

REVIEW

## Humans are not cooperative breeders but practice biocultural reproduction

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### Abstract

**Context:** Alloparental care and feeding of young is often called “cooperative breeding” and humans are increasingly described as being a cooperative breeding species.

**Objective:** To critically evaluate whether the human offspring care system is best grouped with that of other cooperative breeders.

**Methods:** (1) Review of the human system of offspring care in the light of definitions of cooperative, communal and social breeding; (2) re-analysis of human lifetime reproductive effort.

**Results:** Human reproduction and offspring care are distinct from other species because alloparental behaviour is defined culturally rather than by genetic kinship alone. This system allows local flexibility in provisioning strategies and ensures that care and resources often flow between unrelated individuals. This review proposes the term “biocultural reproduction” to describe this unique human reproductive system. In a re-analysis of human life history data, it is estimated that the intense alloparenting typical of human societies lowers the lifetime reproductive effort of individual women by 14–29% compared to expectations based upon other mammals.

**Conclusion:** Humans are not cooperative breeders as classically defined; one effect of the unique strategy of human biocultural reproduction is a lowering of human lifetime reproductive effort, which could help explain lifespan extension.

### Keywords

Alloparenting, human life history, childhood, lifetime reproductive effort, longevity

### History

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### Introduction

Compared with most species of primates, especially the apes, humans have an unusual style of producing and raising offspring that is often described as cooperative breeding (Burkart et al., 2009; Hrdy, 1999, 2009). This special issue of the *Annals of Human Biology* focuses on “Human Biology of the Past” and the evolution of the human biocultural style of reproduction is a central feature of the topic. Here we review evidence and provide new analyses showing that, although sharing many features with cooperative breeders, the human strategy of reproduction and child rearing is distinct from that of most cooperative breeders. We argue that the human species practices *biocultural reproduction*. Biocultural reproduction describes a suite of biological and sociocultural adaptations, including: (1) cognitive capacities for non-genetically based marriage and kinship behaviour that provide demographically and ecologically flexible, but culturally universal, alloparental care for offspring, (2) a life history phase of childhood, characterized by the absence of nursing but considerable ongoing nutritional dependence, creating extended opportunities and needs for the provision of care by individuals other than the parents, (3) early weaning, leading

to an increased rate of reproduction and (4) decreased lifetime reproductive effort, which likely contributed to decreased mortality and lifespan extension.

### Cooperative breeding vs human cooperation in reproduction

We begin by making our case for the introduction of the neologism *biocultural reproduction*, as distinct from recent work that groups the type of highly social childcare practiced in human social groups as cooperative breeding (Burkart et al., 2009; Hrdy, 1999, 2009; Meehan et al., 2014). To be “cooperative” in breeding is often defined to mean that individuals of a species live in groups and that members of the group help to feed, care for or protect offspring that they did not bear (Burkart et al., 2009). Individuals providing these services are called alloparents. Another commonly cited criterion is that the provisioning, care and protection that alloparents provide must come at some cost to the alloparents. That cost may be measured in assisting others to gain access to food or in terms of reducing the alloparents’ opportunities to reproduce (Lukas & Clutton-Brock, 2012; Solomon & French, 1997).

Cooperative breeding species are not common in the Order Primates and, indeed, marmosets and tamarins of South America are the only widely-recognized species of cooperative breeding non-human primates (Fite et al., 2005;

Garber, 1997; Tirado Herrera et al., 2000). Some of the costs incurred by members of these New World monkey species are that only a few females in a social group reproduce, two or more males mate with the same female, which reduces male reproductive success and mothers without sufficient allomaternal support abandon or kill their dependent young (Culot et al., 2011).

Ethnographic work among contemporary human foragers provides detailed examples of the extent of cooperative alloparental care and its role in human societies and also shows that this care comes at a cost to the care provider. As one instance, Marlowe (2010) reported that during the first year that Hadza women are breast-feeding a current infant the mothers' ability to produce food is reduced to an average of 1713 kcals/day. This compares to an average food production of 3016 kcals/day for women without offspring less than 8 years old. Food contributions of married men increased from an average of 2990 kcals/day to 3851 kcals per/day during the first year of breast-feeding by their wives. The women's decrease in food productivity averages 1307 kcals/day and the increase of food provisioning by husbands averages only 861 kcals/day. The shortfall of 446 kcals/day is made up by increased provisioning by other members of the camp, especially maternal grandmothers of the nursing infant (Hawkes et al., 1989, 1997; Marlowe, 2010). These are important intergenerational resource transfers between alloparent, mother and child which carry non-trivial and measureable costs for the alloparents. More detailed discussion of the importance of human intergenerational transfers may be found in Kaplan and Robson (2002) and Gurven et al. (2012).

In another example, Meehan et al. (2013) report that, among Aka, tropical forest foragers living in the Central African Republic, mothers with children <35 months old were observed and quantitative measures of the mothers' energy expenditure were calculated. Assistance to mothers by alloparents significantly reduced mothers' working energy expenditure by up to 216 kcal during the 9-hour observation period. Assistance from grandmothers provided a one-to-one exchange of maternal direct care, while direct infant care from fathers decreased maternal care by almost 4 to 1.

In a review of 45 studies of mostly natural fertility societies, Sear and Mace (2008) found universal evidence of assistance in rearing offspring, leading them to suggest that alloparenting is a human universal. They also found that the benefits of alloparenting varied greatly and often depended on the kinship relation. Assistance from maternal grandmothers and siblings living with the mother tended to improve offspring survival rates. Assistance from paternal grandmothers was associated with both greater offspring survival and mortality, depending on the population, whereas help from fathers showed benefits in only about one-third of the studies. Sear and Mace mention the likely importance of matrilineal vs patrilineal residence as a determinant of these costs and benefits, but do not provide a formal analysis.

These examples illustrate that, while alloparental care is ubiquitous in human societies, the benefits vary widely across societies. In some instances, what may seem to be alloparental care may, in fact, involve costs to the recipient that could detract from reproductive success (Digby et al., 2007; Hrdy, 2009). Hrdy (1999, 2009) described the loss of tens of thousands of

infants who died due to the practice of using allomaternal wet-nurses in 17<sup>th</sup> and 18<sup>th</sup> Century Europe. Unless employed or enslaved by wealthy families, these wet-nurses often provided too little milk to too many infants, under neglectful conditions, resulting in high infant mortality.

