Cooperative Breeding in Humans Pyter Douwe Bootsma - 02-07-2021



The evolution of childhood

The role of children in human life history, cooperative breeding, and sociality

Pyter Douwe Bootsma - s3811840

BSc. Biology, major Ecology & Evolution

Bachelor's Thesis

02-07-2021

Supervised by Prof. Dr. Hannah L. Dugdale Euan Young



5568 words

Abstract

Anthropology is a continuous effort of understanding the evolutionary origins of the modern human, and the implications of features that are uniquely human and have coevolved for millions of years. One theory considers childhood as an essential life-history element of the modern human. The implications of childhood are profuse: early weaning, a short interbirth interval, and raising multiple dependents at once. This would require high-quality nutrition and cooperative breeding to be possible, providing an argument for the evolution of sociality and a large brain. Yet modern human biology is so complementary that these traits seem prerequisites for one another and the evolutionary origins are difficult to dissect. I this thesis I try to answer the question "Is the evolution of childhood the original (coevolutionary) stimulant for the evolution of cooperative breeding and the concurrent uniquely human life history?" and I make an argument against the evolutionary significance of childhood in a literature study. Although childhood is unique to humans and important in the human cooperative breeding system, archaeological dental evidence reveals that childhood may have evolved much later than thought and not concurrent with other life-history traits such as brain size. Lastly, I formulate a novel hypothesis about the origins of childhood.

Introduction

We are the stranger in our midst. Humans are the exception in the great ape family. Bipedalism, naked skin, our large brains, the use of tools and fire and language are all novel traits in the evolution of the genus Homo (Crittenden, 2020). Humans have spread across the world in a demographically rapid expansion (Kramer, 2010; Vitousek et al., 1997). What sets us apart from other apes to be so successful: Large brains, sociality, extensive cooperation, culture, and childhood. Three traditional explanations for childhood are a period of extended brain growth, a period of learning adult skills, and "time for socialization, play, and the development of complex social roles and cultural behaviour" (Bogin, 2020). Childhood is thought to be revolutionary in the coevolution of life human life history, brain size, sociality, and what eventually made us a successful species.

Children play an important role in the human family. Although they cannot support themselves, they cooperate with their siblings, parents and others to divide and share labour and food resources (Bogin, 2020; Crittenden, 2020; Hrdy, 2011; Kramer, 2005a, 2011). Common tasks for children in traditional societies are gathering food or taking care of younger siblings. Especially young children require adult help or assistance or teaching. As children grow up, they become more capable of adult tasks related to the human diet, such as harvesting, hunting, butchering, preparing foods, and cooking. Still, their consumption outweighs their production until they are about 16 years old (Kramer, 2005a, 2014). Often, juveniles continue living with their families even though they are self-sustaining. Cooperative breeding (and kin selection) and a division of labour can explain help by parents, siblings, grandparents, and even unrelated individuals (Kramer, 2011). During this period, juveniles can gain (indirect) fitness benefits by helping their families and siblings when they cannot reproduce yet themselves (Kramer, 2011).

Sibling cooperation and continued help from juveniles are regarded as one aspect of a broader pattern of human cooperation in food provisioning and breeding (Kramer, 2011). Life history seems to be centred around and has evolved convergently with cooperative breeding and sociality (Burkart et al., 2009; Crittenden, 2020; Leigh, 2001). Many distinctly human traits are associated with providing help or requiring help from others. Especially in the latter category, many of these traits are associated with early human life and motherhood (Crittenden, 2020). The period between infancy and maturity is filled in very different in human and ape life history and can be immediately linked to cooperative breeding. Bogin (1997) argues that this period, which has a major impact on the ecology of human breeding, includes a life stage that is unique to humans: "the period following infancy, when the youngster is weaned from nursing but still depends on older people for feeding and protection."; in one word: childhood.

Human mothers care for multiple children at a time. Offspring is stacked and families consist of siblings of varying ages and needs. As such, mothers require help (Crittenden, 2020). Luckily, the social system provides helpers in the form of siblings, grandmothers, fathers, and even friends. It is argued that life history and cooperative breeding are so complementary they must have evolved at once (Burkart et al., 2009; Kramer, 2014) and possibly soon after the evolutionary split between the apes and early humans (Kaplan et al., 2000; van Schaik & Burkart, 2010).

The evolution of childhood is a disputed topic. Some oppose theories of allometry (Charnov & Berrigan, 1993) and gradual evolution of human (and ape) ontogeny (Leigh, 2001; Robson & Wood, 2008), and instead suggest the insertion of childhood during human evolution as a unique and novel life stage (Bogin, 1997). Yet others say that the multitude of life-history traits most likely not evolve at the same time, but separated in time (Robson & Wood, 2008). Therefore, the theory that cooperative breeding and childhood evolved during or soon after the split between Pan and Homo may be debunked. The consensus is that our high offspring survival rate is only possible because of cooperative breeding (Bogin, 2020; Hrdy, 2011; Kramer, 2005a) and that human life-history traits coevolved with cooperative breeding. This means that if childhood evolved rapidly, so did other life-history traits and cooperation. This begs the question: Is the evolution of childhood the original (coevolutionary) stimulant for the evolution of cooperative breeding and the concurrent uniquely human life history?

Evolution of cooperative breeding – theory

Humans have a tendency to form groups and the capacity to form complicated cooperative networks. How and why this behaviour evolved to be so much more complex than in the apes is one of the major questions in anthropology (Enfield & Levinson, 2006). In this thesis, the focus is cooperative breeding, so this will be specifically addressed.

When Charles Darwin wrote his 'On the Origin of Species' (Darwin, 1859), he pondered what the implications of cooperation were for his theory of evolution (Dugatkin, 1997), for cooperation is a behaviour that is beneficial to the receiver but can be costly to the helper (Nordell & Valone, 2021). Time and energy spent helping others cannot be allocated to your own wellbeing and reproduction. As such, cooperation seems to be costly and would not be expected to persist under natural selection.

This paradox endures because it is not immediately clear how the helper benefits. With mutualistic interactions, all cooperators benefit, which outweighs the costs (Brown, 1983). However, in altruism, or one-way cooperation, this is not the case. Hypotheses about the benefits and evolution of cooperation range from genetic relatedness (Hamilton, 1964a) to tit-for-tat (Axelrod & Hamilton, 1981) to more complex mechanisms among which debatable multi-level selection (Avilés, 1999). Cooperation in humans is complex, such that most mechanisms can be observed in human life and thus play a role in evolution.

