitness under natural fertility and mortality conditions representative of our evolutionary past." Our model, simulated with deterministic difference equations (Kim et al., 2012), was an initial step in providing quantitative support.

Here we build on our 2012 model (Kim et al., 2012) to develop a probabilistic, agent-based model (ABM) of grandmother effects. As before, our assumptions about grandmothering are restrictive. Only post-fertile females are eligible, which means we exclude the help known to come from younger grandmothers (Sear et al., 2000; Lahdenperä et al., 2012). Grandmothers can support only one dependent at a time, so we ignore the decreasing need for help of older juvenile dependents and likely economies of scale for subsidizing more than one. Grandmothers do not care selectively for their daughters' offspring. Thus, their help can go to non-descendant users, undercutting relative advantages to their own descendants. We are also guided by evidence from both living people and other great apes (Sear and Mace, 2008; Boesch et al., 2010) that mothers are nearly irreplaceable caregivers before the age of 2 years, so we only allow dependents to be eligible for grandmother care after that age.

Our model begins at an equilibrium corresponding to great-ape-like expected adult lifespans just over 20 years, which we take to represent the ancestral condition. Our simulations then show that the benefit provided by grandmothering could drive the evolution of increased longevity past the end of female fertility toward human-like expected adult lifespans of over 40 years.

The differences between the ABM and the deterministic model (Kim et al., 2012) are (A) the ABM is probabilistic rather than deterministic, and (B) events in the ABM can occur at any time rather than at discrete intervals. However, by altering these two assumptions and making the model more realistic, we obtain several different and unexpected results, including (1) grandmothering does not guarantee evolution toward human-like expected adult lifespans over a fixed time interval, (2) the time of transition between a great-ape-like and human-like equilibria takes substantially longer (approximately 5–10 times as long) than in the deterministic model, (3) two locally-stable equilibria, corresponding to great-ape-like and human-like lifespans, can coexist with grandmothering, whereas in the deterministic model the lower equilibrium becomes unstable with grandmothering, (4) by using variable rather than fixed time intervals, the ABM eliminates artifacts of a fixed time interval, such as zigzagging functions of population growth and irregular evolution rates, (5) the ABM can run much more quickly than the previous model, allowing a thorough parameter sensitivity analysis, which we report, and (6) the ABM proves to be much more sensitive to the male fertility–longevity tradeoff, since male tradeoffs end up affecting long-term equilibria more smoothly rather than in sporadic jumps.

2. Model

Our probabilistic ABM follows the Gillespie method of determining times to next events (Gillespie, 1976). However, our approach differs from the usual Gillespie implementation by determining event sequences for all individuals and then sorting events among individuals, rather than directly determining the next event of the entire system. The ABM has the following features.

2.1. Birth, weaning, independence, and death

Each individual progresses through a period of nursing, weaned dependency, and independence. These transitions occur at times τ_0 and $\tau_1(L)$, where the age of independence, $\tau_1(L)$, is a function of the individual's expected adult life span, L. For simplicity, we assume mortality rates are constant, so that each individual has a lifetime mortality rate of $1/L$. In addition, the population is subject to an extrinsic, population-dependent death rate that affects everyone equally. Specifically, if the population surpasses a carrying capacity, K, the algorithm randomly selects an independent individual with uniform probability and removes him or her from the system. In the event that the individual is a female with a dependent child, the dependent child is also removed.

2.2. Fertile ages

A female is fertile between ages $\tau_2(L)$ and τ_3, where $\tau_2(L)$ and τ_3 are her ages of sexual maturity and end of fertility, respectively. In addition, a post-fertile female of age τ_3 to $\tau_4(L)$ is eligible to grandmother, i.e., adopt a weaned dependent, where $\tau_4(L)$ is her age of frailty. A male is eligible to compete for paternities between the ages of male eligibility, ρ_1 and $\rho_2(L)$.

2.3. Mating, conception, and delivery

Only fertile females without dependents can conceive. For simplicity, we assume females without dependents conceive and give birth at a constant rate c throughout their fertile ages. When a female is eligible to conceive, all eligible males compete for the paternity. A particular male's probability of success is $\alpha(L)/(\sum_i \alpha(L_i))$ where L is the male's expected adult life span and the summation is taken over all eligible males at the current time.

Offspring inherit the (geometric) mean of the expected adult lifespans of their parents with the possibility of a mutational shift. Mutations occur with probability p and result in a shift in L by a random factor following a lognormal distribution with mean 0 and standard deviation σ. By using a geometric mean and lognormal distribution, we are applying a logarithmic scale to L, meaning that we measure mutations in terms of relative, rather than linear, changes. For example, we would consider shifts in L from 20 to 21 and from 40 to 42 both as 5% relative changes up, rather than as 1 and 2 year linear shifts, respectively.

2.4. Grandmothering

As in our previous model (Kim et al., 2012), we assume that females who are eligible to grandmother can take care of any weaned dependent in the population, not only direct matrilineal descendants. This generalization weakens grandmother effects on longevity because the subsidies can go to non-descendants; but simplifies model formulation, since we do not track matrilineal lineages.

For convenience, we still use the term grandmothering to refer to general transfers of dependents between fertile and post-fertile females. In our model, grandmothering occurs whenever a female who is no longer fertile and has no current dependent adopts a weaned dependent from a female of fertile age, freeing the fertile female for another conception.

When a grandmother adopts a child, she functions thereafter as though she were the child's only caretaker. This assumption limits the influence of grandmother effects, because grandmothers cannot cooperate with living mothers to improve the survival of offspring. In addition, we assume that grandmothers can only adopt dependents after they reach the age of weaning.

We also restrict grandmothering eligibility to females who are past the fertile ages, but have not reached frailty, $\tau_4(L)$, thus excluding grandmother effects that occur before the age of 45 (Sear et al., 2000; Lahdenperä et al., 2012).

In our model, transfer of a dependent can occur after two types of events. If the dependent of a fertile female reaches weaning age, the ABM checks to see if there is an eligible grandmother who can adopt the dependent, and makes the transfer if one can be found. If a female becomes eligible to grandmother by reaching the end of fertility without a dependent or if a female of grandmothering age loses a dependent through death or independence, the ABM checks to see if there are any weaned dependents that are still being cared for by fertile females and transfers the eldest such dependent to the eligible grandmother.

2.5. Parameter estimates

Parameters and functions for life history transitions are taken from our previous paper (Kim et al., 2012). We assume that the female conception and delivery rate, c, is independent of life expectancy and equals 1/year. This value corresponds to an average total time of conception and gestation of 1 year. We base this estimate on waiting times in human natural fertility populations and chimpanzee study sites (Bongaarts and Potter, 1983; Wood, 1994; Knott, 2001; Emery Thompson, 2013). If we assume half a year to conception plus 8 months, 8.5 months, and 9 months of gestation (chimpanzee, gorilla and human respectively), we obtain a waiting time from eligibility to delivery of less than 1.5 years, which we simplify to 1 year.