### Humans are not cooperative breeders

In surveys of the literature on breeding systems, Clutton-Brock (2002) and Hrdy (2009) reported that between 5–10% of mammalian species are cooperative in breeding. Building on decades of research, Hrdy (2009) and others (e.g. Kramer, 2011; Meehan et al., 2013) make the case that humans are the only species of cooperatively breeding ape. In a recent systematic review, Lukas and Clutton-Brock (2012) provided a framework for characterizing breeding systems that recognizes only 1.8% of mammal species as cooperative breeders and, in contrast, they do not include humans among these species. They make a distinction between cooperative breeders, communal breeders and social breeders, with cooperatively breeding species being those in which most of the females do not breed regularly and instead provide alloparental care to the offspring of a breeding female (typically only one) to whom they are genetically related, often as siblings or half-siblings (see Lukas & Clutton-Brock, 2012 for details). Humans clearly do not meet this definition as virtually all women in traditional forager, horticultural and pastoral societies reproduce regularly if fecund (Bogin, 2001). Lukas and Clutton-Brock (2012) define other characteristics of cooperative breeding species, such as near-exclusive monogamous breeding and birthing of litters of altricial young, and interested readers may consult their article for further details. Only nine species of non-human primates (1.5% of the 612 total primate species listed at <http://www.alltheworldsprimates.org/Home.aspx>), all members of the New World Callitricidae (marmosets and tamarins), meet all of their criteria for cooperative breeding.

Lukas and Clutton-Brock (2012: 2151) define communal breeders as those species in which, "... most adult females breed regularly and share care such as allonursing or feeding offspring...". They identified four species of primates as communal breeders (two New World monkeys and two lemurs). They do not include *Homo sapiens* in their list of communal breeders because in communal breeding species the females are close genetic relatives, usually sisters or half-sisters, as the females remain in their natal social group. Human alloparents may be close genetic relatives, but often are not due to the variety of post-marital residence patterns. Surveys of traditional foragers and non-foragers find that human societies most often permit bilocal residence (either with the wife's or the husband's social group) and most often practice patrilocal post-marital residence (with the husband's social group)—matrilocal residence is least common (Alvarez, 2004; Marlowe, 2010).

Lukas and Clutton-Brock (2012) define social breeders as species in which the females live in groups and virtually all breed, but rarely, if ever provide allomaternal care to others. The majority of the non-human primate species are social breeders. It is important to emphasize that the ranks of the social breeding species include all of the African apes, which

are closest phylogenetically to humans. Humans, in contrast, are not social breeders, as alloparental care is the rule in human societies.

### Human biocultural reproduction vs cooperative and communal breeding

Humans certainly show cooperative and communal assistance, support and mutual aid in relation to reproduction, care of pregnant women and the rearing of offspring. Indeed, humans have been called “super cooperators” in these regards (Nowak & Highfield, 2011). Lukas and Clutton-Brock (2012) observed that, as none of the African apes practices either cooperative or communal breeding, it seems probable that these cooperative tendencies in raising offspring evolved in hominins after they split from the last common ancestor with living apes. They are not original in this proposal, as it was also offered by Hrdy (1999, 2009) and Burkart et al. (2009). We agree that the “super cooperation” practiced by humans is an evolutionarily derived trait. We differ, however, from Hrdy and Burkart et al. in that they equate the human style of reproduction with cooperative breeding in non-human mammals, whereas we find fundamental differences that set human reproduction apart from any other type of cooperative/communal breeding.

We feel that the most important difference between the human system and that of non-human cooperative breeders is that the provisioning of human allocare and related resource transfers is often uncoupled from genetic relatedness. This is rare in other species. Humans, of course, rely to a great extent upon genetic kin to support and help raise dependent offspring, but human alloparenting is unusual, perhaps even unique, among mammals in relying on many non-kin for care and provisioning. The restriction of breeding to usually one female and one, or only a few, males amongst cooperative breeders (Lukas & Clutton-Brock, 2012) leaves the siblings and half-siblings of the breeders with little choice for direct fitness enhancement. Hamilton (1964) formally identified the next best strategy, which he called inclusive fitness. By assisting their close genetic relatives, the non-breeding alloparents help to ensure that copies of parts of their own genome survive in their close genetic kin.

In the following section we show that human care and provisioning for the offspring of others is not governed by the close genetic relatedness found in all cooperative breeders, but is structured by sets of local, culturally-defined rules, hence our new term, biocultural reproduction. We begin our discussion with a brief review of the life history characteristics of humans that underlie the capacity and, indeed, the need for a strategy of reproduction based upon flexible, culturally-defined rules, rather than a strict adherence to genetic relatedness.

### Derived traits of human life history

The evolution of a protracted period of childhood dependence in hominin evolution greatly expanded opportunities and needs for care to be provided beyond parents and immediate kin (Bogin, 1999). The place of childhood in the stages of human ontogeny is given in Table 1 and Figure 1. When in evolutionary history and with which species the childhood

stage evolved is not known with precision, but some level of extension of the pre-adult period of development may already have occurred about 2 million years ago with the appearance of the genus *Homo* (Bogin & Smith, 2012). It seems likely that some form of genetically-driven cooperative/communal breeding strategy would have been necessary to sustain the evolution of childhood and its increased requirements for prolonged and more intensive care, although these details may not be reconstructed based upon current fossil evidence. What does seem clear is that, over evolutionary time, the bonds of genetic relatedness which likely initially fostered the ancestral hominin strategy of raising offspring was replaced with the current flexible, culturally based systems of kinship and marriage that prescribe that a range of individuals provide care.

Burkart et al. (2009) proposed that cooperative breeding by human ancestors facilitated the evolution of larger brains and cognitive development. Lukas and Clutton-Brock (2012) seem to reject this proposal as they find no evidence of an association between cooperative breeding and brain size in mammals, especially primates, and cite Iwaniuk and Arnold (2004) for the lack of such an association in corvid birds. Alternative proposals are that other selection pressures, perhaps related to greater reliance on stone tools, the use of fire and other extractive technologies (Wells & Stock 2007), the development of language skills (Locke & Bogin, 2006) or the increasing size and complexity of social groups (Dunbar, 2003) initiated brain/cognitive expansion. All of these proposals are speculative, but all assume an evolutionary trend within the hominin lineage toward greater cooperation in tool production, foraging and social relations which may have fostered alloparenting and social cooperation in reproduction.

The transition to biocultural reproduction may have co-evolved with the biological, behavioural and cognitive characteristics which coalesced with the appearance of *Homo sapiens*. We have argued elsewhere that the evolution of the adolescent life history stage and full symbolic language are coincident with *Homo sapiens* (Bogin, 1999; Bogin & Smith, 2012). Dental evidence indicates that key features of the growth pattern of childhood were likely in place by ~160 000 years ago in *Homo sapiens* (Smith et al., 2007). Adolescence, full symbolic language, systems of marriage and non-genetic kinship determination probably have more recent evolutionary origins, although exact dates are impossible to specify with current evidence.