Kin selection

Although Darwin did not know about genetics and relatedness, he predicted that selection may act at a level of kin rather than the individual (Axelrod & Hamilton, 1981). This solution to his paradox forecast the theory of kin selection by Hamilton (1964a). According to Hamilton, not individuals, but genes are the units of selection. This means that natural selection favours the propagation of copies of an individual's genes rather than an individual's reproduction.

The crux of kin selection theory is that all genes (mutations aside), are and have copies and it does not matter which copy of the gene is passed on. Direct reproduction is a favourable strategy because it is the most direct way of propagating genes; The benefits from this are

Cooperative Breeding in Humans Pyter Douwe Bootsma - 02-07-2021

called personal fitness. Because relatives share genes from a common ancestor, some of the shared gene copies will also be passed on if a relative reproduces. As such, kin selection explains cooperative breeding behaviour in which individuals forego direct reproductive potential to increase the reproductive potential of relatives (Hamilton, 1964a). The indirect benefits to the helper are called inclusive fitness.

Yet, for cooperative breeding to be favourable, more gene copies must be passed on by helping than are lost from direct reproduction (Hamilton, 1964b). Because relatedness is de facto the proportion of shared genes, this influences the fitness return from helping. This is spelt out in Hamilton's rule: r*b > c. In other words, this means: the inclusive fitness benefits, which is relatedness (r) multiplied with the relative's direct benefits (b), must outweigh personal fitness costs (c) of foregoing direct reproduction. Only then, helping is favourable. So, in situations in which individuals cannot reach a high direct reproductive potential themselves, they should help. In humans, such situations are for example found when people continue living after reproductive cessation (Lahdenperä et al., 2004) or when juveniles have not yet reached sexual maturity (Kramer, 2011).

Reciprocity

Humans are very social and interact and cooperate intensively with both related and unrelated individuals. Close friends are often treated the same as kin, especially by women (Ackerman et al., 2007). Women in their reproductive period and older are known to form cooperative breeding groups, foraging with and caring for the children (Hawkes et al., 1997; Hrdy, 2011). Especially in patrilocal mating systems, these groups include non-kin (Pasternak et al., 1997). Such shared tasks play a role in social bonding (Wolf et al., 2016). Yet, this behaviour cannot be explained by kin selection*. Instead, reciprocity may explain cooperative behaviour among non-kin.

Direct reciprocity is based on repeated encounters between individuals that cooperate or defect (fail to cooperate) (Sachs et al., 2004; Trivers, 1971). Tit-for-tat is a simple mechanism that explains cooperation (Axelrod & Hamilton, 1981). If in repeated encounters, one individual cooperates, the other will cooperate too. However, if they defect, 'eye for an eye' interactions, there is no cooperation. The first interaction between individuals may be a prisoner's dilemma (Luce & Raiffa, 1989): two suspects can either confess (defect) or deny (cooperate) involvement in a crime. The two individuals can benefit most (they go free) if they both cooperate. However, if the other defects, cooperation would be more costly (longer sentence) than when both individuals defect (reduced sentence). As such, the safest option is to defect. This would lead to defection by definition (Selten & Hammerstein, 1984). However, humans are empathic, prosocial, and generous (Waal, 2012) and are not likely to defect but cooperate when others do not. Also, people may not always run into the same individuals again.

^{* (}except if biases in kinship recognition are considered that avoid the more costly error of not recognising kin in favour of falsely recognising close individuals as kin (Haselton & Nettle, 2005).

In human sociality, cooperation surpasses individual interactions. Within social groups, reputation as a cooperator or defector plays a role (Nowak & Sigmund, 1998). Communication about previous interactions within a group forms a social pressure to cooperate to not be excluded. In modern society, this system of reputation and social pressure developed into morality and ethics (Alexander, 1987). In the human ultra-social society people are expected to cooperate and regarded as trustworthy until they prove otherwise.

The evolution of ultra-sociality is interesting because there may be a role for multi-level selection (J. M. Smith, 1976), which is a disputed topic **. According to multilevel selection theory, individuals in cooperative groups have a fitness advantage and can outcompete groups of defectors, even if defecting would be a better strategy within a group of cooperators (Traulsen & Nowak, 2006).

Groups of cooperators are more successful hunters, foragers, breeders and defenders (J. E. Smith et al., 2012). cooperation is thought to have influenced human expansion to endure harsh demographic and ecological conditions, periods, and areas (Avilés, 1999). Still, it is observed in humans that under inter-group conflict, (male) friendship bonds tend to be stronger (Geary & Flinn, 2002; Taylor et al., 2000).

Competition between groups can also be explained by green beard dynamics (Gardner & West, 2010; Riolo et al., 2001). Individuals with a certain trait, a so-called green-beard, help others with the same trait, or are spiteful towards others without the trait (figure). Humans do not necessarily have such green-beard traits, but can create green-beard like dynamics through social or cultural processes. Nationality, ancestry, beliefs, politics, language (Lindenfors, 2013), complexion (Price, 2000), chauvinism, and even more arbitrary requirements (such as affiliation for the sake of being a group) in humans lead to (organised) cooperation, spitefulness, or exclusion (Dunham & Emory, 2014). Cooperation has been proposed to have coevolved with the emergence of culture in humans (Silk & House, 2016).

Human life history and cooperation

Humans have an extraordinary life history. The entire human life is dictated by cooperation. The evolution of sociality is linked to the rise of culture (Enfield & Levinson, 2006), cooperative food provisioning (J. E. Smith et al., 2012), and cooperative breeding (Kramer, 2010). Cooperative hunting most likely evolved as a means of sustaining the energetic requirements of human life history and cooperative breeding. Culture probably evolved only after sociality. As such, cooperative breeding probably evolved first and is most directly linked to our ecology. Interestingly, not only social but also many life-history traits can be linked to cooperative breeding.

^{**} multilevel selection is not a mechanism that drives the evolution of cooperation. Multilevel selection only could maintain cooperation, yet this is like stating you need cooperators to cooperate, which is the case by definition. This can be explained on the individual level by a system of cooperation and reputation system to prevent defection within groups.

Cooperative Breeding in Humans Pyter Douwe Bootsma - 02-07-2021

Like all apes, human life history is slow. This is characterised by slow development, few but energetically expensive offspring, late maturity, a high survival rate, and long lives (Charnov & Berrigan, 1993). In humans, the slowness of these traits is exaggerated (Leigh, 2001); Human life history is the slowest of all apes (Robson & Wood, 2008). Relatively late age at first birth at about 18-20 years (compared to 13-14 in our closest relatives, the genus *Pan*, including chimpanzees and bonobos) old allows for slower and longer growth, resulting in larger-bodied mothers that can produce larger, expensive offspring (Crittenden, 2020; Robson et al., 2006).

