

# Cooperative Breeding and Human Evolution

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## Abstract

The demographic success of humans compared to other closely related species is one of the remarkable stories of our evolutionary history. This can be attributed both to high fertility and improved chances of survival. But it is also fundamentally shaped by features of human parenting, cooperation, and social organization. The concept and theory of cooperative breeding combines these features and is a useful framework to consider child-rearing patterns characteristic of humans. Cooperative breeding theory was developed in biology to explain a social system found in relatively few animals in which nonparental members of a social group help to support offspring. In traditional human societies, numerous studies document that a variety of kin and nonkin of different ages and sex help mothers and contribute to infant childcare and provisioning juveniles. Cooperative breeding theory offers a well-developed theoretic and empirical context in which to evaluate cross-cultural diversity and to understand why humans cooperate in this way. This review situates humans compared to other species of cooperative breeders by outlining what we share in common and what are distinctly human aspects of parenting and childrearing. Attention is paid to both foundational research and new questions that have more recently surfaced through comparative research. Cooperative breeding is relevant to recent debates concerning the evolution of human life history, sociality, and psychology and has implications to demographic patterns, family formation, and social organization in the past as well as in today's world.

## INTRODUCTION

*Cooperative breeding* was a concept developed in biology that refers to a social system in which group members other than parents help to support mothers or raise their offspring. Because human mothers rarely raise children on their own and routinely rely on the help of others, cooperative breeding is a useful context to consider the parenting, reproductive, and social patterns characteristic of our species. While cooperative breeding does not leave an archaeological, fossil, or molecular record, it is expected to have emerged with a suite of other derived human traits in *Homo erectus*-grade species some

two million years ago (van Schaik & Burkart, 2010). These associated traits include a longer period of juvenility, short infancy, the division of labor and other derived aspects of our life history and sociality. For example, birth intervals and offspring survivorship, which impact demands for maternal care, have likely undergone significant transformation during human evolution. Birth intervals are two to three times shorter in natural fertility populations than in wild chimpanzee populations, and survival to maturity has almost doubled. This combination of short birth intervals and high survival means that mothers support multiple dependents of different ages, something other primates rarely do. These evolutionary changes affect an almost doubling of surviving fertility. Because infants, young children, and older children each require different kinds of time and energy investments, mothers are challenged to meet the needs of multiple dependents on their own. In the past decade, cooperative breeding has generated considerable traction as a framework to explain how humans support both high-quality offspring and a fast reproductive pace by redistributing the cost of childrearing through cooperatively raising young.

#### FOUNDATIONAL RESEARCH

Cooperative breeding is relatively uncommon among animals, occurring in about 3% of bird and 2% of mammalian species. Despite its rareness, cooperative breeding has evolved numerous times within and across diverse taxa of rodents, wild canids, foxes, meerkats, and several primate species. Among nonhuman cooperative breeders, helpers may guard young from predation, help forage for food to feed young, defend territory boundaries, build and clean nests, or carry and groom young. One reason cooperative breeding is suggested to be relatively uncommon among mammalian species is because the dependence of young on others terminates at weaning, which limits opportunities to help (Russell, 2004). Because human juveniles also receive assistance, food and shelter from others, which introduces a wide range of cooperative behaviors not seen in other cooperative breeders. Cross culturally, human mothers only provide about 50% of the care that an unweaned child receives (Kramer, 2010). In addition to assisting with the other 50% of minding infants, mothers also receive help feeding and caring for weanlings and juveniles. Since Turke's seminal study (1988) introduced cooperative breeding into anthropology, attention has centered on the importance of grandmothers (Hawkes, O'Connell, & Blurton Jones, 1989; Hawkes, O'Connell, Blurton Jones, Alvarez, & Charnov, 1998), fathers (Kaplan, Hill, Lancaster, & Magdalena Hurtado, 2000; Lancaster, Kaplan, Hill, & Hurtado, 2000; Marlowe, 2003; Quinlan, 2003) and older siblings (Kramer, 2005a, 2011, 2014) as critical helpers to mothers and dependent offspring.