We estimate the age of weaning, τ_0, to be 2 years. We choose this age based on data from living people and other great apes. Sear and Mace surveyed ethnographic accounts and noted that "the mother effect is strongly dependent on the age of the child. The consequences of losing a mother in very early life are catastrophic… [Yet] five studies found that the mother effect disappeared entirely after the child reached 2 years of age" (Sear and Mace, 2008, p. 5). Our assumption of a deeper evolutionary history for this pattern is based on accounts of chimpanzee infants as young as two surviving their mothers' death upon adoption by another caregiver (Boesch et al., 2010).

Other life history parameters are as follows. Children become independent at age $\tau_1(L) = L/6$; females reach sexual maturity at age $\tau_2(L) = L/2.5 + \tau_0$; female fertility ends at age $\tau_3 = 45$; females become too frail to grandmother at age $\tau_4(L) = \min\{2L, 75\}$; males become eligible to compete for paternities at age $\rho_1 = 15$; and males become too frail to compete at age $\rho_2(L) = \min\{2L, 75\}$, the same age at which females become too frail to grandmother.

As indicated by the definitions, most ages of transition scale with respect to expected adult life span. For example, if $L = 24$, the age of independence is $\tau_1(L) = 4$, the age of female sexual maturity is $\tau_2(L) = 11.6$ so that the average age of first birth is $\tau_2(L) + 1/c = 12.6$, and the age of frailty is $\tau_4(L) = 48$. If $L = 42$, the age of independence is $\tau_1(L) = 7$, the age of female sexual maturity is $\tau_2(L) = 18.8$, the average age of first birth is $\tau_2(L) + 1/c = 19.8$, and the age of frailty is $\tau_4(L) = 75$. We chose our scaling functions based on empirical patterns in other primates (Charnov, 1993), especially chimpanzees (Hill et al., 2001; Emery Thompson, 2013; Muller and Wrangham, 2014), using hunter-gatherers for the human range (Knott, 2001; Robbins et al., 2006; Robson et al., 2006; Gurven and Kaplan, 2007; Sellen, 2007). In addition, we limit the maximum age that a post-fertile female can assume care of a weaned dependent or that a male can compete for paternities to 75, which is consistent with hunter-gatherer mortality data (Gurven and Kaplan, 2007). The upper age limit counteracts the possibility of grandmothering or fathering at unrealistically high ages that may result from our assumption of a constant mortality rate.

We assume that males between ages $\rho_1 = 15$ and $\rho_2(L) = \min\{2L, 75\}$ can compete for paternities. Our assumption is based on data from great apes, especially gorillas and chimpanzees. In gorillas and chimpanzees, dominants gain the largest share of paternities. Gorilla males reach full adult size at 15–16 years and either disperse or wait to become dominant with an average tenure length of 4.72 years in one sample (Robbins, 1995). Twenty chimpanzee alpha males from 5 study sites attained that status at an average 19.9 years and held it an average of 4.7 years (Budongo Conservation Field Station; Jane Goodall Institute; Kibale Chimpanzee Project; Nishida, 1990; Boesch and Boesch-Achermann, 2000). Although aging males may lose dominance, many continue to successfully compete for paternities for much of the remainder of their lives (Boesch et al., 2006). On these grounds we estimate the beginning of male eligibility to compete for paternities at $\rho_1 = 15$ and, as with female frailty, we set the upper limit for male paternities at $\rho_2(L) = \min\{2L, 75\}$ to eliminate the possibility of winning paternities at unrealistically high ages.

We model a cost of increased longevity for males by assigning a weighting function $\alpha(L)$ that represents the relative likelihood that a male will outcompete others for a chance at paternity. Based on one of Williams's deductions about the effects of natural selection on senescence, that "successful selection for increased longevity should result in decreased vigor in youth" (Williams, 1957, p. 410), we assume $\alpha(L)$ is a decreasing function of L.

We assume that the probability of mutation, p, per conception is 0.05 as in (Kachel et al., 2011) and assume that mutational shifts in L have standard deviation $\sigma = 0.05$, or 5%.

We assume that the population carrying capacity $K = 1000$. This value allows the population to possess sufficient size and heterogeneity to produce consistent results. On the other hand, it is small enough to be simulated quickly. Table 1 lists parameters and estimated values. We use these values as base estimates, but we vary several of them in Section 3 to determine the parameter sensitivity of the model.

For simplicity, we begin the initial system with 500 independent females and 500 independent males with average expected lifespans of $L=20$ and ages $15+20n/365$, for $n=0,\ldots,500$, i.e. the female and male populations consist of individuals spaced 20 days apart. We apply this initial state simply as a seed population. The system rapidly converges to a steady age and demographic distribution within several generations, which is negligible in the evolutionary timescale of the model.

3. Results

We coded the agent-based model in Python and ran simulations on Unix and Linux machines. Throughout the paper we calculate average expected adult lifespans using the geometric mean. The use of a geometric mean is consistent with how we calculate the inheritance of expected adult lifespans from both parents and the use of the lognormal distribution for mutational shift sizes. In any case, the geometric and arithmetic means differ at all time points by less than 0.01 years.

3.1. Female fertility–longevity tradeoff

For populations with fixed expected adult lifespans, L, we estimate the net growth rate, r, at a steady-state age distribution.

Table 1
Parameters and estimates.

Parameter	Description	Estimate
L	Average expected adult life span (yr)	Variable
τ_0	Age of weaning (yr)	2
$\tau_1(L)$	Age of independence (yr)	$L/6$
$\tau_2(L)$	Age of female sexual maturity (yr)	$L/2.5+\tau_0$
τ_3	Age female fertility ends (yr)	45
$\tau_4(L)$	Age of female frailty, i.e. ineligibility to adopt (yr)	$\min\{2L, 75\}$
ρ_1	Age male eligibility starts (yr)	15
$\rho_2(L)$	Age male eligibility ends (yr)	$\min\{2L, 75\}$
c	Rate of female conception and delivery (1/yr)	1
$\alpha(L)$	Male weighting factor for mating	Decreasing function of L
p	Probability of mutation in L at birth	5%
σ	Standard deviation of mutations	5%
K	Population carrying capacity	1000

To estimate the population growth rate, we remove the population carrying capacity and simulate the system for 2000 years for constant L and mutation probability $p=0$. Since simulations are probabilistic we take the average of 10 simulations. Plots of the growth rate versus expected adult lifespan are shown in Fig. 1a.

In Fig. 1a, we see that without grandmothering, the growth rate declines as L increases past 18. Furthermore, the population cannot survive for $L \geq 29$, since the growth rate passes below 0 at this point. The decrease in r results from increasing ages at first birth, decreasing fertile periods, and increasing ages of independence, which causes a steadily increasing birth interval (see Fig. 1b).

On the other hand, grandmothering allows the population to have a positive growth rate for L up to 60. This high growth rate at high L occurs because mothers can transfer weaned dependents to grandmother care at ages below the rising age of independence, which allows birth intervals to increase more slowly (see Fig. 1b).