Especially brain development is energetically expensive, which explains why larger brained species, such as primates, have slower life histories (Barton & Capellini, 2011). Thus, Charnov & Berrigan (1993) explain, based on allometry, that primate lifespan is long because large brains are costly to develop. Counter to allometry, however, human gestation length is short relative to our body and brain size. As such, human babies are secondarily altricial, under-developed and helpless, at birth (Crittenden, 2020; Foley et al., 1991). This means that an important part of early human development is post-natal, requiring continued intensive parental effort, such as nursing and weaning. Yet human infants are relatively heavy at birth,

which is mainly the result of large fat stores Mothers too are relatively fat, which is probably related to sustaining milk production under periods of malnourishment (Lee, 1987; Ulijaszek, 2002).

Most apes wean their infants when they reach about 1/3 of maternal body weight (Charnov & Berrigan, 1993) and the first permanent molar erupts (H. B. Smith et al., 1994); In humans, this would be about 6-7 years of age (Lee et al., 1991) (and 4.5 years in the genus Pan) (Robson & Wood, 2008). However, again counter to allometry, the human nursing and weaning period is relatively very short at 2.8 years. This allows for a short interbirth interval so mothers can get offspring in rapid succession (Alvarez, 2000; Walker et al., 2006). That is every 3 years, compared to 6 years in chimpanzees (Robson & Wood, 2008). Usually, there is a trade-off between a longer period of weaning and a high infant survival rate or a shorter inter-birth interval and lower infant survival (N. B. Jones, 1986). Yet compared to other apes, humans wean their infants earlier, have a shorter inter-birth interval, and higher infant survival; how is this possible?

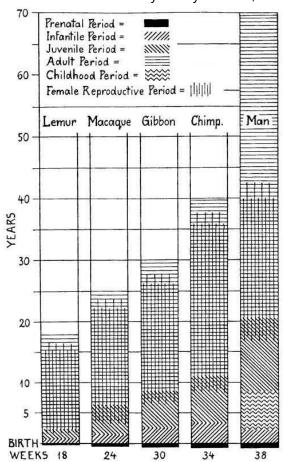


Figure 1: the timing and duration of different primate life history stages in years of total life. Note the long post-reproductive lifespan in humans, which could be called elderhood and the addition of the 'childhood' period between the infantile and juvenile periods. (Adapted from Bogin, 1997; Schultz, 1960)

Pyter Douwe Bootsma - 02-07-2021

BOX 1: HUMAN NUTRITION AND CHILDREN

Food provisioning requires a large skillset (Kramer, 2005a); Apart from procuring food through foraging, harvesting, or hunting, many foods require extensive processing, such as butchering, cracking, hulling, winnowing, shelling, leaching, pounding, grinding, drying, salting, smoking or cooking before it is edible. Children are often physically unable or too inexperienced to carry out such tasks. Thus, adults have to prepare the foods (Kramer, 2005a). It is our large and fast-growing brain that necessitates a high-quality diet (Leonard & Robertson, 1994) and especially weaning and children's foods need to be nutritious and easily digestible because of fast growth and an immature digestive system (Bogin, 1997). Humans can create foods that can be fed to infants earlier, reducing the weaning period.

As children grow up, they become more able to procure and process foods (Bock & Johnson, 2004). Young children quickly learn to forage for foods such as fruits and shellfish, which they can process and eat themselves (Draper & Cashdan, 1988; Hawkes et al., 1997). Children can procure up to 50 per cent of their consumption when they are 5-6 years old (Kramer, 2002), yet children's dependency on adults varies with what foods are available (Kramer, 2005a). Most foods require more processing and proper nutrition consists of a variety of foodstuffs. As such, the preparation of a full meal requires a multitude of tasks of different skill levels. This is represented in an age-graded division of labour (Kramer, 2014). For example, men and older juvenile boys hunt for large game (R. A. Gould et al., 1980), younger juveniles harvest enough vegetables such as maize to provide for the whole family, and the raw materials are processed by women and older sisters (Kramer, 2005b).

A major role is reserved for the period that follows infancy but precedes the juvenile stage: childhood. According to Bogin (1997), this is a unique developmental life stage that evolved in humans. Others suggest that the characteristics of childhood are the result of heterochrony or the evolution of timing and duration of developmental processes (S. J. Gould, 1985; McNamara, 2012).

Childhood is characterised by immature dentition, a small digestive system, and a large and quickly developing brain (Bogin, 1997). At the same time, children are not capable of providing for themselves and need adult help, in part due to the high-quality (Leonard & Robertson, 1994) nature of human nutrition, which requires extensive preparation (Box 1) (Kramer, 2005a). Only cooperative breeding can provide the energetic demands of human reproduction.

When infants reach nutritional independence, the juvenile period starts. As mentioned before, apes are weaned when they reach about 1/3 of maternal body weight and the first permanent molar erupts. That is 4.5 years old for chimpanzees and the human equivalent would be 7 years of age (Bogin, 1997), which happens to be when human brain growth slows down (Bogin, 2020). Although humans are not yet nutritionally dependent at 7, able of producing only about 50 per cent of their own consumption (Kramer, 2005a), this is established as the end of childhood and the start of the juvenile period (Bogin, 1997). Humans reach nutritional independence at about 15 years of age, and then continue living with the family until they can reproduce themselves; usually, sexual maturity is reached at 19-20 years old (Kramer, 2005a).

From these characteristics of human life history, an unusual, and uniquely human, family structure emerges: mothers care for multiple dependent offspring of different ages and

different (dietary) needs at the same time (Crittenden, 2020). This may seem impossible for a single mother... and it is. An estimate of the nutritional requirement of raising an infant to nutritional independence is about 13 million Kilocalories (Crittenden, 2020). At the extreme point, total family consumption for up to 7 'stacked' offspring needs to be provided by 45 hours of food provisioning a day (Kramer, 2005a). This requires provisioning efforts of multiple people; in other words, cooperative breeding is essential for the human breeding system.

