Supporting Information

Coxworth et al. 10.1073/pnas.1599993112

The Agent-Based Model of Life History Evolution

Our simulated data come from a two-sex, stochastic, agent-based model. To determine the effect of grandmothering on OSR and ASR, we ran 30 simulations for 1 million y without grandmothering, then, from that equilibrium, 30 more 2-million-y simulations with the addition of grandmothering. Because details of the model are reported in-depth elsewhere (13, 15), we provide a brief summary here (see Table S1 for model parameters). Expected adult lifespan, or L, is the only heritable trait and offspring inherit the geometric mean of their parents' longevities, with a 2% probability of a mutation. Mutations result in a proportional shift governed by a lognormal distribution with mean 0 and an SD of 2% (i.e., a 2% chance of a shift in longevity based on a lognormal distribution with SD 2%). As shown in Table S1, we assume that many aspects of life history scale with L, whereas other components remain fixed. Our justifications for these assumptions come from theory (99, 100) and empirical evidence [e.g., infant survival depends on mothers in both chimpanzees and humans until age 2 y (101, 102) and oldest parturitions are in the forties for all living hominids (4, 5)]. For further justification of model assumptions, see Kim et al. (13, 15).

Agents progress through a number of sex-specific life stages, starting with conception and birth. After birth, individuals are dependent on their mothers for the first 2 y of life; if their mother dies, so do they. They are still dependent at age 2 y and, in simulations without grandmothering, they remain with their mothers until independence. In simulations with grandmothering, they become eligible for adoption. We assume that grandmothers are just as good as mothers at keeping dependents alive. If a grandmother adopts a weaned dependent, its mother conceives and delivers her next offspring within a year. Mothers or grandmothers care for juveniles until the age of independence.

Females then go through a period of immature independence until fertility begins at $\tau_2(L)$ and lasts until age 45. In simulations with grandmothering, females older than 45 y may then adopt weaned dependents. They are eligible to adopt until they reach frailty at age 75 y or $2L$, whichever comes first. We include a frail period to guard against improbably old grandmothers—a consequence of constant mortality ($1/L$).

Males also live through a period of immature independence before first reproduction. Unlike females, males become eligible to compete for paternities once they mature at age 15 y. They remain eligible until $\rho_2(L)$, at which point they become frail and no longer eligible, a limit on improbably old fathers. In contrast to constant female fertility, males compete for paternities with variable competitive competence, $\alpha(L)$, that decreases with expected adult life span. The likelihood of winning a paternity depends upon a male's own competence and those of the other males in the population.

Our model specifications make adult sex ratios simple to compute (fertile males, m, are those between ρ_1 and $\rho_2(L)$; fertile females, f, are between $\tau_2(L)$ and τ_3):

$$ASR = \frac{m}{f}. \quad \textbf{[S1]}$$

The OSR is a subset of fertile adults: only those currently capable of a conception. To calculate it, we rely on the formula for nonseasonal breeders derived by Mitani et al. (33), where

$$OSR = \frac{m \cdot B \cdot 365}{f \cdot \sum_{i=1}^{n} s}. \quad \textbf{[S2]}$$

In Eq. **S2**, m and f are the numbers of fertile males and females, respectively; B is the average birth interval; and 365 is the days per year that males can compete for a paternity. The summation in the denominator is the fecundable days per birth interval for fertile females. It depends on the number of conception risk days per estrous cycle (s) and the number of cycles per conception (n).

As noted by Marlowe and Berbesque (37), estimates of OSR can vary widely depending on which individuals are counted as adults. For our simulations, that part of the equation is simply the ASR, Eq. **S1**: m = males between ρ_1 and $\rho_2(L)$, f = females between $\tau_2(L)$ and τ_3. The model also computes the mean birth interval in the population. For female risk days per cycle (s), our assumptions differ from those of Emlen and Oring (19) and the formulations of both Mitani et al. (33) and Marlowe and Berbesque (37) by quantifying fecundability, not receptivity, because our concern is actual conceptions. For number of days a female can conceive during each cycle we use observations from humans (34) and fix $s = 6$. The number of cycles to conception, n, varies widely in great apes (32), so we use human data (35) to set $n = 4$.

