



When mothers need others: The impact of hominin life history evolution on cooperative breeding



Karen L. Kramer^{a, b, *}, Erik Otárola-Castillo^b

^a Department of Anthropology, University of Utah, 270 S 1400 E, Salt Lake City, UT 84112, USA

^b Department of Human Evolutionary Biology, Harvard University, 11 Divinity Ave., Cambridge, MA 03128, USA

ARTICLE INFO

Article history:

Received 10 February 2014

Accepted 1 October 2014

Available online 3 April 2015

Keywords:

Human evolution

Juvenility

Intergenerational transfers

Parental care

ABSTRACT

The evolution of cooperative breeding is particularly complex in humans because many other traits that directly affect parental care (shorter birth intervals, increased offspring survivorship, juvenile dependence, and older ages at dispersal) also emerge during the Pleistocene. If human cooperative breeding is ancient, it likely evolved in a hominin lacking a fully modern life history. However, the impact that changing life history traits has on parental care and cooperative breeding has not been analytically investigated. We develop an exploratory model to simulate an economic problem that would have arisen over the course of hominin life history evolution to identify those transitions that produced the strongest pressures for cooperative childrearing. The model generates two central predictions. First, help within maternal-offspring groups can support early changes in juvenile dependence, dispersal age, birth intervals, and fertility. If so, maternal-juvenile cooperation may be an important but understudied step in the evolution of human cooperative breeding. Second, pressure to recruit adult cooperation is most pronounced under more derived conditions of late dispersal and later ages of juvenile dependence, with a strong interaction at short birth intervals. Our findings indicate that changes in life history traits that affect parental care are critical in considering background selective forces that shaped the evolution of cooperative breeding.

© 2015 Elsevier Ltd. All rights reserved.

Introduction

Compared to other closely related species, humans wean infants at a young age, have short birth intervals, and raise multiple dependents at the same time. Juveniles depend on others for their well-being and adults cooperate to raise young. Because mothers rely on others to help provision offspring, humans have been characterized as cooperation breeders (Foster and Ratnieks, 2005; Hrdy, 2005a, 2009; Kramer, 2005a, 2010; Sear and Mace, 2008; Burkart et al., 2009; Hill and Hurtado, 2009; Russell and Lummaa,

2009; Strassman and Kurapati, 2010; van Schaik and Burkart, 2010; Crepsi, 2014).¹ However, this suite of traits did not always characterize humans. We likely evolved from an ape-like animal with long birth intervals, independence at weaning, mothers who raised young on their own, and juveniles who were self-sufficient foragers. While cooperative breeding is often presumed to be ancient (i.e., dating to *Homo erectus*-grade hominins), the impact that other evolving life history traits have on its emergence has not been analytically explored. Our goal is to model an economic problem that would have occurred during hominin life history evolution and to estimate the relative influences that these changes have on pressure to recruit allocares.

Evolutionary changes in dependent juveniles, birth intervals, and cooperative breeding

The pace at which mothers reproduce and how long offspring are dependent have considerable effects on parental care and have likely undergone significant transformation during hominin evolution (Dean, 2006; Hawkes and Paine, 2006; Smith et al., 2010; Kramer, 2011). Great ape mothers nurse infants for 4–6 years

* Corresponding author.

E-mail address: karen.kramer@anthro.utah.edu (K.L. Kramer).

¹ Cooperative breeding is a rare mammalian reproductive strategy in which group members other than parents help to support mothers or their young (Russell, 2004). Because both breeding females and nonbreeders (pre- and post-reproductives) share in caring for and provisioning young, humans have been described as having aspects of both communal and cooperative breeders (Lukas and Clutton-Brock, 2012). Because the definition of cooperative breeding is debated, and we wish to avoid focusing on typological issues, we use cooperative breeding in its most general sense as a reproductive system in which nonparental members of the social group help to support offspring or other mothers (Russell, 2004).

(Emery Thompson, 2013). In contrast, modern children are weaned on average between the ages of 2–3 years (Kennedy, 2005; Emery Thompson, 2013). While we cannot know the length of birth intervals in the past, paleontological evidence (Humphrey, 2010; Kelley and Schwartz, 2012) and adult onset of lactase decline (Sellen, 2006) suggest that ancestral weaning ages were late, similar to those in great apes, and gradually declined over time (van Noordwijk et al., 2013).

The lives of juveniles have also changed substantially during hominin evolution. Because all other ape juveniles are independent foragers (Knott, 2001), juveniles in the past were likely self-sufficient at younger ages, and the direction of selection was toward a longer period of dependence. While age at independence varies among modern juveniles, even among hunter-gatherer societies considered evolutionarily relevant (Supplementary Online Material [SOM] Fig. 6), weaned children provide some, and sometimes a substantial portion of their own caloric intake. Thus, over the last two million years the duration of lactation and infancy has shortened, and support has been extended to juveniles. This combination of derived traits commits modern human mothers to raise multiple dependents of different ages. This has important implications for reproductive rates, which are 2–5 times faster in modern natural-fertility populations, compared to other primates adjusting for body size, and are the highest among the great apes (Alvarez, 2000).