The evolution of helpers

Cooperative breeding is interrelated with many life-history traits (Hamilton, 1966). So much so that it is unclear whether cooperative breeding is a requisite or the result of human life history and childhood in particular (Bogin, 1997; Walker et al., 2006). Brain size, for example, is suggested to be the driver of high-quality human nutrition (Leonard & Robertson, 1994), which requires cooperative food provisioning. Yet Dávid-Barrett & Dunbar (2013) suggest larger brains evolved to communicate as a response to larger group sizes that were necessary to provide food for another reason. The complementarity of cooperation and human life history (childhood and ontogeny) is sometimes explained by rapid coevolution (Aiello & Key, 2002; Hrdy, 1999, 2011; Salmon & Shackelford, 2007) and sometimes linked to the split between the genera *Homo* and *Pan* (Kaplan et al., 2000). Others provide evidence for a gradual and independent evolution of ontogenetic traits (Leigh, 2001; Robson & Wood, 2008), leaving the link with cooperative breeding enigmatic.

The traits mentioned in the previous section apply to mother and offspring and seem to necessitate cooperative breeding. However, some helpers' life-history traits seem to be specially adapted to breeding cooperatively. Grandmothers, for example, seem paradoxical. Unlike the apes, which generally do not survive long after female reproductive cessation, humans have an extraordinarily long post-reproductive lifespan (Ellis et al., 2018). A general pattern is that mammals reproduce until the end of life to maximise their fitness (Ellis et al., 2018; Packer et al., 1998). Yet humans live long after reproductive cessation. Menopause is at a similar timing to the apes' menopause at about 40-45 years of age. Yet where apes die shortly after, humans live another 20-30 years (Robson & Wood, 2008). Since women can also not reproduce in the considerably long period before maturity, the total female reproductive period is only 1/3rds of the total lifespan (see the reproductive period in figure 2). This is an incredibly small proportion compared to other mammals' reproductive lifespans (Ellis et al., 2018).

Common helpers (Box 2), also known as allomothers, are fathers (Marlowe, 2000), grandmothers (Alvarez, 2000; Coall & Hertwig, 2010; Hawkes et al., 1998), and siblings (Bogin, 1997; Kramer, 2005a, 2011, 2014; Turke, 1989; Zeller, 1987), as well as other relatives and (unrelated) friends (Wade & Hompe, 2018). In box 2, highlighted also are the evolution of paternal care and monogamy, family structure, the cooperative food provisioning and breeding system, and patrilocality. These elements of human life seem to have evolved in response to or reciprocally with the evolution of cooperative breeding.

BOX 2: WHY ALLOMOTHERS HELP	
FATHERS In most mammals, including chimpanzees and bonobos, fathers have no role in parental care (Clutton-Brock, 2019). This is the result of low paternal investment and a low certainty of paternity. In humans, fathers are expected to be allomothers because paternal investment is necessary for offspring survival (Clutton-Brock, 2019). Then, monogamy likely coevolves with parental care as increased paternal efforts are only likely if the certainty of paternity is high. This requires mate guarding, which conversely reduces the opportunity of extra-pair matings (Geary, 2000). Also, if males in a group are related, such as under patrilocality (Pasternak et al., 1997), they gain inclusive fitness from other pairs' reproduction, further reducing benefits (and costs) of extra-pair matings. Moreover, ovulation in humans is concealed such that it is unclear whether women are receptive to pregnancy (Burley, 1979), further decreasing the benefits of polygamy (Geary, 2000).	GRANDMOTHERSForelderwomen, greater risks are associated with reproduction and childbirth, resulting in decreasing average fitness returns of direct reproduction. As such, the costs of menopause are limited, but not nil.ItItis hypothesised that the evolution of menopause at an age at which women from the next generation start breeding can prevent intergenerational breeding competition (Cant & Johnstone, 2008). Under patrilocality (Pasternak et al., 1997) such as in humans, the younger generation is comprised of immigrant women, and older women are more related* to group members (Cant & Johnstone, 2008).As such, older women lose the least and gain the most from helping and so lost the evolutionary conflict for direct reproduction (Johnstone & Cant, 2010). Then, the increased post- reproductive lifespan can be directly linked to the inclusive fitness benefits of cooperative breeding (Alvarez, 2000).
SIBLINGS Like grandmothers, siblings help when they are not capable of direct reproduction. Human siblings are relatively ^{**} related (r=0.5) in monogamous mating systems (Hagen & Barrett, 2009), so the inclusive fitness benefits are large. Children continue living with the family up to nutritional dependency (16 Y), maturity (19-20 Y) (Hagen & Barrett, 2009), and possibly beyond if there are no suitable mates. These older siblings do not compete with younger, dependent siblings for resources as individuals older than 16 on average produce more than they consume (Kramer, 2005b). Group dynamics provide a steady rate of nutrition (see BOX 1) and cooperative siblings are suggested to have evolved within this framework (Kramer, 2011). Cooperative efforts sometimes decrease personal survival, but this seems limited in humans because survival after childhood is generally very high (Kaplan et al., 2000).	FRIENDS Here, helpers that are not related are considered. They do not get any direct or inclusive fitness benefits from helping. Yet unrelated helpers may be part of the cooperative breeding and food provisioning system, in which every group member has a role (Taylor et al., 2000). Because of patrilocality (Pasternak et al., 1997), especially young women happen to be unrelated to most group members. This may explain why women are more likely to perceive and treat friends as kin (Ackerman et al., 2007; Geary & Flinn, 2002). Some tasks, such as hunting large game, protecting, raising children, or meal preparation*** simply require multiple people to carry out. Then, individuals can gain direct fitness benefits by helping. For example, someone who helps preparing food gets a share of the meal. If this is the only reason for helping, this is called pseudoreciprocity (Sachs et al., 2004). This may explain why unrelated individuals pertain to the group dynamics.

* This relatedness increases with age: unrelated brothers and fathers in law die of old age and younger males are of her descent (Johnstone & Cant, 2010)

** e.g. r= 0.25 for grandmothers and -children

*** considering the procurement and preparation of multiple food resources

Evolution of human ontogeny and childhood

Finally, the last step can be taken in the reasoning to answer the research question "Is the evolution of childhood the original (coevolutionary) stimulant for the evolution of cooperative breeding and the concurrent uniquely human life history?" From the previous sections, it has become clear that cooperative breeding, childhood, nutrition, and female life history are interrelated (also, S. J. Gould, 1985). Cooperative breeding (Miller et al., 2019; Robson & Wood, 2008), and childhood are all suggested to have played a major role in the evolution of the female life history (Robson et al., 2006). Other theories ascribe slow human development to harsh ecological conditions (J. H. Jones, 2011) requiring the build-up of fat stores as a buffer or to the energetic requirement of developing a large brain, (Ulijaszek, 2002; Walker et al., 2006).

