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

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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.

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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 allocare.

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

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[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*.

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

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

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.

Because we are interested in the effects that evolutionary changes in the duration of juvenile dependence have on the net cost of overlapping dependents, we include a range of production values. The baseline empirical data used in the best-fit model are taken from ethnographic observations for a population for whom detailed time allocation data are available and net production (juvenile independence) is reached at age 15 (SOM Appendix 3). By adjusting the model's parameters (shown in red in Eq [1]), the age at net production can be expressed as a continuous term that varies from age 10 (early juvenile independence) to age 20 (late juvenile independence; SOM Fig. 5). This range is intended to simulate the evolutionary transition from a juvenile who covers a greater proportion of their consumption and is self-supporting at a fairly young age to one who contributes little to their own consumption and is dependent until older ages. This range is conservative in not including an age at net production where juveniles become autonomous feeders at weaning, which occurs around the age of 5 in chimpanzees for example. Although calorically independent, chimpanzee juveniles continue to forage in the company of their mother until about age 10, which is the youngest age at net production that we include in parameter values. While we use ages 10–20 as the duration of juvenile dependence, this range can be easily varied in future studies for other research questions and other species.

The same age-specific C schedule is used in all models to highlight the effect that changes in children's production have on net value. We believe this is reasonable because age-specific consumption for children growing up in traditional, subsistence-level societies is expected to be closely related to changes in body size and not to vary appreciably above or below resources needed for growth and survival.

From the fitted age-specific values, a child's net value at age x can then be computed as $P_{xj} - C_{xj}$ (SOM Appendix 1.2; SOM Fig. 4). This value may be positive (net producers) or negative (net consumers) depending on an individual's age and how much they produce relative to their consumption. The age at which net value exceeds 0 indicates the age of juvenile independence.

Accounting for evolutionary changes in dispersal age

Dispersal age is added to the model because the time at which offspring leave their natal group (a mother and her nulliparous offspring) may be independent of the age at net production (Kaplan, 1994; Lee and Kramer, 2002). Dispersal has a parameter range of age 14–20, 14 corresponding to mean age at first birth in chimpanzees and 20 to mean age at first birth in modern ethnographic populations (Kaplan et al., 2000:158). Dispersal is included in the model by considering an offspring's coresidence in its natal unit up until he or she leaves and stops both consuming from it and contributing to it. The probability of staying becomes the complement of dispersal as follows:

$$P(S_{x_j}) = 1 - \int_{-\infty}^{\infty} \frac{1}{\sqrt{2\pi\sigma^2}} e^{-\frac{(x_j - \mu)^2}{2\sigma^2}} \qquad [3]$$

Where x_j is individual age x at time j and μ is the mean age at dispersal (at the population level, ranging between age 14 and 20), and σ is the standard deviation surrounding the mean. Here we chose a standard deviation of two years. We then calculate $P(D)$, the probability of dispersing at a given age, by scaling Equation [3] to the appropriate mean and standard deviation and integrating to x_j (SOM Fig. 7).

Grouping these terms together, the net value of an individual offspring adjusted for the probability of being coresident at a given age, x_j is (SOM Fig. 8):

$$\text{Net}_{x_j} = P(S_{x_j}) \cdot (P_{x_j} - C_{x_j}) \qquad [4]$$

Accounting for maternal fertility

We also need to account for the biological limits to a mother's fecundity. To avoid making an explicit assumption about maternal age at first birth, we begin with a mother who gives birth at $t = 0$ and can reproduce for 20 years. This time span is included in the model as an indicator function (1,0). If t exceeds 20 years, no new births occur; otherwise females reproduce at their scheduled birth interval (described in next section).

I = indicator function denoting $p(\text{birth})$ at year t;

$$\text{I} = \begin{cases} 1 & \text{if } t \leq 20 \\ 0 & \text{if } t > 20 \end{cases}$$

Accounting for evolutionary changes in birth intervals and number of dependents

Most cost of children analyses consider only the age-specific cost or cumulative cost of a single offspring. Because this may bias the cost of children, the method developed here accounts for the human pattern of raising multi-aged children by integrating the adjusted net values of individual children at each year in a mother's reproductive career. This can be visualized as a stepped matrix, similar to a lexis diagram, across t—the years after a mother gives birth to her first child. A simple illustration of this process is given in SOM Table 2 where children are born at an average birth interval and census out at independence. We vary birth intervals from 6 to 3 years. Six years is equivalent to a chimpanzee-like birth interval, and three years to the mean for modern human natural fertility populations (Alvarez, 2000). These are expressed as discrete values to facilitate graphing and interpreting the model.