### Childhood and biocultural reproduction

Although many of the evolutionary details remain uncertain, the eventual evolution of the childhood stage in hominin evolution likely co-evolved with human biocultural reproduction. Humans are highly unusual among mammals in weaning offspring before they are nutritionally independent. Extensive provisioning of dependents by genetic kin and genetically unrelated individuals allows humans to “stack” offspring and spread the burden of provisioning across alloparents, thus facilitating both relatively high fertility, despite the intensity of investment, and high survival of each offspring (Bogin, 1999; Gurven & Walker, 2006; Hill & Hurtado, 1996; Hawkes et al., 1998; Kaplan et al., 2000).

Table 1. Stages in the human life cycle (modified from Bogin 1999). The duration of each stage is a median or modal value. There is some variation about these average values in healthy individuals, especially from the Infancy stage onward. Literature sources for the construction of this table are given in Bogin (1999).

Stage	Duration	Events
First trimester of pregnancy	Fertilization to week 12	Embryogenesis
Second trimester of pregnancy	Months 4 to 6	Rapid growth in length
Third trimester of pregnancy	Month 7 to birth	Rapid growth in weight and organ maturation
Neonatal period	Birth to 28 days	Extra-uterine adaptation, most rapid rate of post-natal growth and maturation
Infancy	Month 2 to end of lactation (usually by 36 months)	Rapid growth velocity with steep deceleration in velocity with time, feeding by lactation, deciduous tooth eruption, many developmental milestones in physiology, behaviour and cognition
Childhood	30–36 months to 6.9 years	Moderate growth rate, weaned but dependency for feeding, mid-growth spurt, eruption of first permanent molar and incisor, cessation of brain growth by end of stage
Juvenile	7–10 (girls) or 12 (boys) years	Slower growth rate, capable of self-feeding, cognitive transition leading to learning of economic and social skills
Puberty	Brain: 9–10 years Body: girls 10 years, boys 12 years	In the brain, puberty is an event of short duration (days or a few weeks) that reactivates the hypothalamic GnRH pulse generator leading to a massive increase in sex hormone secretion; on the body, puberty is noted by a darkening and increased density pubic hair
Adolescence	The 5–8 years following onset of puberty	Adolescent growth spurt in height and weight, permanent tooth eruption virtually complete, development of secondary sexual characteristics; socio-sexual maturation, intensification of interest and practice in adult social, economic and sexual activities
<i>Adulthood</i>		
Prime and transition	18–20 years for women to 45 years (end of child-bearing) and from 21–25 years for men to ~50 years	Commences with completion of skeletal growth; homeostasis in physiology, behaviour and cognition; menopause for women by age 50
Women's post-reproductive	10–20 years following menopause	Bioculturally defined stage of women's life, often characterized by investments of time and energy in the caring for daughters and grandchildren
Old age and senescence	From end of child-bearing years to death	Decline in the function and repair ability of many body tissues or systems
Death		

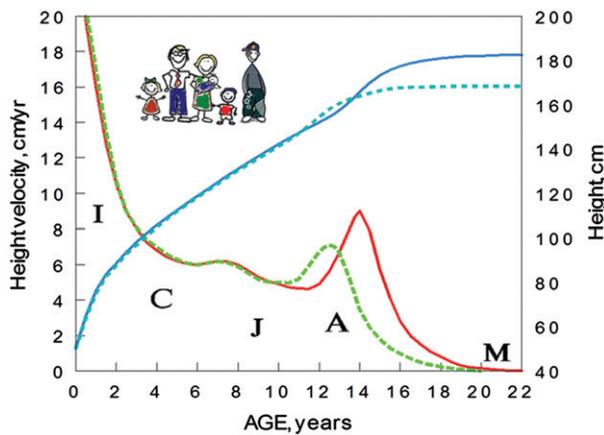


Figure 1. Distance and velocity curves of growth for healthy, well-nourished humans. Boys, solid line; girls, dashed line. These are modal curves based on height data for Western Europe and North American populations. The stages of post-natal growth are abbreviated as follows: I, infancy; C, childhood; J, juvenile; A, adolescence; M, mature adult (modified from Bogin 1999). The distance curve (right y-axis) indicates the amount of height achieved at a given age. The velocity curve (left y-axis) indicates the rate of growth at a given age. Growth velocity during infancy is rapid with a steep deceleration. Childhood growth is relatively constant at ~6 cm per year. Growth rate slows during the juvenile stage and then accelerates during the first phase of adolescence—the adolescent growth spurt. Growth rates decline during the second phase until all growth in height stops at the onset of the adult stage. The image of the “family” is not meant to promote any particular type of family as desirable or normal, rather the cartoon figures illustrate the stages of human life history between birth and adulthood.

Human reproductive behaviour increases genetic fitness of parents over that of any other ape by enabling women to give birth to new offspring while allowing existing dependent offspring to receive care and feeding from close kin and other members of the social group (Bogin, 2001, 2006). The evolution of human childhood may be viewed as critical to this human reproductive strategy.

The biological constraints of childhood—including an immature dentition, small digestive system and a calorie-demanding brain that is both relatively large and growing rapidly—necessitate care and feeding from older individuals, which greatly expands the opportunities for allocare within human societies. Although women tend to provide the majority of care to infants for at least 3 years in most traditional societies (Sear & Mace, 2008; Marlowe, 2010), many other individuals are also involved in the care, provisioning and social lives of infants and young children. Indeed, by the stage and age at which human mothers tend to wean their infants, which is, on average, between 30–36 months in forager and other subsistence societies (Bogin, 2001; Marlowe, 2010; Walker et al., 2006), a greater percentage of the care of offspring tends to be provided by other family members including fathers, older siblings, aunts and grandmothers (Gettler et al., 2011; Hawkes et al., 1998; Hrdy, 1999; Kramer, 2005; Meehan et al., 2014; Valeggia & Ellison, 2004).

The point we make again here in order to re-enforce its importance is that, although genetic kin are clearly important

as care providers, in most human societies family members with no close genetic relationship and non-family members also play crucial roles in the cooperative care and feeding of children. For instance, recent work among Hadza foragers found that physical proximity and genetic relatedness explained about equally the likelihood of cooperation, including childcare, between individuals (Apicella et al., 2012). Indeed, all human social groups include a variety of childcare and feeding arrangements which make use of both biological kin and socially-defined relationships such as in-laws by marriage, fictive kin, servants, friends or employees paid in cash or kind (Lancy, 2008).