Raising multi-aged dependents has well-recognized implications for human sociality and is hypothesized to be associated with the emergence of cooperative breeding (Lee and Kramer, 2002; Kramer, 2005a, b; Hrdy, 2005b, 2007, 2009; Gurven and Walker, 2006). While it may seem that a trajectory toward a longer period of dependence and shorter birth intervals would exceed a mother's ability to raise offspring on her own, the interaction effects of these life history changes on maternal time and energy budgets have not been investigated. Further, because none of these traits leaves unambiguous fossil evidence, an archaeological record, or a genetic signature, the sequence of life history changes and their causal relationships are unknown. Nor is there a cooperative breeding great ape model to guide us in terms of what intermediary forms might look like. We address this empirical gap by developing an exploratory model to assess the impacts that evolving life history traits have on the rate of change in the *force of dependence*. We measure the force of dependence as the net cost of overlapping offspring as a function of juvenile dependence, dispersal age, and birth intervals. The model is used to predict those life history transitions under which mothers would be unable to support children on their own and pressure would have been strongest to recruit adult help.

Modeling the force of dependence

The model incorporates several novel elements so that we can formally test the hypothesis that evolutionary changes in the duration of juvenile dependence, dispersal age, and birth intervals have directional effects on the force of dependence. First, we use life history parameters that span the ancestral hominin pattern of long birth intervals and juveniles who are self-provisioning at a young age to a modern pattern of short birth intervals and juveniles who are dependent until older ages. While most cooperative breeding models and cost of children analyses assume a modern life history, our approach allows us to expand beyond relying on contemporary ethnographic examples as a direct analogy to the conditions under which cooperative breeding evolved. Second, the model accounts for the derived hominin pattern of raising multiple dependents at the same time—some younger and more dependent on provisioning from others, and some older and self-provisioning.

This differs from traditional cost of children analyses that consider the net or cumulative cost of only a single child (SOM Fig. 11). The effects of overlapping young are incorporated into the model by integrating the net cost of all children alive in each year of a mother's reproductive career. This more closely reflects the demographic pressures that the hominin reproductive pattern generates on mothers and others. Third, we use time allocation as the unit of measure for net cost. Because the human feeding niche is based on high-quality foods that require technology to access, food processing, and many other activities that do not have a caloric value, the time allocated to these activities—not only the calories that children consume—is a more comprehensive measure of the force of dependence and demands for parental and nonparental investment.

Methods

Calculating juvenile dependence

In the first step we develop an underlying model to calculate the duration of juvenile dependence. Since weaning does not correlate with independence in human children, we use the age at which children produce more resources than they consume, which marks the crossover from being a net consumer to a net producer (SOM Part 1, 3; SOM Figs. 1–5).

An individual consumes a certain amount and produces another amount according to his or her age. Although specific values may vary, the general shape of these functions for human and nonhuman primates varies with age such that both production and consumption are relatively low when young, begin to accelerate at some age, then at an inflection point they begin to decelerate, and finally reach an asymptote (Kaplan, 1994; Kramer, 2005b; Gurven and Kaplan, 2006). This maturation process was modeled using seven nonlinear mathematical equations that approximate these age-related behavioral properties of children's maturation as consumers and producers (SOM Appendix 1.1; SOM Figs. 1, 2 and 4). The models were fitted to empirical production and consumption data (see below) using maximum likelihood, which were converted to Akaike Information Criterion (AIC) values to select the best fit model. For both production and consumption, the best-candidate model was a 4-parameter logistic, which accounts for the increase in variance (SOM Figs. 1 and 2). This general 4-parameter function is used to model production [1] and consumption [2] values for an individual at age x .

$$P_{x_j} = a_p + \frac{b_p - a_p}{1 + e^{c_p(d_p - x_j)}} \quad [1]$$

$$C_{x_j} = a_c + \frac{b_c - a_c}{1 + e^{c_c(d_c - x_j)}} \quad [2]$$

Where x_j is the age value, a is the lower asymptote, b the higher asymptote, c the rate of change of production/consumption as offspring age, and d the inflection point (acceleration to deceleration; SOM Fig. 3). The age at which production exceeds consumption we use to denote the duration of juvenile dependence.

This modeling approach is advantageous compared to smoothing individual values because the parameters serve as useful point estimates that can be compared across groups, populations, or species. This facilitates future hypothesis testing, for example, about differences between males and females in terms of the rate of age-related change, or the age at which the asymptote is reached.

Download English Version:

<https://daneshyari.com/en/article/4555956>

Download Persian Version:

<https://daneshyari.com/article/4555956>

[Daneshyari.com](https://daneshyari.com)