Although it is difficult to find archaeological evidence for cooperative breeding and human life history, fossils provide ample evidence about dental and skeletal development, which are a proxy for human life history and so, childhood (Robson & Wood, 2008; Wood & Lonergan, 2008). Growth rates in the legs, trunk, head, face, jaws, teeth, and body differ and change in relation to the developmental stage an individual is in (Bogin, 1997). As growth rates can be detected from fossil evidence, the relative growth rates of body parts in early hominids can be compared to modern human ontogeny. Changes that can be reliably found in the fossil evidence of the evolution of the *Homo* genus are the size and shape of the canines and mandible, the morphology of the limbs, and cranial development (Robson et al., 2006).

Based on estimates derived from fossil evidence, there was an apparent fast and substantial increase in the mean body about 2 Mya, before which hominins were chimpanzee sized (Robson & Wood, 2008). Yet for *H. rudolfensis* and *H. habilis*, this body size increase was earlier, about 2.4 Mya. Modern human sexual dimorphism seems to have evolved more gradually and a larger cranial or brain size evolved only in later *Homo* species (*sapiens, neanderthalensis, heidelbergensis*) (Robson & Wood, 2008). As such, there is a discrepancy in body and brain size development that contradicts coevolution.

Also, dental development is an important indicator of life history (B. H. Smith, 1989). This development is especially related to nutrition, which is an important characteristic of human childhood. T. M. Smith et al. (2007) show that the dental development of a neanderthal juvenile (estimated at 8 years old) is comparable to that of several years older modern human juveniles. In agreement with earlier studies (Bromage & Dean, 1985; B. H. Smith, 1989), this suggests that *H. sapiens* dental development is delayed compared to its closest (extinct) relative and that prolonged childhood is unique to *H. sapiens* (T. M. Smith et al., 2007). Recent developments in the field are more nuanced in their age estimates, which means early *Homo* dental development falls within the range of variation between modern humans (Dean & Liversidge, 2015).

All in all, the evolution of human body size, brain size, and dental development are not necessarily related to one clear shift of human life history, which would include childhood. Even if childhood would be dismantled and only represented by dental development, there is no consensus for when "a modern human-like schedule of dental development" appeared in the fossil record (Dean & Liversidge, 2015), with some assuming very early (Dean & Liversidge,

2015; Wood & Collard, 1999) in hominid evolution and others very recently (T. M. Smith et al., 2007). Other life-history traits suggest maybe somewhere in the middle (Robson & Wood, 2008), in agreement with (Bogin, 1997). However, it seems that life-history traits evolved independently, gradually and at different times; it is likely that within genus *Homo*, there have been life histories different from what we know of modern humans and apes (Robson & Wood, 2008).

I think that, still, developments in cooperation and diet quality (Dunbar, 2014) seem to have made possible larger body and brain size (Antón et al., 2014; Dávid-Barrett & Dunbar, 2013), increased longevity, and a short interbirth interval (Crittenden, 2020). It is still unclear what drove the need for high diet quality, cooperation and unusual female life history (Hrdy, 2011). In my opinion, one theory explains well the evolutionary foundation of a slow history and potentially large brain size, which would require and enable cooperation: Fat babies and mothers in response to periods of harsh ecological conditions (J. H. Jones, 2011; Ulijaszek, 2002; Walker et al., 2006).

Larger and fatter mothers need to invest a smaller proportion of their daily energy budget in fetal tissue, which is observed in larger primates and especially the *Hominidae* (Ulijaszek, 2002). This allows for a relatively large investment in fetal tissues, among which fats and the brain, longer gestation and slower growth in general. Then, although humans are altricial, infants are relatively heavy and large-brained at birth. As such mothers and infants would be able to survive periods of malnutrition. In periods of no malnutrition, human infants could continue developing; initially quickly, then slower (as observed in childhood (Bogin, 1997)). Although this theory provides a starting point, still, the dynamics of further coevolution of life history, brain size, and cooperation are unclear, though cooperation could also be a response to harsh conditions (Walker et al., 2006).

Conclusion

The scientific consensus is that the clear distinction in life history between humans and the other apes suggests a simultaneous adaptive evolution of these traits. Possibly, this would have been one (rapid) (co-)evolutionary event that is related to the split between genera *Homo* and *Pan* or early hominins such as *Australopithecus*. If so, this could explain why childhood is sometimes regarded as a novel and unique life stage in humans instead of a series of heterochronous, ontogenetic adaptations The insertion of childhood in human development (possibly with *Homo* habilis about 2.3-1.5 Mya) would be the major breakthrough that sets apart humans from other hominids and started a rapid coevolutionary revolution in human life history, cooperation, brain (and body) size, nutrition and food provisioning, and sociality.

To answer the research question "Is the evolution of childhood the original (coevolutionary) stimulant for the evolution of cooperative breeding and the concurrent uniquely human life history?", I would say no.

On one hand, childhood is unlikely to have evolved in one evolutionary event, but rather is a conglomeration of life-history traits that probably evolved gradually and at different times. As such, the insertion of childhood as a novel human life stage, and the starting point seems

unlikely. Despite this, the human reproductive system is complicated and unique in many ways and children play an important role in the cooperative breeding system. Extinct species from the genus Homo likely featured equally unique life histories, other than any known from extant hominids.

On the other hand, Hypotheses about the evolution of cooperative breeding, life history, large brains, and sociality are accumulating and no consensus has yet been reached. It is unclear what could have been the evolutionary stimulus, because the elements seem to be, more than just complementary, a prerequisite for one another. As such, a reasonable assumption is the coevolution of these traits, which has now reached relative scientific consensus. In this sense, childhood, whether as a defined life stage or just a period in human development, certainly can be regarded as a stimulant, though not definitively the starting point. Still, it is unclear what could have sparked the coevolution of these traits and how it was adaptive before it consolidated into modern human life history.

On that note, lastly, I would like to formulate an alternative hypothesis for the evolution of early weaning and a short interbirth interval and childhood, which I did not encounter in the scientific literature: Humans use endless food processing practices to procure and produce very high-quality nutrition. It is not unimaginable that humans were able to create potent weaning foods, highly nutritional and easily digestible, that could be fed to infants much earlier than before. As such, this may have opened up an opportunity for women to stop weaning earlier. This could thus have resulted in the progressive evolution of a shorter interbirth interval and childhood.