Both with and without grandmothering, the growth rates and birth intervals coincide up to 22.5 years, since this is the point at which the age of frailty, $\tau_4(L)$, starts to exceed the end of female fertility, τ_3. Only then can the benefits of grandmothering take effect.

3.2. Male fertility–longevity tradeoff

Because there are two sexes, the long-term average adult life expectancy of the population is determined by a compromise between female and male fertility–longevity tradeoffs. As discussed in Section 2, we model the male tradeoff with a decreasing weighting function $\alpha(L)$. As the expected adult lifespan L increases, the chance of a male surviving through the reproductively eligible ages between ρ_1 and $\rho_2(L)$ also increases. However, the decreasing weighting $\alpha(L)$ reduces the relative chance of paternity for longer-lived males. The balance between probability of survival and chance of paternity determines how the male tradeoff influences the long-term equilibrium of the population.

To investigate the influence of the male tradeoff on long-term behavior, we define the change in the weighting function $\alpha(L)$ by the function $\delta(L)=\alpha'(L)/\alpha(L)$. Since we assume that $\alpha(L)$ is a decreasing function, the change $\delta(L) \leq 0$ for all L. In addition, the function $\delta(L)$ uniquely determines $\alpha(L)$ up to a scaling factor by the expression

$$\alpha(L)=\exp\left\{\int_{L_0}^{L}\delta(u)du\right\}. \tag{1.1}$$

where L_0 is constant. For convenience, we set $L_0=20$. To assess the effect of changes in $\alpha(L)$ on the long-term behavior of the population, we simulate the system with and without grandmothering for cases when $\delta(L)=\delta_0$ is constant. As indicated

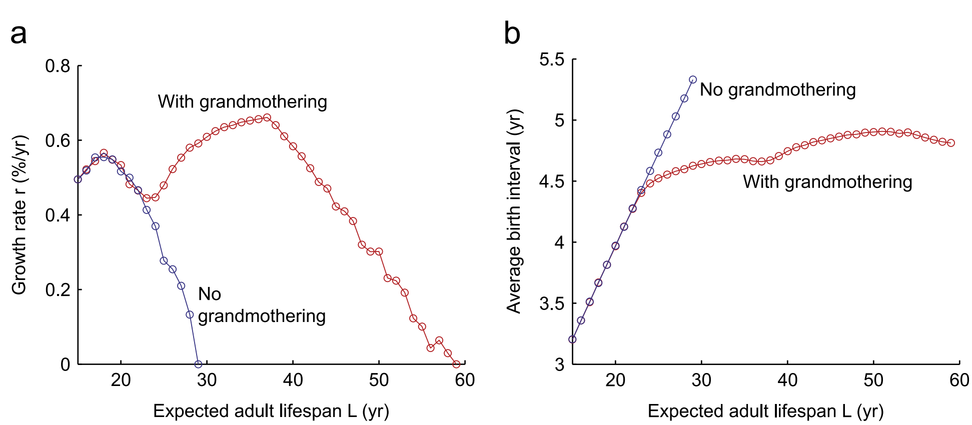

Fig. 1. Effects of grandmothering and adult lifespan on female fertility. Plots of (a) population growth rate and (b) average birth interval versus expected adult lifespan, L, with and without grandmothering.

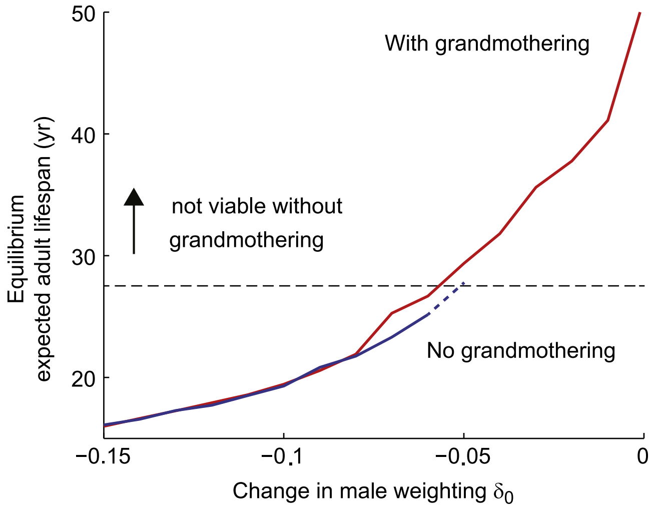

Fig. 2. Effects of male tradeoff on population equilibria. Equilibrium expected adult lifespans with and without grandmothering for $\delta_0 = -0.15, -0.14, -0.13, \ldots, 0$, where the change in the male weighting function $\alpha(L)$ is defined by $\alpha'(L)/\alpha(L) = \delta_0$. The dotted segment of the no-grandmothering curve represents the average expected adult lifespan of the population before it went extinct prior to the end of simulation.

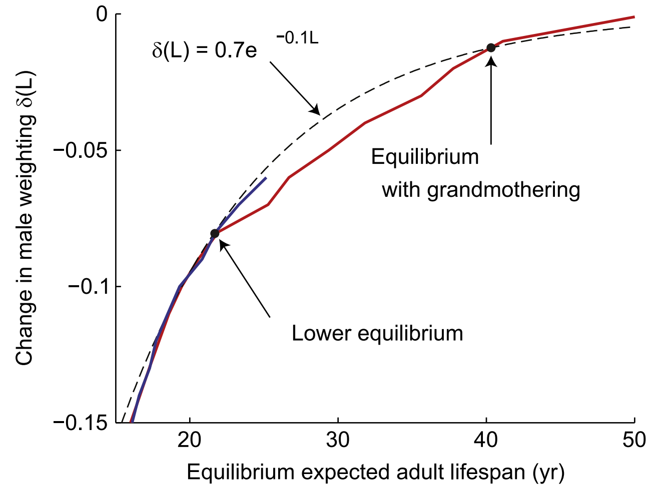

Fig. 3. Predicted long-term equilibrium adult expected lifespans. Change in the male weighting function, given by $\delta(L) = -0.7e^{-0.1L}$, versus expected adult lifespan L. Intersections of $\delta(L)$ with curves from Fig. 2 help predict the locations of long-term equilibria with and without grandmothering.

explicitly in (1.1), a constant $\delta(L) = \delta_0 \le 0$ means that as L increases, a male's competitive ability decreases at a constant (proportional) rate. For example, if a male with $L = 21$ had a 5% smaller chance of winning a paternity than a male with $L = 20$, then a male with $L = 22$ would have a 5% smaller chance of winning a paternity than a male with $L = 21$ and so on.

For different values of δ_0, we simulate the system for 2 million years, and take the average expected adult lifespan of the population over the last 1.5 million years to numerically estimate the equilibrium expected lifespan. The initial 0.5 million years is well over enough time for the system to reach an equilibrium age and demographic distribution. Fig. 2 shows equilibrium expected adult lifespans versus δ_0.

From Fig. 2, we see that as the magnitude of δ_0 decreases, the equilibrium increases with and without grandmothering. This result is expected, because as the magnitude of δ_0 decreases, males incur less competitive disadvantage when they gain the survival advantage of an expected adult lifespan increase. Consequently the equilibrium shifts higher. Both with and without grandmothering, the equilibria coincide up to 22.5 years, since this is the point at which there is an opportunity for grandmothering before frailty disallows it.