Mapping the force of dependence across all life history combinations

Aggregating these components, at a kth birth interval, the net cost can be calculated as the sum of the age-specific net values for all children at age x_j at each ith year after a mother's first birth. This yearly calculation can be computed across a mother's reproductive career between the years after first birth t_0 until some year t_i. Thus, the force of dependence is the summation of all children's dispersal-adjusted net value for each year in a mother's reproductive career.

$$\text{Force of Dependence}_k = \sum_{t=0}^{i} \text{Net}_{x_j} \qquad [5]$$

Where t = year after birth i:{0, 1, 2, ... 20}; k = BI: {6, ... 3}.

Model parameters are perturbed within their specified ranges across 100 interpolated values for juvenile dependence (age 10–20) and dispersal (age 14–20), and four birth interval values (6, 5, 4, and 3 years). This simulation produced a total of 40,000 unique sets of parameter combinations (100:100:4), with net cost mapped onto a 3-dimensional response surface (see SOM Fig. 9 for an interactive rotational display).[2] While the individual effects of these

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[2] We include the life history combination of juveniles dispersing before independence because in many ethnographic populations, young people may marry before they reach the asymptote in production or become net producers (Kaplan, 1997). This also occurs among some animals. Great apes do not achieve adult levels of foraging efficiency until late in juvenility or early adulthood, long after weaning and feeding independence from their mothers.

variables may seem intuitive, how these life history traits behave in concert when multiple offspring of different ages are considered is unknown. Our emphasis is on determining the relative influences of these variables on the force of dependence.

Caveats and limitations

Although other life history variables have directionally changed during hominin evolution, we focus on those variables that impact the cost of children. While child mortality is not specifically parameterized, because the length of a mother's reproductive career is controlled, surviving fertility is implied through the birth interval term. At a 6- to 5-year birth interval, a mother who completes a 20-year reproductive career produces four surviving children, at a 4-year birth interval, five surviving children, and at a 3-year birth-interval, seven surviving children. At premodern mortality levels (Gurven and Kaplan, 2007), surviving fertility would be equivalent to the reproductive output in the model's 6- to 5-year birth interval. As an approximation, in a population of hunter-gatherer women, if 40% survive to age 45 (Gurven and Kaplan, 2007), surviving fertility of four children for women completing their reproductive career would generate the relatively low population growth characteristic of pre-Neolithic populations (Gignoux et al., 2011).

The model can incorporate other production and consumption values and be reconfigured under different life history assumptions. For example, for simplicity and not to add assumptions about past behaviors, we do not distinguish between male and female dispersal ages. However, for future research questions focused on modeling sex differences, sex can be incorporated as an added parameter. Although all possible ethnographic adjustments cannot be made here, as a rule of thumb any modification that would increase the negative net value ($P_{xi} - C_{xi}$) would raise the force of dependence. Likewise, any modification that would decrease net value ($P_{xi} - C_{xi}$) would lower the force of dependence and demand for parental/allo-care. While other variables can be added to account for specific population or species attributes, most factors affecting net cost are expected to filter through juvenile dependence, dispersal age, and birth interval.

While evolutionary changes in birth interval and dispersal age can be fairly securely bracketed by spanning the range in living apes and contemporary humans, consumption and production behaviors may have other possible but unobservable scenarios not represented by extant species. We compensate for this by including a broad range of juvenile independence values (ages 10–20) rather than assuming that any one modern ethnographic group is representative of the past. We also assume that if a juvenile's production exceeds their consumption and they have not yet dispersed, their surplus is shared with others. In ethnographic populations, juveniles have been shown to increase the reproductive output of their mothers through shortening birth-intervals and increasing child survivorship (Lee and Kramer, 2002; Sear and Mace, 2008; Kramer, 2009). When such cooperative behaviors emerged is currently unknown. If juveniles do not share, net cost may be underestimated. (Depending on age of net production, this may be on the order of .5–1.5 h per day). We compensate for this potential underestimate in statistical analyses by using the maximum net cost, which considers the point in a mother's reproductive career when children are the most expensive they ever will be given other life history parameters. Our question here is not to address why humans share but, instead, to assess what combinations of life history traits could not have evolved (or were constrained) unless mothers had access to help from other adults. If adult cooperate, the assumption that juveniles cooperate seems reasonable. Evidence for this is found among many other cooperative breeding mammals

(and social insects), where subadults are important helpers (Thorne, 1997; Clutton-Brock, 2002; Russell, 2004; Gilchrist and Russell, 2007), and in the comparative cognitive research on the ontogeny of sharing, fairness, and theory of mind in young children (Herrmann and Tomasello, 2006; Warneken and Tomasello, 2006; Warneken et al., 2007; Tomasello and Vaish, 2013).

