12 Allocare

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Human mothers rarely raise children on their own. Rather, others commonly help support their children. Biologists refer to this reproductive system as “cooperative breeding,” which is found across relatively few but diverse taxa. Because cooperative breeding is not a trait shared with other great apes, its emergence in the human lineage marks a significant departure in reproductive and parenting strategies that has far-reaching consequences for human life history, sociality, and the demographic success of our species.

Mothers and children benefit from the assistance of others in numerous ways. However, recruiting help is not simple (Hamilton 1964; West et al. 2007), setting up the central evolutionary problem of cooperative breeding: How and why do individuals spend valuable time and energy helping to support another’s offspring? Much of what has been theoretically developed to solve this puzzle has been established in the nonhuman literature. This provides a useful framework to consider what becomes the characteristically human pattern of shared parenting. But it also raises a challenge, because, although humans share many traits in common with other cooperative breeders, they are atypical in several key ways. This chapter addresses these and other points about the unifying characteristics of cooperative breeding species and how humans fit in. What are the benefits of help to mothers and their offspring, and how do helpers overcome the costs and obstacles of helping? Who are the key helpers, and what do they do? Why cooperative breeding developed in humans but not in other great apes is also considered, as are some of the downstream life history and cognitive effects of cooperatively raising children. Examples focus on research in natural fertility and small-scale societies because they more closely represent the high-fertility, high-mortality demographic conditions in which cooperative child-rearing became a predominant human strategy. The last section then turns to the implications for cooperative breeding following the modern demographic transition. Because cooperative breeding is unusual among hominoids, its evolution brings together ideas about life history, our cooperative nature, group and family structure, and other traits that characterize human modernity.

12.1 Foundational Knowledge

12.1.1 What Is Cooperative Breeding?

Cooperative breeding is variously defined in both the nonhuman literature, where the concept originated, and the human literature (see Clutton-Brock 2006 for a discussion of cooperative breeding classifications). It is used in this chapter in its general sense as a reproductive and social system in which individuals other than parents (referred to as *alloparents*) help to raise offspring who are not their own. Cooperative breeding has evolved numerous times across various taxa, including in insects, spiders, crustaceans, fish, birds, and mammals (Emlen 1991 [1978]; Solomon and French 1997; Koenig and Dickinson 2016). Although expressed in diverse taxa, cooperative breeding is relatively rare, occurring in only an estimated 9% of birds (Cockburn 2006) and 3% of mammalian species (Russell 2004).[1] In mammals, cooperative breeding is predominantly found in wild canids, carnivores, meerkats, rodents, and primates. Among primates, reproductive cooperation is best documented for humans, tamarins, and marmosets (McKenna 1987; Tardif 1997). Although care by nonparents occurs across a range of other primate species (Mitani and Watts 1997; Ross and MacLarnon 2000), cooperative breeding is not a nonhuman great ape-reproductive strategy (Lancaster and Lancaster 1983; Hrdy 2005a), and therefore, its emergence is relevant to hominin evolution.

Who helps mothers and their young varies considerably across cooperative breeders. In birds, helpers are usually sexually mature siblings, as they are in some mammals (Russell and Lummaa 2009). Among the eusocial insects, Hymenoptera (bees, wasps, ants) helpers tend to be either fertile or sterile adults (Hughes et al. 2008), while Isoptera (termites) juveniles are likely to help (Boomsma 2013). In many cooperative breeding mammals, juvenile helpers are typical (Clutton-Brock et al. 2002; Russell 2004; Gilchrist and Russell 2007; Russell and Lummaa 2009), as they are in humans (Kramer 2011, 2014). While food transfers to grandoffspring are exceedingly rare in wild populations, exceptions are found among pilot and killer whales (Croft et al. 2015) and African elephants (Péron et al. 2019), and grandmaternal investments are common in human societies (Hawkes et al. 1997). The investment of fathers (social or biological) in their offspring is also well documented across human societies and is associated with improved survivorship, well-being, and maternal fertility (Gurven and Hill 2009; Meehan et al. 2013; cf. Sear and Mace 2008 for discussion of the facultative nature of paternal investment). Among evolutionary biologists, however, biparental care is usually subsumed under parental investment theory rather than cooperative breeding (Clutton-Brock 1991; Lukas and Clutton-Brock 2012). Following this convention, this chapter focuses on nonparental helpers, and their effects on mothers and her offspring, while Chapter 11 addresses parental care and the role of fathers.

12.1.2 How Humans Fit in as Cooperative Breeders

Although cooperative breeding systems vary across species, two commonalities are widely shared. First, nonparental individuals who provide care are currently not

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[1] Estimates vary depending on how narrowly or broadly cooperative breeding is defined. About 1% of mammals are estimated to be cooperative breeders if cooperative breeding is specified as "systems where a small number of breeding individuals are reared by nonbreeding helpers or workers" (Clutton-Brock and Manser 2016:294). When cooperative breeding is more broadly defined, an estimated 3% of mammals are cooperative breeders (Russell 2004).

breeding (Brown 1987; Emlen 1991 [1978]; Russell 2004) either because they are not yet mature (juveniles), are permanently sterile (sterile workers, post-fertile females), or because they are temporarily constrained from breeding (sexually mature, but nonreproducing helpers). The second commonality, one that distinguishes reproductive help from other forms of cooperation, is that helping behaviors are directed toward another's offspring or toward mothers to facilitate reproduction now or in the future.

Human child-rearing, however, also differs from other cooperative breeding systems in several key ways (Hrdy 2009; Kramer 2010; Crespi 2014). First, although humans might best be described as cooperative breeders (Clutton-Brock 2006), they also incorporate elements of communal breeding (Box 12.1). Beside nonbreeders, other mothers may help women raise their children, a trait of communal breeding. While human reproductive support is diverse and flexible, *cooperative breeding* is used throughout this chapter as the best term to encapsulate common usage of a reproductive system where mothers rely on others, without diluting too much of its theoretical intention as developed in evolutionary biology.

Second, female reproductive skew, which is an essential feature of cooperative breeding in some definitions (Lukas and Clutton-Brock 2012), is comparatively low in humans (Betzig 2012). In some species of cooperatively breeding birds and mammals, one or a small group of dominant females monopolize reproduction, and subordinate females help to raise their offspring (Clutton-Brock 1998; Johnstone 2000; Magrath et al. 2004). These dominant females often have unique physiological or behavioral traits, and aggressively suppress the breeding efforts of subordinate females. Among African meerkats, for instance, dominant females produce about 80% of the group's litters (Clutton-Brock et al. 2001b; Grueter et al. 2012). Female skew is not characteristic of human sociality. Instead, we live in multilevel groups with multiple breeding females, referred to as *plural breeding* in the cooperative breeding literature (Grueter et al. 2012).

Some have argued that reproductive senescence in human females is a case of reproductive suppression and coercion (Cant and Johnstone 2008; Mace and Alvergne 2012). While compelling as an explanation for grandmothering, we first have to rule out that menopause is simply explained by the deep ancestral mammalian pattern of age-related atresia. Across mammals, the cessation of reproductive function is pleiotropically linked to restricted oocyte production, in which humans do not appear to be biologically exceptional (Ellison 2001; Walker and Herndon 2008). Thus, the question for humans becomes not why reproductive function declines but why life span is extended.

