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3

Comes the Child before Man

How Cooperative Breeding and Prolonged Postweaning Dependence Shaped Human Potentials

Sarah Blaffer Hrdy

The causal chain of adaptive evolution . . . begins
with development.

Mary Jane West-Eberhard,
Developmental Plasticity and Evolution

INTRODUCTION: A NEW PARADIGM EXPANDS

Back in my mother's day, educated women were under the impression that if a baby cried and his mother rushed to pick him up, she would spoil him, conditioning the baby to cry more. According to psychological wisdom of the day, babies were born "blank slates" ready to be molded and shaped by caretakers. It was the second half of the 20th century, before baby books influenced by British evolutionary psychiatrist John Bowlby began to tell a different story. Bowlby (1969) argued that baby primates are born powerfully motivated by the "set goal" of remaining in contact with their mother, and that infants need a "warm, intimate and continuous" relationship, an "attachment," in order to develop normally.

At the time Bowlby was developing attachment theory, not much was known about childrearing among hunter-gatherers (Konner, Chapter 2 in this volume). Bowlby relied heavily on clinical observations of children along with field observations of nonhuman primates, particularly wild chimpanzees, gorillas, and baboons and mother-infant studies of captive

rhesus macaques. As it happened, infant care in these species is exclusively by the mother, who carries her baby everywhere. Extrapolating from these sources, Bowlby emphasized cases where human infants as well were exclusively with their mothers. If babies find it comforting to be held and carried by their mothers, this he reasoned is because in humankind's "environment of evolutionary adaptedness," this is where babies would be safest from predators. Bowlby envisioned this mother-infant dyad nested within a nuclear family composed of husband and wife plus baby.

Influenced by Mary Ainsworth and her observations of infant care in Ugandan households, Bowlby somewhat qualified this mother-focused model. He noted that the term "mother" was meant as a literary convenience to signify "the person who mothers the child and to whom he becomes attached" (1969:221, footnote 2). In time Bowlby also acknowledged the role of the father and other secondary attachment figures. But scratch him hard, and at his core Bowlby retained a chimp- or rhesuslike template for human infants' environment of evolutionary adaptedness, a world where the mother carried her baby everywhere. Indeed, the reason Bowlby gave for selecting chimps and baboons as models was that he assumed their lifeways resembled that of early man (Bowlby 1969:229).¹ "Only in more economically developed societies, and especially in Western ones," Bowlby argued, "are infants commonly out of contact with their mothers for many hours of the day" (p. 246).

Bowlby's profound insight concerning the human infant's need for a "secure base" has become widely accepted, and remains one of the greatest contributions to human well-being ever made by an evolutionary theorist. In the last two decades, however, evolutionary anthropologists like Pat Draper, Henry Harpending, Barry Hewlett, and Jim Chisholm, along with anthropologically oriented psychologists like Michael Lamb, have started to rethink Bowlby's assumptions about the exclusivity of the mother-infant relationship and the insularity of the mother-father unit. They questioned the simple dichotomy that infants were either securely and adaptively attached to their mothers or else not (Lamb et al. 1985; Ahnert and Lamb, in press; Chisholm 1996, 1999, and references therein). At the same time, the evolutionary paradigm was expanding to consider the role of *alloparents*, group members other than the parents, who might also care for infants (especially older infants) and help provision both children and their mothers. Mothers were embedded in a wider social network, and family compositions were less stable, more variable, and dynamic than previously assumed. Within such flexible arrangements it is not always possible to identify the genetic father so it may be more precise to refer to helpers other than the mother, or *allomothers*. In this chapter, both terms are used. Allomothers may include a child's siblings, uncles, aunts, and grandmothers as

well as its father or because of a sexual relationship with the mother, men who *might* be fathers, as well as nonkin like foster children living in the group. Instead of one track (infant is or is not securely attached to mother) developmental trajectories varied with the availability and willingness of such caretakers.

Bowlby correctly observed that infant survival in nomadic, foraging context required close physical contact with *someone*. But as anthropologists like Paula Ivey Henry, Gilda Morelli, Ed Tronick (Chapter 9), and Barry Hewlett have shown, in such cases as the Efe or the Aka, that “someone” was not necessarily the mother. Furthermore, new information (reviewed here) suggests that in environments with high levels of child mortality, alloparental care and provisioning is more than helpful; it is *essential* for child survival.

Most social scientists continue to favor “mother-as-caretaker-within-the-nuclear-family” models. However, I believe that human family patterns were more flexible, and assistance from group members other than genetic parents (“alloparents”) were essential for successful childrearing. Hence, in this chapter I will stress allomaternal contributions in addition to those of the lactating mother. For comparisons, I will also draw on the extensive literature on “cooperative breeding” in other animals to explore the ways that cooperative child childrearing might have transformed the social and ecological context in which early hominid infants developed. Because cooperative breeding allows slower maturation without compromising survival, allomaternal assistance would have facilitated the evolution of prolonged periods of nutritional dependence—the life phase we know as “childhood.” Such allomaternal care and provisioning is heavily dependent on inducements from immatures themselves, so I will also examine how this need to elicit and maintain succor affected the evolution of specific human cognitive and emotional capacities. I argue that a cooperative breeding model provides a more compelling explanation for distinctive human emotional and mental aptitudes than do competing hypotheses.

THE “SEX CONTRACT” MODEL UNDER FIRE

Even as this shift to a cooperative breeding paradigm was under way, human behavioral ecologists were beginning to dismantle support for the main alternative “sex contract” hypothesis, and with it the presumption that prolonged childhood evolved in the context of mated pair with a labor clearly divided between nurturing mothers and provisioning by hunter-fathers (Hawkes 1991; Hawkes et al. 1998; Blurton Jones et al., Chapter 10 in this volume). Ever since Darwin, anthropologists had taken for granted that increasingly efficient hunting by genetic fathers subsidized the slow

maturation of human progeny. According to this conventional wisdom, long childhoods were required for extended development of large brains and for the prolonged socialization and learning of language, cultural traditions, and tool-based subsistence technologies that characterized our species. Supposedly, survival and reproductive benefits from uniquely human capacities like symbolic thought and language more than offset the costs of large brains and slow growth (with the attendant risk of dying before maturity and any chance at all to reproduce). If long childhoods required paternal investment to subsidize full maturation into a fully sapient adult, it was argued, human mothers would just need to choose mates accordingly. A "sex contract" between the mother and her mate evolved: in exchange for exclusive sexual access, the male provided for the female and her young, subsidizing much longer periods of dependency than are found in other apes and providing the economic underpinning of the nuclear family.²

But there has been growing unease with this model. Improved brain capacity would not pay off in evolutionary terms unless smarter individuals outbred dumber but faster maturing apes. Could being smarter possibly pay off enough to offset several years' delay in the time when a young female breeds? How could an organ so costly as the human brain, together with such a long delay in maturation, be selected for? Worse, evidence emerging from still extant foragers was not always consistent with other assumptions of the sex contract model.