As the equilibrium expected adult lifespan increases beyond 22.5, the curves corresponding to the cases with and without grandmothering diverge, and, with grandmothering present, adult lifespan increases. Fig. 1a shows that the population without grandmothering cannot survive as individuals' expected adult lifespans pass 28 years. Hence the system without grandmothering is not viable above the dotted line in Fig. 2. In contrast, the population with grandmothering can survive up to an average expected adult lifespan of around 50 years.

The results imply that grandmothering can provide a divergent selection pressure toward increased adult lifespan even when it occurs at the low levels present when population average adult lifespans are 22.5. Grandmothering levels are very low at this point because only females with L above the average 22.5 have a period of eligibility to adopt between the end of fertility (at 45) and before frailty (at $2L$). On the other hand, the population without grandmothering remains at the ape-like expected adult lifespans regardless of the male tradeoff function, because the females cannot replenish the population as expected adult lifespans exceed 28 years. Such a scenario would drive the population to extinction.

The curves in Fig. 2 help us assess how different male weighting functions $\alpha(L)$ are likely to affect the long-term equilibrium behavior of the population. Since the model is probabilistic and the curves are generated as time averages of probabilistic simulations, it is always possible that a simulation will deviate from predicted long-term behavior. Nonetheless, the curves provide a useful tool for assessing probable behavior without running numerous simulations. In particular, consider the curve $\delta(L) = -0.7e^{-0.1L}$ for relative change as a function of L. Fig. 3 shows a plot of $\delta(L)$ and the curves for equilibrium expected adult lifespans with and without grandmothering, but, compared to Fig. 2, we switch the horizontal and vertical axes in Fig. 3 to show $\delta(L)$ as a function of L.

In Fig. 3, the curve $\delta(L)$ closely follows the equilibrium curves with and without grandmothering up to an expected lifespan of around 22.5 years, where the equilibrium curves diverge. Consequently, if the male tradeoff is governed by the curve $\delta(L)$, the population without grandmothering has very little advantage to shift away from the lower equilibrium where the curves intersect around 21 years. Furthermore, in the absence of grandmothering, shifts toward significantly higher expected lifespans favored by advantages through males may result in the population going extinct.

In the presence of grandmothering, on the other hand, the equilibrium curve shifts toward higher values, meaning that the population has an advantage to move toward higher expected adult lifespans until the curve $\delta(L)$ intersects with the equilibrium curve with grandmothering around 41 years. Using this $\delta(L)$ and Eq. (1.1), we can obtain an expression for $\alpha(L)$. As mentioned previously, the model behaves probabilistically and the equilibrium curves are estimated probabilistically, so the predictions of the actual equilibrium points are not precise, and we must simulate the full model to determine where the population will evolve over time. Nonetheless, as we will see, these predictions end up very close to the actual simulated equilibria.

3.3. Time evolution without grandmothering

We simulate the system using parameter values in Table 1 and the male weighting function $\alpha(L)$ corresponding to $\delta(L) = -0.7e^{-0.1L}$. We first simulate the system for 1 million years without grandmothering. Fig. 4a shows the time evolution of population average expected adult lifespans, $\bar{L}$, for 30 simulations. Since the model involves two sexes, the evolution of the system is influenced by both female and male fertility–longevity tradeoffs.

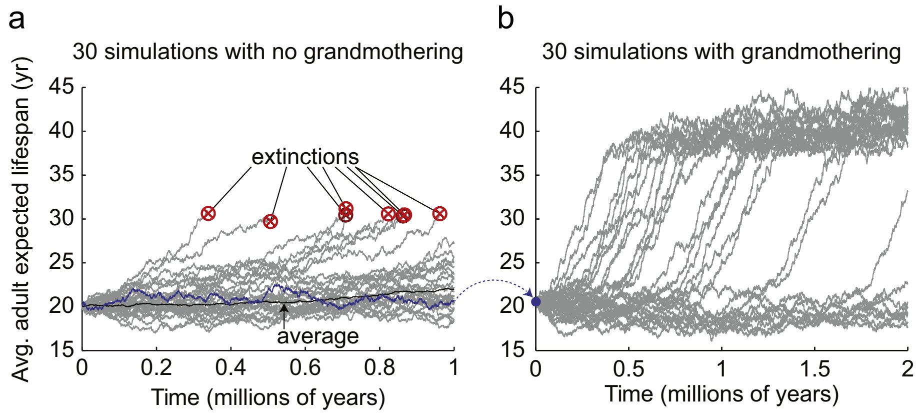

Fig. 4. Time evolutions of the average expected adult lifespans with and without grandmothering. (a) Thirty simulations over 1 million years without grandmothering. Each simulation is shown in gray. In eight simulations, the populations went extinct at the times shown by the red circled *X*'s. The average among the 22 simulations that did not go extinct is shown in black and ends at an overall average expected adult lifespan, $\overline{L}$, of 22.0. The ending point of the simulation shown in blue serves as the starting point for 30 new simulations with grandmothering. (b) Thirty simulations over 2 million years with grandmothering. By the end of the simulation, 21 populations have progressed and stabilized at average expected adult lifespans of over 38. These simulations end at an overall average expected adult lifespan, $\overline{L}$, of 41.1. One population is progressing toward an increased lifespan, and eight populations have remained at lifespans below 23. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Of the 30 simulations in Fig. 4a, eight rise above $\overline{L}=30$ and become extinct. In addition, it appears that simulations are likely to remain under $\overline{L}=25$, but once a simulation passes $\overline{L}=25$, it appears have a high chance of progressing to higher $\overline{L}$ without returning to lower values. On the other hand, as $\overline{L}$ increases past 29, female fertility cannot maintain the size of the population, because the average population growth rate becomes negative, leading to extinction (see Fig. 1a). Because the model is probabilistic, the population has a nonzero chance of exiting a great-ape-like average expected adult lifespan even without grandmothering; however, the female fertility–longevity tradeoff prevents the population from surviving for long when $\overline{L}>29$. Of the 22 simulations in Fig. 4a that do not result in extinction, the ending overall average adult expected lifespan is 22.0 – within the great-ape-like range.

Some simulations evolve to extinction without grandmothering because advantages through males can push population longevity to levels that are not only higher than the optimum overall growth rate, but too high for females to maintain population viability. Selection is very strong through males, and males can experience large disparities in reproductive success, making their tradeoffs very high stakes. Although it would not make sense for females to drive a population toward extinction as female life histories are sensitive to growth rates and lower growth rates would be selected against, for males, it is paternities that matter. Even as female productivity declines with greater longevity, sex conflict from male tradeoffs can push the population to decreasing growth rates and extinction.

3.4. *Time evolution toward increased longevity with grandmothering*

To simulate the influence of grandmothering, we take a simulation shown in Fig. 4a and use its end point at 1 million years as a starting point for 30 new simulations with grandmothering. We chose a simulation, shown in blue in Fig. 4a, with $\overline{L}=20.6$ at 1 million years.