An important consideration in placing humans in the context of other cooperative breeders is that most theory building has been developed in biology, based initially on bird models (Brown 1987; Skutch 1987; Emlen 1991 [1978]; Koenig and Dickinson 2004), subsequently applied to mammals and only relatively recently to humans (see Russell 2004). Originally, attention was focused on nonbreeding, sexually mature helpers, who present a particularly thorny evolutionary problem. Not only does cooperation have to be explained (i.e., why an individual expends

Box 12.1 **Are Humans Cooperative or Communal Breeders?**

Cooperative and communal breeding are variously defined in both the nonhuman and human literature, which has led to unfortunate confusion. In this chapter, I refer to Lukas and Clutton-Brock's (2012:1) distinction: "in a small proportion of species, breeding females either pool their young and share care and provisioning (communal breeders), or are assisted in protecting and feeding their offspring by non-breeding helpers (cooperative breeders)." Communal breeders appear to derive from different phylogenetic lineages, mating systems, and evolutionary pathways than cooperative breeders, and are associated with species such as mice, bats, elephants, whales, and social carnivores. In communal species, mothers may band together during the breeding season or live in groups of plural breeders, and they may pool young into nursery groups or crèches for warmth or protection. Communal babysitting occurs in some species (primates, whales, cats, coatis are examples) when one or more mothers stay with the nursery group, while others are absent. In these cases, breeding females often provide little direct care to non-offspring (Lewis and Pusey 1997). However, mothers mutually benefit from group-size effects on offspring survival through enhanced social thermoregulation or protection from predators or infanticidal conspecifics. A notable exception is allonursing, which is more common in species that roost together (bats), are communal reproducers (social carnivores, rodents), bear young in confined spaces (seals), or give birth to large litters (Packer et al. 1992). The frequency of allonursing, however, is usually rare in these species.

Various forms of these behaviors occur in humans. Mothers may care for the young of another, or form nursery groups. Communal care of non-offspring by other mothers is known, for example, among Shingu River native South Americans and Australian Aborigines; however, these helpers are less common than nonreproductive helpers, such as juveniles and grandmothers. Allonursing is noted in many societies, but it is a normative behavior in relatively few (Hewlett and Winn 2014). Among hunter-gatherers, allonursing is commonly observed among the Aka and Efé (Congo River hunter-gatherers), occurs, albeit rarely, among the Savanna Pumé (South American hunter-gatherers), and is absent in the !Kung and Hadza (for an overview, see Hewlett and Winn 2014).

Communal breeding in the animal literature is usually associated with minimal and indirect care. Although mothers help each other in human societies (as mentioned previously), many others do as well, nonbreeders in particular. Because human reproductive help is often direct and provided by nonbreeders and other reproductive-aged individuals, cooperative breeding seems to be the most inclusive moniker to situate humans.

time and energy helping), but also why individuals delay or forgo their own reproduction to do so. Although the reasons are widely debated, most biologists concur that some group dynamic, ecological, or life history factor gives rise to sexually mature individuals benefiting from staying in their natal group. Benefits may include fitness gains, improvements to their own survival, coercion, or ecological constraints (Emlen 1995; Hatchwell and Komdeur 2000; Clutton-Brock 2002; Hatchwell 2009; Sparkman et al. 2011).[2] In human studies, the postponement of marriage and low marriage rates in historic Europe have been associated with constraints in the land or wealth required to attract mates (Boone 1988; Clarke 1993; Strassman and Clarke 1998).

Although great strides have been made in understanding why sexually mature helpers help, evolutionary biology's focus on them as helpers has detracted from thinking more broadly about the costs and benefits for other nonbreeders to help (e.g., juveniles, grandparents). For example, subadult helpers are well documented in eusocial species, birds, fish, and mammals, including primates (Emlen 1990; Fairbanks 1990; Alexander et al. 1991; Solomon 1991; Gursky 2000; Clutton-Brock et al. 2002; Taborsky 2016). However, juveniles are seldom the target of investigation or theory building, perhaps because they present less of an evolutionary puzzle than do sexually mature helpers.

A fourth substantive difference between human and nonhuman cooperative breeders is that humans assist not only infants but also juveniles. One reason cooperative breeding is suggested to be uncommon among mammals is because the dependence of young generally terminates at weaning, which limits the needs and opportunities for help (Russell 2004). Because humans provide food, shelter, and protection through the juvenile stage, it introduces a wide range of potential helping behaviors not seen in other cooperative breeders. Importantly, assisting a nursing infant versus a weaned juvenile has very different implications for the cost of helping (Kramer 2011).

Primary among these divergent costs is that infant care requires helpers to spend time in activities that they would not otherwise do for themselves, such as carrying, holding, feeding, and babysitting. In contrast to infant care, because juveniles consume adult foods and resources, helpers can integrate provisioning into their own daily routines. For instance, a portion of the wild roots that a foraging 10-year-old collects is consumed by herself, and a portion is consumed by her parents and younger siblings. However, the time she spends holding or carrying her young brother is an added time and energy expenditure. While infants are too young to reciprocate, juveniles produce, process, and share food with others, and they are important contributors to domestic tasks (fetching water and firewood, washing, etc.) in most preindustrial societies (Blurton Jones et al. 1994b; Hawkes et al. 1995; Kramer 2005b, 2014; Tucker and Young 2005; Crittenden et al. 2013).

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[2] Subsequent studies pointed out that staying in one's natal group does not necessarily imply that these individuals help and that explanations for staying and helping might be different (Bergmüller et al. 2007; Cockburn 1998; Russell 2004).

This means that at least part of the cost to help a juvenile is recouped or offset, because juveniles give back (Kramer 2011). This point, though obvious, is not well incorporated into ideas about the cost of reproduction, the cost of children, and evolutionary explanations for human pair-bonding, male parental care, or the sexual division of labor.

In sum, cooperative breeding has much to offer as a framework to think about reproductive cooperation and to explain the human life history of early weaning, short birth intervals, high fertility, and a long juvenile period. When applying cooperative breeding approaches to humans, it is important to keep in mind that much of the theorizing originated in biology to explain care directed toward hatchlings and infants and to explain the cooperation of nonbreeding sexually mature helpers. Consequently, several key elements of human cooperative breeding – the role and implications of help from juveniles, grandmothers, and other reproductive-aged kin and nonkin – are largely unaddressed in the nonhuman behavior ecology literature. In studying human behavior, our charge then is to expand existing theory and empirical research to generate new hypotheses and predictions that address this gap and explain the diversity of child-rearing networks.

12.1.3 Notes on Terminology

Throughout, *allocare* and *allocaretaker* are used when referencing infant care, and *help* and *helper* more generally refer to either childcare or economic aid directed toward mothers and children. *Alloparent* refers to nonparental helpers and *allomother* to nonmaternal helpers. *Infant* refers to a nursing child, and *juvenile* is used in the general mammalian sense for an individual from weaning to sexual maturity. An *adult* refers to a reproductive-aged individual. *Child* and *children* are used as general terms for all subadult states. Consistent with other analyses of human childcare, infant care is subset into direct care and indirect care. *Direct care* refers to intimate childcare behaviors that imply close physical proximity, which includes nursing, feeding, carrying, holding, and grooming (dressing, bathing, delousing, minor medical tasks). *Indirect care* refers to behaviors such as walking alongside a child, laying in a hammock with a child, playing with a child, talking to a child, comforting a child, watching, or keeping a child out of trouble.[3]

12.2 The Evolutionary Puzzle of Cooperative Breeding

12.2.1 Benefits of Help to Mothers and Offspring

Generally across taxa, the help that mothers receive benefits them by redistributing the cost of raising young, which may have a positive effect on maternal fertility or offspring outcomes. For example, among meerkats, the number of helpers per pup

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[3] Note that direct and indirect childcare are both forms of direct investment, *sensu* Kleiman and Malcolm (1981). Indirect childcare should not be confused with indirect investment, which refers to territory defense, nest construction, resource provisioning, and other similar behaviors (Kleiman and Malcolm 1981).

has a positive influence on pup food intake and daily rates of weight gain (Clutton-Brock and Manser 2016). In nonhuman primates, allocare is associated with accelerated infant growth, shorter weaning times, and faster reproductive rates (Fairbanks 1990; Mitani and Watts 1997; Ross and MacLarnon 2000). In several species of callitrichid monkeys, the number of helpers in a group is associated with increased infant survival and decreased energetic burden on parents (Bales et al. 2000). If helpers transport young, as they commonly do in primates, then mothers can forage more efficiently and reallocate energy from carrying to lactation and reproduction (Hrdy 1977; Goldizen 1987; Koenig 1995; Tardif 1997; Bales et al. 2000).