Mutation Rates and the Time Course of Life History Shifts

Because the life history parameter values are set by real-world data, the time scale in Fig. 1 in the main text is real years. However, the mutation rate strongly affects the time it takes these simulations to escape the basin of attraction surrounding ape-like longevities and sex ratios. The mutation rate also determines how long it takes to move to the human-like equilibrium. In Fig. 1 the mutation rate is 2%. In Fig. S1 we show example trajectories for the evolution of the ASR and the OSR with the mutation probability and SD of L set to 1, 2, and 4%, respectively.

Trajectories can, however, vary widely from simulation to simulation. Although not shown, we ran 30 simulations for each of the three cases and measured the first time in each that L reached 25 y and then 35 y, representing, respectively, our thresholds for escape from the previous, chimpanzee-like equilibrium and arrival at the new, human-like longevity.

Of the 30 simulations corresponding to a mutation parameter of 1%, only 8 reached the human-like threshold within the 2 million y of simulation. Of these eight, the mean ± SD transition time from the first to the second threshold was 372,000 ± 91,700 y. When the mutation parameter was set at 2%, all 30 simulations reached the human-like equilibrium within 2 million y, crossing the first threshold in 187,000 ± 147,000 y and rising from there to the human-like threshold in 134,000 ± 147,000 y. With a mutation parameter of 4% all 30 simulations crossed the first threshold in only 23,500 ± 11,500 y and reached the second after 9,770 ± 4,770 y more.

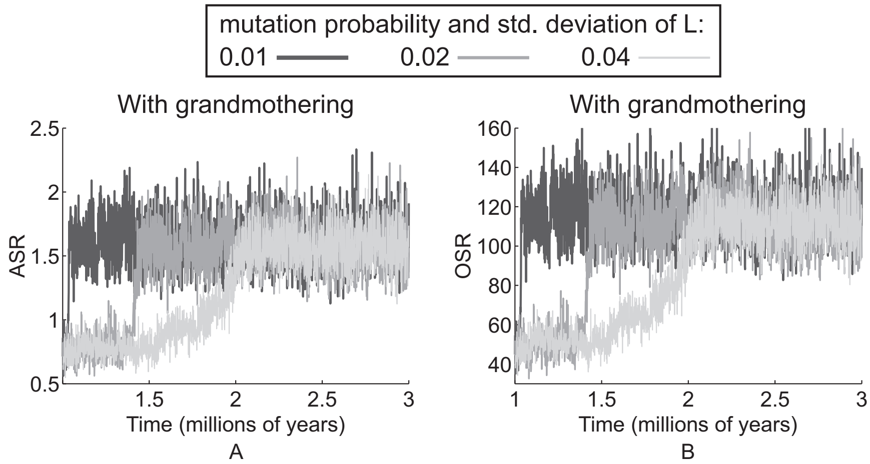

Fig. S1. Evolution time depends on the mutation parameter. Example time evolutions of (*A*) ASRs and (*B*) OSRs with grandmothering for cases when the mutation probability and SD of *L* are set to 1% (light gray), 2% (medium gray, used in the text and Fig. 1), and 4% (black).

Table S1. Parameters of the agent-based model

Parameter	Description	Estimate
L	Average expected adult life span, y	Variable
τ_0	Age of weaning, y	2
$\tau_1(L)$	Age of independence, y	$L/6$
$\tau_2(L)$	Age of female sexual maturity, y	$L/2.5+\tau_0$
τ_3	Age female fertility ends, y	45
$\tau_4(L)$	Age of female frailty (i.e., ineligibility to adopt), y	$\min\{2L, 75\}$
ρ_1	Age male eligibility starts, y	15
$\rho_2(L)$	Age male eligibility ends, y	$\min\{2L, 75\}$
c	Rate of female conception and delivery, 1/y	1
$\alpha(L)$	Male weighting factor for mating	Decreasing function of L
p	Probability of mutation in L at birth, %	2
σ	SD of mutations, %	2
K	Population carrying capacity	1,000