Cooperative Breeding in Humans Pyter Douwe Bootsma - 02-07-2021

Bibliography

Ackerman, J. M., Kenrick, D. T., & Schaller, M. (2007). Is friendship akin to kinship? Evolution

and Human Behavior, 28(5), 365–374.

https://doi.org/10.1016/j.evolhumbehav.2007.04.004

Aiello, L. C., & Key, C. (2002). Energetic consequences of being a Homo erectus female.

American Journal of Human Biology, 14(5), 551–565.

https://doi.org/10.1002/ajhb.10069

Alexander, R. D. (1987). The Biology of Moral Systems. Transaction Publishers.

Alvarez, H. P. (2000). Grandmother hypothesis and primate life histories. American Journal of

Physical Anthropology, 113(3), 435-450. https://doi.org/10.1002/1096-

8644(200011)113:3<435::AID-AJPA11>3.0.CO;2-O

- Antón, S. C., Potts, R., & Aiello, L. C. (2014). Evolution of early Homo: An integrated biological perspective. *Science*, *345*(6192). https://doi.org/10.1126/science.1236828
- Avilés, L. (1999). Cooperation and non-linear dynamics: An ecological perspective on the evolution of sociality. *Evolutionary Ecology Research*, 1(4), 459–477.

Axelrod, R., & Hamilton, W. D. (1981). The Evolution of Cooperation. *Science*, *211*(4489), 1390–1396. JSTOR.

Barton, R. A., & Capellini, I. (2011). Maternal investment, life histories, and the costs of brain growth in mammals. *Proceedings of the National Academy of Sciences*, *108*(15), 6169–6174.

Bock, J., & Johnson, S. E. (2004). Subsistence ecology and play among the Okavango Delta peoples of Botswana. *Human Nature*, *15*(1), 63–81.

Bogin, B. (1997). Evolutionary hypotheses for human childhood. *American Journal of Physical Anthropology*, *104*(S25), 63–89. https://doi.org/10.1002/(SICI)1096-

8644(1997)25+<63::AID-AJPA3>3.0.CO;2-8

Bogin, B. (2020). Patterns of Human Growth. Cambridge University Press.

- Bromage, T. G., & Dean, M. C. (1985). Re-evaluation of the age at death of immature fossil hominids. *Nature*, *317*(6037), 525–527. https://doi.org/10.1038/317525a0
- Brown, J. L. (1983). Cooperation—A Biologist's Dilemma. In J. S. Rosenblatt, R. A. Hinde, C.
 Beer, & M.-C. Busnel (Eds.), *Advances in the Study of Behavior* (Vol. 13, pp. 1–37).
 Academic Press. https://doi.org/10.1016/S0065-3454(08)60284-3
- Burkart, J. M., Hrdy, S. B., & Schaik, C. P. V. (2009). Cooperative breeding and human cognitive evolution. *Evolutionary Anthropology: Issues, News, and Reviews*, 18(5), 175–186. https://doi.org/10.1002/evan.20222
- Burley, N. (1979). The Evolution of Concealed Ovulation. *The American Naturalist*, *114*(6), 835–858. https://doi.org/10.1086/283532
- Cant, M. A., & Johnstone, R. A. (2008). Reproductive conflict and the separation of reproductive generations in humans. *Proceedings of the National Academy of Sciences*, *105*(14), 5332–5336.
- Charnov, E. L., & Berrigan, D. (1993). Why do female primates have such long lifespans and so few babies? Or Life in the slow lane. *Evolutionary Anthropology: Issues, News, and Reviews*, 1(6), 191–194. https://doi.org/10.1002/evan.1360010604
- Clutton-Brock, T. H. (2019). The Evolution of Parental Care. In *The Evolution of Parental Care*. Princeton University Press.

http://www.degruyter.com/document/doi/10.1515/9780691206981/html

Coall, D. A., & Hertwig, R. (2010). Grandparental investment: Past, present, and future.

Behavioral and Brain Sciences, 33(1), 1–19.

https://doi.org/10.1017/S0140525X09991105

Crittenden, A. (2020, November 23). Exploring The Human-Ape Paradox: The Foundations of

Cooperative Breeding.

https://www.youtube.com/watch?v=qymmM7yaa9s&list=LL&index=1&t=600s

- Darwin, C. (1859). On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life. Read Books Ltd.
- Dávid-Barrett, T., & Dunbar, R. I. M. (2013). Processing power limits social group size:
 Computational evidence for the cognitive costs of sociality. *Proceedings of the Royal Society B: Biological Sciences*, *280*(1765), 20131151.
 https://doi.org/10.1098/rspb.2013.1151

111ps.//doi.org/10.1090/15pb.2013.1131

- Dean, M. C., & Liversidge, H. M. (2015). Age estimation in fossil hominins: Comparing dental development in early Homo with modern humans. *Annals of Human Biology*, 42(4), 415–429. https://doi.org/10.3109/03014460.2015.1046488
- Draper, P., & Cashdan, E. (1988). Technological Change and Child Behavior among the !Kung. *Ethnology*, *27*(4), 339–365. https://doi.org/10.2307/3773398
- Dugatkin, L. A. (1997). *Cooperation Among Animals: An Evolutionary Perspective*. Oxford University Press.
- Dunbar, R. (2014). Human Evolution: A Pelican Introduction. Penguin UK.
- Dunham, Y., & Emory, J. (2014). Of affect and ambiguity: The emergence of preference for arbitrary ingroups. *Journal of Social Issues*, *70*(1), 81–98.

Ellis, S., Franks, D. W., Nattrass, S., Cant, M. A., Bradley, D. L., Giles, D., Balcomb, K. C., & Croft,
D. P. (2018). Postreproductive lifespans are rare in mammals. *Ecology and Evolution*,
8(5), 2482–2494. https://doi.org/10.1002/ece3.3856

Enfield, N. J., & Levinson, S. C. (2006). Roots of human sociality. New York: Berg.

Foley, R. A., Lee, P. C., Widdowson, E. M., Knight, C. D., Jonxis, J. H. P., Widdowson, E. M.,
Whiten, A., & Bone, Q. (1991). Ecology and energetics of encephalization in hominid evolution. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 334(1270), 223–232. https://doi.org/10.1098/rstb.1991.0111

Gardner, A., & West, S. A. (2010). Greenbeards. *Evolution*, 64(1), 25–38.

https://doi.org/10.1111/j.1558-5646.2009.00842.x

- Geary, D. C. (2000). Evolution and proximate expression of human paternal investment. *Psychological Bulletin*, *126*(1), 55–77. https://doi.org/10.1037/0033-2909.126.1.55
- Geary, D. C., & Flinn, M. V. (2002). Sex differences in behavioral and hormonal response to social threat: Commentary on Taylor et al. (2000). *Psychological Review*, 109(4), 745– 750. https://doi.org/10.1037/0033-295X.109.4.745
- Gould, R. A., Gould, & Gamble, P. of G. C. (1980). *Living Archaeology*. CUP Archive.