Based on ethnographic data from contemporary hunter-gatherers like the Hadza, Blurton Jones et al. (Chapter 10 in this volume) and Hawkes (1991) proposed that obtaining meat had more to do with "showing off" so as to increase sexual access to women (i.e., mating effort) than provisioning progeny (parental effort). Pursuing the logic that sociobiologists use to explain the evolution of nuptial gifts in animals (e.g., Weddell 1993) Hawkes hypothesized that males used meat to advertise their worth and to compete for access to mates.

Unquestionably, animal protein and fat provided by hunters increased the fecundity of women as well as the survival of their children [Marlowe (2001); see also O'Connell et al. (2002) for extension of this argument back in time to include our Pleistocene ancestors], and unquestionably this desirable commodity was exchanged for sex, often with the father of a woman's children. But Hawkes argued that the *primary* payoff to men was *more sex*, not necessarily the increased survival of children men had already fathered. "Father-as-hunter-and-sole-provider" might have characterized Paleolithic hunters from northern latitudes as well as bourgeois patriarchal families, the type of Victorian society most familiar to Darwin, but Hawkes, O'Connell, and Blurton Jones were starting to question whether such sex contracts constituted the fundamental economic unit for

provisioning children among hunting-gathering ancestors in the African tropics hundreds of thousands of years ago.

Using comparative data from foraging societies, Hillard Kaplan (1994) calculated that it takes some 13 million calories to rear immatures to a point where they produce as much as they consume. Because it takes more calories than a mother by herself could produce (over and above her own needs) to get to this point, offspring would have needed nutritional subsidies from allomothers until they were 18 years of age, or older. In contrast to all other apes, human mothers produce a new baby before her previous, weaned infant is nutritionally independent (Lancaster and Lancaster 1983; Kaplan et al. 2000). How could natural selection have favored an ape female who produced offspring so far beyond her means to rear? Such mothers must have had help. In hunting and gathering societies, help from fathers was important, sometimes critically so, but what about when due to death, defection, or inadequacy, a deficit remained? Then who helped? It is not that contributions by husbands or hunters are unimportant, but that a mother who relied exclusively on a sex contract with the father to provision their children, risked failure. What were her alternatives?

THE COOPERATIVE BREEDING HYPOTHESIS

The cooperative breeding hypothesis presumes that mothers evolved in groups where a broader range of individuals—not just the genetic father—assisted the genetic mother in protecting, carrying, or provisioning offspring, thereby permitting her to produce and rear costlier, slower-maturing offspring than otherwise would survive. Divisions of labor between breeders and nonbreeding helpers would have permitted mothers to reproduce faster. Concomitant sharing and cooperation also permitted reliance on a wider range of resources and with it the option to move into new habitats. This is one reason why cooperative breeding has independently evolved in a small but diverse array of arthropod, avian, and mammalian species (Stacey and Koenig 1990; Emlen 1991; Solomon and French 1997a). Somewhere between 8 and 17 percent of birds (Heinsohn and Double 2004) and perhaps 3% of mammals breed cooperatively. In the case of humans, I believe it was cooperative breeding that originally allowed them to spread out of Africa and expand into diverse habitats around the globe as also occurred in other geographically successful cooperative breeders like canids, lions, elephants, and various corvids.

Alloparental assistance by genetic relatives is well explained by Hamilton's rule. Individuals help when the cost of caring is less than the benefits to their charges calibrated by degree of relatedness. But high degrees of relatedness between an allomother and his or her charges are not the only

motivations for helping. Ways in which helpers benefit include obtaining a safe refuge while buying time to mature, acquire subsistence skills, practice parenting skills, or awaiting opportunities to breed; acquiring improved social status or opportunities to signal quality to prospective mates; obtaining occasional mating opportunities; enhancing the territory or cooperating community in ways that improve future breeding opportunities or increase the helper's chance of inheriting access to these resources (for review, see Cockburn 1998). Ecological constraints may facilitate the evolution of cooperative breeding if breeding territories or other inherited resources critical for reproduction are in short supply (Emlen 1991; Pen and Weissing 2000:2417ff.).

Individuals who lack help, access to resources, or relevant skills have little chance of breeding successfully anyway. This reduces the fitness costs of helping. Furthermore, when helpers have the option to strategically schedule assistance, they can limit helping to phases when they are well nourished or can spare the time. When helping does interfere with their own reproduction, however, allomothers may decline to help (Russell et al. 2003). Finally, allomothers at or near the end of their reproductive careers have little if anything to lose by helping, which may explain selflessness in defense of infants sometimes exhibited by old female primates (Hrdy and Hrdy 1976).

REQUIREMENTS AND HALLMARKS OF COOPERATIVE BREEDING: COMPARATIVE EVIDENCE

Philopatry and a high degree of sociality are essential for shared caretaking to evolve in the first place. To set the stage for the evolution of cooperation, one sex or the other has to remain in its natal group in order to be susceptible to infant solicitations (Emlen 1995; Solomon and French 1997a). Another requirement is sufficient phenotypic flexibility so individuals can shift between nonreproductive and reproductive caretaking roles.

Flexibility and opportunism are hallmarks of cooperatively breeding species. Wild dogs provide a classic example. Typically, wild dog packs have a single breeding pair attended by allomothers who provision the alpha female while she gestates and lactates; bring predigested meat back to her pups; guard them while the alpha female hunts; and also allow her pups once weaned and past the age of receiving predigested "baby food" to eat first at kills. Nevertheless, when feasible, subordinate female "helpers" ovulate and breed themselves. Genetic analyses reveal that most pups are produced by the alpha female, but as many as 8 percent are borne to subordinates. Even when the alpha female has a dominant mate, 10 per-

cent or more of pups may be sired by subordinates (cited in Creel and Creel 2002). Typically pups are suckled by their mother, but they may also be suckled by an allomother who undergoes pseudopregnancy and lactates without giving birth. The Creels even observed one subordinate nullipara begin to lactate ten days after the litter was born. Thereafter, she ended up spending more time with the pups than the mother and did most of the suckling.

Following Sherman et al. (1995), cooperative breeding occurs along a continuum ranging from modest assistance (like carrying or protecting infants while mothers forage) to extensive assistance that includes prolonged babysitting, provisioning, or even suckling. Helping behavior ranges from facultative to obligate assistance, depending on how feasible it is for mothers to rear offspring on their own, but food sharing and allomaternal provisioning of young are probably essential for the prolonged periods of nutritional dependency I focus on here.