Results

To illustrate how the force of dependence changes across a mother's reproductive career with specific life history combinations, eight profiles are taken from the full model at the end points of the parameter range for the three life history variables (Fig. 1). The ancestral combination of life history traits is shown in the upper left box, and the most derived combination in the bottom right. Negative values indicate the net cost, or amount of time (daily hours), that mothers or others have to spend subsidizing offspring. Negative values are greatest under the most derived combination of traits when juveniles are dependent until older ages, birth intervals are short, and dispersal age is late (bottom right box). In contrast, the net cost of overlapping young is low when juveniles reach independence at a young age, regardless of other parameter values (top row).

To statistically compare the relative effects of juvenile dependence, birth intervals, and dispersal age, we extract the greatest negative net cost from each of the 40,000 life history profiles in the full model (shown by stars for eight of the profiles in Fig. 1). This represents the point at which children are most expensive during a mother's reproductive career (SOM Appendix 2). Extracting maximum net costs has several advantages. In reality, the distribution of net costs across a mother's reproductive career (for an example see SOM Fig. 11) will vary within a sample of mothers with the same average life history traits because individual children will differ to some extent in their age at independence, birth intervals, and dispersal age. However, the maximum net cost should not vary. It could be less (if for example mortality were particularly high for any one mother) but will not be greater under a given set of life history parameters. Thus, if the model's net cost values are biased, they will be in the direction of overemphasizing the cost of children to mothers and others.

Figure 2 gives the composite of the maximum net cost as three dimensional surfaces illustrating the effects of juvenile dependence and dispersal age at 6- to 3-year birth intervals (see SOM Fig. 10 for an interactive rotational display). This figure illustrates, for example, that the maximum net cost is 6 h/day across all values of dispersal age for a mother who gives birth at 3-year birth intervals (Fig. 2, bottom right panel) and her juvenile offspring become self-sufficient at age 10. Maximum net cost is also standardized as the difference between the ancestral state of early juvenile independence, long birth intervals, and early age at dispersal, and the derived pattern of later independence, shorter birth intervals, and later ages at dispersal (Table 1). These standardized values indicate the magnitude of change in the force of dependence from the ancestral state and allow us to compare the relative effects of each trait on net cost.

Results are summarized by four major findings. Our first finding is that *early modifications of the ancestral pattern of long birth intervals, singleton dependents, and independence at weaning do not generate large net costs*. When juveniles are independent at a relatively young age, the maximum net cost of raising overlapping children is less than 5 h/day across the range of decreasing birth intervals and increasing dispersal ages (Fig. 1, top row). The net cost is even less throughout much of the rest of a mother's reproductive career. While it cannot be known how much time mothers in the past spent foraging or providing food and childcare to dependents,
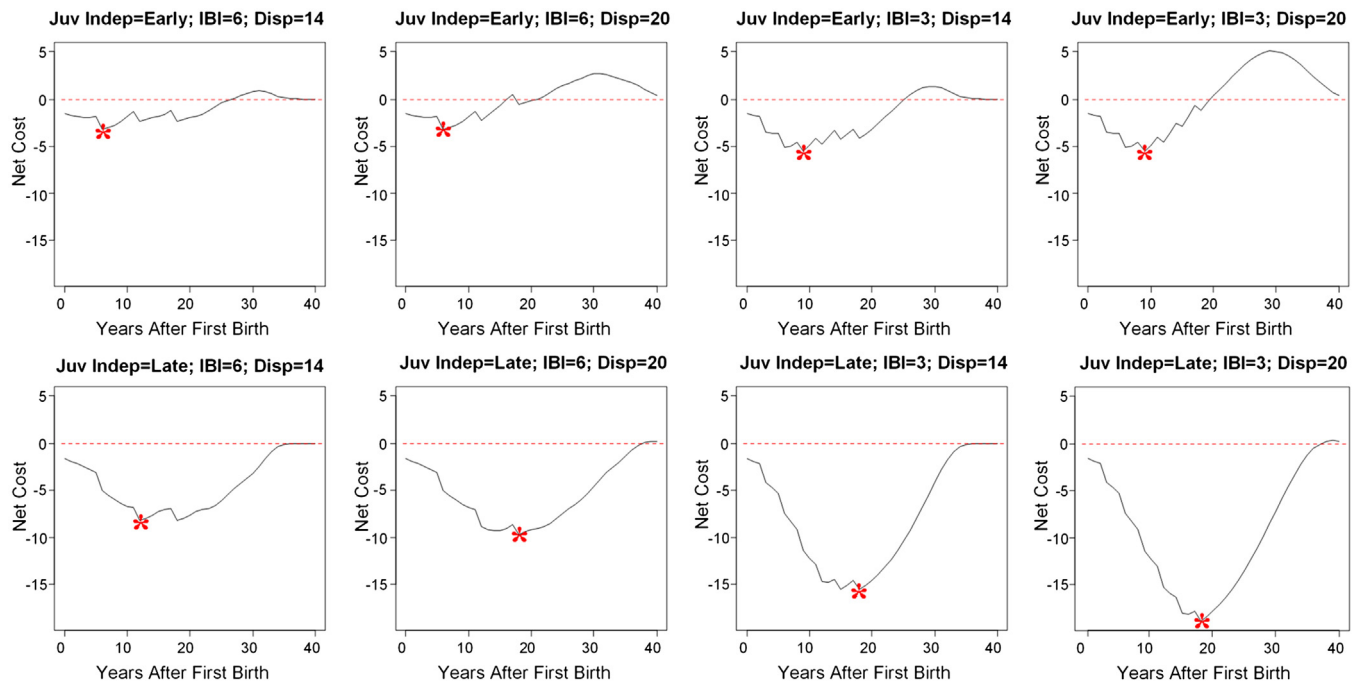
Figure 1. Net cost of overlapping offspring across a mother's reproductive career (years after first birth). Eight profiles from the full force of dependence model (SOM Fig. 9) are taken from the end points of the parameter range for age at independence (Juv Indep), dispersal age (Disp), and birth intervals (IBI). Negative values indicate the time (daily hours) mothers or others have to spend subsidizing offspring. The stars show the point of maximum net cost. The ancestral combination of life history traits is shown in the upper left box, the most derived traits in the bottom right. Positive values indicate that children as a group generate a surplus.