Cooperating to raise the offspring of another presents a classic evolutionary puzzle and has generated two central questions. From the vantage point of the helper, why spend time and energy helping to support another's reproductive interests? And, does helping make a difference to maternal fitness and child well-being? *Kin selection theory* (a more specific formulation of inclusive fitness theory that predicts when and why cooperative behaviors might develop) has had broad appeal as the evolutionary basis to explain why helpers help. Before its formulation by Hamilton (1964), there was no satisfying way to understand helping behavior, which was seen as an enigmatic expression of altruism. Hamilton's rule, which articulates the conditions under which cooperation might evolve, predicts that helping behavior will be favored when  $rb > c$ , where  $r$  is the coefficient of relatedness,  $b$  is the benefit to the recipient, and  $c$  is the cost to the helper.

Studies among a range of insect, bird, and mammalian species support Hamilton's predictions and the dominant role that kinship plays in the evolution of cooperative breeding. Three points can be taken from these studies. First, the decision to help or not is strongly determined by kinship, although the amount of care contributed by helpers appears more influenced by personal costs and benefits. For example, studies show that when choosing between assisting close relatives, distant relatives, or unrelated individuals, strong preferences are typically shown for helping close relatives (Cornwallis, West, & Griffin, 2009). Second, helpers have more significant effects on recipients in species where kin are preferentially helped compared to species where they are not. Third, the extent to which species can discriminate among kin increases with the degree of benefits that helpers provided (Griffin & West, 2003). These observations are consistent with case studies in traditional human societies that associate the probability of being closely related with who helps and the amount and quality of the help that they provide (Crittenden & Marlowe, 2008; Ivey, Morrelli, & Tronick, 2005; Kramer, 2009; Leonetti, Nath, Heman, & Neill, 2005).

In answer to the second question, do helpers really make a difference, as observed in other cooperative breeders, human helpers also have a demonstrated positive effect on maternal fitness and on the health, growth, and survival of offspring (Kramer, 2010: Table 2). Juveniles and grandparents have been shown to increase the fertility of their mothers and daughters, respectively, primarily through affecting shorter birth intervals and increasing child survivorship (Hawkes, O'Connell, & Blurton Jones, 1997; Kramer, 2009; Lahdenpera, Lummaa, Helle, Tremblay, & Russell, 2004; Lee & Kramer, 2002; Sear & Mace, 2008). Fathers as well have positive effects on maternal and child outcomes. In most cases, these effects are primarily due to food provisioning rather than to direct childcare (Hill and Magdalena Hurtado, 2009;

Kaplan *et al.*, 2000; Lancaster *et al.*, 2000; Marlowe, 2003; Meehan, Quinlan, & Malcom, 2013; Quinlan & Quinlan, 2008).

### CUTTING-EDGE RESEARCH

Researchers agree that human mothers and children reproduce and survive with the help of others. In this respect, humans share many features in common with other cooperative breeders. But they also differ in ways that have recently been highlighted (Crepes, 2014; Hrdy, 2009; Kramer, 2010). These differences have raised debate about how to define cooperative breeding in its application to humans, and whether the selective pressures that gave rise to cooperative breeding differ in humans. To situate humans compared to other cooperative breeders, distinct features of human parenting and reproduction that have come to the fore in recent research are discussed.

Cooperative breeding in many species of birds and mammals tends to be associated with high *female reproductive skew*, meaning that one or a small group of dominant females breed and reproduce, while other sexually mature females help raise their offspring. These dominant females may have unique physical traits and behaviors, and aggressively suppress the breeding efforts of other females so they can be solicited as helpers. Good examples are cooperatively breeding naked mole rats, meerkats, and mongoose. In contrast, female reproductive skew is low in humans, and mothers receive help without suppressing the reproductive effort of other females in the group. In traditional human societies, most sexually mature females are married or otherwise pursuing their own reproductive careers.

This leads to a second significant difference between human and non-human cooperative breeders. Among nonhuman cooperative breeders, individuals who help mothers or provide care to their offspring are usually, but not always, sexually mature adults who stay in their natal group and delay or forego their own reproduction to raise the young of others (Clutton Brock, 2009). In human societies, while other mothers may help, juveniles and grandmothers are the predominant helpers. This has significant implications to lowering the cost of helping in humans compared to other cooperative breeders. Nonfertile juveniles and grandmothers are not competing for mating opportunities or for reproductive help. Nor do they compromise their own reproductive effort during the life stage when they help. Consequently, they do not incur the same opportunity cost as do sexually mature helpers in delaying or foregoing their own reproduction by helping (Kramer, 2011).

