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Evolution of longevity, age at last birth and sexual conflict with grandmothering

Matthew H. Chan [a],*, Kristen Hawkes [b], Peter S. Kim [a]

[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*

HIGHLIGHTS

- We model the evolution of longevity and age at last birth in a population.
- We find two locally stable equilibria corresponding to great ape-like and hunter–gatherer longevity and age at last birth.
- Grandmothering enables the transition between these two equilibria, without extending the end of fertility.
- Male competition effects play a significant role in determining whether this transition is possible.

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ABSTRACT

We use a two-sex partial differential equation (PDE) model based on the Grandmother hypothesis. We build on an earlier model by Kim et al. (2014) by allowing for evolution in both longevity and age at last birth, and also assuming that post-fertile females support only their daughters' fertility. Similarly to Kim et al. (2014), we find that only two locally stable equilibria exist: one corresponding to great ape-like longevities and the other corresponding to hunter–gatherer longevities. Our results show that grandmothering enables the transition between these two equilibria, without extending the end of fertility. Moreover, sensitivity analyses of the model show that male competition, arising from a skew in the mating sex ratio towards males, plays a significant role in determining whether the transition from great ape-like longevities to higher longevities is possible and the equilibrium value of the average adult lifespan. Whereas grandmothering effects have a significant impact on the equilibrium value of the average age at last birth and enable the transition to higher longevities, they have an insignificant impact on the equilibrium value of the average adult lifespan.

1. Introduction

A key feature that distinguishes humans from our closest evolutionary cousins is a much higher longevity; for example, the marked increase in age-specific mortality in the common chimpanzee starts at approximately 20 years, whereas in hunter–gatherer populations the rise occurs at about 45 years and is noticeably less steep (Hawkes, 2003). However, for both humans and other great apes, the average end of female fertility is around 45 years (te Velde and Pearson, 2002; Hawkes et al., 2009). A consequence of this is that humans are the only primate to have a significant proportion of adult females living beyond their fertile years (Levitis et al., 2013; Alberts et al., 2013; Croft et al., 2015). Although it is widely assumed that survival past menopause is only a recent phenomenon due to improvements in life expectancy from medical and public health technology, this assumption is based on a misunderstanding. Life expectancy is an average that is strongly affected by high infant and juvenile mortality rates. Data on historical and hunter–gatherer populations show that females who survived past their juvenile years are much more likely than not to survive past menopause, even though life expectancies in these populations are less than 40 years (Gurven and Kaplan, 2007). Moreover, in classic model life tables built from national census data, a tripling of life expectancy (from 20 to 60 years) has a trivial effect on the proportion of elders in the population (Hawkes, 2004; Coale and Demeny, 1968). As noted by Levitis et al. (2013), "even the worst surviving human population has Postreproductive Representation higher than the highest recorded value for nonhuman primates in protected environments."

The human mismatch between the end of fertility and longevity is seemingly paradoxical as natural selection generally

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* Corresponding author.
E-mail addresses: M.Chan@maths.usyd.edu.au (M.H. Chan), Hawkes@anthro.utah.edu (K. Hawkes), PKim@maths.usyd.edu.au (P.S. Kim).

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favours traits that increase life-time reproduction. However, there is evidence from hunter–gatherers of grandmothers supplying foods that just weaned juveniles cannot acquire effectively for themselves (Hawkes et al., 1995, 1997). In other mammals, including other great apes, weaned juveniles can feed themselves, while humans continue to depend on provisioning after weaning. The help of older women allows their daughters to have next offspring while the previous one is still dependent. This prompted the "Grandmother hypothesis" to explain the evolutionary origins of our distinctive post-menopausal life stage (Hawkes et al., 1998; O'Connell et al., 1999). The hypothesis proposes increased longevity was favoured in our lineage without an increase in the age female fertility ends when ancestral populations began to rely on foods weaned juveniles could not handle for themselves. Under those ecological circumstances, mothers would have to feed their offspring longer, but with subsidies from grandmothers they could have next offspring sooner; and longer-lived grandmothers, without infants themselves, could support more grandchildren. Moreover, the increase in both body size and delay in maturation age are expected consequences of greater longevity according to Charnov's model of mammalian life history, which aims to explain the ways female life histories vary across the mammals (Charnov, 1993). In Charnov's mammal model, age at independence, age at maturity and adult body size all increase in predictable ways with increases in adult lifespan.

In this study, we build upon a mathematical model by Kim et al. (2012) and a more sophisticated agent-based model by Kim et al. (2014). The Kim et al. (2014) model tracks the evolutionary trajectory in longevity, while fixing the age at last birth based on the similarity in oldest ages at parturition in humans and other great apes. While that model addresses the question "could grandmothering drive the evolution of increased longevity while keeping the end of female fertility fixed?", it leaves unanswered the question why female fertility ends at about 45 years. We formulate a partial differential equation (PDE) model which shares many of the same assumptions as Kim et al. (2014), but allows for evolution in age at last birth, restricts grandmothers to support only their daughters and uses a more realistic mortality function which in turn generates a more realistic age structure at both the great ape-like equilibrium and hunter–gatherer equilibrium.