some insights can be taken from living populations. Great ape adults spend on the order of 5 h/day feeding (Hunt, 1989; Doran, 1997). Some portion of this supports the energetic cost of lactation, but great ape mothers do not produce surpluses to feed juveniles. In modern ethnographic populations, women 20–50 years of age on average spend 8.93 h (std = 2.04, n = 15 groups) in productive work (7.56 h) and childcare (1.38 h; see SOM Fig. 12 for detail).[3] This suggests that maximum net costs within this range would have been reasonable, and that help outside maternal-offspring groups may not have been required early in the transition to modern life histories.

Our second finding is that the *force of dependence is least sensitive to changes in dispersal age* compared to other life history traits that affect the cost of children. The marginal value of dispersal while holding other variables constant is 9.36 compared to changes in juvenile dependence or birth intervals (marginal values = 66.32 and 21.32, respectively; Table 1). These effects are evident in Figure 2, where at a given birth interval and level of juvenile independence, the increased maximum net cost negligibly increases across dispersal age. In contrast, the force of dependence is most sensitive to age of juvenile independence.

Our third finding is evidence of *an interaction that substantially increases the force of dependence under modern life history conditions* (Fig. 2 bottom right panel). For every year offspring independence occurs at a later age, the maximum net cost increases a half-hour per day (slope = −.51; Table 2) when dispersal is early and birth intervals are long. However, at a 3-year birth interval, maximum net cost increases by an hour per day (slope = −1.00; Table 2). Thus, although age at independence has an important influence on net

cost, its impact is pronounced only when interactions with other life history variables are strongest—when age at dispersal is late, birth intervals are short (4–3 years), and mothers have high levels of surviving fertility (5–7 surviving children; Fig. 3, left to right). The importance of this interaction is that early evolutionary changes in life history traits have the least impact on the cost to raise children, while more derived changes result in substantial increases.

This interaction implies our fourth result. The force of dependence is greatest and *pressure to recruit adult help most pronounced under more derived life history conditions* of late juvenile independence when the interaction is strongest at 3-year birth intervals (Figs. 2 and 3, bottom right, Fig. 1, bottom row columns 3 and 4). For much of our evolutionary history, surviving fertility for a population of women completing their reproductive careers would likely not exceed four surviving children. This rate is equivalent to a 5–6 year birth interval in the model. In this interval range, help outside the maternal-offspring unit may not be necessary to support more ancestral life history changes.