The key feature of cooperative breeding is that when available, allomaternal assistance alters basic quantity-versus-quality life-history trade-offs underlying maternal decision-making. In a paradoxical departure from the usual trade-offs, mothers in a cooperative breeding system can produce more, larger, or more closely spaced offspring even as total cost of rearing each offspring to independence increases. They can invest less per offspring and give birth again sooner, without sacrificing child survival. Divisions of labor between reproductive and nonreproductive group members lowers the costs of mothering as allomothers in addition to mothers respond to signals of infant and juvenile needs by providing protection, care, and/or provisioning. Allomaternal provisioning also permits offspring to remain dependent longer, because they can afford to take longer to grow up without risking starvation. Buffered by allomaternal assistance, mothers in cooperatively breeding species also tend to survive longer presumably because they are healthier, better provisioned, and remain in safer locales (in a hive, in a den, near camp; e.g., Rowley and Russell 1990; Keller and Genoud 1997).

Whether we are talking about dunnocks or acorn woodpeckers, wild dogs, mongooses, or elephants, mating arrangements in cooperative breeders are very variable. Breeding associations range from reproductively "single" mothers or monogamous pairs surrounded by nonbreeding helpers (some social mongooses or marmosets), to socially bonded pairs who are also facultatively polyandrous or polygynous where alloparental male help is very important (e.g., other marmosets; many birds). Helpers may be either close relatives or hopeful immigrants waiting to inherit a territory. Helpers may be totally excluded from breeding opportunities or have occasional opportunities to breed. This flexible style of

family life varies with local ecologies (or economics) and depending on which sex currently has the most leverage, a not uncommon pattern in traditional human societies (Emlen 1995; Hrdy 2002).

If humans evolved as cooperative breeders, there would be no need to invoke the development of sapient brains or other uniquely human rationales as the original selection pressures favoring longer childhoods. Improved child survival, and with it slower maturation (Hamilton 1966) along with prolonged periods of postweaning dependence, would have evolved as routine corollaries of cooperative breeding. So far the strongest evidence in support of this proposition comes from birds.

COOPERATIVE BREEDING AND LONG "CHILDHOODS"

The link between cooperative breeding and prolonged dependence was first demonstrated by behavioral ecologist Tom Langen in a comparative study of birds. Of 261 passerine birds, 217 species did not ever breed cooperatively, 10 did so occasionally, while 34 species were frequent cooperative breeders. Average duration of postfledgling nutritional dependence was twice as long (just over 50 days) for birds that frequently bred cooperatively compared to birds who never bred cooperatively (just over 20 days). Species that occasionally bred cooperatively fell in between, at just over 30 days (Langen 2000:Figure 1). Cooperating and noncooperating species do not differ in duration of incubation or nesting periods, but they differed significantly in duration of nutritional dependence postfledging.

Langen (2000) argues that prolonged postfledging dependence is made possible because additional care from alloparents reduces the cost of parenting, and offspring have less incentive to become independent. A new sort of division of labor develops as nonbreeders feed fledglings, freeing breeders to initiate the next nesting attempt (p. 367). Langen's terminology is aviocentric, but his logic applies more generally. In theory, the same arguments should apply to social mammals. Unfortunately though, mammals have not been as intensively studied as birds have, and it is also harder to pinpoint the timing of independence. As yet, no comparable analysis across mammals has been done. Hence we cannot extend Langen's arguments to mammals with the same conviction with which we apply them to birds. That said, the greater prenatal and postnatal costs of rearing young documented in best studied species of cooperatively breeding mammals (especially perhaps those with suppressed ovulation) are consistent (see Creel and Creel 1991:Table 2). Consider also the case of Calitrichids, who according to Harvey et al. (1987:Figure 16-4) appear to mature almost as slowly as humans do provided that their much lower birth weights are taken into account and controlled for. Allomaternal provi-

sioning means that offspring can take their time maturing without risking starvation, even though their mothers wean them, conceive again and produce new offspring. This is the case with wolves and wild dogs, where alloparents provide regurgitated meat to pups. Premasticated "baby food" means that even in mammals (where only lactating females provide the earliest food) males can provision older immatures, just as both sexes are able to do in birds and humans. Even after pups outgrow the milk and "formula" phase, parental and alloparental forbearance buffers less-than-self-sufficient, still inexperienced, hunters over long apprenticeships during which they become proficient hunters. Experienced grown-ups tolerate youngsters at kills and may even allow them feeding priority. Although scramble competition at kills would normally mean that smallest group members feed last, least, or not-at-all, this is not what happens among cooperatively breeding carnivores like wild dogs, where preferential access to food by pups and cubs is typical (e.g., see Malcolm and Marten 1982; Creel and Creel 2002:165).

I hypothesize that dependents were similarly buffered among our ancestors and that cooperative breeding thus helps to explain prolonged and delayed childhood and adolescence in humans (compared to other apes), a developmental process that may have begun with *Homo erectus* (Tardieu 1998:173–174), although this proposition remains controversial). The hypothesis that allomaternal buffering provided the initial condition permitting delayed growth spurts does not rule out the possibility that once started delayed maturation and greater brain growth coevolved.

ALLOMATERNAL ASSISTANCE AMONG NONHUMAN PRIMATES

The central assumption of the cooperative breeding hypothesis is that allomothers increase the reproductive success of mothers. Do they? After all, allomothers might have their own reasons for "helping," like obtaining practice by babysitting. It is now well documented for some species of cooperatively breeding birds and mammals that alloparental assistance permits mothers to breed more rapidly and/or increases offspring survival (e.g., Stacey and Koenig 1990; Emlen 1991; Langen and Vehrencamp 1999; Solomon and French 1997a), but such evidence has been slow in coming for primates. The main problem in demonstrating alloparental effects has been the difficulty of obtaining information on lifetime reproductive success for long-lived primates. In addition, the mother-centered models for our own species—reinforced by data from the other apes—were so compelling that many anthropologists and psychologists tended to overlook the role of other caretakers even though primatologists had been reporting

on rudimentary cooperative breeding (allomaternal care without provisioning) in primates for many years (e.g., Hrdy 1976).

Across primates, allomaternal assistance ranges from simple protection or occasional interventions during disputes, to carrying babies, to cases where allomothers (often males likely to be the father) spend *more* time holding infants than mothers do (see continuum of primate allomaternal care in Figure 3.1). If we include paternal care, on the order of half or more of all 175 or so species of primates are characterized by some degree of shared caretaking. Allomaternal attention to infants is a far more important feature of primate behavior than has been generally realized (Hrdy 1999).

Mothers in species with “infant-sharing” depend on allomothers less than full-fledged cooperative breeders where allomothers provision as well as care for youngsters. Nevertheless, in infant-sharing Hanuman langurs, infants are carried by females other than the mother up to 50 percent of daylight hours from the first day of life (Hrdy 1977). Energetic savings to the mother mean the mother can conceive again sooner, and breed at a faster rate without impairing her own or her offspring’s survival (Mitani and Watts 1997; Ross and MacLarnon 2000). Without allomaternal provisioning weaned youngsters are under pressure to provision themselves, ruling out leisurely development as an option.