With these sources of childcare assistance, human women may reproduce every 2–3 years without sacrificing their own health or the health of their current offspring. In contrast, chimpanzees have a median interval of 5.9 years between successful births, that is, between births where the infant survives for at least 4 years (Emery Thompson et al., 2007). In some traditional, non-contracepting human groups there may be a birth every 3 years over a 20-year reproductive career (Bogin, 2001; Lee & Kramer, 2002, see discussion below). The resulting assemblage of six or seven dependent offspring range in maturational status from infant to child, juvenile, adolescent and even young adult (see Table 1 for chronological ages). These “litter-like” assemblages of offspring are both a cause and consequence of the socially diverse sources of alloparenting afforded by biocultural reproduction.

### The nature of human biocultural reproduction

As practiced by human societies, biocultural reproduction may be defined as the set of marriage and kinship based rules for extra-maternal cooperation in the production, feeding and care of offspring. The human strategy of reproduction and offspring care, which is based on both genetic and non-genetic relationships, is distinct from that of all other mammals, including our closest genetic cousins the African apes. It is vitally important to state here that we are not discussing human mating, which takes place within and outside of stable pair bonds and marriage. Instead, we focus on the cultural rules for the care and provisioning of offspring, regardless of the genetic relationship to the caregivers. Our point is that, in every human society so far observed, or for which historical records exist, there are biocultural rules for the extra-maternal (alloparental) care of dependent offspring. This is especially the case for traditional societies, which include foraging groups, pastoralists and horticultural societies, but it is also true for nation-states based on intensive agricultural or industry and contemporary post-industrial states.

Marriage and kinship based rules include delegating responsibilities for feeding, clothing, housing and educating the infants, children and youth of the society and often similar rules for the care of women of reproductive age. The rules may extend to responsibilities of alloparents for arranging the marriage of offspring.

Above we speculated that human childhood and biocultural reproduction co-evolved as derived characteristics of our species. In addition, human biocultural reproduction likely also required the evolution of other human-specific

characteristics, such as the cognitive capacities that allow for what is often described as “theory of mind” (Premack & Woodruff, 1978). This phrase is often taken to mean the ability of one individual to impute or attribute mental states to self and to others. To have “theory of mind” requires an appreciation that others may have desires, intentions or beliefs that may be different from one’s own and, based upon this appreciation, the ability to predict behaviour on the basis of such states. There are debates as to which animal species have “theory of mind”. We do not enter into these debates here; rather we accept that living humans have a “theory of mind” and related behaviours which surpass those of other primates. We also assume that these human cognitive and behavioural capacities evolved or were at a minimum augmented substantially, since the hominin split from the last common ancestor with chimpanzees, without speculating on when or how this occurred.

Human “theory of mind” emerges during development in a sequence from infant to child, juvenile, adolescent and adult. Two of the crucial changes in cognition which underlie theory of mind emerge at the transition from human infancy to childhood, at ~3–4 years of age. These are the capacities for pretense and the attribution of false belief in other people (Baron-Cohen, 1995; Leslie, 1987). Bananas provide an example of pretense. Infants accept only the reality of the banana as a fruit that may be eaten. Children are capable of the pretense of a banana as a telephone or some other imagined object. A common test for false belief is to allow a child and another person to see a banana hidden in a basket. The other person then leaves the room; the banana is re-hidden in a box and then the other person returns to the room. Infants and younger children will expect that the other person knows that the banana was re-hidden. Children with theory of mind will make the attribution of false belief and say that the other person thinks that the banana remains in the basket (a graphic explanation is available at <http://labspace.open.ac.uk/mod/resource/view.php?id=482989>).

With these new abilities, the child may use pretense and attribution of false belief in many contexts. A kindly neighbour may be called an “aunt”, while two unrelated but socially-close girls may call each other “sisters”. Older individuals also make use of pretense toward the child, as illustrated by the kindly neighbour accepting the kinship name of “aunt” as well as the associated responsibilities for allocare, even though she is genetically unrelated to the child. Many of the human social rules for alloparental care of offspring are a “pretense” of the genetic relatedness which drives cooperative breeding in other species. In the larger social arena of human behaviour, these types of pretense and false beliefs are essential supports for the rules for kinship and marriage. The essential point is that, in the human species, relationships defined by marriage and kinship rules often take the place of genetic closeness.

Humans, of course, build on the foundations of primate biology and psychology that foster intimacy between mother and offspring (Hrdy, 2009; Konner, 2010; Okamoto-Barth, unpublished). These foundations are necessary for human biocultural reproduction, but the degree of mother–offspring intimacy in non-human primates would not likely be sufficient to sustain the more complex and expansive human

networks of affection and alloparental care that extend to many kin and non-kin. A deeper ability to impute or attribute mental states to self and to others is required. Tomasello et al. (2005) proposed that this new, deeper “theory of mind” is found only in the human species and they label it as “shared intentionality”. To evolve from communal or cooperative breeding to the human practice of biocultural reproduction would have required the new emotional capacities of shared intentionality.

Goldschmidt (2006: 47) went further and emphasized the importance of another human emotion called “affect hunger”, which he defined as “. . . the urge to get expressions of affection from others”. For humans this often means affection from many others. Konner (2010) discussed examples of the importance of affection with many people, in addition to the mother, for the healthy development of human children in forager societies. Especially noteworthy is the affection between children with members of the social group who serve as alloparents and also as teachers of essential survival skills. These people may be quite distantly related to the child in any genetic sense.

Hrdy (2009, in press) focuses on the ways in which intense alloparenting by human ancestors “changed our minds”, reflecting the fact that infant attachment was spread across many alloparents rather than just the mother. She provides evidence that having a broader range of alloparents and attachments changes mental phenotypes and promotes the ability and desire to adopt the mental perspective of others (i.e. “theory of mind”). Hrdy (2009, in press) also proposes that the new emotional capacities of hominin ancestors promoted those human cognitive accomplishments which distinguish our species from other apes.

Based upon these analyses, one may conclude that human emotion and cognition are among the features that set our species apart from other mammals, even the apes, and undergird our capacity for emotional attachments to a range of individuals other than direct genetic kin. Our ability to form strong social bonds, not only with mothers but also with many other people through social institutions such as marriage and kinship, are critical to understanding how biocultural reproduction operates.

