Journal of Theoretical Biology 353 (2014) 84–94

Contents lists available at ScienceDirect

Journal of Theoretical Biology

journal homepage: www.elsevier.com/locate/yjtbi

Grandmothering drives the evolution of longevity in a probabilistic model

Peter S. Kim [a,1], John S. McQueen [a,1], James E. Coxworth [b,c], Kristen Hawkes [b,*]

[a] School of Mathematics and Statistics, University of Sydney, NSW 2006, Australia
[b] Department of Anthropology, University of Utah, Salt Lake City, UT 84112, USA
[c] Utah Population Database, University of Utah, Salt Lake City, UT 84112, USA

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.

ARTICLE INFO

Article history:
Received 14 December 2013
Received in revised form
5 March 2014
Accepted 6 March 2014
Available online 14 March 2014

Keywords:
Human evolution
Life history
Sexual conflict
Agent-based modeling
Human longevity

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

* Corresponding author.
E-mail addresses: pkim@maths.usyd.edu.au (P.S. Kim), john.mcqueen@sydney.edu.au (J.S. McQueen), james.coxworth@anthro.utah.edu (J.E. Coxworth), hawkes@anthro.utah.edu (K. Hawkes).
[1] Contributed comparably.

http://dx.doi.org/10.1016/j.jtbi.2014.03.011
0022-5193/

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