Discussion

If cooperative breeding is ancient and appears in *H. erectus*-grade hominins (Hrdy, 2009; van Schaik and Burkart, 2010), it likely developed under not yet fully modern phenotypic expressions. Although birth interval length, dispersal age, and juvenile dependence directly affect parental investment, the impact of their changes has not been previously explored in its evolutionary context. Our goal is to develop a model to predict those life history transitions where selective pressure would have been strongest for cooperative childrearing.

The force of dependence model simulates an economic problem that would have arisen during the hominization of birth intervals, juvenile dependence, and dispersal ages. We take this approach to establish the underlying costs, constraints, and interactions among

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[3] Of the daylight hours that a mother spends in economic activities, about a third are net production, which increases and plateaus early in her reproductive career. In addition, she may spend up to several hours per day in childcare depending on the age of her children.
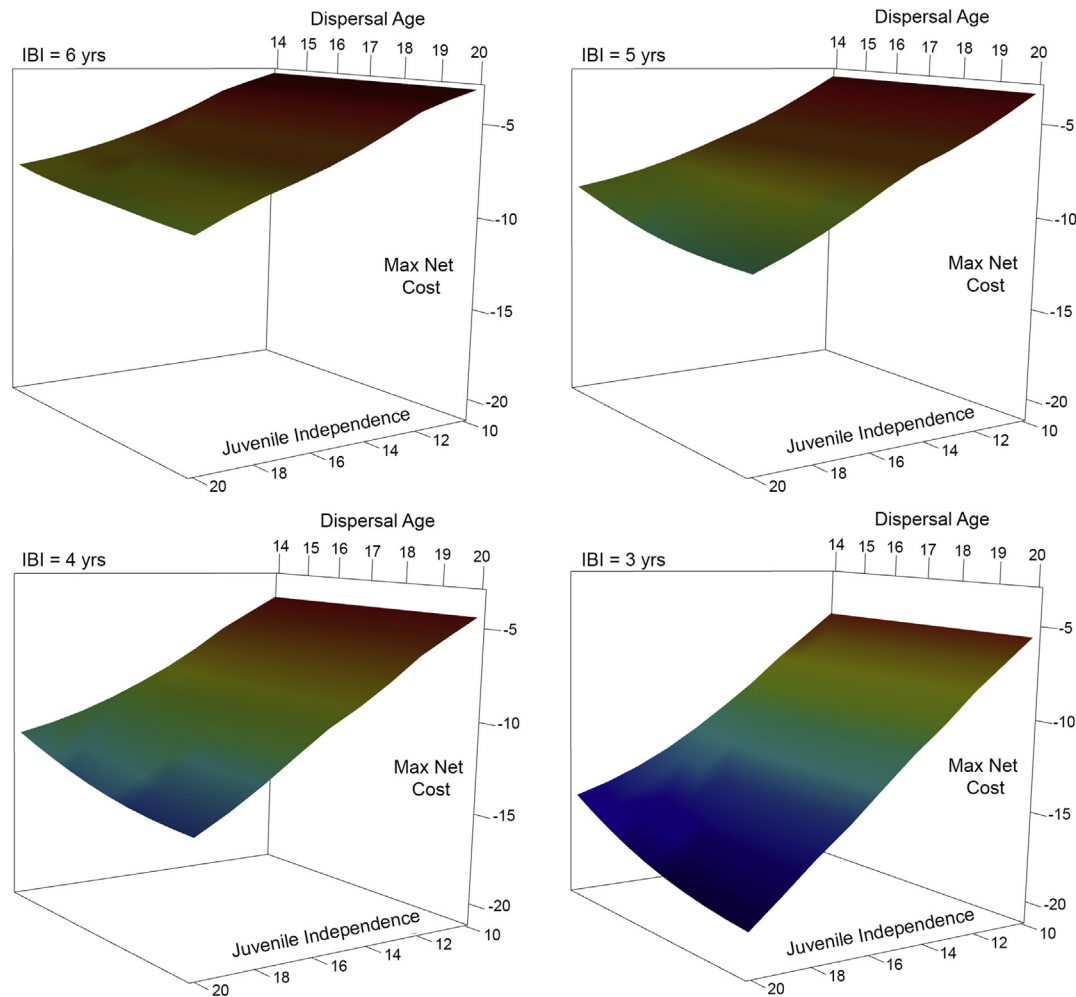
Figure 2. Maximum net cost of overlapping offspring stratified by 6- to 3-year intervals (IBI). Surfaces show the influence of age at juvenile independence (y-axis), dispersal age (x-axis), and birth intervals, and are the composite of the maximum net cost points from each of the 40,000 profiles in the full model (SOM Fig. 9). Color gradients follow the z-axis, where maximum net cost increases from red to blue. See SOM Fig. 10 for an interactive rotational model display.

life history variables that directly affect parental investment. In future research these can be incorporated into evolutionary models that consider fitness tradeoffs of alternative strategies. The model generates two central predictions related to cooperative breeding. First, the net cost of early changes in life history traits do not exceed demands that can be feasibly supported by maternal-offspring groups. Second, pressure to recruit adult reproductive cooperation follows under more derived conditions of late dispersal, late juvenile dependence, short birth intervals, and higher levels of surviving fertility.