Human mothers and children have been shown to benefit from cooperative child-rearing in two important ways. First, it alleviates maternal time constraints of simultaneously raising both younger and older children, a distinctive human life history feature. For example, among the Aka (hunter-gatherers) and Ngandu (agriculturalists) of Central Africa, mothers hold their infants less when engaged in work, and allomothers effectively offset this decrease in maternal care (Hewlett et al. 2000; Meehan 2009). In managing the competing demands of supporting younger and older children, nursing mothers tend not to compromise direct infant care. In a number of ethnographic cases, mothers find the extra time to care for a newborn by downwardly adjusting their investment in economic activities (Hurtado et al. 1985, 1992; Hames 1988; Hawkes et al. 1997; Kramer 2009). For instance, among Maya subsistence farmers (Yucatan, Mexico), mothers with young nursing infants spend no time working in their fields, which is an investment in food production that benefits older children and requires mothers to leave their infants at home (Kramer 2009). To compensate for their reduction in agricultural work, husbands and older children increase their effort. In other cases, caretakers allow nursing mothers to increase the time spent in economic activities (Ivey et al. 2005).

Second, cooperation is associated with positive fitness outcomes, since help from others can have important mitigating effects in permitting mothers to reproduce at a faster rate without compromising child survival (Hrdy 1999a; Kramer 2005b). Using demographic variables as proxies for the help available to mothers, case studies and meta-analyses indicate that the presence of potential helpers in a household (either a grandmother or older siblings) is associated with higher fertility (Draper and Hames 2000; Crognier et al. 2001; Lahdenpera et al. 2004) or improved probabilities of child survival when controlling for other variables that may affect mortality (Sear et al. 2002; Leonetti et al. 2005; Mace and Sear 2005; Sear and Mace 2008; but see Voland and Beise 2002; Strassman and Kurapati 2010).

While demographic studies often utilize historic and large-scale census data, behavioral observations provide detailed accounts of what helpers actually do and their effects on maternal fitness. Behavioral observation studies show that labor substitution by sons and daughters saves mothers considerable time and effort, which is associated with higher maternal fertility and improved sibling outcomes (Turke 1988; Bereczkei 1998; Bove et al. 2002; Lee and Kramer 2002; Kramer 2005a, 2009). For instance, the economic contributions of older Maya children not only offset a substantial portion of their own costs, but early-born children enable their mothers to continue childbearing when parents exceed the time they have available each day to support their family (Lee and Kramer 2002). Among the Aka of the Central Africa Republic, allocare provided to young children reduces a mother's energy expenditure by up to 216 kcal over a 9-hour period (Meehan et al. 2013), a caloric savings that can be directed to other reproductive goals.

In addition to these benefits, reproductive cooperation appears to have important cognitive and emotional benefits for children. Exposure to multiple caretakers expands a child's social sphere and is associated with cognitive and psychological benefits (Weisner and Gallimore 1977; Wilson 1986; McKenna 1987; Pope et al. 1993; Burkart et al. 2009; Isler and van Schaik 2012). Cooperative child-rearing also has important implications for the development of prosociality (van Schaik and Burkart 2010; Isler and van Schaik 2012), and it is a vital factor in learned sociability (Hrdy 2001; Gottlieb 2009).

12.2.2 Why Helpers Help

As a cooperation problem, we have to square evidence across taxa that mothers and offspring benefit from cooperative breeding with the potential cost to helpers (Fisher 1930). Helpers could spend their time in other, and perhaps more, valuable, ways. Besides an *opportunity cost* (the foregone benefit from an alternative time or energy expenditure), the effort allocated to helping others could compromise their own growth, survival, or fitness. Consequently, cooperative breeding raises a classic evolutionary question: Why would an individual spend time and energy helping to support another's reproductive interests? The theoretical expectation is that if helping incurs a cost, then it should be offset by some benefit (Chapter 5). For cooperative breeding, most explanations fall into three broad categories: indirect kin-selected benefits, direct fitness benefits, and mutual benefits.

12.2.2.1 Kin-Selected Benefits

Prior to Hamilton's inclusive fitness theory (1964), there was no satisfactory theoretical framework to explain helping behaviors, which were seen as enigmatic expressions of altruism. Kin selection as an explanation for why helpers help builds upon Hamilton's Rule that cooperation can develop when helpers and recipients are closely related. Three general observations have been made from empirical studies relating kin-selected benefits to cooperative breeding. First, both case studies and meta-analyses show that when choosing between assisting a close relative, distant relative, or unrelated individual, strong preferences are shown for helping close relatives (Cockburn 1998; Hatchwell et al. 2001; Griffin and West 2003; Cornwallis et al. 2009). Because of this added value, kin-selected benefits have had broad appeal as the evolutionary basis for cooperative breeding (Cockburn 1998; Hughes et al. 2008; Boomsma 2009). Second, while the decision to help is strongly related to kinship, the amount of care a helper gives is more influenced by personal costs and benefits (Griffin and West 2003; Cornwallis et al. 2009). Third, helpers are more likely to help when the effect is substantial (Griffin and West 2003). These observations are well supported in cooperative breeding species (Skutch 1987; Emlen 1991 [1978], 1997; Koenig and Rothe 1991) and are consistent with case studies in human societies that associate the probability of relatedness with who helps and the amount and quality of the help they provide (Ivey et al. 2005; Leonetti et al. 2005; Crittenden and Marlowe 2008; Kramer 2009).

Because kin-based benefits are diluted under widespread promiscuity, biologists have hypothesized that an ancestral history of monogamy was a critical step to raise relatedness within groups and sibships (Boomsma 2007, 2009; Hughes et al. 2008; Lukas and Clutton-Brock 2012). The logic is that in a promiscuous or polyandrous mating system, a sexually mature individual is more likely to be closely related to one's own offspring (Wright's $r = .5$) than to siblings who may have different fathers (Wright's r between siblings = .25–.5). Consequently, after sexual maturity one's fitness is generally maximized by investing in one's own offspring rather than helping to raise siblings. All else being equal, continuing to help would require either halving the costs or doubling the benefits. In a monogamous mating system, however, the value for a sexually mature sibling to stay in their natal group and help full siblings is equal to that of rearing one's own offspring (Wright's $r = .5$ for both) (Boomsma 2007, 2009; Lukas and Clutton-Brock 2012).

Although monogamy undoubtedly raises relatedness between siblings and increases the probability that sexually mature helpers will care for full siblings rather than half siblings, it is not a necessary condition to explain human cooperative breeding (Box 12.2). Foremost, an ancestry of monogamy is important to explain why sexually mature adults help. Cooperation between mothers and her juvenile children or between grandmothers and her daughters can be favored irrespective of breeding system as long as helpers can identify their mothers and siblings.

While kin selection is commonly given as the reason why helpers help, recent explanations have become more nuanced. In particular, they raise the question whether kin selection alone suffices to explain cooperative breeding (Cockburn 1998; Heinsohn and Legge 1999; Clutton-Brock 2002). While kin may ultimately benefit, because fitness payoffs often are time delayed, especially in long-lived animals, factors other than kin selection may be needed to motivate cooperative behaviors (Silk 2006; de Waal 2008; Coall and Hertwig 2010). In the human case, several emotional mechanisms have been forwarded as incentivizing helping behaviors, including empathy, fairness, and sympathy (de Waal 2008; Coall and Hertwig 2010; Blake et al. 2015).