In nonhuman cooperative breeders, the challenge has been to explain why sexually mature helpers engage in such reproductively costly behaviors. In humans the challenge to integrate theories why multigenerational male

**Table 1**  
 Select Studies that Discuss Benefits to Help for Various Classes of  
 Helpers for Human Cooperative Breeders

Helper's Status	Types of Explanation	Select Sources
Sexually mature, nonbreeding related sibling	Delayed dispersal, ecological constraints	Strassman and Kurapati (2010)
	Indirect fitness benefits (kin selection)	Dugatkin (1997), Emlen (1991)
Nonrelated adults	Reciprocal altruism	Ivey (2000)
Postreproductive females	Kin selection	Hawkes <i>et al.</i> (1989, 1997, 1998), Hill and Magdalena Hurtado (1991), O'Connell, Hawkes, and Blurton Jones (1999); Crittenden and Marlowe (2008), Hrdy (2009)
Fathers	Resource provisioning	Irons (1983), Lancaster and Lancaster (1983), Kaplan <i>et al.</i> (2000), Marlowe (2003), Quinlan and Quinlan (2008)
	Male competition over sexual access	Blurton Jones, Marlowe, Hawkes, and O'Connell (2000)
	Kin selection	Crittenden and Marlowe (2008)
Juveniles	Benefits of learning and gaining maternal experience	Hrdy (1999), Ivey (2000), Ivey <i>et al.</i> (2005), Lancaster (1971), Weisner (1987)
	Kin selection	Crittenden and Marlowe (2008)
	Age division of labor, mutual benefits, kin selection	Kramer (2005a, 2005b, 2009, 2011, 2014), Lee and Kramer (2002)

and female helpers cooperate. Depending on a helper's developmental and reproductive status, the costs and benefits of helping involve different payoffs and explanations (Table 1). Consequently, rather than define cooperative breeders by associated attributes (skew, delayed dispersal of sexually mature helpers) and create typologies based on traits, it is useful to think about cooperative breeding in its broadest sense, as a reproductive and social system in which nonparental members of a social help to raise the young of others, and the selective pressures that gave rise to it. Most theoretic formulations for the evolution of cooperative breeding in nonhumans have focused on monogamy as the mechanism that raises relatedness within groups and

sibships and consequently increases the benefit of kin-based cooperation (Lukas & Clutton Brock, 2013). However, alternative pathways such as shorter birth intervals, polygynous mating systems, and selection for non-fertile helpers may be relevant to set the stage for the evolution of kin-based cooperation in humans (Kramer & Russell, 2014).

## FUTURE RESEARCH

Cooperative breeding theory provides a rich theoretic and empirical platform from which to appreciate the parenting, social, and reproductive behaviors that characterize humans. In humans today, cooperative childrearing is embedded in a complex sociality and long-term reciprocal labor and food sharing relationships that occur across all ages and sex. This complexity provides fodder for future research directions, and has generated several debates discussed here.

### EXPLAINING “WHY HELP”: KIN SELECTION, AND MUTUAL OR DIRECT BENEFITS?

Kin selection has been widely accepted as the basis for cooperative breeding and is supported by the genetic relatedness often noted between helpers and those they support and the amount of allocare they provide. In human societies, childrearing is typically kin based. Grandparents are closely related to their grandchildren. Full siblings are even more closely related, as are biological fathers. While there is often a strong relatedness association between helpers and recipients, other reasons have been brought to the fore to explain cooperation. Further, kin selection cannot address why humans, but not other closely related species, are cooperative breeders.

Kin selection as the explanation for cooperative breeding has been reexamined from two perspectives. First, the emphasis placed on indirect benefits may eclipse potential *direct benefits* (gains to the helper’s own survival or reproduction) and *mutual benefits* (both the helper and the recipient benefit) and overstate the cost to help (Clutton-Brock, 2002; Griffin & West, 2002). Mutual benefits may be particularly germane to human cooperative childrearing and help explain why cooperative breeding develops in humans but not other great apes. Evolutionary changes in the human subsistence niche include an increased diversity of plant, animal, and aquatic resources. Most of these resources require multistage processing and complex technology to access. These changes offer novel opportunities for the age and sexual division of labor, which increases foraging efficiency and labor economy (Kramer, 2014). The mutual benefits of a division of labor have been documented in other cooperative breeders (Clutton-Brock, 2006; Silk, 2009). Help directed to infants, since they do not return the favor, may be motivated by

kin selection. But provisioning juveniles is based on long-term, and often mutualistic food-sharing and labor exchange in which juveniles also participate. Thus, the opportunity cost for adults to help juveniles may be relatively low because the time and energy spent provisioning others are embedded in the same set of tasks they otherwise do to support themselves (Kramer, 2010).