Currently the only primates counted among full-fledged cooperative breeders—where allomothers provision as well as carry their charges—are at the extreme end of the primate continuum of shared care, among marmosets and tamarins. Adult males—typically former sexual partners of the mother—are so eager to carry the babies (usually twins) that by the second week after birth, males carry them as much as 60 percent of the time. Unlike cooperative breeding birds where allomothers feed immatures right from hatching, or those carnivores where subordinate females serve as wet nurses, only the lactating mother has ever been observed to suckle Callitrichid babies. Nevertheless, by one week, an adult male is doing most of the carrying, and by three weeks—with weaning still more than two months away—marmoset allomothers supplement the mother’s milk with “finger food” in the form of crickets and other small-prey items. The more males in the group, the higher the mother’s reproductive success (Snowdon 1996; Bales et al. 2002). Such help is costly to males, who spend less time foraging and fail to gain weight until after their charges are mobile.

Cottontop tamarin mothers are so dependent on this assistance, that regardless of how old or experienced the mother is, if adult or sibling caretakers are not available, mothers short on assistance abandon their young at high rates (Johnson et al. 1991; Bardi et al. 2001). Humans are the only other primates with such high rates of abandonment. (Detailed evidence

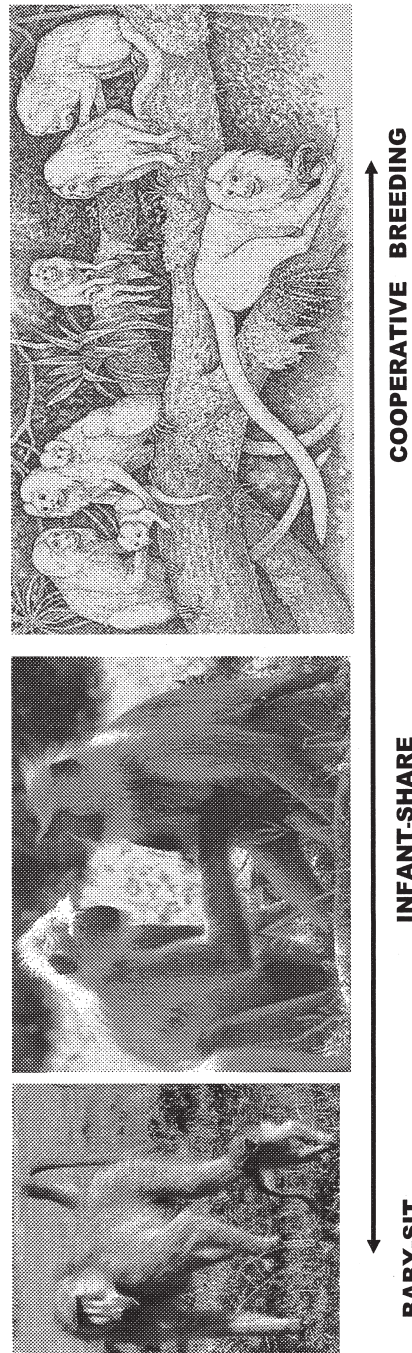


Figure 3.1. Please provide caption.

for unusually situation-dependent and contingent maternal commitment is summarized in Hrdy (1999: Chapters 8, 12, 14); the main exception to the pattern is in inexperienced first-time or “primiparous” mothers, which may have trouble rearing infants in other primates as well as in humans without social support) (see Figure 3.2).

HUMAN EVIDENCE THAT ALLOMOTHERS HELP

Anthropologists have long been aware that older siblings, cousins, and other family members play important roles as child-minders (Weisner and Gallimore, 1977; Tronick et al. 1987; Hames 1988; LeVine et al. 1996; Konner, Chapter 2 in this volume). The more attention one pays to the original field studies and the less attention is paid to categorical statements from the secondary literature, the less monotropic maternal caretaking seems (discussed in Konner, Chapter 2 in this volume). Yet it was the end of the 1980s before sociobiologists began to consider the evolutionary implications and to collect the data showing that allomaternal assistance actually affected reproductive success. In a pioneering 1988 paper, Paul Turke at the University of Michigan linked the availability of allomaternal assistance to increased maternal reproductive success among the Truk islanders in Micronesia. In this matrilineal and matrilocally living population, women



Figure 3.2. Please provide caption.

who bore a daughter first had higher reproductive success than those women whose first two children were sons. Similarly in a study of a Trinidadian village in the Caribbean, nine mothers who lived in households with nonreproductive helpers on hand—usually daughters—had significantly higher reproductive success than 29 mothers without (Flinn 1989). In a study of Mandinka horticulturalists in the Gambia of West Africa, children had better survival than did same-age children without older sisters (Sear et al. 2002:58). As in the Truk case, daughters helped more than brothers, but Truk was the only place where birth-order (having a daughter first) seemed to matter.

All of these studies documented beneficial effects from having a big sister. Elsewhere though, benefits from having older siblings did not show until later in life, when younger siblings themselves reproduced (e.g., see demographic data analyzed for !Kung hunter-gatherers in Botswana by Hames and Draper 2001). Mechanisms responsible for this correlation are not known, but it seems possible that adult siblings may provide shelter or food in times of crisis, contributing that way to the survival of nieces and nephews. Although most research in this area has focused on prereproductive helpers, it is worth keeping in mind that collateral kin can help at any point in their life cycle.

Ever since Hawkes and coworkers (1989) became intrigued by how hard and efficiently postreproductive women were working at food gathering among Hadza foragers in East Africa, evidence has been accumulating that the presence of older matrilineal kin (both grandmothers and great-aunts) enhances the growth and survival of immature relatives. Such data are all the more remarkable because the correlation is found over a broad socioecological spectrum. The best documented cases come from East and Central African hunters and gatherers (Hawkes et al. 2001b; Ivey 2000; Ivey Henry, Chapter 9), West African horticulturalists in the Gambia (Sear et al. 2000), 18th-century German peasants (Volland and Beise 2002), and rice-growing peasants in Tokugawa, Japan (Jamison et al. 2002). Among South Asian swidden agriculturalists (Leonetti et al. 2002). Grandmothers also contribute to shorter birth intervals, although exactly how is not known.

For both 18th-century Germany (Volland and Beise 2002) and the Gambia (Sear et al. 2002), the survival advantage to having a maternal grandmother nearby showed up around the age of weaning—a very vulnerable life phase attended by emotional stress and the introduction of new foods. The timing of the effect suggests provisioning is at issue. However, mothers in the Gambia population were primarily Muslim, living patrilocally in their husband's home. At first glance then, it seems odd therefore, that it would be the *maternal* grandmother's presence that mattered so much. But Sear et al. (2002:59) note how common it is for West African mothers to

foster babies out around weaning in order to help their babies “forget the breast.” Hence the most solicitous available caretaker not already a household member would be—were she still alive, and nearby—the maternal grandmother.