12.2.2.2 Direct Benefits

Helpers may directly benefit by increasing their own survival or mating prospects or by learning to become a competent mother. For example, recently fledged or matured individuals may improve their survival prospects by delaying dispersal and staying in their natal group to assist their parents to raise the next brood or litter (referred to as "pay-to-stay," Dunn et al. 1995). Helpers also may directly benefit if engaging in cooperative behaviors increases their mating success (referred to as the "prestige hypothesis," Grinnell et al. 1995; Zahavi 1995;

Box 12.2 Is Monogamy a Necessary Condition for Cooperative Breeding to Evolve in Humans?

Behavioral ecologists have long recognized that breeding and parenting systems are closely associated. Phylogenetic studies offer compelling evidence that an ancestry of monogamy preceded the evolution of cooperative breeding across insect, bird, and mammalian taxa (Hughes et al. 2008; Cornwallis et al. 2010; Lukas and Clutton-Brock 2012). Although these studies suggest that monogamy provides a general rule for evolutionary transitions to cooperative breeding (Boomsma 2013), it may not apply to humans (overview in Kramer and Russell 2015). First, an ancestry of monogamy as the mechanism to raise relatedness in groups has strong support to explain why sexually mature helpers help, but it is not needed to explain why juveniles and grandmothers help. Because neither is able to produce offspring currently (or in the future in the case of grandmothers), helping does not carry the same reproductive or opportunity cost for juveniles or grandmothers, who can gain an immediate indirect fitness benefit by helping to raise the reproductive potential of their parents and descendants, respectively (see Section 12.2.2.1). Second, traits typically associated with monogamy (testes size, concealed ovulation, body size dimorphism, cross-cultural mating pattern) are inconclusive in characterizing ancestral human mating patterns as monogamous (Dixson 2009; reviewed in Martin and May 1981; Marlowe 2000b; Plavcan 2012; Kramer and Russell 2015). Third, even if past breeding patterns were monogamous, serial monogamy was likely the norm throughout most of the human past. Because of relatively high mortality and long breeding careers, both males and females in small-scale populations often have more than one spouse over their lifetime. For example, among largely monogamous Savanna Pumé hunter-gatherers, 40% of adults reenter the mating market after their first marriage due to spousal death or divorce (Kramer et al. 2017). If cooperative breeding is ancient, it likely emerged in a mating environment of multiple partners, not monogamy. Juvenile and post-fertile female cooperation can be favored in the absence of lifetime monogamy, while a more constrained breeding system (female monandry), which increases relatedness among siblings, is a pathway to favor helping by adult siblings.

Cockburn 1998; Zahavi and Zahavi 1999; Bergmüller et al. 2007). In humans, cooperation as a costly signal of male quality and status has largely been discussed in the context of hunting and meat provisioning (Hawkes 1991; Hawkes and Bliege Bird 2002). Of note, both pay-to-stay and prestige benefits pertain specifically to the payoff for sexually mature individuals to help.

Juvenile helpers may directly benefit by learning skills that enhance their future success in raising offspring of their own (Hrdy 1976; McKenna 1987; Fairbanks 1993; Tardif 1997). For example, longitudinal observations of vervet monkeys show that females who spent more time carrying infants as juveniles were significantly more likely to have a firstborn who survived (Fairbanks 1990). While the learning-to-mother payoff has been proposed for humans (Lancaster 1971; Ivey 2000), the challenge of testing this hypothesis is the scarcity of large samples of longitudinal data that track girls from childhood into their reproductive careers.

Another direct benefit is group size augmentation (Cockburn 1998; Clutton-Brock 2002; Russell 2004; Bergmüller et al. 2007). If individuals survive and reproduce better in larger groups, they may benefit if caring for another's offspring augments breeder survivorship or fertility, thereby increasing the group's size (Brown 1987; Pusey and Packer 1987; Kokko et al. 2001).

12.2.2.3 Mutual Benefits

Helpers may also benefit by engaging in mutualistic cooperative interactions (Clutton-Brock 2002). For example, among social birds, juveniles may contribute to building a communal nest that they will utilize as adults. The benefits of mutual cooperation may be particularly germane to cooperative breeding in humans for several reasons related to the human feeding niche.

The human diet is distinguished by its broad diversity of plant, animal, and aquatic foods, which are often located in disparate locations on the landscape and transported long distances back to base camps. Daily foraging ranges are large, and most food resources require multistage processing, central-place foraging, and complex technologies to access and process (Kramer 2019). Simply said, there are insufficient hours in the day for any one person to get the plants and animals they need, to procure and process raw materials to manufacture the tools, to haul water, to chop firewood, to construct clothing and shelter, to take care of children, and to maintain the social and information networks that are needed to access geographically dispersed resources. This introduces a time allocation constraint for an individual of any age to be self-reliant, making it difficult for juveniles as well as adults to be independent. These distinctive features of the human diet present both opportunities and benefits for the division of labor, which is central to many explanations for cooperative breeding (see Section 12.4).

12.3 Human Cooperative Breeders: Who Helps and How

Turke's (1988) seminal study among Micronesian islanders first introduced humans as cooperative breeders. Using time allocation data, he showed that Ifaluk mothers who bore girls, who are valuable household helpers, early in their reproductive careers had greater completed fertility than if their firstborn children were boys. This study was followed by Ivey's (1993) examination of the range of childcare helpers among the Efé (Ituri Forest hunter-gatherers). Since then, reproductive cooperation has become a central explanation for the evolution of human life history and sociality (Hrdy 1999a). Individuals who cooperate with mothers vary culturally, demographically, and situationally, and they may include mothers, grandparents, juveniles, and a variety of other kin and nonkin (Ivey 2000; Kramer and Veile 2018; Helfrecht et al. 2020). The discussion here is focused on juveniles and grandmothers in natural fertility settings. This emphasis does not obviate the overall importance of diverse and flexible caregiving networks for humans.

12.3.1 Who Helps

Distinct theoretical arguments have been made for the evolutionary importance of grandmothers (Hawkes et al. 1998; Alvarez 2000) and juveniles (Kramer 2011, 2014). Grandmothers are closely related to their daughters and grandchildren, and since they are often postmenopausal, helping provides a means for them to further their inclusive fitness. Likewise, juveniles cannot reproduce, and because they are closely related to their mother and siblings, they can leverage their non-fertile status into a higher reproductive potential for their mother, increasing their inclusive fitness. If juveniles contribute, either through direct calorie transfers by producing and sharing food or by performing tasks that reduce their mother's energy expenditure, they can make the most of growing slowly and receive an immediate fitness benefit rather than having to wait until they are sexually mature. This time-discounting advantage may be important in selecting for slow juvenile growth, especially in high-mortality environments where up to 10% of juveniles who survive weaning may not survive to reproductive age (Reiches et al. 2009; Kramer and Ellison 2010).

Juveniles might incur a disadvantage if the caloric cost to helping is high. The potential trade-off with compromising the energy available for growth has been examined in small mammalian cooperative breeders. Researchers found that for meerkats, while the energy expended in helping resulted in a short-term growth cost, there was no enduring fitness cost (Russell et al. 2003b; Clutton-Brock 2006; Clutton-Brock and Manser 2016).