Second, cooperative behaviors may be motivated by factors besides kin selection. Researchers have raised the point that kin selection is an ultimate cause focused on fitness payoffs. Because these payoffs often are time delayed, kin selection may be insufficient to explain the motivation to cooperate. Several emotional mechanisms have been forwarded as incentivizing helping behaviors, including empathy, fairness, and sympathy (Coall & Hertwig, 2010; de Waal, 2008).

#### RECONSIDERING ECOLOGICAL CONSTRAINTS AS AN EXPLANATION FOR COOPERATIVE BREEDING

One widely accepted hypothesis about the evolution of cooperative breeding is that it is an outcome of ecological constraints and delayed dispersal. Delayed dispersal occurs when sexually mature offspring stay in their natal territory and delay their own reproduction when constraints exist either in mating opportunities or in the availability of the resources and/or territory necessary to compete for mates and successfully reproduce. When young reach sexual maturity and are reluctant to leave because of an ecological or breeding constraint, they may benefit from staying in their natal group and helping either because of direct benefits, improvements to their survival, or they are coerced to do so. In several human case studies, the postponement of marriage and low marriage rates are associated with ecological constraints in the accessibility of land or wealth necessary for reproduction (Strassman & Clarke, 1998).

Ecological constraints as an explanation for cooperative breeding, however, is limited in not predicting why cooperative breeding evolves in some species and lineages but not others (Hatchwell & Komdeur, 2000). Recent research has suggested alternative hypotheses including life history characteristics, and the mutual and direct benefits of group augmentation and load lightening. In addition, the ecological constraints hypothesis only explains why sexual mature helpers help, not why juveniles, grandmothers or fathers cooperate.

#### WHO HELPS?

Because cooperative breeding is not a reproductive and social system shared with other great apes, it has raised many questions and speculations about its evolution in humans. Distinct theoretic arguments have been made for



the evolutionary importance of grandmothers (Hawkes, O'Connell, Blurton Jones, Alvarez, & Charnov, 1998), fathers (Kaplan *et al.*, 2000) and juveniles (Kramer, 2014). The incorporation of different classes of helpers requires different social preconditions. For example, to explain kin-based benefits for cooperating adult males or sexually mature siblings, some mechanism that increases paternity and relatedness within sibships needs to be in place. This mechanism is often assumed to be monogamy. However, other agents (shorter birth intervals, longer tenure of dominant males, polygyny) may have similar effects in modulating relatedness and be important in human evolution (Kramer & Russell, 2014). On the other hand, if the opportunities for and benefits from cooperative breeding did arise in the past (Crespi, Summers, & Dorus, 2009; Hrdy, 2009; Kramer, 2011), juveniles and maternal grandmothers, who are closely related to their mothers and daughters, respectively, can realize kin-based benefits regardless of the background mating system. The most parsimonious interpretation may be that cooperating groups of mothers and children, which does not require the additional social transition to a pair-bonded mating strategy, developed before more complex forms of cooperative breeding that require a significant change in mating patterns. Comparative research across species offers future insights into the potentially far-reaching effects and outcomes that cooperative breeding has on other aspects of human sociality.

#### COEVOLVING TRAITS

The evolution of cooperative breeding is particularly complex in humans because many other traits that directly affect parental care likely were evolving at the same time. The cooperative breeding literature often presumes a modern life history (as characterized by ethnographic populations, especially hunter-gatherers) as the selective background for its evolution. However, this may not be an adequate model of the past. Modern humans wean infants at a young age, have short birth intervals, and raise multiple dependents at the same time. Juveniles depend on others for their well-being and adults cooperate to raise young. However, this suite of traits did not always characterize humans. We likely evolve from an ape-like life history of long birth intervals, independence at weaning, mothers who raised young on their own, and juveniles who were self-sufficient foragers. If the life history traits that directly affect parental care have undergone considerable modification, then the evolution of cooperative breeding should be considered against this changing life history landscape (Kramer, 2014). Models that simulate the evolutionary transition from long to short birth intervals and early to late ages of maturity show that early in this transition, mothers can support their younger children with the help of their older children alone. Only more recently in this life



history transition do mothers require the help of other adults to meet the cost of their children (Kramer & Otárola-Castillo, in press). The development of other dynamic models is needed to further our understanding of the selective forces that shaped cooperative breeding.

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