### Marriage, kinship and culture in human reproduction

Marriage is a uniquely human practice with strong ties to human systems of social, economic and political organization, as well as moral codes, religious behaviour and other forms of ideology (Fox, 1984; Keesing, 1975). As noted previously, human mating is not confined to marriage and in some societies there is little correlation between the two. However, all human societies practice marriage and, along with systems of kinship, these cultural behaviours are the central organizing principles for alloparental care in small scale human societies, which collectively describe human social organization for more than 99% of the evolutionary history of *Homo sapiens*. It was within traditional small-scale societies that the biology of childhood and the cultural power of marriage and kinship fostered the emergence of human biocultural reproduction.

Based on a survey of 563 mostly traditional human societies, Murdock (1981) found that ~18% of human

cultures prescribe monogamous marriages, ~80% permit polygynous marriage and the remaining 2% permit polyandrous marriage. In practice, the most common form of marriage is one man with one woman, on account of the often high material resource costs of marriage to multiple partners. Marital dissolution due to death, divorce (legal or *de facto*) and abandonment is known in all human cultures and re-marriage is also common. This leads to “serial monogamy” and polygynandrous mating, with both men and women having multiple marriages or mating partners.

Human marriage is one basis for kinship determination, although there are others. Human societies define kinship relations on the basis of familial and social ties. Humans are the only species to use language and the cultural institution of marriage to define kinship categories. The application of non-biological criteria results in what is sometimes called “fictive kinship”, the application of kinship names to people unrelated by marriage or genetic descent. Fictive kinship can at times be a tie between people which is as strong, or stronger, than biological kinship. Because the social nature of human kinship often overrides biological descent, some anthropologists avoid making any distinction (Carsten, 2000; Schneider, 1984). Here, we use the distinction to emphasize the integrated biocultural nature of human reproduction and alloparental care.

Within the context of human biocultural reproduction, fictive kinship serves to enhance social relations including affection, concern, obligation and responsibility towards each other’s offspring. Our previous example was calling the close friend of one’s mother by the name “Aunt Maria” instead of Mrs Smith. “Aunt Maria” may provide food, supervision, protection, gifts and other types of parental investment to her “niece” and the “niece” is expected to behave in accordance with the rules of interaction between family members. An ethnographic example of fictive kinship in traditional societies comes from the Hadza. Each Hadza person treats all other Hadza as kin (Kaare & Woodburn, 1999). Each person knows and uses a kinship name that would apply to every other Hadza, irrespective of genetic relationships. Given the relatively small population of ~1000 Hadza (Marlowe, 2010), this kinship naming may not seem unusual as it is possible for any Hadza person to know a sizeable fraction of other Hadza. However, the Hadza practice is typical of much larger societies, including much of the population of China, totalling more than 1.3 billion people. In traditional Han Chinese culture it is regarded as an offense to refer to, or address, a more senior person or family relation by his or her given name. The use of the appropriate kinship term is the only acceptable form of address (Baker, 1979). Our point is that fictive kinship, as defined anthropologically, is a common way that people in all human societies structure relationships, especially those for the transfer of allocare, education, material resources, wealth and status.

Some cross-cultural examples where fictive kinship is an essential feature of social organization include: (1) *Compadrazgo* in Latin America (Foster, 1953), where friends become “co-parents” of each other’s offspring, (2) adoption and foster care in most human cultures, by which biologically unrelated infants and children are treated

as biological kin by the adopters, (3) cultures practicing Hawaiian kinship terminology where, for example, all women of one's mother's generation are referred to with the kinship name of "mother" and (4) the military of many nations where soldiers call each other "brother" and, in some cases, where new recruits are "twinning" with an older soldier. It is also common for anthropologists conducting fieldwork to be given a kinship name by their hosts. Doing so defines, justifies and facilitates social relationships. Well-known ethnographic examples are provided by Lee (1979), who lived with the !Kung (or Ju/'hoansi), foragers of Namibia, and by Chagnon (1992), who lived with Yanomamö, a horticultural and foraging society of South America. Similar fictive kinship designations were given to the present authors during fieldwork in Guatemala and the Philippines. Bogin was adopted as the "son" of a middle-class family in Guatemala City, while Kuzawa is treated as a "son" by someone from the neighbourhood in Cebu City where he has lived in the Philippines. These fictive kin designations came with much of the affection and the responsibilities of biological kinship.

### Human social groups are based on social kinship

Hill et al. (2011) surveyed 32 present-day foraging societies, including the !Kung (Ju/'hoansi), the Ache of South America and the Hadza and reported that human hunter-gatherer societies have a social structure that is unique among all primates. Hill et al. found that, on average, 75% of individuals in residential groups were genetically unrelated or at least not genetically related by descent from common parents or grandparents. This is due to the practice by both men and women of dispersing or remaining in their natal group. Migrations to new groups dilute genetic relationships and require social kinship designations to help structure new relationships. In our view, these types of socially-based kinship arrangements, which operate in addition to genetic kinship, are the essence of what sets human biocultural reproduction apart from the forms of cooperation found in other species. Hill et al.'s findings complement and extend those of Apicella et al. (2012), who reported that Hadza camps are comprised of people with distant genetic relationships: first order genetic relatives comprised less than 10% of residential camps.

People will marry and reproduce according to the rules of kinship, often with disregard to their degree of genetic relationship. Lee (1979) found that !Kung regard people with the same name as equal in kinship. A man will regard all women with the same name as his sister as a sister. Marrying a sister is forbidden, so all women a man calls sister are unmarriageable.

Chagnon (1992) reported that the Yanomamö practice a type of kinship classification by which a man calls his mother's sisters and some other women by the kinship name "mother". The daughters of these "mothers" are not eligible for marriage. A shortage of eligible women is often a problem for Yanomamö men. Chagnon described the social mechanisms by which a man can change the kinship name of his mother's sister from "mother" to "mother-in-law", which thereby makes her daughters eligible for marriage.