Beside siblings and grandmothers, aunts (usually mother's sister), grandfathers, other relatives, and nonrelatives may provide care, food, shelter, and assistance to mothers and children. For example, among the Maya, young children receive 8% of their direct care from their aunts (Kramer 2010). Among the Ye'kwana of Venezuela, young children receive 6.6% of their direct care from aunts (Hames 1988). Aunts and uncles provide 4.5% of the care that young Trinidadian children receive (Flinn 1992). Most published studies aggregate non-grandmother adult helpers as "other relative" or "nonrelative," who, together in the case of Australian Aborigines, provide up to 30% of a young child's care (Scelza 2009).

The few studies that specify the contributions of elder men (grandfathers and uncles are often combined in reporting) concur that they provide little direct childcare. Among the Aka, who are well documented for paternal infant care, infants were held by grandfathers less than 1% of the time (Hewlett 1991b:79). Efé grandfathers and uncles spend approximately 2.5% and 1% of their time in allocare, respectively (Ivey

2000:860). While older men do not commonly take on active childcare roles, they may provide important food, resources, property, and social access (Hooper et al. 2015b). Aché, Hiwi, Hadza (Kaplan et al. 2000), and Maya men (Kramer 2005b) over the age of 50 on average remain net producers for another decade, suggesting that some of their food surplus flows to younger generations. In Tanzania, Hadza men's foraging returns remain consistent after the age of 40, and older men may provide meat calories to grandchildren (Marlowe 2000a). In many small-scale societies, older men are vital in brokering social status, settling disputes, providing agonistic support, promoting group cohesion, and arranging marriage ties, which affect the lives and success of younger generations (Wiessner 2002). For example, the presence of an uncle or grandfather lowers the age of a Martu boy's initiation, which is correlated with future reproductive success (Scelza 2010). Aside from these few studies, understanding the function of grandfathering in small-scale societies is generally understudied.

12.3.2 Not All Helpers Are the Same

Because of paternity uncertainty and the expectation that cooperators will bias their investment toward kin, the role of maternal grandmothers is most frequently highlighted. Where resources are shared, an investment in female kin is assumed to more likely be transformed into benefits for children than an investment in male kin, who may alternatively allocate resources to mating effort. Ethnographic exceptions are noted, particularly in patrilineal societies where mothers extend help to their sons' children.

For similar reasons, a distinction between maternal and paternal grandmother effects is observed in many studies. Generally, positive effects on grandchild survivorship (and other outcomes) are associated with maternal grandmothers (Sear et al. 2002; Voland and Beise 2002; Leonetti et al. 2004; Gibson and Mace 2005; Sear and Mace 2008), while paternal grandmothers exhibit a range of positive (Sear and Mace 2008), neutral (Griffiths et al. 2001; Sear et al. 2002), and negative associations with child survival (Voland and Beise 2002). Besides the sensitivity of cooperative behaviors to kin selection and paternity certainty, negative effects are also suggested to arise from resource competition in households where paternal grandmothers have a stake in biasing the sex or number of heirs. Others suggest that the inconsistent results in grandmothering effects derive from confounding differences in X-chromosome relatedness between maternal and paternal grandmothers (Fox et al. 2009). The range of positive, negative, and neutral findings suggests that complex economic and socioecological factors condition grandmaternal effects.

12.3.3 What Helpers Do

12.3.3.1 Infant Allocare

In a cross-cultural sample of time allocation studies, mothers on average provide about half of infant care, and allocaretakers provide the balance (Kramer and Veile 2018). While allocaretaking may be considerable, it is also quite variable across societies. Among the Efé, allocaretakers provide 60% of the care that an infant receives at 18 weeks (Ivey 2000). Young Aka children ages two to four are fed by someone other than their mother about 60% of the time (Fouts and Brookshire 2009). Hadza allomothers hold children four and younger only 31% of the time (Crittenden and Marlowe 2008). !Kung infants in particular stand out as receiving much more of their care from their mothers, who account for 75–80% of all physical contact that an infant receives in the first 20 months of life (Howell 2010; Konner 2010).

Of allocaretakers, a study using the same data collection methods in two groups of agriculturalists and a group of hunter-gatherers found that unmarried siblings, and specifically children ages 7–14 years old, invested the most time caring for infants (Kramer and Veile 2018). The tendency for young children to be childcare specialists has been qualitatively noted by many ethnographers (Barry and Paxson 1971; Weisner and Gallimore 1977; Nag et al. 1978; Hames 1988; Whiting and Edwards 1988). Humans are not unusual in this regard; juvenile allocaretaking is common in many cooperative breeding species (Clutton-Brock 2002; Russell 2004; Gilchrist and Russell 2007). One possible explanation is that because subadults and adults are stronger, more skilled, and efficient at a greater range of economic tasks, the opportunity cost for them to allocate time to childcare is higher than for younger children who have fewer competing ways that they can spend their time (Bock 2002). This explanation accords with analyses that find that the time children allocate to childcare does not predict a decrease in time spent playing, in economic activities, or school (Kramer and Veile 2018).

Older women may care for their young grandchildren while their daughters spend time away from home foraging or in other economic pursuits (Hrdy 2009). In other instances, mothers with young children might reduce the time they spend in economic activities, while grandmothers take on these support tasks rather than helping with childcare (Hawkes et al. 1989, 1997; Hurtado et al. 1992; Gibson and Mace 2005; Leonetti et al. 2005). In a study of the energetic effects of helping, Aka grandmothers reduce maternal workloads by about 200 kcal per day while also offsetting the time that mothers spend in direct care (Meehan et al. 2013).

Many studies infer grandmother effects from demographic data (i.e., counts of living family members) rather than from direct observations of assistance. One question that arises from demographic studies is whether the association between the presence of a grandmother in a household and child survival is due to phenotypic correlation rather than helping. That is, healthier women who survive to older ages may produce grandchildren who exhibit better health and survivorship (see Box 2.1). If larger families are associated with a living grandmother, is it because the grandmother is easing maternal constraints by helping or because long-lived women pass on the survival advantage to their grandchildren? Furthermore, while an individual may be counted as a caretaker, how much help they give is unknown without observational study. For instance, among the Savanna Pumé and the Maya, older siblings, fathers, and grandmothers allocate between 0–17% and 0–33% of their time to childcare, respectively. In other words, these potential allomothers may do nothing or a lot, and consequently they may be either a cost or benefit to a mother.

Although childcare tends to be a family affair (Kramer and Veile 2018: Figure 1; Helfrecht et al. 2020: Figure 2), childcare network size can be large and diverse. For example, Efé focal infants interact with 11 allocaregivers on average during focal observations (range from 2 to 21; Ivey 2000:860). A similar network size is found among Central African hunter-gatherers, where childcare networks average 12.1 caretakers per 9 hours of observation (range 3–24; Helfrecht et al. 2020, Table 1). Furthermore, this same study demonstrates that larger caregiver networks are associated with a decrease in the frequency of maternal care, suggesting that diversity itself is an important variable attenuating time allocation conflicts for mothers (Helfrecht et al. 2020).

12.3.3.2 Juveniles Are Both Subsidized and Provision Their Siblings

Across all human societies, weaned children are fed and cared for in various ways. Because of this, adult provisioning is often highlighted as a defining feature of human evolution. But children also cooperate to provision and care for others, an equally defining human trait. Children are caretakers, share resources, and exchange labor with their mothers, siblings, and others, something other primate juveniles rarely do. Indeed, cross-culturally, toddlers are observed to go through a helpful developmental stage (Lancy 2018), and in early childhood, much of the cognitive and emotional architecture develops that establishes the human capacity for coordination and cooperation (Tomasello et al. 2005; Hrdy 2009; Tomasello and Vaish 2013).