THE VERY VARIABLE ROLE OF FATHERS

The most surprising finding from this West African horticultural society in the Gambia was not that maternal grandmothers mattered so much. Rather it was how little difference the presence of the father or older brothers made. Even when the father was absent altogether, alloparents were able to compensate (e.g., Sear et al. 2002; Blurton Jones et al., Chapter 10 in this volume). Yet where game is more important, as among Ache foragers of Paraguay, the death of a child's father undermined his survival chances (Hill and Hurtado 1996). Perhaps not surprisingly, mothers under such conditions cover their bets by lining up several possible “fathers.” Whereas in some societies, a wife suspected of adultery puts herself in peril, in others, her options for manipulating information about paternity are enhanced by customary beliefs about how long pregnancy lasts, or about how many men contribute to the formation of a fetus.

Across vast areas of South America, there is a prevailing belief that a fetus is built up from contributions of semen from all the men a woman has sex with in the ten months preceding birth. This presumably quite ancient belief encompasses multiple language groups, from the Ache and Kaingang people in Paraguay, all the way north as far as the Yanamami and Bari in Venezuela, eastward to the Canela, Mehinaku, and Arawete peoples in Brazil, westward to the Matis of Peru. Over a vast region, mothers rely on the convenient biological fiction that it takes contributions of semen from more than one man to “make” a baby to reduce male sexual jealousy and facilitate sexual sharing of a woman by possible “fathers” who will jointly help provision both the mothers and their children (Beckerman and Valentine 2002). Among the Bari and the Ache, the only two groups for which we have data on child survival rates, children with two “fathers” survived better than those with only one. However, children ascribed to too many “fathers” survived less well, presumably because men may balk at provisioning them (Hill and Hurtado 1996; Beckerman et al. 1998).

Many cooperatively breeding mammals *do* routinely bear litters with more than one genetic father (e.g., wild dogs, wolves, dwarf mongooses, lions). But humans do not. Nevertheless, a belief in partible paternity presumably persists because in a part of the world where provisioning by males is unpredictable, and where mothers need more help than one man

by himself can provide, the willingness of several men to provision mothers and their children is critical for the survival of patrilineal as well as matrilineal lines. Generation after generation having multiple "fathers" (along with any "memes" that facilitated it) paid off. As soon as a Bari woman misses a period she may attempt to seduce one of the better fishermen or hunters in her group. This may be the flip side to the observation that the best hunters and the best fisherman have the most lovers (e.g., Hill and Hurtado 1996).

Such a belief system makes it is easier for mothers to draw several men into a web of possible paternity. The custom may also facilitate cooperation and alliances among men (often kin) belonging to the same community. Ritual reinforces these beliefs. Among the Canela of Brazil, for example, sex with multiple partners takes place during public ceremonies, in full view of everyone, and with the approval of the community. Subsequently, all the men a woman had intercourse with are publicly acknowledged as cofathers to the next infant she bears. Within limits, traditional beliefs about shared paternity function to diminish, not necessarily eliminate, sexual jealousy. In large areas of Central Africa, as well as in parts of Western Asia, there is customary sharing of wives within fraternal clans and among both genetic and fictional "brothers" (Hrdy 2001c). We are still in the early days of the study of the reproductive consequences of "polyandrous motherhood" (Guyer 1994). Already though it is clear that we need to reexamine the reflexive assumption that children develop best reared in nuclear families and cared for exclusively by mothers, for whether or not these presumptions pertain depends on economic and social circumstances.

If our ancestors lived among groups of relatives, as is true among most hunter-gatherers, generalized tendencies to behave altruistically toward needy group members would be adaptive (Wiessner 2002). Wiessner argues persuasively that among the !Kung San, successful hunters are not just provisioning other group members, who are more likely than not kin. They are also providing incentives for capable, willing allomothers to remain in their group. Meat becomes a reward hunters can use to produce long-term residential and political configurations favorable to rearing their children, as well as increasing the resource-holding potential of the group as a whole (Wiessner 2002:427, Tables 3 and 4).³

It is now clear for many species that degree of relatedness affects whom individuals help and how much (Emlen 1995). Once again, cooperatively breeding birds provide the best-documented examples. For example, among dunnocks, provisioning by alpha and beta males is calibrated to each male's probability of paternity (Davies 1992). The calculus for caring can be especially complex in the case of possible progenitors [see Westneat and Sargent (1996) for an excellent overview]. Whereas in some species or situations, males respond to decreased certainty of paternity by

withholding care or even by destroying offspring, in others, even males who are less than certain of paternity help [e.g., see Osorio-Beristain and Drummond (2001) for birds; Palombit (1999), Buchan et al. (2003) for baboons]. In this respect, humans exhibit marked intraspecific variation, depending on circumstances. In some situations a father is essential for child survival, while in others the effects of his presence are hard to even document. Among the Ache, a child whose father dies may be killed by a stepfather, or preemptively eliminated by the mother herself (Hill and Hurtado 1996). Similarly, among modern Canadians there is a significant increase in the risk of abusive treatment if a stepfather (or boyfriend) rather than the baby's father is living with the mother (Daly and Wilson 1988). Yet in modern Sweden, where extensive social welfare allotments defray costs to unrelated "fathers", no such effect was found (Temrin et al. 2000). Consider also the Mandinkan case from the Gambia, West Africa. There allomothers play an important role in subsidizing the costs of childrearing and death of the father made no detectable difference unless the mother remarried and thereby placed her child at risk from a stepfather (Sear et al. 2002). It is not my intent here to downplay the importance of fathers, but only to call attention to how variable is the role they play, depending on what other sources of support, alloparental or otherwise, are available.

THE IMPORTANCE OF REAL AND PERCEIVED ALLOMATERNAL SUPPORT

For all mammals, the best single predictor of infant survival is maternal commitment. But in humans, this commitment—at least initially—is influenced by the mother's own perception of social support. Mothers register social signals given off by those around them, and translate this information into how much material support is likely to be forthcoming. Thus, even when the mother is *initially* the main caretaker (almost always the case in lactating mammals), availability of allomaternal support matters. The ethnographic and historical record for societies in which child survival is far more uncertain than in our own provides ample evidence that mothers short on allomaternal support are more likely to abandon infants at birth (Hrdy 1999:372 ff.).

Even small increases in level of social support make a difference. Adolescent U.S. mothers (even those where the father remains with them) are more sensitive to their infants' needs and have more securely attached infants if a supportive grandmother is also on hand (Spieker and Bensley 1994). Women visited in their homes during their pregnancy by trained nurses and during the first two years after birth had a lower incidence of child abuse (Olds et al. 1986). Follow-up studies confirmed the long-term benefits (in terms of these allomaternal interventions (Olds et al. 2002).