### Costs and fitness in biocultural reproduction

These examples, and hundreds of others described in the literature on cross-cultural kinship research, show that human biocultural reproduction is based upon social relationships that are qualitatively distinct, in their definition, extent and complexity, from those of cooperative or communal breeding systems. Human kinship and marriage systems cast new light on Hamilton's Rule for the evolution of cooperation and cooperative breeding (Hamilton, 1964). Hamilton's Rule is expressed as  $C < rB$ ; where  $C$  is the cost in fitness to the actor,  $r$  is the genetic relatedness between the actor and the recipient and  $B$  is the fitness benefit to the recipient. If the reproductive cost to the actor is less than the product of genetic relatedness multiplied by the reproductive benefit to the recipient, then a "helpful" behaviour toward the recipient's reproductive success is expected to be favoured by natural selection. If reproductive costs are greater than the product of  $rB$ , then apparently altruistic behaviours such as alloparenting will never evolve. Our review shows that human biocultural reproduction is a system of alloparenting which violates Hamilton's Rule in that alloparents often incur costs greater than the product of  $rB$  because, unlike in other cooperating species, the genetic relatedness between the human actor and recipient is often small or, essentially, zero. As the value of "r" approaches zero the costs of alloparenting far exceed the benefits. In reality, the cost in fitness to the alloparent becomes quite difficult to measure, as the actor is part of elaborate kinship networks and families created by marriage, which structure the flow of energy and other resources in ways that do not always map onto genetic relatedness. Equally important, the obligations and prohibitions entailed by kinship categories result in emotional costs and benefits which may offset any material or biological costs. The fitness benefit ( $B$ ) to the recipient also becomes more complicated to measure for the same reasons. In addition to the metrics used to understand evolutionary selection pressures in non-human animals, such as survival, growth and future reproduction, human reproduction also involves non-biological contributions to the members of the social group, such as emotional affection, the teaching of culturally acquired skills and transfers of material goods and other wealth (Gurven et al., 2012). In these ways, biocultural reproduction differs from cooperative and communal breeding because it not only contributes to the inclusive fitness of parents and genetically-related helpers, but it also serves to continually reproduce and recreate the social, economic, political and moral cohesion of social group members.

### Why do humans rely upon such diversity in kinship and allocare strategies?

One hallmark of the human system of biocultural reproduction is extreme flexibility. Local ecological conditions vary across the range of environments that traditional subsistence level human societies inhabit today and have inhabited for millennia. It is likely that the effective patterns of allocare, including kinship and marriage-defined rules for provisioning, holding, protecting and educating the young varied remarkably over time and place. One well researched ethnographic example are the Hadza, among whom heavy

and difficult to dig tubers are a key food resource. Hadza grandmothers have the knowledge and physical strength to dig them, allowing them to play a central role as allocaregivers (Hawkes et al., 1989).

Another common pattern of child care in many traditional cultures is to have juveniles assume caretaking responsibilities for younger children. This occurs among two well-studied African hunting and gathering societies, the !Kung (Konner, 2010) and the Mbuti (Turnbull, 1983a, b). In these societies, mothers carry their infant and still nursing child (nursing a child to age 4 years is common in these cultures) with them while foraging. Weaned children must stay ‘‘home’’, that is at the base camp, as pre-adolescent children have neither the strength nor stamina to follow their parents while gathering or hunting. At !Kung camps children of various ages play together within the camp boundaries while juveniles discharge many caretaking functions for younger children. The children seem to transfer their attachment from parents and other adults to the juveniles, behaving toward them with appropriate deference and obedience. The age-graded play group functions to transmit cultural behaviour from older to younger generations and to facilitate the learning of adult parental behaviour (Konner, 2010). Of course, the children and juveniles are never quite left on their own, as there is always one adult or more in camp at any time, but this person is not directly involved in childcare. Rather, he or she is preparing food, tools or otherwise primarily engaged in adult activities.

The Mbuti, who are nomadic hunters and gatherers of central African rain forests, have a similar childcare arrangement. After weaning, toddlers enter the world of the *bopi*, the Mbuti term for the children’s playground, but also a place of age-graded childcare and cultural transmission. Between the ages of 2–3 years to 8–9 years of age, children and juveniles spend almost all of their day in the *bopi*. There they learn physical skills, cultural values and, even, sexual behaviour. Turnbull (1983b: 43–44) notes ‘‘Little that children do in the *bopi* is not of full value in later adult life’’.

The age-graded play group provides for both the caretaking and enculturation of the young, freeing the adults from these tasks so that they may provide food, shelter and other necessities for the young who may be at various stages of development. A formal mathematical treatment of the reproductive benefits of an age-graded division of labour for alloparenting was provided by Kramer (2014). The ethnography and the formal analysis both show that a woman may be pregnant, have a child weaned within the past year and have one or more older offspring simultaneously. Kramer’s ethnographic fieldwork with Maya horticulturalists of Mexico found that the average Maya woman will be able to give birth and rear 7 offspring during a 20-year reproductive career (Lee & Kramer, 2002). As children, juveniles and adolescents, those offspring contribute time and labour toward the alloparenting of their younger siblings, cousins and others. It is not until the offspring are ~20 years old that they achieve independence in terms of the ability to leave their natal social group to begin their own families.

As we proposed previously, the selective advantage of a greater number of surviving offspring afforded by age-graded caretaking may, in part, account for the evolution of

childhood in the hominin lineage. In addition, the play group, in the protective environment of the home base or camp, provides children and juveniles with the freedom to explore and experiment, which tends to encourage learning, tool using, socialization, physical development and emotional well-being (Bogin, 1999, 2002).

These examples illustrate how humans, unlike other species, have adopted a system of biocultural reproduction and offspring care that is flexible and responsive to local opportunities and constraints. Having our kinship and marriage systems, including fictive kinship and many styles of marriage practices, emerge locally, allows greater opportunities for plasticity in behavioural accommodation of local ecological realities. In contrast, other species that practice cooperative or communal breeding have relatively narrowly-constrained systems of collective care based on close genetic relationships.

We are mindful that there is no simple correlation between types of marriage and kinship systems and local ecologies. Styles of human alloparental care likely developed due to many historical factors that are often challenging to reconstruct from the fossil record. We only mean to emphasize that human alloparental care based on biocultural rules for kinship and marriage responsibilities provide human populations with enormous flexibility to adapt effectively to the unusually wide range of ecologies that our species has colonized (Wells & Stock, 2007).

### Biocultural reproduction and lifetime reproductive effort

In this final section we tie together our discussion of the biocultural nature of human reproduction and the childhood stage of life history by analysing their consequences for lifetime reproductive effort (LRE) and the broader implications of these ideas for understanding the evolution of the human life history. LRE may be defined as the metabolic energy devoted to reproduction, relative to maintenance costs, over the average adult life span. To explain this definition of LRE we first provide background on reproductive effort (RE). Within the life history theory literature, RE is often defined as including expenditures of energy and time in: (1) mating, that is, searching for, finding/attracting and keeping a mate(s); (2) offspring production, including gametogenesis, siring and gestating offspring along with (in mammals) milk transfers during infancy; and (3) parental investment, which includes all expenditures of the parents’ time and energy on any one offspring. All of these expenditures are viewed as coming at a cost to parental abilities to invest in their own somas and in other current—or future—offspring (Hamilton, 1964, 1966).