Because juveniles are helped and are helpers themselves, both of these derived human traits are evidently important to the origins of cooperative breeding. Although children receive difficult-to-acquire food and resources from others, they are also able to produce other easy-to-acquire resources (fruits, nuts, berries, small game) that contribute directly to their own energy budget and are often shared with others (Kramer 2005b, 2014; Crittenden et al. 2013). Hadza children living in sub-Saharan Africa spend five to six hours a day foraging for food. By the age of five, during some seasons, they supply about 50% of their own calories (Blurton Jones et al. 1989a:367). Maya children produce 50% of what they consume by age six (Sullivan Robinson et al. 2008), and much of what they produce is shared with other household members. On days that they forage, Savanna Pumé boys have an average return rate (amount of food produced per foraging trip) of 4.5 kg of wild fruit (~3200 kcal), and 0.5 kg of fish (~700 kcal). This is what a boy returns to camp after whatever field snacking that he might do on the trip, and it is a sufficient caloric return to feed himself and at least some of his family. On days that she forages, his sister brings home an average of 1.1 kg of roots (~3850 kcal), some of which she will eat, but much of which are shared with others.

While juveniles both produce and consume food, foraging returns, and calorie counting do not capture other important contributions. For example, although !Kung children are known for contributing little to food production (Blurton Jones et al. 1994a; Howell 2010), by the age of eight they crack most of the mongongo nuts they eat, a substantial portion of their diet (Lee 1979). Hadza girls under the age of five spend more time food processing than any other age class (Hawkes et al. 1998). Many food processing and domestic activities (firewood, water), which are critical to the human feeding niche, do not have readily measurable caloric equivalents. Thus, analyses that limit children's contributions to calorie acquisition will inevitably conclude that children do little for themselves and are costly. If the human adaptation is contingent on high-quality food requiring complex access and processing solutions, considering the time allocated to these tasks is critical to understand both the effect that juvenile dependence has on maternal time budgets and on cooperative breeding.

If how children allocate their time to this broader range of food processing and other labor is considered, in most societies there are noteworthy increases between middle childhood and adolescence (Figure 12.1). If what juveniles do is standardized as a proportion of the adult mean, in many societies, juveniles work at least 50% as much as their adult counterparts (Kramer 2019). This is not insignificant if you consider that a 10-year-old, for example, is on average about 60% of adult body mass. Although children are not working equally proportional to their body size, they go a long way toward it, and while they underproduce some resources, they also overproduce others.

While hunter-gatherer children are often thought to do less to support themselves than children in other subsistence economies, the empiricial data suggest otherwise. Hunter-gatherer children have both some of the highest and lowest participation in economic activities (see Figure 12.1). This suggests that the helpfulness of juveniles is not a function of whether a child is a forager, an agriculturalist, or a pastoralist. Rather, children's contributions vary with ecology, kinds of subsistence tasks, the costs to participate, dangerousness of the environment, and how children learn to become competent adults.

Another reason that human children are often characterized as an energetic burden is because the effects of overlapping dependents are not considered. Although any one child may be a net cost, how mothers experience the day-to-day support of multiple dependents is analogous to a mortgage, where others need to pay only the daily balance of what children cannot fund themselves. Because juveniles are both producers and consumers, and mothers raise children of various ages at the same time, a different picture emerges from analyses that combine these features of human families. Using a framework that incorporates the combined costs of older and younger children, food and labor exchanges between children within a family cover a substantial portion of their total costs (Lee and Kramer 2002; Kramer 2014; Kramer and Otárola-Castillo 2015). For instance, when data is modeled across a Maya woman's reproductive career, fathers contribute as much time as mothers to child support, but parents nonetheless fall short in meeting their children's consumption needs. Juveniles fill this gap and are especially critical to family survival after the last child is born, when parents have the maximum number of dependents (Kramer 2005b).

While many reasons have been forwarded for why helpers would help, they also should be self-interested. In the case of juveniles, competition between siblings and a reluctance to cooperate might be expected. Several studies that have looked at sibling

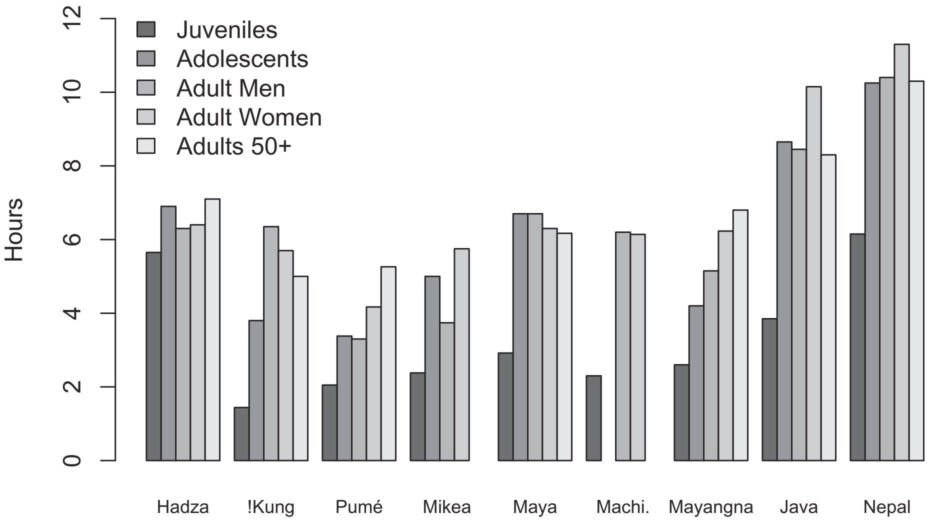

Figure 12.1 The average number of daily hours that younger juveniles ages 6–14, adolescents ages 15–19, reproductive-aged males and females, and adults over the age of 50 spend in economic activities among hunter-gatherers and subsistence agriculturalists. Economic activities are defined, unless otherwise indicated, as time allocated to food production (foraging, hunting, fishing, caring for animals, working in fields, etc.) and domestic production (chopping firewood, fetching water, food processing, etc.). Male and female values are averaged for juveniles, adolescents, and adults over the age of 50. The sample includes known published time allocation data stratified by age and sex. Age categories vary slightly from study to study. Missing bars indicate unreported data. Sources: Hunter-gatherers: Hadza (Hawkes et al. 1997:556); observation period 12 daylight hours, reported as weekly means; instantaneous scan samples (*n* = 1700 observations; 90 individuals); !Kung (Lee 1979; Draper and Cashdan 1988); Pumé (Kramer and Greaves, unpublished data); observations period 12 daylight hours 6:00 a.m.–6:00 p.m.; instantaneous scan samples (*n* = 24,924 observations, *n* = 87 individuals); Mikea (Tucker and Young 2005, Figure 7.2); observation period 12.5 daylight hours; instantaneous scan samples (*n* = 6637 observations, 46 individuals); Agriculturalists: Maya (Kramer 2005b); observation period 11 daylight hours 7:00 a.m.–6:00 p.m.; instantaneous scan samples (*n* = 18,500 observations, 112 individuals); Machiguenga (Johnson 1975, Tables 1 and 2); observation period daylight hours 6:00 a.m.–7:00 p.m.; instantaneous scan samples (*n* = 3495 observations, 105 individuals); Mayangna (Koster 2007, Tables 5.4 and 5.5); observation period 5:30 a.m.–6:00 p.m.; instantaneous scan samples (*n* = 14,653 observations, *n* = 195 individuals); Java (Nag et al. 1978, Tables 1 and 2); 24-hour recall collected every 6th day over the course of a year (*n* = 105 individuals); Nepal (Nag et al. 1978, Tables 3 and 4); 24-hour recall collected every 6th day over the course of a year (*n* = 498 individuals).

competition have not found negative impacts on growth outcomes, however. The effects of younger and older siblings (Kramer et al. 2016), closely aged siblings (Helfrecht and Meehan 2016), male and female siblings (Hagen and Barrett 2009), and caregiver presence (Meehan et al. 2014) instead reveal a positive relationship with developmental outcomes, suggesting that sibling helpfulness outweighs competition in these circumstances.