Fig. 4b shows the results of 30 simulations with grandmothering over a span of 2 million years. Of the 30 simulations, 21 progress from a great-ape-like expected adult lifespan less than 23 and stabilize at a human-like expected adult lifespan greater than 38. Of these simulations, the average adult expected lifespan at the end point of 2 million years is 41.1. Unlike the simulations without grandmothering, these populations can survive due to a positive growth rate at human-like expected adult lifespans (see Fig. 1a). In Fig. 4b, one simulation is in the process of transitioning from great-ape-like to human-like expected adult lifespan, and eight simulations have remained at a great-ape-like expected adult lifespan.

From the results shown in Fig. 4b, we see that simulations that shift to a human-like expected adult lifespan take approximately 250,000–300,000 years to pass from $\overline{L}=23$ to 38. This transition rate is substantially slower than the ones obtained by our deterministic model (Kim et al., 2012), which indicates that probabilistic effects play a significant role in determining the time of evolution.

Because the model is probabilistic, not all populations increased or even began to increase to greater lifespan over the duration of the simulations. From Fig. 4b, we can deduce that all simulations will eventually transition to human-like expected adult lifespans. It is a well-known result that if an event, e.g., passing above the threshold of $\overline{L}=23$ or $\overline{L}=25$, has nonzero probability, it will occur in a finite amount of time. Nevertheless, the timing of a simulated population's transition to greater adult life span may vary greatly.

The tendency of the system to remain at a lower $\overline{L}$ for up to a few million years suggests that the lower equilibrium of approximately $\overline{L}=21$ shown in Fig. 3 is still a possible long-term equilibrium for populations with grandmothering. This suggestion is further supported by the observation that the equilibrium curves with and without grandmothering almost coincide for $\overline{L}<22.5$. As noted previously, an expected adult lifespan of 22.5 is the first point at which the age of frailty, $\tau_4(L)$, starts to exceed the end of female fertility, τ_3. Prior to this point, only the small fraction of the population with $\overline{L}$ above the average 22.5 is eligible to grandmother. As a result, the population has to probabilistically drift above $\overline{L}=22.5$ in order to realize the possibility of grandmothering. When it does, the increasing numbers of eligible grandmothers push the population toward the higher equilibrium around $\overline{L}=41$. When a population begins to progress, more or less steadily, toward increased lifespan depends on the probability that a population exits the basin of attraction of the lower equilibrium.

The results of Fig. 4b also strongly imply that once a population reaches an $\overline{L}$ of 25, it is very unlikely that the population will go back to a substantially lower $\overline{L}$ of below 23. It may probabilistically wander around each value before moving upward, but none of our simulations resulted in a population turning around from this point and returning to a great-ape-like expected adult lifespan. (Strictly speaking the probability of reverting to a great-ape-like expected adult lifespan, even from a human-like state, is nonzero, so such an event would occur after some arbitrary number of simulations; however, the probability of such an event is probably so unlikely as to be negligible.)

3.5. Sensitivity analyses

To gain a better understanding of the effect of our assumptions about life history parameters, we conducted sensitivity analyses by investigating how variation in age of weaning,τ_0, age of independence, $\tau_1(L)$, age of female sexual maturity, $\tau_2(L)$, and the age of female frailty, $\tau_4(L)$ affect model behavior. We vary these parameters by 80%, 90%, 110%, and 120% of the values or expressions in Table 1. For these analyses, we leave the end of female fertility fixed at $\tau_3 = 45$, since a similar age of end of fertility in the forties seems to be conserved in the great ape lineage (Robbins et al., 2006; Robson et al., 2006). Also, we keep male life history and other parameters fixed, since we have already discussed the effects of varying the male weighting function $\alpha(L)$ in the section *Male fertility–longevity tradeoff*. In general, higher tradeoffs, i.e., higher $\alpha(L)$, lead to lower equilibrium $\overline{L}$, and lower tradeoffs lead to higher equilibrium $\overline{L}$ as expected. The results of our sensitivity analyses are summarized below.

3.5.1. Weaning age

A variation of $\pm 20\%$ of weaning age, τ_0, does not affect the simulations with or without grandmothering. This result is due to the small effect of a $\pm 20\%$ variation on τ_0 (corresponding to a range of values from 1.6 to 2.4). In the case without grandmothering, females cannot conceive new offspring until their current child reaches the age of independence, which remains well above 2.4 for the values of L that occurred in our simulations. In the case with grandmothering, we see from Fig. 1b that on average grandmothers only adopt weaned dependents of around 4.5 years or older. Adoption of dependents well after weaning age is due to our assumption that grandmothers start by adopting the oldest weaned dependent. Thus, in our model, grandmothers have little to no effect on offspring of 2.4 years or younger.

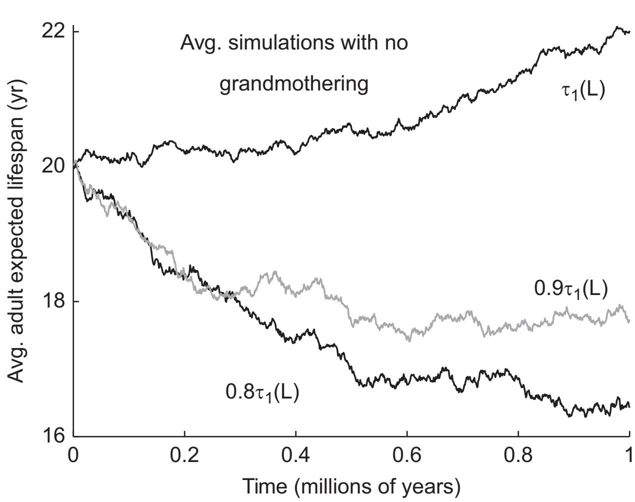

Fig. 5. Time evolutions of the average expected adult lifespan without grandmothering for ages of independence set to $0.8\tau_1(L)$, $0.9\tau_1(L)$, and $\tau_1(L)$, where $\tau_1(L)$ is defined in Table 1. The curves for $0.8\tau_1(L)$ and $0.9\tau_1(L)$ show the averages over 10 simulations. None of these simulations resulted in extinction. The curve for $\tau_1(L)$ is the same as the average over the 22 simulations that did not go extinct in Fig. 4a. The three curves end at overall average adult expected lifespans of 16.4, 17.7, and 22.0, respectively.

3.5.2. Age of independence

Fig. 5 shows averages over multiple simulations without grandmothering when the ages of independence are set to $0.8\tau_1(L)$, $0.9\tau_1(L)$, and $\tau_1(L)$. The curves for $0.8\tau_1(L)$ and $0.9\tau_1(L)$ show averages of 10 simulations each, and the curve for $\tau_1(L)$ is the average curve in Fig. 4a. The three curves end at values of 16.4, 17.7, and 22.0, respectively. The 10 simulations for $0.8\tau_1(L)$ and the 10 simulations for $0.9\tau_1(L)$ vary by less than 12% and 16%, respectively, of their averages over the span of 1 million years. When ages of independence are set to $1.1\tau_1(L)$ and $1.2\tau_1(L)$, all simulations lead to rapid extinction, because the birth interval is too long for the population to maintain itself.