Human reproductive effort is highest between the ages of 18–40 years in most societies. In traditional societies, especially foragers, reproductive careers are typically initiated after 17 years of age, with 19 years being the modal age at first birth for women (Bogin, 2001; Marlowe, 2010). After about 35 years of age, women’s biological capacity to conceive (fecundity) begins to decline slowly until menopause, which can be defined as the cessation of monthly menstrual cycling and the absence of ovulation in adult women. Menopause is usually reached by ~50 years of age,

although there is some evidence that it may occur earlier when women have been subjected to poor-quality environments in terms of nutrition, infection or heavy workloads (Murphy et al., 2013). In societies in which there is no parity-specific limitation on the number of children and hormonal contraception is not used, completed fertility rates may exceed 15 per women (Larke & Crews, 2006). Relatively high fertility likely characterized much of human history, as opposed to modern high income settings in which birth control is common and fertility typically falls below two per woman. Men's reproductive success follows closely that of women in the same population, although in some traditional settings a larger variance in men's total fitness is observed due to inter-male competition for access to mates via aggression and/or cultural rules which channel women to older, wealthier or more socially dominant men (Alexander & Noonan, 1979; Chagnon, 1979; Crews, 2007; Marlowe, 2000).

Extensive, high quality parental investment is a hallmark of human reproductive effort and it sets humans apart from all other mammals and other large-bodied apes (Lancaster & Lancaster, 1983). The intensive parental investment that characterizes human biocultural reproduction is made possible by kinship and marriage rules, noted above, which organize patterns of energy and labour transfers by alloparents to mothers and their offspring. This style of alloparental care allows human societies to maintain extremely high investment in each offspring, while also allowing human women to achieve the highest fertility and shortest inter-birth intervals of all the apes (Bogin, 2001; Bogin & Smith, 2012; Hrdy, 1999; Kramer & Ellison, 2010; Reiche et al., 2009; Short, 1976).

### Lifetime reproductive effort

Early historical “seeds” of the modern notion of reproductive effort (RE) were planted by Fisher (1930), who formulated the concept of “reproductive value”, which he described as the direct reproductive contribution that an individual of a given age, on average, will make to future generations. Fisher wrote that this is “. . . of some interest, since the direct action of Natural Selection must be proportional to this contribution” (Fisher, 1930: 27). Lack (1947) extended this concept when he analysed egg clutch size in birds and reported a trade-off between the number vs size of offspring, concluding that, “The parental feeding rate tends to increase if the brood is larger, but not proportionately, so that each nestling gets a smaller share of the food in a large than a small brood” (Lack, 1947: 331). Lack's observations have been cited by subsequent theorists as part of the early development of life history thinking (Ricklefs, 2000). Building on Fisher, Lack and others, Williams (1966) proposed an elegant way to express the propagative part of these basic trade-offs. He called this “Reproductive Effort” (RE) and defined it as that portion of adult body mass devoted to reproduction per unit time (Williams, 1966). There has been much discussion of how best to measure RE (e.g. Gadgil & Bossert, 1970; Hirschfield & Tinkle 1975; Smith & Fretwell, 1974), but William's definition remains the most commonly used method.

Charnov et al. (2007) further extended the RE concept by devising a method for estimating a species' average lifetime

reproductive effort (LRE) by taking the RE of an average reproductive bout multiplied by the average number of bouts across the reproductive lifespan of a female of that species. It is important to distinguish LRE from a related measure called lifetime reproductive success (LRS). The LRS of a female equals the total number of surviving offspring that she produces in her lifetime (Robbins et al., 2011). It is well known that humans have the highest RS of all primates and a RS higher than many mammals (Bogin 2001; Walker et al., 2008). In contrast, LRE encapsulates the direct metabolic burden of reproduction over a female animal's lifecourse and, thus, is a way of expressing the total amount of energy a typical female member of a species allocates to reproduction, on average, over her lifecourse.

Specifically, Charnov et al. (2007) express LRE as:

$$\begin{aligned} & (\text{litters per year}) \times (\text{litter size}) \times (\text{average reproductive lifespan}) \\ & \times \left( \frac{\text{offspring mass at independence}}{\text{adult mass at first reproduction}} \right) \end{aligned}$$

Charnov et al.'s (2007) use of the word “litter” also includes other terms to denote birthing events, such as clutches and broods. Calculating LRE for 54 lizard species, they find a mean LRE of 1.43 (1.3–1.5, 95% confidence interval) and, for 40 mammal species, a mean LRE of 1.41 (1.2–1.6, 95% CI). No primates were included in the analysis. These results indicate that, across this range of animal species, with varying growth and production rates, the average female in a typical mammal or lizard will generate a mass of offspring ~1.4-times her own body weight. Charnov et al. (2007: E135) explain that LRE is of theoretical importance because it “. . . is a key component of fitness. . . and it encompasses the central core of 40 years of life history thought—reproductive allocation, size at maturity, and adult life span. This places it central to the study of life histories”.

Following the approach developed by Charnov et al. (2007), Burger et al. (2010) calculated the average LRE of human women using data from 17 small-scale, traditional societies. By multiplying the average fertility rate, offspring size relative to maternal body mass and reproductive lifespan of women within these populations, they calculate an average LRE of 1.45 ( $\pm 0.12$ , 95% CI). This value is statistically indistinguishable from the predicted average LRE value calculated by Charnov et al. (2007) for other mammals, suggesting that humans may be typical mammals in this regard.

While an important initial step, the assumptions employed by Burger et al. do not fully account for the energetic and reproductive benefits accrued to human mothers through the processes of biocultural reproduction discussed above. Burger et al.'s analysis relies on the assumption that maternal per-offspring RE is reflected in the size of an offspring at nutritional independence from maternal metabolism. Nutritional independence from the mother is relatively simple to estimate for a reptile—when the egg is laid or the viviparous offspring are birthed (Somma (2003) describes some rare exceptions). For most mammals, nutritional independence from the mother is achieved at weaning (end of lactation). Cooperative breeding mammals are exceptions, as some food provisioning may be common to weaned young.

Charnov et al.'s (2007) definition of nutritional independence is central to their estimation of LRE in non-human species. That definition of nutritional independence clearly does not apply to species with extensive nutritional transfers from alloparents. The human species is most notable in this regard. For humans, weaning is not equivalent with nutritional independence from the mother as she is likely to continue to supply food for many years. A further complication for humans is that both prior to weaning and for many years post-weaning other people will supply food to infants, children, juveniles, adolescents and even adults (Reiches et al., 2009; Kramer & Ellison, 2010). Accordingly, the definition of LRE likely needs modification when applied to the bioculturally reproducing human species.