Gould, S. J. (1985). Ontogeny and Phylogeny. Harvard University Press.

- Hagen, E. H., & Barrett, H. C. (2009). Cooperative Breeding and Adolescent Siblings: Evidence for the Ecological Constraints Model? *Current Anthropology*, 50(5), 727–737. https://doi.org/10.1086/605328
- Hamilton, W. D. (1964a). The genetical evolution of social behaviour. I. *Journal of Theoretical Biology*, 7(1), 1–16. https://doi.org/10.1016/0022-5193(64)90038-4
- Hamilton, W. D. (1964b). The genetical evolution of social behaviour. II. *Journal of Theoretical Biology*, 7(1), 17–52. https://doi.org/10.1016/0022-5193(64)90039-6

- Hamilton, W. D. (1966). The moulding of senescence by natural selection. *Journal of Theoretical Biology*, *12*(1), 12–45. https://doi.org/10.1016/0022-5193(66)90184-6
- Haselton, M. G., & Nettle, D. (2005). The paranoid optimist: An integrative evolutionary model of cognitive biases. *Manuscript under Review*.
- Hawkes, K., O'Connell, J. F., & Blurton Jones, N. G. (1997). Hadza Women's Time Allocation, Offspring Provisioning, and the Evolution of Long Postmenopausal Life Spans. *Current Anthropology*, *38*(4), 551–577. https://doi.org/10.1086/204646
- Hawkes, K., O'Connell, J. F., Jones, N. G. B., Alvarez, H., & Charnov, E. L. (1998). Grandmothering, menopause, and the evolution of human life histories. *Proceedings of the National Academy of Sciences*, *95*(3), 1336–1339.
- Hrdy, S. B. (1999). Mother nature: A history of mothers, infants, and natural selection.
 https://static1.squarespace.com/static/56a7cac4e0327c116bd2394a/t/599f1ef9893fc0
 5aebcf8ebb/1503600378151/Mother+Nature+NYT+Excerpts.pdf
- Hrdy, S. B. (2011). Mothers and Others. Harvard University Press.
- Johnstone, R. A., & Cant, M. A. (2010). The evolution of menopause in cetaceans and humans: The role of demography. *Proceedings of the Royal Society B: Biological Sciences*, *277*(1701), 3765–3771. https://doi.org/10.1098/rspb.2010.0988
- Jones, J. H. (2011). Primates and the Evolution of Long, Slow Life Histories. *Current Biology*, *21*(18), R708–R717. https://doi.org/10.1016/j.cub.2011.08.025
- Jones, N. B. (1986). Bushman birth spacing: A test for optimal interbirth intervals. *Ethology* and Sociobiology, 7(2), 91–105. https://doi.org/10.1016/0162-3095(86)90002-6
- Kaplan, H., Hill, K., Lancaster, J., & Hurtado, A. M. (2000). A theory of human life history evolution: Diet, intelligence, and longevity. *Evolutionary Anthropology: Issues, News,*

and Reviews, 9(4), 156-185. https://doi.org/10.1002/1520-6505(2000)9:4<156::AID-

EVAN5>3.0.CO;2-7

Kramer, K. L. (2002). Variation in juvenile dependence. Human Nature, 13(2), 299–325.

https://doi.org/10.1007/s12110-002-1011-8

Kramer, K. L. (2005a). Children's Help and the Pace of Reproduction: Cooperative Breeding in Humans. *Evolutionary Anthropology: Issues, News, and Reviews, 14*(6), 224–237. https://doi.org/10.1002/evan.20082

Kramer, K. L. (2005b). Maya Children. Harvard University Press.

- Kramer, K. L. (2010). Cooperative breeding and its significance to the demographic success of humans. *Annual Review of Anthropology*, *39*, 417–436.
- Kramer, K. L. (2011). The evolution of human parental care and recruitment of juvenile help. *Trends in Ecology & Evolution*, *26*(10), 533–540. https://doi.org/10.1016/j.tree.2011.06.002
- Kramer, K. L. (2014). Why what juveniles do matters in the evolution of cooperative breeding. *Human Nature*, *25*(1), 49–65.
- Lahdenperä, M., Lummaa, V., Helle, S., Tremblay, M., & Russell, A. F. (2004). Fitness benefits of prolonged post-reproductive lifespan in women. *Nature*, *428*(6979), 178–181. https://doi.org/10.1038/nature02367
- Lee, P. C. (1987). Nutrition, fertility and maternal investment in primates. *Journal of Zoology*, *213*(3), 409–422. https://doi.org/10.1111/j.1469-7998.1987.tb03717.x
- Lee, P. C., Majluf, P., & Gordon, I. J. (1991). Growth, weaning and maternal investment from a comparative perspective. *Journal of Zoology*, *225*(1), 99–114. https://doi.org/10.1111/j.1469-7998.1991.tb03804.x

- Leigh, S. R. (2001). Evolution of human growth. *Evolutionary Anthropology: Issues, News, and Reviews, 10*(6), 223–236. https://doi.org/10.1002/evan.20002
- Leonard, W. R., & Robertson, M. L. (1994). Evolutionary perspectives on human nutrition: The influence of brain and body size on diet and metabolism. *American Journal of Human Biology*, 6(1), 77–88. https://doi.org/10.1002/ajhb.1310060111
- Lindenfors, P. (2013). The green beards of language. *Ecology and Evolution*, *3*(4), 1104–1112. https://doi.org/10.1002/ece3.506
- Luce, R. D., & Raiffa, H. (1989). *Games and Decisions: Introduction and Critical Survey*. Courier Corporation.
- Marlowe, F. (2000). Paternal investment and the human mating system. *Behavioural Processes*, *51*(1), 45–61. https://doi.org/10.1016/S0376-6357(00)00118-2
- McNamara, K. J. (2012). Heterochrony: The Evolution of Development. *Evolution: Education and Outreach*, 5(2), 203–218. https://doi.org/10.1007/s12052-012-0420-3
- Miller, I. F., Churchill, S. E., & Nunn, C. L. (2019). Speeding in the slow lane: Phylogenetic comparative analyses reveal that not all human life history traits are exceptional. *Journal of Human Evolution*, 130, 36–44. https://doi.org/10.1016/j.jhevol.2018.12.007

Nordell, S. E., & Valone, T. J. (2021). Animal behavior: Concepts, methods, and applications.