Figure 12.2 Cooperative breeders vary in who they are and what they do. Savanna Pumé aunts, siblings and grandmothers shown grooming (a), preparing food (b), providing childcare (c, e, f) and food (d). Photo credits: Russell Greaves.

The idea of hardworking grandmothers has received significant traction as an evolutionary explanation for longevity (Hawkes 2003; Kim et al. 2012, 2014). Several demographic studies show an association between a maternal grandmother being alive and child survivorship. However, relatively few studies report what grandmothers actually do. Those that record time expenditures for older adults indicate that they continue to make important economic contributions throughout much of their lives (Turke 1988; Hawkes et al. 1989, 1997; Hurtado et al. 1992; Kaplan 1994; Gibson and Mace 2005; Kramer et al. 2009; Kramer and Greaves 2011a) (Figure 12.1). Other cross-cultural studies suggest that food transfers from older females are nuanced. For example, older Hadza women spend significantly more time foraging during some seasons of year, but not others. Post-reproductive Savanna Pumé females overproduce some resources (small wild roots), but not others (large wild roots or fruit) (Kramer and Greaves 2011a). Among the Hiwi, who live within 100 km of the Savanna Pumé in a similar Savanna environment, post-reproductive women spend more time foraging than younger women during certain seasons of the year (Hurtado et al. 1992), but their return rates for roots and fruit decline after about age 50 (Kaplan et al. 2000).

Comparative time allocation studies, where age-specific consumption data are paired with production data, show that among several groups of hunter-gatherers and horticulturalists, older adults often acquire more food than they can consume (Hawkes et al. 1989; Hurtado et al. 1992; Lee et al. 2002; Hill and Hurtado 2009; Kramer et al. 2009). Because food sharing is particularly difficult to document, overproduction is often assumed to be transferred to juveniles. However, overproduction may have other destinations (feasting, status competition) besides being shared with children (Codding et al. 2010).

In sum, researchers emphasize the contributions of different age and sex classes of potential helpers. Although grandmothers, siblings, and fathers often are treated as mutually exclusive sources of help, helpers of different age and sex may be key at different points in a mother's reproductive career, and under different ecological and demographic conditions. In addition to variable mortality schedules, small-scale populations are subject to pronounced stochastic swings in age and sex distribution, affecting the availability of potential helpers. Because both male and female labor and resources are important to survival and subsistence, there is strategic value for mothers to have access to a range of helpers. As a child, you only ever have two grandmothers, and under preindustrial mortality schedules, if your grandmother is alive, you are likely to have only a few years when your lives overlap (Chapman et al. 2018). Data from four Savanna Pumé camps show that 64% of mothers ages 15–30 have a surviving mother, while only 31% of mothers ages 31–45 do. This compares closely to the Aché, among whom 32% of women 36–45 have a surviving mother (Hill and Hurtado 2009). In contrast, unless juvenile mortality is particularly high, a natural fertility mother will have an increasing number of productive-aged juveniles until about age 40 when children start to leave home. We might then infer that the importance of grandmothers is greatest during early parities, but during their prime reproductive years, many mothers will have to count on the help of juveniles, fathers, and others.

12.4 Why Humans Are Cooperative Breeders

While mothers and their offspring may benefit from help, and a number of reasons for why helpers might help are well-established, this does not answer why cooperative breeding emerged during hominin evolution. By comparison, nonhuman great ape juveniles would surely benefit from help, as would their mothers. Because cooperators potentially have to wait a long time to realize fitness benefits, especially long-lived animals, kin selection itself may be insufficient to motivate cooperative behaviors. Rather, proximate mechanisms may be critical to stimulate cooperation. Indeed, because cooperative breeding occurs across a range of environments – from harsh to benign, stable to fluctuating – recent research suggests that it is not determined by ecological variables alone. Rather, cooperative breeding is associated with social and group benefits that crosscut environmental differences (Shen et al. 2017). Building on this, the mutual benefits of foraging efficiency, labor economy, and the division of labor, which have been documented in other cooperative breeders

(Kokko et al. 2001; Clutton-Brock 2002, 2006; Silk 2009), may be particularly relevant to humans as proximate mechanisms and provide clues why humans became cooperative breeders.

The human feeding niche is characterized by a diverse portfolio of food types, dependence on complex technology, and food processing (see Section 12.2.2.3). When tasks vary in their costs (e.g., feeding vs. protection, foraging vs. food processing, gathering vs. hunting), task specialization is argued to be instrumental in favoring biparental care and a division of labor. Task specialization and the age division of labor (age polyethism) are widespread in many cooperative breeding insects and mammals (Thorne 1997; Clutton-Brock et al. 2002; Toth and Robinson 2007; Crespi 2014). In the human case, the mutual benefits of a division of labor is hypothesized to be critical to the formation and stability of cooperating groups (Leonetti and Chabot-Hanowell 2011) and reinforce cooperative interactions between mothers and her offspring (Chapais 2001, 2006).

12.4.1 Recruiting Helpers on the Path to Cooperative Breeding

The human cooperative breeding pattern involved at least three distinct evolutionary steps: the integration of juveniles, grandmothers, and fathers into cooperative relationships. Each step would have required a payoff to cooperate (see Section 12.2.2), which may have included kin-selected benefits, direct benefits, or mutual benefits. Although most researchers agree that the advantages to cooperate arose at some point in the past, which partnerships were at the root of early cooperation is debated. These debates are not reviewed here, but the broader point is that given a benefit to cooperation, whether juveniles, grandmothers, or fathers were motivated to cooperate depended on breeding systems, dispersal, and resident patterns (Table 12.1).

Juveniles are closely related to their mothers and siblings and have low opportunity costs to cooperate since they do not compete for mating opportunities and benefit by leveraging their own nonreproductive status into indirect fitness gains. Juveniles usually co-reside with mothers until sexual maturity (exceptions exist where fosterage occurs), and extended ties between mothers and juveniles and the mutual benefits of a division of labor can encourage cooperative interactions through reciprocity and mutualism (Silk 2006) and complement the positive effects of kin selection (Silk 2009).

Likewise, a grandmother's relatedness to her daughter (Wright's $r = .5$) or her grandchildren (Wright's $r = .25$) is unchanged by the breeding system (see Box 14.2), and opportunity costs are low to cooperate, which might be favored among post-reproductive individuals. (Paternal grandmothering is more constrained by the breeding system and dispersal patterns.) However, dispersal and residence patterns and age-specific mortality and fertility affect the likelihood that the lives of grandmothers and grandchildren overlapped in sufficient numbers to select for a productive post-reproductive period during which help can be directed to grandoffspring (Chapman et al. 2018).

Table 12.1 Helper status and associated theoretic foundations and breeding systems.

Helper's status	Theoretic foundations	Evolutionary breeding system to realize kin-benefits
Juveniles	Cooperative breeding Kin selection Learn-to-mother Age division of labor and mutualism	Any breeding system
Post-fertile females	Grandmother hypothesis Kin selection	Any breeding system
Sexually mature siblings	Cooperative breeding Monogamy hypothesis Ecological constraints	Female monandry*
Mothers	Communal breeding	Any breeding system
Fathers, grandfathers	Parental investment Prestige hypothesis	Female monandry*
Nonkin	Reciprocity Direct benefits (pay-to-stay, learn-to-mother, prestige, group augmentation)	Any breeding system

* Either a monogamous or polygynous pair-bonded breeding system. Note that once cooperative breeding is favored, breeding system constraints can be relaxed (e.g., Lukas and Clutton-Brock 2012) (see Box 12.1 on Monogamy).