Because modern human juveniles are subsidized, emphasis has traditionally focused on the demands of children driving the need for mothers to recruit adult help. For example, in other primates, help needed to carry young is one explanation for biparental care (Clutton-Brock and Harvey, 1977; Kleiman, 1977). We reconsider this perspective for two reasons. First, while juveniles are often characterized as being expensive, existing cost of children analyses evaluate the net or cumulative cost of a single dependent (Gurven and Kaplan, 2006). In contrast, the force of dependence model integrates the demographic and economic effects of overlapping offspring across a mother's reproductive career. This permits evaluation of potential sources of help both within and exogenous to mother-offspring dyads. Second, juvenility has undergone significant hominization. To account for this we start with an ancestral

juvenile who is self-sufficient at younger ages and then model effects on net cost as juveniles move toward lower levels of self-provisioning and later ages at independence and dispersal. The greatest increase in the cost of children from the ancestral state occurs when both birth intervals are short and juvenile independence is late (Table 1), a life history combination that the model suggests is not sustainable unless mothers can rely on the help of other adults. However, early life history changes generate costs that appear supportable by a mother and her juvenile offspring.

Cooperation within maternal-offspring groups

Among nonhuman species explanations for cooperative breeding have focused on the indirect and direct costs and benefits for a mature individual to delay dispersal or forego reproduction to help raise another's young (Emlen, 1995; Kokko et al., 2001; Hatchwell, 2009; Sparkman et al., 2011). Attention has not centered on the importance of juvenile help in the evolution of cooperative breeding for several likely reasons. First, because juveniles do not forgo or delay their own reproduction by helping, they present less of an evolutionary puzzle than explaining why sexually mature individuals help. Second, although juveniles cooperate in some species (Ratnieks and Anderson, 1999; Clutton-Brock et al., 2000; Clutton-Brock, 2002; Crespi et al., 2009;

Table 1
Change in maximum net cost from the ancestral state of early juvenile independence (age 10), early dispersal (age 14), and a 6-year birth interval.[a]

Juvenile independence	Dispersal		IBI
Early (Age 10)	Late (Age 20)		
Actual difference			
Early	.00	.00	6 yrs
Late	−5.05	−6.48	
Early	−.21	−.21	5 yrs
Late	−6.30	−8.30	
Early	−1.22	−1.22	4 yrs
Late	−8.63	−11.08	
Early	−2.38	−2.39	3 yrs
Late	−12.36	−15.73	
Relative difference			
Early	0%	0%	6 yrs
Late	158%	202%	
Early	6%	6%	5 yrs
Late	197%	259%	
Early	38%	38%	4 yrs
Late	270%	346%	
Early	74%	74%	3 yrs
Late	386%	491%	

[a] Table values give the difference between the maximum net cost at the end points of the parameter range for juvenile independence (difference between age 10 to age 20) and dispersal difference between (age 14 to age 20), and from a 6-year to a 5-, 4-, and 3-year birth interval. These end points are represented at the corner of the layers in Figure 2. Actual difference is the difference in raw values from the ancestral state and relative difference is the percentage change from the ancestral state. The marginal value, or total effect of each variable holding the others constant, is calculated as the sum of the difference of sums in the parameter end points shown in this table. Marginal value for juvenile independence = 66.32, birth interval = 21.32, and dispersal = 9.26.

Uematsu et al., 2010), their help is often sporadic and unreliable (Emlen, 1990). Because juveniles are not fully grown and are less efficient foragers than adults, the marginal value of their help may be of little added benefit to their mothers' fitness. Further, since nonhuman juveniles are independent foragers, diverting time and energy from their own survival to help may incur transient costs (Russell et al., 2003) and increased mortality risks (Crespi et al., 2009). Human juveniles, however, are less constrained as helpers both because they are partially subsidized and because the human subsistence niche offers novel helping opportunities that may positively affect the marginal value of juvenile cooperation (Kramer, 2011).