As shown in Fig. 5, when ages of independence are decreased to 90% or 80% of the original expression in Table 1, the long-term $\overline{L}$ also decreases monotonically. This decrease is, however, not proportional, since the long-term equilibria for $0.8\tau_1(L)$ and $0.9\tau_1(L)$ are much closer than the equilibrium for $\tau_1(L)$. For the cases corresponding to $0.8\tau_1(L)$ and $0.9\tau_1(L)$, we start from example simulations that end close to the overall averages and introduce grandmothering. When grandmothering is introduced, all simulations remain around the same equilibria for the next one million years (results not shown). In contrast, as we found before, when grandmothering is introduced to the case when the age of independence is $\tau_1(L)$, the population has a high chance of shifting to an increased average adult lifespan (see Fig. 4b).

Our sensitivity analysis shows that scaling down the age of independence leads to lower long-term lifespan equilibria without grandmothering, and at this point, grandmothering is much less effective at propelling lifespans out of the lower ranges to higher human-like values. These results concur with the Grandmother Hypothesis, which proposes that increasing ages of independence opened a novel fitness opportunity for grandmothers to provision grandchildren. As implied by this scenario, as ages of independence decrease, the window for grandmother effects diminishes.

3.5.3. Age of female sexual maturity

Fig. 6a shows averages over multiple simulations without grandmothering when the ages of female sexual maturity are set to $0.8\tau_2(L)$, $0.9\tau_2(L)$, $\tau_2(L)$, and $1.1\tau_2(L)$. The curves for $0.8\tau_2(L)$ and $0.9\tau_2(L)$ each correspond to averages of 10 simulations, the curve for $\tau_2(L)$ coincides with the average curve shown in Fig. 4a, and the curve for $1.1\tau_2(L)$ is the result of the single simulation out of 10 that did not result in extinction. The four curves end at values of 16.6, 17.7, 22.0, and 21.3, respectively.

The 10 simulations for $0.8\tau_2(L)$ and the 10 simulations for $0.9\tau_2(L)$ vary by less than 15% and 25% above and below their averages shown in Fig. 6a. As before, for each case, we select an example simulation that ends near the overall average and simulate the system 10 more times with grandmothering for the next 1 million years. When grandmothering is introduced for these two cases, all simulations remain around the same equilibria for the next one million years (results not shown). Although we did not observe a transition to higher lifespan for these simulations, it seems that, with grandmothering, the $0.9\tau_2(L)$ case has a reasonable probability of evolving higher lifespans. We make this observation because some simulations reach values far above the long-term average, in some cases as high as 22.0, which lie close to the range where evolution to higher lifespans begins to occur in Fig. 4b.

In the case of $1.1\tau_2(L)$, nine of 10 simulations result in populations rising to average expected adult lifespans greater than 25, at which point the populations go extinct (results not shown). These results follow the observed pattern in Fig. 6a that as the age of female maturity scales up, the population tends to shift toward higher long-term average expected adult lifespans. It follows that

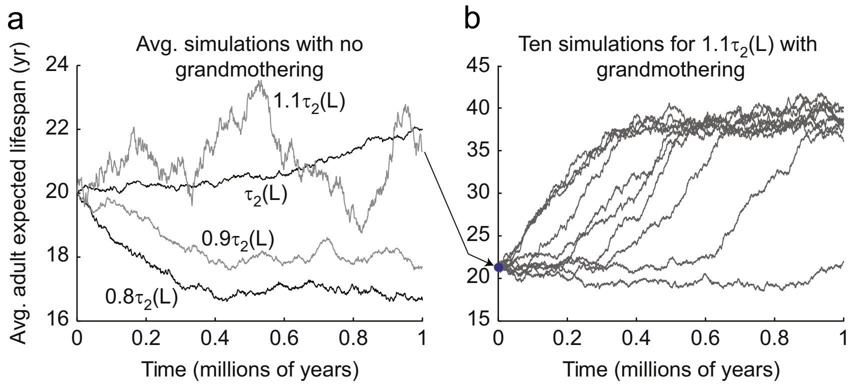

Fig. 6. (a) Time evolutions of the average expected adult lifespan without grandmothering for ages of female maturity set to $0.8\tau_2(L)$, $0.9\tau_2(L)$, $\tau_2(L)$, and $1.1\tau_2(L)$, where $\tau_2(L)$ is defined in Table 1. The curves for $0.8\tau_2(L)$ and $0.9\tau_2(L)$ show the averages over 10 simulations. None of these simulations resulted in extinction. The curve for $\tau_2(L)$ is the same as the average over the 22 simulations that did not go extinct in Fig. 4a. The curve for $1.1\tau_2(L)$ shows the only simulation out of 10 that did not go extinct within 1 million years. The four curves end at overall average adult expected lifespans of 16.6, 17.7, 22.0, and 21.3, respectively. (b) Ten simulations for the case when age of female sexual maturity is $1.1\tau_2(L)$ over 1 million years with grandmothering. By the end of the simulation, nine of 10 populations have progressed and stabilized at average expected adult lifespans of over 36. These simulations end at an overall average expected adult lifespan, $\overline{L}$, of 38.3. One simulation has remained below 22.1, but it appears to be progressing toward increased lifespan.

if the age of female maturity is delayed by 10%, then the average growth rate will be less than the rates shown in Fig. 1a, causing the population to go extinct before $\overline{L}$ reaches 30. We also simulated the case for $1.2\tau_2(L)$, but all the populations went rapidly extinct, since the delayed age of female maturity pushed all growth rates below 0.

3.5.4. *Age of female frailty*

Since the age of female frailty only affects grandmothering, variations to this parameter have no effect on the system without grandmothering, so we do not show additional simulations for these cases. Instead, as before, we use the endpoint of the example simulation in Fig. 4a (blue curve) as a starting point for new simulations with varying ages of female frailty.

Fig. 7a, b, c, and d shows time evolution of 10 simulations with grandmothering when ages of female frailty are set to $0.8\tau_4(L)$, $0.9\tau_4(L)$, $1.1\tau_4(L)$, and $1.2\tau_4(L)$. As we scale the age of female frailty up or down, the number of eligible grandmothers increases or decreases. From Fig. 7, we see that grandmothering appears to push all simulations toward increased lifespans. However, when the ages of frailty are lowest at $0.8\tau_4(L)$ and $0.9\tau_4(L)$, only three of 10 simulations rise out of lower great-ape-like expected adult lifespans within 1 million years. Furthermore, in the case for $0.8\tau_4(L)$, one population goes extinct, due to the lack of eligible grandmothers. In all four simulations, each population has a reasonable probability of progressing to increased lifespan in one million years, but as the age of female frailty increases, so does the probability of moving to the higher equilibrium. These results show that the availability of more eligible grandmothers positively affects both the probability of transition to increased lifespan and the ability of the population to survive at higher lifespans.