Social workers and medical personnel have long been aware that children benefit from living in extended, multigenerational families. Even when socioeconomic conditions are controlled, rates of morbidity and mortality continue to rise among children in single-parent homes (Weitoft et al. 2003). Nor does this effect appear to be due to the absence of the father per se (e.g., Golombok et al. 1997). Rather the evidence suggests that it is the various forms of support provided by multiple caretakers that matters. Furthermore, if maternal competence is compromised by immaturity, by inexperience, by father absence, or by resource scarcity, the presence of alloparents turns out to be more important still. For example, babies born to unmarried, low-income U.S. teenagers tested better on cognitive development at age four if a grandmother was present (Furstenberg 1976). By three years of age, children are able to interpret the feelings and intentions of others, and can even imagine what it is like to be someone altogether different (Harris 2000:54-55). Infants who have older siblings develop this "theory of mind" sooner, and with greater sophistication (Ruffman et al. 1998; Perner et al. 1994). For children at risk, the guidance, emotional support, protection, and material support of grandmothers have a positive effect at all ages (reviewed in Werner 1984).

The most obvious explanation for faster growth rates among the Gambian children with maternal grandmothers nearby (Sear et al. 2000) is that these postmenopausal women, unencumbered by dependent offspring of their own, provided their grandchildren with extra food. However we cannot yet rule out alternative possibilities. Years ago Widdowson (1951) reported that institutionalized children in the charge of an emotionally warm and nurturing matron grew faster. So too, the faster-growing Gambia children may have responded to emotional support from an affectionate grandmother by thriving. Indeed, the cooperative breeding hypothesis specifically predicts that children should be responsive to emotional cues from caretakers since in human environments of evolutionary relevance signals of emotional commitment would have been correlated with prospects of continued provisioning. That is, we should expect human immatures to possess psychological devices for monitoring signals of commitment from both mothers *and* allomothers. Continued rapid growth should be expected when infants perceive these cues, but detection of indifference or neglect should slow growth down so as to conserve resources and increase chances of surviving future anticipated neglect. This may be why even with adequate nutrition available, some children nevertheless "fail to thrive" (Pollitt and Leibel 1980).

A vast historical and sociological literature now documents emotional, cognitive, physiological, as well as material benefits for children growing up in extended families with older siblings, grandmothers, kin, or as-if kin in attendance (e.g., Stack 1974; El Hassan Al Awad and Sonuga-Barke 1992; Spieker and Bensley 1994). Until recently though, few researchers thought

of such advantages in *evolutionary* terms, primarily I suspect because most sociological and psychological studies were done in populations with low rates of infant and child mortality. Not until the sociobiologically oriented field studies of the late 1980s did the actual *survival* advantages from allo-maternal assistance in humans become apparent.

SUMMARY, CAVEATS, AND AN ASIDE ON GENETIC RELATEDNESS

Old paradigms are in flux. As we replace old models based on "sex contracts" with new ones based on cooperative breeding, there is all the more reason to proceed with caution lest the pendulum swing unchecked. As old biases are corrected, and kin-selected altruism moves to center stage, it is time to worry lest a new set of biases replace the old ones.

After years of neglecting the role of alloparents, it may now be time to worry about overemphasizing collateral kin. For example, we should be careful not to cast grandmothers as universally more useful than they really are. This is why it is important to pay attention to outliers, to the odd findings that do not readily conform to the model in hand, and why it is important for journal editors and reviewers to urge publications of "negative results." Consider Draper and Howell's (Chapter 12, in this volume) reexamination of !Kung demography as it relates to the body mass index (BMI) of children. These authors detected no advantage from having grandparents. This could be because the cooperative breeding hypothesis is wrong or, as Draper suggests, because we need to take social context into account. Perhaps it is the band rather than kin group per se that provides critical assistance under these particular demographic and ecological conditions. For genetic relatedness is not the *only* determiner of nurturing. If the cost of caring is low enough and benefits to recipients are high enough, individuals who are only distantly related should still help (Hamilton 1964). This generalization applies in spades to humans, where payoffs from generosity and kindness come in many currencies, and where other group members may react negatively to those who fail to help a child.

HAMILTON'S RULE AND THE PROXIMATE CAUSES OF HELPING

Ultimately, individuals in species with a history of cooperative breeding would be predisposed to help mothers rear their young because their own inclusive fitness (that is, individual fitness plus the fitness effects upon close kin) was enhanced by aiding relatives rear offspring. Helping also

provides valuable practice, increases group acceptance, or paves the way to later breeding opportunities for experienced individuals who inherit mates or territories. But what are the mechanisms? At a proximate level, there must be selection pressure on nonmothers to find infants appealing in the first place. Helpers have to assess and respond to infant needs depending on the urgency of need and the caretaker's own condition. In the case of older females approaching the end of their reproductive careers, "donative intent" goes up (apparently a fairly general rule in primates) but postreproductives nevertheless should prioritize their service depending on degree of relatedness and especially *level of need* (Hrды 1999:Chapter 11; Blurton Jones et al., Chapter 10 in this volume). That said, many primates (perhaps especially females?) exhibit a bias toward helping, as if their internalized version of Hamilton's rule more nearly read: *Find infants appealing and help them if you can, so long as the cost is not prohibitive and so long as it does not interfere with caring for your own new baby*. This may be because the female primates I am most familiar with (humans and langurs) evolved in kin groups.

In many primates, males and females respond differently to solicitations from infants. In infant-sharing species belonging to the subfamily Colobinae, for example, newborn infants exercise a magnetic appeal on females (and this may be why they are born with flamboyantly colored natal coats to advertise their neonativity), but such signals may be less attractive to males (Hrды 1976). Male nonchalance species like langur monkeys contrasts with the fanatically nurturing behavior and the prioritizing of infant care by adult males seen in species with *obligate* male care. For example, among titi monkeys, fathers are actually more responsive to infant signals, and more eager to carry infants than their mothers are.

In humans, however, both sexes respond to attractive behaviors (like smiling or babbling), and both sexes respond to "cuteness" and/or vulnerability (round heads, small face, big eyes, immature body form), but there are nevertheless significant differences in how the sexes respond to them. In one of the few studies of this, Thomas Alley (1983) asked 120 childless undergraduates to examine drawings that only differed in size and how babylike or immature the body proportions were. For both sexes the "mean cuddliness ratings" decreased with perceived age, and for both sexes, having a younger sibling increased responsiveness. However, on average women were significantly more protective than men (i.e., they would intervene if someone struck the infant). Compared to most women, men probably have a higher threshold for responding to infants (e.g., see Babchuk et al. 1985; Silk 2002). Nevertheless, what stands out here is just how responsive men are to prolonged exposure.

The most revealing research in this area been done on prolactin-mediated systems. The first hint that there was a connection between

prolactin levels and “paternal” behavior came from a study of marmosets (Dixson and George 1982). The discovery was initially met with skepticism, in part because prolactin was viewed as a lactation-related hormone linked to *maternal* rather than paternal behavior. Critics protested that prolactin must be a response to stress in these males rather than a corollary of nurturing tendencies. Subsequently, the introduction of improved, noninvasive techniques permitted robust replications of Dixson and George’s discovery (Schradin and Anzenberger 1999 for review), and higher prolactin levels were also correlated with male helping behavior in other cooperative breeders, such as provisioning by male scrub jays (Schoesch 1998). Interestingly, prior experience is a factor in primate male responsiveness as it also is in females, and the rise in prolactin levels is even more pronounced among males with prior caretaking experience (Snowdon 1996).