A self-sufficient chimpanzee spends about 5 h/day foraging (Hunt, 1989; Doran, 1997), equivalent to the time that the model's

Table 2
The daily hourly increase in investment needed to support offspring (maximum net cost) for every year dispersal age and age of juvenile independence increase while holding the other variable constant at its maximum and minimum value, and stratified by birth interval (IBI).[a]

Dispersal		Juvenile independence		IBI
Early net prod (age 10)	Late net prod (age 20)	Early dispersal (age 14)	Late dispersal (age 20)	
.00	.24	.51	.65	6 yrs
.00	.33	.61	.81	5 yrs
.00	.41	.74	.99	4 yrs
.00	.56	1.00	1.33	3 yrs

[a] Values are slopes derived from the linear combinations in Figure 3 (SOM Appendix 2). Because the original maximum net costs are negative, slope values are multiplied by −1 to express more intuitively as the daily hourly change from one life history condition to another.

early net-producer spends working. A hominin juvenile who would otherwise work hard to support himself may incur no added time cost to cooperate while also leveraging his nonreproductive status into a potential indirect fitness benefit. Human subsistence is distinguished by large foraging ranges and a broad diversity of plant, animal, and aquatic resources, most of which require processing and use of technology to access. While juveniles may be provided with difficult-to-acquire resources, they are also able to produce other easy-to-acquire resources (fruits, nuts, berries, fire wood, water, small game) that are often shared with others (Blurton Jones et al., 1994; Hawkes et al., 1995; Tucker and Young, 2005; Kramer, 2005b, 2011; Crittenden et al., 2013). Juveniles today often specialize in tasks at which they are competent but that have greater opportunity costs for older, stronger, and more skilled individuals (Kramer, 2005b, 2011). Further, because juveniles are less efficient than adults as long-distance bipeds (DeJaeger et al., 2001; Ridley and Olds, 2008), juveniles tend to perform subsistence tasks, such as food processing, that occur in or close to residential camps, while adults forage long-distance (Lee, 1979). Task specialization, the age division of labor, and juvenile cooperation, while often overlooked in humans, are well documented in other cooperative breeders (Jarvis, 1981; Alexander et al., 1991; Thorne, 1997; Ratnieks and Anderson, 1999; Clutton-Brock et al., 2000; Clutton-Brock, 2002; Crespi et al., 2009; Uematsu et al., 2010).

Model implications to the past and fossil hominins

Much of the discussion about the evolution of cooperative breeding in humans has centered on adults, particularly the help of grandmothers and fathers (Hawkes et al., 1998; Kaplan et al., 2000; Marlowe, 2003; Flinn et al., 2008; Hill and Hurtado, 2009; van Noordwijk et al., 2013). However, in considering selection pressures from the past forward, we also have to explain what happens to juvenile subsistence effort through time. Juveniles transition from an ancestry of being self-supporting to a modern pattern of greater dependence. We do not expect this transition to occur rapidly since it is linked to many other traits, nor to affect all juveniles equally. Juvenility is long life stage, lasting 10 or more years during which many developmental changes occur. Consequently, younger and older juveniles should have very different abilities as foragers and helpers. Well-dated dental formation and eruption evidence suggest that the human pattern of juvenility is slow to develop, beginning with *H. erectus*, but not assuming a fully modern form until early *Homo sapiens* (Smith and Tompkins, 1995; Dean et al., 2001; Dean, 2006; Smith et al., 2010). Early childhood (age 3–6) is also hypothesized to emerge as a distinct developmental phase in *H. erectus* grade species (Thorne, 1997; Clutton-Brock, 2002; Russell, 2004; Gilchrist and Russell, 2007; Bogin, 2009; Bermúdez de Castro et al., 2010). The insertion of childhood has important implications because weaned but very young children likely produced little. Model results show that older juveniles can self-provision much of their own and their younger sibling's dependence under a range of life history conditions. If so, intergenerational cooperation between a mother and her juveniles may be a critical but understudied initial step in the evolution of human cooperative childrearing.