4. Lessons from the model

We have described a probabilistic ABM of the grandmother effect. Unlike our previous model (Kim et al., 2012), this one probabilistically determines the times of key events for each individual. This modification allows us to simulate the model much more rapidly and removes artifacts of rounding from imposing a fixed time step size. The ABM also results in distinct phenomena that were not present in the previous, deterministic model. In particular, grandmothering induces two distinct, locally-stable equilibria, representing great-ape-like and human-like expected adult lifespans. There are no intermediate equilibria, but both great-ape-like and human-like equilibria coexist, with a probabilistic rate of shifting out of the basin of attraction of the great-ape-like equilibrium and progressing toward the human-like one. The basin of attraction of the human-like equilibrium appears much larger than the basin for the great-ape-like equilibrium, meaning that it is highly unlikely for a population that has reached the human-like equilibrium to revert back to the great-ape-like equilibrium.

In terms of quantitative differences, the time of transition from great-ape-like to human-like expected adult lifespans in the ABM takes approximately 275,000 years as opposed to between 24,000 and 56,000 years in our deterministic model (Kim et al., 2012). In addition, the relationships between population growth rate (shown in Fig. 1b) and expected adult lifespan, both with and without grandmothering, as well as long-term equilibria as a function of male tradeoffs (shown in Figs. 2 and 3) are substantially smoother. This last result indicates greater sensitivity to the male fertility–longevity tradeoff, since even slight male tradeoffs will result in steady shifts of population equilibria. By contrast, in our previous model (Kim et al., 2012), a range of variation in male tradeoffs hardly affected the long-term equilibria and only influenced the rate of transitions from great-ape-like to human-like equilibria.

An important practical benefit of the ABM is that it runs over 10 times faster than the previous model, making more thorough sensitivity analysis feasible. The sensitivity analyses we report here would have been prohibitively time-consuming with the previous model. For our sensitivity analyses, we individually scaled four life history parameters – age of weaning, age of independence, age of female sexual maturity, and age of female frailty – by up to $\pm 20\%$. We found that the age of weaning had no effect on the behavior of the system with or without grandmothering. Scaling the ages of independence or female sexual maturity up or down shifted the long-term equilibrium up or down, although not proportionally. It is not surprising that scaling isolated parameters does not result in proportional shifts in equilibrium lifespans, because of the interactions between parameters. If other parameters are held fixed while one varies, the fixed parameters will restrict the range over which long-term lifespans can vary and still remain viable. Scaling the age of female frailty affected the strength of grandmothering by increasing the probabilistic rate of a population progressing toward the higher human-like equilibrium. In all cases, if the population began at an

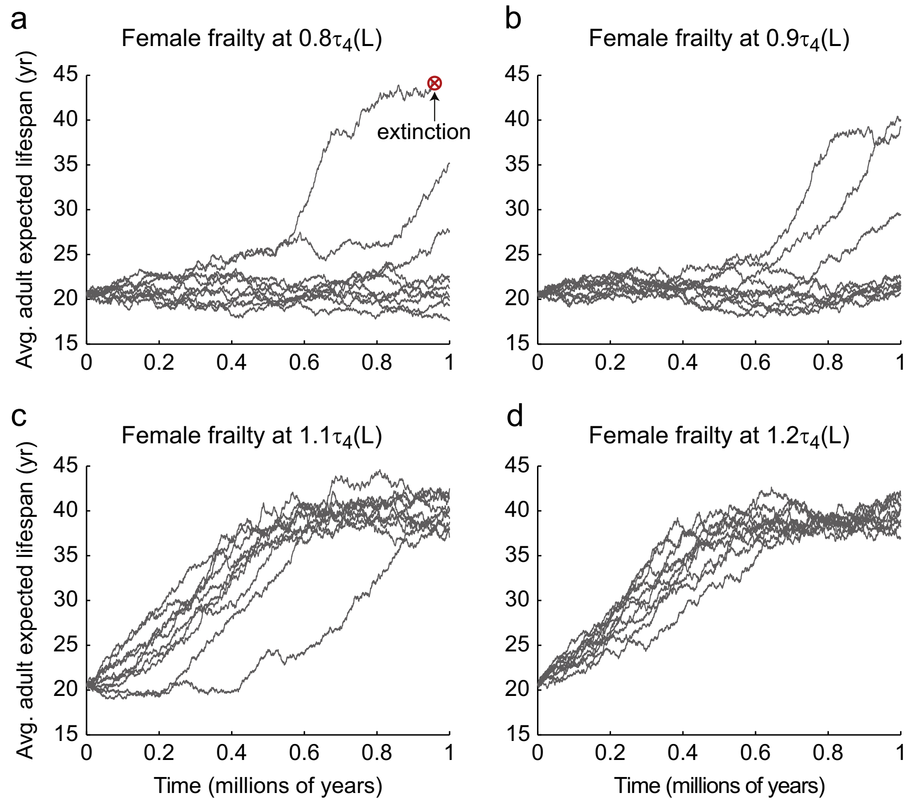

Fig. 7. Time evolutions of average expected adult lifespan with grandmothering. Each plot shows 10 simulations for ages of female frailty set to (a) $0.8\tau_4(L)$, (b) $0.9\tau_4(L)$, (c) $1.1\tau_4(L)$, and (d) $1.2\tau_4(L)$, where $\tau_4(L)$ is defined in Table 1. As the scaling value of the age of female frailty increases, the probabilistic rate of transitioning to increased lifespan also increases.

average expected adult lifespan that was too low, as in the cases for 80% and 90% scaling of ages of independence and sexual maturity, grandmothering did not drive the population out of the basin of attraction of the great-ape-like equilibrium over our observed simulations.

Our sensitivity analyses show that increasing the number of eligible grandmothers increases the chance of evolving greater longevity. On the other hand, shifting a population to lower ages of independence and hence shorter birth intervals or lower ages of sexual maturity greatly weakens the ability of grandmothering to drive selection of increase lifespan. These results suggest that great apes exist at the brink of a critical window where grandmothering could push selection of human-like longevities. Alternative life histories consisting of earlier ages of maturity, shorter birth intervals, and shorter overall lifespans would not favor such a transition – with or without grandmothering.

In this study, our model populations shift from great-ape-like adult life spans into the human longevity range because grandmothers free mothers for another pregnancy sooner without reducing the survival chances of previous offspring. The benefits of greater longevity are increased chances of living through the fertile years. But greater longevity also imposes the cost of later ages of first birth, and longer-lived offspring are dependent to older ages (as holds for mammals generally, see Charnov and Berrigan, 1993). Without grandmothering, the longevity that maximizes female lifetime reproductive success depends on these tradeoffs. Grandmothers' help alters the tradeoffs (see Fig. 1). Our simulations assume that only females past their fertility are eligible to grandmother, that they can subsidize only one dependent at a time, and that grandmothers adopt any dependent, not only their own grandchildren. These assumptions restrict grandmothering to a narrow eligible pool, constrain their help, and allow non-descendants to free-ride on it, all features that weaken grandmothering. Yet its influence is still enough to shift the payoffs for both sexes and drive the evolution of longevity from an ape-like value into the human range.