- Nowak, M. A., & Sigmund, K. (1998). Evolution of indirect reciprocity by image scoring. *Nature*, *393*(6685), 573–577. https://doi.org/10.1038/31225
- Packer, C., Tatar, M., & Collins, A. (1998). Reproductive cessation in female mammals. *Nature*, *392*(6678), 807–811. https://doi.org/10.1038/33910
- Pasternak, B., Ember, C. R., & Ember, M. (1997). Sex, gender, and kinship: A cross-cultural perspective. Pearson College Division.

Price, G. N. (2000). Evolution, green beards, and skin hue wage discrimination. *World Futures*, 55(4), 341–355. https://doi.org/10.1080/02604027.2000.9972787

Riolo, R. L., Cohen, M. D., & Axelrod, R. (2001). Evolution of cooperation without reciprocity. *Nature*, *414*(6862), 441–443. https://doi.org/10.1038/35106555

- Robson, S. L., van Schaik, C. P., & Hawkes, K. (2006). *The derived features of human life history*. https://core.ac.uk/reader/276278010
- Robson, S. L., & Wood, B. (2008). Hominin life history: Reconstruction and evolution. *Journal of Anatomy*, *212*(4), 394–425. https://doi.org/10.1111/j.1469-7580.2008.00867.x
- Sachs, J. L., Mueller, U. G., Wilcox, T. P., & Bull, J. J. (2004). The Evolution of Cooperation. *The Quarterly Review of Biology*, *79*(2), 135–160. https://doi.org/10.1086/383541
- Salmon, C. A., & Shackelford, T. K. (2007). *Family Relationships: An Evolutionary Perspective*. Oxford University Press.

Selten, R., & Hammerstein, P. (1984). Gaps in Harley's argument on evolutionarily stable learning rules and in the logic of "tit for tat". *Behavioral and Brain Sciences*, 7(1), 115– 116. https://doi.org/10.1017/S0140525X00026479

- Silk, J. B., & House, B. R. (2016). The evolution of altruistic social preferences in human groups. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*(1687), 20150097. https://doi.org/10.1098/rstb.2015.0097
- Smith, B. H. (1989). Dental Development as a Measure of Life History in Primates. *Evolution*, *43*(3), 683–688. https://doi.org/10.2307/2409073
- Smith, J. E., Swanson, E. M., Reed, D., & Holekamp, K. E. (2012). Evolution of Cooperation among Mammalian Carnivores and Its Relevance to Hominin Evolution. *Current Anthropology*, 53(S6), S436–S452. https://doi.org/10.1086/667653

Smith, J. M. (1976). Group Selection. The Quarterly Review of Biology, 51(2), 277–283. JSTOR.

- Smith, T. M., Toussaint, M., Reid, D. J., Olejniczak, A. J., & Hublin, J.-J. (2007). Rapid dental development in a Middle Paleolithic Belgian Neanderthal. *Proceedings of the National Academy of Sciences*, 104(51), 20220–20225.
- Taylor, S. E., Klein, L. C., Lewis, B. P., Gruenewald, T. L., Gurung, R. A. R., & Updegraff, J. A. (2000). Biobehavioral responses to stress in females: Tend-and-befriend, not fight-orflight. *Psychological Review*, *107*(3), 411–429. https://doi.org/10.1037/0033-295X.107.3.411
- Traulsen, A., & Nowak, M. A. (2006). Evolution of cooperation by multilevel selection. *Proceedings of the National Academy of Sciences*, *103*(29), 10952–10955. https://doi.org/10.1073/pnas.0602530103
- Trivers, R. L. (1971). The Evolution of Reciprocal Altruism. *The Quarterly Review of Biology*, 46(1), 35–57. https://doi.org/10.1086/406755
- Turke, P. W. (1989). Evolution and the Demand for Children. *Population and Development Review*, *15*(1), 61–90. https://doi.org/10.2307/1973405
- Ulijaszek, S. J. (2002). Comparative energetics of primate fetal growth. *American Journal of Human Biology*, *14*(5), 603–608. https://doi.org/10.1002/ajhb.10088
- van Schaik, C. P., & Burkart, J. M. (2010). Mind the Gap: Cooperative Breeding and the Evolution of Our Unique Features. In P. M. Kappeler & J. Silk (Eds.), *Mind the Gap: Tracing the Origins of Human Universals* (pp. 477–496). Springer. https://doi.org/10.1007/978-3-642-02725-3_22
- Vitousek, P. M., Mooney, H. A., Lubchenco, J., & Melillo, J. M. (1997). Human Domination of Earth's Ecosystems. *Science*, *277*(5325), 494–499.

https://doi.org/10.1126/science.277.5325.494

- Waal, F. B. M. de. (2012). The Antiquity of Empathy. *Science*, *336*(6083), 874–876. https://doi.org/10.1126/science.1220999
- Wade, T. J., & Hompe, C. (2018). Women's Friendship: Allomothering, Cooperative Breeding, and Exogamy as Bases For Effective Strategies For Friendship Formation. *Human Ethology Bulletin*, 33, 37–47. https://doi.org/10.22330/heb/332/037-047

Walker, R., Hill, K., Burger, O., & Hurtado, A. M. (2006). Life in the slow lane revisited:

Ontogenetic separation between Chimpanzees and humans. *American Journal of Physical Anthropology*, *129*(4), 577–583. https://doi.org/10.1002/ajpa.20306

- Wolf, W., Launay, J., & Dunbar, R. I. M. (2016). Joint attention, shared goals, and social bonding. *British Journal of Psychology*, *107*(2), 322–337. https://doi.org/10.1111/bjop.12144
- Wood, B., & Collard, M. (1999). The Human Genus. *Science*, *284*(5411), 65–71. https://doi.org/10.1126/science.284.5411.65
- Wood, B., & Lonergan, N. (2008). The hominin fossil record: Taxa, grades and clades. *Journal of Anatomy*, *212*(4), 354–376. https://doi.org/10.1111/j.1469-7580.2008.00871.x

Zeller, A. C. (1987). A Role for Children in Hominid Evolution. *Man*, 22(3), 528–557. https://doi.org/10.2307/2802504