It took two decades and a paradigm shift in how biologists conceptualized sex roles before anyone studied the hormone profiles of men in proximity with infants. As soon as they did, it became clear that endocrinological shifts in men spending time in proximity to pregnant women and new infants are surprisingly similar to those found among cooperatively breeding male marmosets (Gubernick et al., no date; Hewlett and Aster, no date; Storey et al. 2000; Wynne-Edwards and Reburn 2000). Prolactin levels in cohabiting men gradually rose over the course of their companion’s pregnancy. In addition, men exposed to pregnant women and new babies experience a drop in testosterone after birth (Storey et al. 2000; Grey et al. 2002; Fleming, et al. in prep)—something no one would have expected to find in parents with a strict division of labor between nurturing mothers and protective male hunters. However, male flexibility in this respect is compatible with the hypothesis that humans evolved in cooperative breeding systems where if no other allomother was available, a male might pinch-hit.

Without question, hormonal changes during pregnancy and lactation are more pronounced in mothers than in their male partners. With some important exceptions, female primates tend to be more sensitive to infant signals and solicitations than males are. No one is suggesting that fathers are equivalent to mothers. So different are the physiological and sensory thresholds of the two sexes that experimenters use different scales to measure them. But the point remains, whether caretakers are mice, marmosets, or humans, that *both sexes can potentially be primed to be more nurturing by innate physiological responses to infant stimuli*. The neurological framework is in place. Just being near infants or pregnant mothers renders males or virgin females more nurturing, so that giving birth is not a prerequisite for nurturing.

If humans evolved as cooperative breeders, an obvious prediction would be that some potential for nurturing response to prolonged contact

with infants should be found among males generally, not just in husbands or genetic fathers—something that remains to be seen.

**SPECULATIONS ON COOPERATIVE BREEDING,
AND CHILDHOOD MILESTONES SUCH AS
MIND-READING, MILK TEETH, AND BABBLING**

Once allomothers become important for child survival, selection would have acted on any number of life history traits that made allomothers more available (e.g., delayed dispersal, delayed maturity, longer lifespans). In particular, Hawkes et al. (1998 and elsewhere) have explored the implications of assistance by older matrilineal kin for lifespans that last long past menopause. Selection should also favor emotional traits that make allomothers more helpful and more responsive to signals of need (e.g., increased empathy in particular age-sex classes). One outcome would be that natural selection should have favored humans whose neuronal systems registered the act of helping others (even those they are not related to) as pleasurable. This is precisely what studies show that use magnetic resonance imaging to track the effects of altruistic behavior on pleasure centers in the brain (Rilling et al. 2002). Experiments using “ultimatum games” and other experiments to determine internalized rules used when sharing reveal humans to be far more altruistic than anticipated. Whether in modern or traditional societies, humans appear to employ innate rules about what is fair (Henrich et al. 2001). The discovery that rational self-interest often takes a backseat to internalized rules of sharing and fair play is revolutionizing traditional economic theories (Fehr and Fischbacher, 2003). Remarkable as all this seems, even more momentous selection pressures appear to have been at work on human infants.

Assuming that our ancestors were cooperative breeders among whom maternal commitment was unusually contingent on social support, human offspring would have needed to monitor and interpret the moods and intentions of others more than other apes do. Infants who could engage their mothers right from birth would have an advantage over those who could not. Beyond the discomfort and separation cries characteristic of all infant apes, human infants would have been under greater selection pressure to appeal to both mothers and allomothers. Perhaps not surprisingly then, right from birth human infants seek out human faces, and initiate contact with others. Remarkably early in development, babies imitate faces, smile, and laugh in ways that apes reared exclusively by their mothers have not been observed to do (Meltzoff and Prinz 2002; Papousek et al. 1991). Early learning biases persist, and are refined and reinforced through experience (see esp. Tomasello 1999), as babies become more discriminating. Eyes play

a key role in the attendant social engagements (Baron-Cohen [1995] 2001). Human infants seek out and fixate on eyes, and preferentially respond to a direct gaze. By three to four months, infants smile less at adults who avert their gaze, and resume smiling when the adult looks straight at them (Farroni et al. 2002). The sociocognitive tools for monitoring others and reading their intentions by seeking out their eyes, following their gaze, etc., are more developed in humans than in other apes (Baron-Cohen [1995] 2001). Emerging evidence for chimpanzees reveals that other apes are capable of observational learning and imitation (Whitten et al. 2003), but humans appear to be unusually eager to do so, and are unusually adept at it. Just how different chimps and humans are in respect to reading intentions (Tomasello 1999) remains a matter of debate. But by and large, humans are better able at understanding what someone else is trying to do and why, and from an early age they are more interested in sharing the experiences of others. Understanding how someone else is thinking about a task, along with shared interest in their goals, improves our ability to learn through observation, and makes humans especially prone to accumulate and transmit new knowledge. Indeed, Simon Baron-Cohen ([1995] 2001) and James Chisholm (2003) have argued that mental aptitudes for reading what is in the minds of others evolved *because* they proved valuable for identifying and interpreting the intentions of others. I agree. But why should humans and chimps differ in this respect? Why (to use Tomasello's excellent descriptor) are humans so "hyper-social"?

According to proponents of the "Machiavellian intelligence" hypothesis, reading the minds of others was a strategic advantage in competitive worlds characterized by shifting alliances—as is typical of many primate societies (Byrne and Whitten 1985). But since many primates, and certainly other apes, live in complexly competitive social worlds, the Machiavellian intelligence hypothesis still does not explain why humans are so much better at imagining the intentions of others, even unseen others, than other apes seem to be. Chimpanzees, after all are at least as dominance-oriented and competitive as humans are, probably more so. So we are still left with the question of why capacities for formulating "theories of mind" and especially for shared engagement are so much better developed in humans (Tomasello 1999).

I suggest that what really distinguishes humans from other apes is not so much our competitive heritage as our more cooperative one, and that cooperative breeding left offspring who grew up in such systems with neuronal underpinnings for shared engagement. Infants born into cooperative breeding systems are desperately seeking caretakers, and even their own mother's commitment (far and away the most important factor in their survival) is going to be contingent not just on the cues she receives from her infant, but on her perception of how much support from allo-

mothers she is likely to have. To be so dependent and still prosper, infants have to be adept at reading their mother's intentions and soliciting other caretakers if needed. As Chisholm (2003) stresses, "theory of mind" reduces the uncertainties such youngsters would face, helping them to predict how others (both mothers and allomothers) are going to respond. In other words, it was the discriminative solicitude of mothers themselves that imposed the necessity that was the mother to this inventiveness. Through practice and conditional rewards, infants get incrementally better at reading the intentions of their caretakers, learning to engage them, and eliciting solicitude.