Female monandry (either through monogamy or polygyny) is usually argued as a critical step for the inclusion of fathers, sexually mature siblings, or other collateral kin to realize kin-selected benefits for cooperating. One parsimonious interpretation is that cooperative breeding has its origin in cooperating groups of mothers and juveniles since it does not require a priori selection for a specific breeding system, dispersal pattern, or advances in offspring or old-age survivorship. With subsequent changes in life history and sociality, more complex forms of cooperative breeding follow that involved grandparents, fathers, sexually mature siblings, and other ascendant kin (Kramer and Orárola-Castillo 2015).

12.4.2 The Evolution of Cooperative Breeding and Life History Traits

In contemporary natural fertility societies, mothers wean infants at a young age and have short birth intervals while juveniles rely on others in part for their well-being and have a good probability of surviving. This combination of life history traits, which means that mothers have multiple dependents of different ages, is often evoked as the reason why mothers need others. However, this suite of traits did not always characterize human life history and likely did not reach its *modern* form until the terminal Pleistocene (Dean 2006). In asking questions about the evolution of cooperative breeding, it is important to keep in mind that the very life history traits that directly impact parental care (birth intervals, survivorship, juvenile dependence, dispersal) have undergone considerable, and likely recent, modification. In other words, if cooperative breeding is ancient, it likely evolved under not fully modern life history conditions.

Although substantial reorganization in life history, parental care, and energy flows occurred during hominization, these changes leave ambiguous fossil, archaeological, and molecular records. Neither is there a great ape model to help inform us what the transition from autonomous mothers and juveniles to economic interdependence might have looked like. While we often turn to ethnographic populations, particularly hunter-gatherers, they may not be that informative about the emergence of cooperative breeding in our species since they express a modern life history. Alternatively, we can simulate the transition from a general apelike pattern of long birth intervals, nutritional independence at weaning, and juveniles who were self-sufficient foragers to a modern life history of early weaning, short birth intervals, and extended juvenile dependence. Predictions can then be generated for how constraints on a mother's time change within this evolutionary space. Models predict that early in this transition, cooperating groups of mothers and juveniles could have supported early life history modifications such as shorter birth intervals and later ages at maturity, dispersal, and independence (Kramer and Otárola-Castillo 2015). Models also predict that the modern life history parameters of a three-year birth interval and high juvenile survivorship have a marked interaction in raising the costs of children and would have required the help of other adults for mothers to support large families.

In sum, the cooperative breeding literature often assumes a modern life history as the selective background for its evolution. However, if traits that directly affect parental care have undergone considerable modification, this assumption may mislead interpretations of causal relationships and selective pressures. Multiple lines of evidence suggest that cooperative breeding as we know it today was a multilevel process that developed on a changing life history landscape and involved several transitions to incorporate juveniles, grandmothers, other relatives, and fathers.

12.5 Implications for Cooperative Breeding Following the Demographic Transition

Mothers in post-demographic transition societies face new challenges to the same time allocation dilemma of providing competent childcare while finding time to maintain their economic and domestic activities. While this trade-off is as relevant today as it was in the past, living in a market-based economy, having smaller families and living longer alter both the demands and opportunities for help, though not always in expected directions.

Although post-demographic transition mothers have on average fewer children, balancing childcare and resource provisioning may become even more demanding. For much of human history, maternal work and childcare were combined. In small-scale societies, nursing children often accompany mothers on their daily activities, while toddlers are left in home bases to the care of older children. Although mothers can interrupt foraging, agricultural, and domestic work to care for young children, wage work is often incompatible with childcare. Additionally, schooling separates younger children from their older-sibling caretakers. As wage earners, mothers also often have less flexibility. In managing the competing demands of finding time to support younger and older children, mothers in small-scale societies spend less time in economic activities (foraging for food, in agricultural or domestic work, depending on their subsistence base) when they have a nursing infant (Hurtado et al. 1985, 1992; Hames 1988; Kramer 2009). Instead, mothers give priority interest to childcare, while others substitute for their food production and domestic tasks. To maintain their economic position and pursuits, wage earner mothers often opt to pay for childcare. Effective contraception also allows mothers to solve competing demands in new ways by delaying first births, extending birth intervals, or limiting family size.

The kinds of assistance that benefit mothers and offspring, and why helpers help, also change in a monetary economy after the demographic transition, where helper effects become disassociated with child survival. The rise in infant survivorship, a defining feature of the demographic transition, is largely accounted for by the institution of immunization, improved nutritional and sanitation conditions, and child and maternal public health programs, which reduce an infant's exposure to mortality and morbidity risks. While helpers may be less critical to child survival, helpers continue to convey fitness benefits in other ways. Grandparenting, for example, has an important effect on the fertility decisions for working mothers (Coall and Hertwig 2010; Sear and Coall 2011). In a three-generation study of grandparents in the Netherlands, grandparental childcare increased the probability that parents have an additional child over the next decade (Kaptijn et al. 2010).

While some traditional roles may be supplanted, new measures such as financial well-being, educational achievement, or status attainment may be more appropriate in evaluating helper effects in post-transitional societies. For example, close, supportive grandfather relationships are associated with improved grandchild emotional well-being, especially in single-parent households (Ruiz and Silverstein 2007). Although extended family members are more likely to geographically live at a distance and be unable to provide childcare, a monetary economy allows them to contribute from a distance with cash transfers, financial assistance, and purchased goods and services, such as paying for daycare or school fees.

As siblings and juveniles fall out as helpers, opportunities for others increase. The demographic transition is accompanied by changes in both child and old-age survivorship, both of which affect the probability that ascendant and younger generations will be alive at the same time. A large genealogical Finnish sample over a 170-year period found that before the demographic transition, while 65% of children had a living maternal grandmother at birth, shared time varied between 0 and 2 years (estimate across years) (Chapman et al. 2018). After the demographic transition in the mid-nineteenth century, shared time steadily increased with a high of 80% of children having a living maternal grandmother in the 1950s and an overlap of 14 years. Trends in shared time with paternal grandmothers were similar, but much lower both before and after the demographic transition.

Surveys across European countries found that many grandparents, including grandfathers, report caring for a grandchild (Hank and Buber 2009). While grandparenting generally may become more central, grandfathering in particular appears to rise in importance (overview in Coall et al. 2016). Not only are grandparents more likely to be alive, but the role of grandfathers has changed (Sear and Coall 2011), and may make particularly important differences in grandchild outcomes in single-parent and low-income families (Coall et al. 2016).

In sum, as generational time lengthens, family size reduces to one or two children, and families are more prone to geographic dispersion, child-rearing support networks often shrink. Support to raise children in post-demographic transition populations often shifts from kin to nonkin-based assistance such as paying for childcare or utilizing institutional assistance. The indirect value of helping, which may be diluted in larger families, becomes more concentrated in smaller families, and may explain the increasing role of grandparental assistance.

12.6 Conclusion

Similarities and differences between human and nonhuman cooperative breeders are rooted in the human feeding niche and the diverse social and economic interactions that characterize human behavior. Resolving how humans fit into the framework of cooperative breeding will benefit from further theoretical debate and empirical research. Because humans target high-quality resources with complex access problems, it means that not only children but also adults are constrained from being self-reliant. Because human cooperative breeding is embedded in a generalized pattern of food sharing, labor cooperation, and long-term reciprocal relationships that occur across all ages and sex, the integration of cooperative breeding and cooperation theory is likely to be a productive path for future research (Bergmüller et al. 2007). The life history of high fertility and relatively high juvenile survival rates that we document in small-scale and natural fertility populations today is feasible because mothers utilize many forms of offspring support. As an ancestral strategy, however, cooperative breeding likely emerged in stages that coevolved with other features of our life history and sociality.