As in our previous model (Kim et al., 2012), we include two sexes with different tradeoffs, which introduces sexual conflict over optimal longevities. The optimum expected adult lifespan for females alone, which maximizes growth rate, is different from the compromised equilibrium reached with males added. Helpful grandmothering makes even greater longevity advantageous through males (see Fig. 2). The influence of sexual conflict underlines the importance of including both male and female tradeoffs when investigating the evolution of human-like expected adult lifespans.

The link between grandmothering and increased longevity is not automatic. In particular, it is not guaranteed that the grandmother effect can overcome the tradeoff necessary to pull the population away from the fitness plateau that corresponds to a great ape-like life history toward an alternative plateau corresponding to a human-like life history. In our model, we investigate the effect of male tradeoffs on the locations of higher and lower equilibrium longevities with and without grandmothering (see Fig. 3). If the male tradeoff were much higher (i.e. above the dotted curve in Fig. 3), so that increased longevity would come with great penalty to males, then there would likely be only one equilibrium with grandmothering, coinciding with the equilibrium without grandmothering. If the male tradeoff were much lower (i.e. below the dotted curve in Fig. 3), so that males could increase longevity almost for free, then there would be no viable equilibrium without grandmothering, since sex conflict from males would drive the population to increasing longevities at the expense of decreasing growth rates.

5. Discussion

Other mathematical models have examined the important role the economic productivity of elders plays in maintaining distinctively human life history. Lee (2008) showed that intergenerational transfers selected against increasing senescence in a human-like age structure using a one-sex model. In a two-sex model, Kachel et al. (2011) used the Grandmother Hypothesis as the basis for a probabilistic, agent-based model of grandmother effects on the evolution of lifespan, but assumptions about male fertility hijacked their result (Hawkes et al., 2011). Our 2012 model (Kim et al., 2012) was stimulated by theirs.

More recently, Morton et al. (2013) used the stopping-early framework we critiqued above to explain the evolution of the human mismatch between longevity and female fertility. They assumed an ancestor with our longevity, but female fertility extending to much older ages. In their model it was the introduction of a male mating preference for younger females that led to the evolution of mid-life menopause by allowing the accumulation of fertility-reducing mutations affecting fertility in older females (Morton et al., 2013). However, while a preference for young females is evident in men (e.g., Jones, 1996), this is not true of other primates (Anderson, 1986), with contrary preference for older females best established in our closest living relatives, chimpanzees (Muller et al., 2006). Morton and colleagues do not suggest a source for the human preference, which might likely be a consequence, rather than a cause, of our post-fertile life spans (Hawkes et al., 2000).

In addition, their model (Morton et al., 2013) assumes that new births exactly compensate deaths to maintain an equilibrium population, so mating and conception only occur when someone dies. When a conception opportunity arises, males and females randomly form mating pairs and compete for the next conception. The first mating pair to successfully conceive gains the new birth, while females who did not conceive must wait for another opportunity. This pattern generates a strong selective pressure on females to continually compete for maternities, which is part of the reason why the model results in a shrinking female fertility window.

In contrast, we assume that only males compete for mating opportunities as in most sexual reproducers. In mammals, reproducing females are committed to gestation and lactation, and in most primates, including humans, each female can produce at most about one baby a year. Each male, on the other hand, could produce many more – if the other males would let him. The number of new offspring attainable is, therefore, constrained by the number of fertile females. This formulation reflects the active male competition for fertile females that generally characterizes primates (Strier, 2011). In our model, female fertility determines the rate of conceptions, and we rely on a population-dependent death rate to maintain an equilibrium population size.

Morton et al. (2013) share the assumption that male mating preferences shape human life history with other previous models. In particular, Marlowe (2000) suggested a patriarch hypothesis in which the fertility of older males maintained human longevity. Tuljapurkar et al. (2007) built a formal two-sex model to derive evolutionarily stable life histories in which late fertility in men maintained human longevity. However, these investigators assumed the contemporary patterns and did not address their evolution.

From a different angle, Kaplan and Robson (2002) modeled the evolution of human longevity in a one-sex model based on ideas about longevity payoffs for increased skills learning without addressing the timing of female fertility decline. Then Kaplan et al. (2010) extended the logic of that model to address the mismatch between longevity and female fertility by showing that, in living humans, later ages of female fertility would produce unsustainable economic deficits in families.

Cant and Johnstone (2008) framed the mismatch between survival and fertility in women as stopping early and explained it with a model of reproductive conflict among females who disperse and then mate locally. Such female biased dispersal characterizes genus *Pan* and, because hunter-gatherers have long been assumed to be patrilocal, the apparent similarity had suggested that female natal dispersal was an ancestral condition retained throughout human evolution (e.g., Ghiglieri, 1987; Wrangham, 1987; Foley and Lee, 1989; Chapais, 2008). Recent empirical re-examination has shown those longstanding assumptions about hunter-gatherer patrilocality to be incorrect (e.g., Alvarez, 2004; Wilkins and Marlowe, 2006; Hill et al., 2011). Cant and Johnstone (2008) also assumed a *Pan*-like ancestral condition that put older females in competition with their sons' mates for childrearing assistance. This competition drove the population to an evolutionarily stable strategy in which older females stopped bearing early to allocate their effort to assisting grandchildren. We show here that without constraining assumptions about sex-biased dispersal, skill based learning, or pair bonds, weak grandmothering alone is sufficient to favor the evolution of human-like post-fertile longevity.

Unlike our previous model (Kim et al., 2012), the model formulated in this paper provides more flexibility for modification and future extension. It also highlights some of the enormous effects that chance can have on these evolutionary shifts. In our previous simulations (Kim et al., 2012) using deterministic difference equations, the same weak grandmothering assumed here drove the ancestral ape-like adult lifespans to the human like equilibrium in 24,000–56,000 years, depending on the steepness of the male tradeoff between longevity and competitive ability. That provided a striking demonstration of the evolutionary effects of grandmothering, but the unrealistic speed of the change was notable. The stochasticity added here shows the change is not inevitable and the incorporation of chance slows things down by about an order of magnitude.

The transition between the two equilibria that arises in this model, one like the other great apes, one like us, depends on the population escaping from one local region of stable attraction to another. Based on the ecological assumptions of the Grandmother Hypothesis, that escape would have been the beginning of genus *Homo* (O'Connell et al., 1999).

Our current simulations are consistent with arguments that once grandmothering began to propel the evolution of ancestral life histories, there were no stable intermediates. Perhaps further variation in fertility–longevity tradeoffs, as well as stronger grandmothering and help for mothers from other sources (Hrdy, 2009) will find other locally stable regions between the great ape and human-like equilibria. But the simplest reading of our results is that human life history did not begin with our species, but with our genus. If so, it may have been helpful grandmothering that allowed the spread of genus *Homo* out of Africa and into previously unoccupied regions of the temperate and tropical Old World (O'Connell et al., 1999; Lordkipanidze et al., 2013).

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