In their estimation of human LRE, Burger et al. treat humans as if there were no pre-weaning alloparental transfers. Burger et al. (2010) also assume that the age of independence in humans occurs at the age of complete weaning, which they define as 3 years after birth. They then use values for average offspring weight (in grams) at that age for the variable "litter size" in their empirical estimation of LRE. Elsewhere, we have examined in greater detail these assumptions and explored strategies for calculating LRE that account for more of the features of our unique strategy of biocultural reproduction (Bragg et al., 2012). Here we present a summary of these considerations.

Across all placental mammals, three distinct phases of maternal investment in reproduction can be identified: (1) direct metabolic transfers during gestation, (2) a period of exclusive breastfeeding when all of the infant's nutritional needs are met via breast milk and (3) in many mammals, a period of "mixed" feeding during which infant nutritional requirements are met by a blend of infant self-provisioning and breast milk (Langer, 2008). The nature of this third, transitional feeding phase is greatly modified in humans compared to all other great apes and non-cooperatively breeding primates (van Noordwijk et al., 2013a). In wild Bornean orangutans, offspring are entirely dependent upon milk and do not initiate self-foraging until mid-way through the second year of life, with full weaning from milk occurring at an average of 6.5 years (van Noordwijk et al., 2013b). Humans, rather than shifting from milk to a combination of milk and self-provisioning, shift from milk to "complementary feeding" wherein still-dependent and nursing offspring are fed nutritionally-rich, specially prepared foods (Bogin, 1999; Knott, 2001; Lancaster & Lancaster, 1983; Lee, 1996; Sellen, 2006). Complementary feeding of human infants generally begins ~6 months of age and often earlier, which means that, for the majority of the period of lactation, infants receive both their mother's milk and foods supplied from outside the mother's body. These complementary foods should *not* be included in the calculation of LRE which, according to Charnov et al. (2007), is reserved for the amount of energy that mothers provide as direct metabolic transfers to offspring.

The highest energetic output that an average human woman achieves during lactation is ~2.7 MJ/day (Prentice et al., 1996; Sellen, 2007), which is already outstripped by infant energy requirements at 6 months of age (Butte et al., 2000). Because energy needs continue to increase with age, the

proportion of infant needs met by breastfeeding will tend to progressively decline following peak lactation (Lee, 1996; Sellen, 2007). All of this theoretical discussion is consistent with empirical observations, from ethnographic research of human societies, of the role of both mothers and alloparents in providing a variety of foods to still breast-feeding infants, which can even include breast milk from wet-nurses (e.g. Hrdy (1999) for historical sources and Tronick et al. (1987) for a contemporary forager society example). Taking such factors into consideration, Sellen (2006, 2007) has estimated that supplementary feeding could account for 1.8 MJ/day of infant needs during the first year, which is the equivalent of about two-thirds (67%) of the energetic cost of peak lactation.

Using the same dataset as Burger et al. (2010), we re-estimated human LRE by modifying the equation for LRE to reflect these unique, species-defining characteristics of the human life history (Bragg et al., 2012). We re-calculated LRE by "adjusting" offspring size at weaning to reflect the proportion of offspring weight gained from conception through size at weaning "paid for" by maternal metabolism, as well as the portion paid for by complementary feeding. We followed Burger et al. (2010) and assumed age 36 months to be the age at weaning. We used the same data set of 15 small-scale forager and traditional subsistence-based societies. We re-calculated human LRE based on both "high" and "low" estimates of the energy savings afforded by complementary feeding, which were derived from the empirical data for infant energetic requirements and maternal breast milk production. With these modifications, we estimate that the LRE of human women is on the order of 1.02–1.23, assuming high (67%) to low (33%) proportions of the energetic needs of weanlings older than 6 months being met by complementary foods in lieu of breast milk (Bragg et al., 2012).

Our estimates of human LRE are 14–29% lower than that calculated by Burger et al. (2010). This difference represents a significant saving of energy expended on reproduction in both statistical terms and also in biological function. Statistically, the difference between Burger et al.'s (2010) mean LRE of 1.44 (SD = 0.22) and our conservative mean estimated LRE of 1.23 (SD = 0.20) results in a  $t = 2.65$  with  $p < 0.01$ . Biologically, our new human LRE values, ranging from 1.02–1.23, result in substantial energy savings that may be invested in other functions or needs. These include defense against infection, maintenance of the mother's body, food production and social interactions.

We have speculated that another life history change derived from associations between the evolution of childhood, biocultural reproduction and lower LRE may be greater longevity than any other primate species (Bogin, 2009; Kuzawa & Bragg, 2012). The energy savings invested in body maintenance may have slowed the senescence of somatic capacities and capital and prolonged human lifespan by several decades more than our closest great ape kin (Bragg et al., 2012; Crews & Bogin, 2010; Gurven et al., 2012; Kuzawa & Bragg 2012). In this way, the distinctive features of human biocultural reproduction, which co-evolved with the stage of human dependence known as childhood, may be directly linked with the evolution of our unusually long lifespan.

## Conclusions

In this review we propose that a new term, biocultural reproduction, best describes the human style of alloparental care of offspring. The evolution of the childhood life history stage in the human lineage made possible new opportunities for reproductive success, in particular by allowing infants to be weaned earlier and shortening inter-birth intervals. This strategy would only be favoured by natural selection if the increased rate of offspring production was also followed by the survival of the offspring to adulthood. Perhaps in service of this need, the evolution of human childhood was accompanied by a shift from the typical mammalian pattern of a unique attachment dependence between the infant and the biological mother to the human pattern, in which attachment is expanded outward to other members of the social group in a locally- and culturally-defined fashion via rules of kinship and marriage. It is this decoupling of allocare from genetic relatedness, more than anything, which sets humans apart from cooperative breeding species. In a re-evaluation of recent work, we estimate that the human strategy of biocultural reproduction results in a sizeable reduction in lifetime reproductive effort in humans. The excess maternal energy freed up through this strategy may have played an important role in the demographic success of humans over that of other ape species. In particular, lower human lifetime reproductive effort may have contributed the metabolic “fuel” necessary to slow the pace of ageing and extend lifespan, thereby expanding the pool of late life allocaregivers and possibilities for inter-generational transfers, which are critical to human biocultural reproduction.

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## Declaration of interest

The author reports no conflicts of interest. The authors alone are responsible for the content and writing of the paper.

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