Evolutionary changes in growth and development have generated considerable interest in recent years. While generalized changes in hominin growth trajectories are well-recognized, early *Homo*, archaic *Homo* (i.e., *Homo ergaster, H. erectus, Homo heidelbergensis*), and early anatomically modern humans now appear far more morphologically diverse than previously thought (Gunz et al., 2009; Hammer et al., 2011). Ontogenetic differences may help to account for some of this variation. Previous research has shown that how quickly juveniles approach and asymptote (specifically the rate of change, *C*, and the
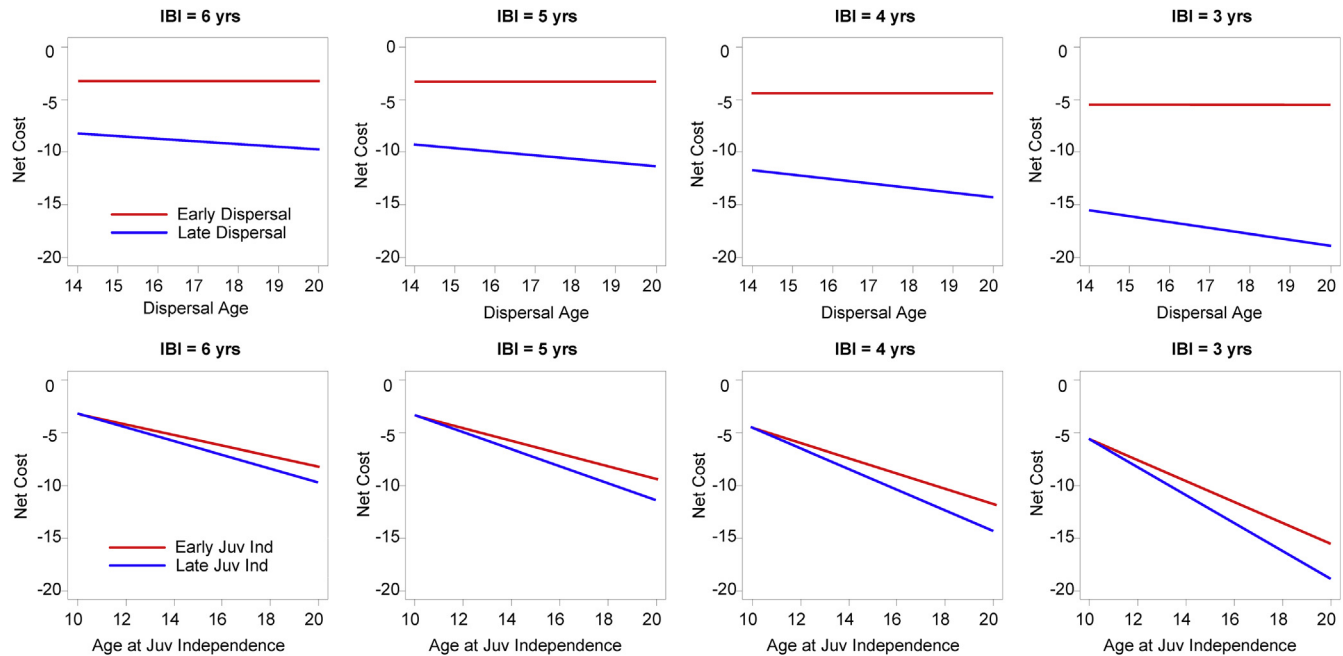
Figure 3. Linear combinations of the maximum net cost as a function of dispersal age and age at juvenile independence across 6- to 3-year birth intervals (IBI). The top row illustrates the effect of a later dispersal age (14–20) at early (age 10) and late (age 20) age of juvenile independence. The bottom row shows the effect of increasing age at juvenile independence (10–20) at early (age 14) and late (age 20) dispersal age. Slopes estimates given in Table 2.

inflection point, D, in the production function; SOM Fig. 3) at adult production levels is particularly sensitive to local food ecology and whether task difficulty is related to skill or strength (Kramer, 2005b). As hominins expanded into new and varied environments, juvenile activities likely became more variable in terms of foraging ranges, burden loads, mobility patterns, and foraging party composition. These aspects of subsistence condition selective pressures for juveniles to achieve adult levels of locomotor efficiency and have behavioral implications for the age-division of labor, juvenile dependence, and cooperation (Kramer, 2011). These factors influence differences in growth rates, the onset of growth spurts and rates of achieving adult lower limb proportionality.

Conclusions

Model results show that the demands and opportunities for cooperative breeding are sensitive to assumptions made about other life history traits. The cooperative breeding literature often supposes a modern life history as the selective background for its evolution. However, in species where life history traits that directly affect parental care have also undergone considerable modification, this assumption may mislead interpretations of causal relationships and selective pressures. This is particularly relevant for humans because juvenile dependence, late maturity, and short birth intervals are derived since the last common ancestor and likely do not reach their modern forms until the terminal Pleistocene among *H. sapiens* (Dean, 2006). Model results indicate that these traits interact and affect demands for parental care that in some combinations incur little cost and in others a substantial cost. If hominin cooperative breeding is ancient, its evolution should be considered against this changing life history landscape.

Acknowledgments

Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.jhevol.2015.01.009.

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