The aim of the study is to determine whether there can even exist an evolutionary trajectory from a great ape-like equilibrium to a hunter–gatherer-like equilibrium under reasonable parameter settings, many of which are based on empirical data (the exceptions being the male and female fertility-longevity tradeoff functions, see Sections 2.3.1 and 2.3.2 for details). We note that in our study we require both the great ape-like and hunter–gatherer-like equilibria to match empirical data on life expectancy, age at first birth, age at last birth and lastly age profile of wild chimpanzees and hunter–gatherers respectively. As such, our definitions for both of these equilibria are more stringent than in previous studies which examine the evolutionary effects of grandmothering such as by Kim et al. (2012, 2014), Pavard and Branger (2012) and Kachel et al. (2011a). We show that such an evolutionary trajectory exists, whereby grandmothering is the sole mechanism responsible for the transition between the two equilibria. Moreover, in Section 4 we show that the existence of such an evolutionary trajectory is not automatic, but is instead sensitive to the parameters of the model.

2. Model

We consider an age-structured system with two compartments, male and female population densities, denoted by $u_m(a, M, L, t)$ and $u_f(a, M, L, t)$ respectively, where $a \in [0, \tau_3]$ denotes age, $M \in [0, 1]$ is a measure of the age at last birth, $L \in [0, 1]$ is a measure of an individual's longevity and t denotes time. The population age-structure and mortality dynamics are given by the McKendrick-von Foerster equations

$$\begin{cases} \dfrac{\partial u_f}{\partial t} = -\dfrac{\partial u_f}{\partial a} - \mu(a, L) u_f, \\ \dfrac{\partial u_m}{\partial t} = -\dfrac{\partial u_m}{\partial a} - \mu(a, L) u_m, \end{cases} \tag{1}$$

where $\mu(a, L)$ is the age-specific mortality rate for an individual with longevity L.

The boundary condition for system (1) governs several mechanisms of the model: whether individuals are eligible to mate, how individuals mate, whether a female has a mother who is alive and eligible to grandmother, the benefit from grandmothering effects and how offspring inherit their parent's longevity and age of last birth trait values. We first explain the assumptions behind these mechanisms and then introduce the mathematical formulation of the boundary condition in Section 2.5.

2.1. Fertility

We assume all individuals simply progress from birth through to sexual maturity. Unlike Kim et al. (2014), we do not include stages of nursing, weaned dependency or independence for simplicity. Females are fertile between ages $a = \tau_1(L)$ and $\tau_2(M)$ respectively, where

$$\tau_1(L) = \tfrac{1}{3}(35L + 29) \tag{2}$$

and

$$\tau_2(M) = 20 + 55M. \tag{3}$$

Thus, the age of female sexual maturity ranges from 9.6 to 21.3 and the age at last birth ranges from 20 to 75, depending on trait values M and L. We design these functions such that $(M, L) = (0.455, 0.2)$ and $(M, L) = (0.455, 0.8)$ correspond to great ape- and hunter–gatherer-like values respectively. This translates to great apes having a female sexual maturity of 12 years and humans having a female sexual maturity of 19 years, with both having an age at last birth of 45 years. These approximately match the data in Sugiyama (1994), Hill and Hurtado (1996), Walker et al. (2006) and Hawkes et al. (2009). We intentionally let $\tau_1(L)$ and $\tau_2(M)$ have unrealistically large ranges to investigate the M and L trait values selected by the population. The form for both $\tau_1(L)$ and $\tau_2(M)$ were chosen such that they are linear within the ranges. We let the age of frailty for both males and females to be $\tau_3 = 75$. As with Kim et al. (2014), we assume males compete for paternities from age 15 until frailty, regardless of their M or L traits. Kim et al. (2014) base this on data from living great apes (Robbins, 1995; Boesch et al., 2006).

2.2. Mortality

All individuals have a mortality rate $\mu(a, L)$ dependent on age a and longevity L, where there are three distinct stages: early, middle and late mortality stages. This serves as a simplified model of the age-specific mortality data shown below in Fig. 2. Distinguishing early, middle and late stages allows for a more realistic mortality function than the constant mortality rate assumed by Kim et al. (2014). The form and parameters of the mortality function are chosen such that the survivorship curves and age-specific mortality rates generated in Fig. 1a are consistent with survivorship data in Gurven and Kaplan (2007) and age-specific mortality data in Fig. 2. We assume that the early mortality stage lasts three years regardless of L, but the length of the middle stage increases with increasing longevity. The mortality rates in both of