In the case of creatures as intelligent and manipulative as all apes are, such precociously expressed abilities to read and interpret the intentions of others continues to develop throughout the first years of life. There is a racheting effect as early attempts to monitor mother (and perhaps others) develop into sophisticated mind-reading and experience-sharing abilities (Tomasello 1999:67; Baron-Cohen [1995] 2001). Being able to intuit and care about what others are thinking, to cognitively and emotionally put oneself in someone else's shoes, and to think about what they are thinking (and learn from it) has in turn had spectacular repercussions in the evolution of our peculiarly "hypersocial," information-sharing, and culture-transmitting species (Tomasello 1999), a species preadapted for all manner of cooperation. Sociocognitive development right from birth plays an important role in the development of the neural underpinnings for such talents. Indeed, it is intriguing to note that chimp infants raised from birth in experimental situations with both their mother and human allomothers, also engage their caretakers more, gazing into their faces and smiling far more than has ever been observed among wild or exclusively mother-reared, chimps (Matsuzawa 2001; Bard in press). Such observations may help us to imagine the first steps in the transition to human sociocognitive aptitudes. The point I stress here then is that increased reliance on allomaternal care and provisioning, and with it prolonged maturation, *preceded* the emergence of peculiarly human talents, and facilitated (even permitted) their evolution since natural selection cannot favor traits at the genetic level before they are already useful at the phenotypic level (West-Eberhard 2003).

Continuing in this speculative vein, I am struck by some of the unusual traits that humans share with other cooperative breeders, talents that in chimpanzees and other apes are either poorly developed, or else only present in individuals raised in close association with humans. In most cases, the capacity to extract information from human signals such as finger-pointing and looking at something while tapping on it is better developed in dogs than among highly intelligent fellow apes (Hare et al. 2003). (The only known exceptions involve chimpanzee infants reared in intimate

contact with human allomothers, Matsuzawa 2001). Domestic dogs, however, not only descend from cooperatively breeding wolves—who presumably would have benefited from being neurologically equipped to read intentions—but also have a 15 thousand year history of coevolving with—and depending on handouts from—humans. In this sense, domestic dogs share an evolutionary heritage similar to that of children—depending on handouts from other humans. Similarly, like humans, cooperatively breeding tamarins turn out to be remarkably astute at assessing the “character” of individuals with whom they share food. In experimental situations where one individual has to help another before it can get access to a food treat, tamarins were more likely to assist an unrelated individual who had a past history or “reputation” for sharing and reciprocation, than to help individuals known not to reciprocate (Hauser et al. in press).

Babbling—the repetitive, rhythmical vocalizations long assumed to be uniquely human—represents the strangest of all these convergences. Babbling spontaneously emerges around seven months, about the time babies begin to accept preweaning foods. This is also roughly the same time that babies begin to grow their “milk” teeth, beginning with two tiny incisors at the bottom, then four more on top, eventually twenty in all, sharp little teeth to help chew their first foods, mostly solids mashed or premasticated by someone else. Far from unique, babbling is also found in Callitrichids, the only primates (unless we count humans) known to have full-fledged cooperative breeding. In pygmy marmosets, babbling emerges between the first and third weeks, just about the time allomothers take over most of the care (Elowson et al. 1998). My guess is that babbling in human babies, like smiling, originated for the same reason that babbling developed in Callitrichids. As Snowden points out, babbling is an alluring behavior that attracts the attention of caregivers and elicits interest, solicitude, and edible tidbits.

It has long been assumed that infants babble because the practice helps them learn to talk. No doubt it does. But I suspect that babbling evolved before language, and for a different reason. Our ancestors were born clever apes who babbled at caretakers because they needed to engage them. Best babblers were best fed, and also learned to talk, thus entering into a whole new world of possibilities.

CONCLUSION: LONG CHILDHOODS IN COMPARATIVE PERSPECTIVE

To the extent that anthropologists thought about childhood at all, most viewed it as a prolonged developmental phase between weaning and the end of brain development that was a “unique stage in the life history of human beings” evolving around two million years ago to provide extra

time for large brains to develop and for children to learn necessary skills (see extensive reviews in Bogin 1996; 1998). According to this view, "Much of human evolution, especially the evolution of childhood and adolescence, the human capacity for symbolic language, and culture are the result of the introduction of new life stages into the general pattern of growth and development" (1999, p. 171–72). Taking a broad sociobiological perspective however, prolonged developmental phases between weaning and maturity are not unusual. Long periods of offspring dependence are routine corollaries of cooperative breeding. From this perspective, we do not need to invoke peculiarly costly brains, tool use, or uniquely human cognitive, symbolic, or linguistic skills—the uniquely human traits that long childhoods supposedly evolved to accommodate—in order to explain the origin of long childhoods in the hominid line. Other cooperative breeders from crested magpie jays to wolves had long "childhoods" nutritionally subsidized by allomothers.

So why did such extraordinary gifts evolve in humans but not in other apes? After all, chimpanzees living in the Tai forest obtain massive amounts of calories from nuts that they laboriously crack open, using skills acquired through their mothers. Surely chimps would also benefit from improved subsistence skills and learning capacities (Boesch and Boesch-Achermann 2000). Enhanced learning capacities should be useful for any creature as social and manipulative as a chimp is. Yet chimps never evolved human-sized brains: Why not? Brains are energetically extremely costly, and delayed maturity extremely risky (Aiello and Wells 2002). How could a chimp marginally better at nutcracking garner sufficient reproductive rewards to make delayed maturation and a little bit bigger brain worthwhile? The slightly dumber nutcracker would still be more likely to outbreed him or her. But this constraint would be far less of an obstacle if we assume that the line of apes leading to humans had already embarked on cooperative breeding, and hence already matured slowly. Under those conditions, the costs of large brains would evolve at a discount (Hrdy 1999:86–87). I believe it was the ecological release that cooperative breeding generates along with the special sociocognitive aptitudes that contingent care demands from infants if they are to survive, that unleashed the coevolutionary processes resulting in sapient brains.⁴

This explanation for sapient intelligence is not incompatible with other coevolutionary models based on the proposition that prolonged childhoods and big brains are useful (Kaplan et al. 2000b; Bock, Chapter 5 in this volume). But the cooperative breeding hypothesis specifically predicts that shared care and provisioning along with longer childhoods among *Pan*-like ancestors came first.⁵ That is, longer childhoods *preceded* and set the stage for the coevolutionary processes that selected for bigger brains and other trademarks of the hypersocial human species (cf. Bird and Bliege Bird, Chapter 6 in this volume). Costly brains and the spectacular

linguistic, symbolic, and technological capacities they permit evolved at a discount because among our cooperatively breeding ancestors, maturation was already delayed. Small reproductive payoffs from being smarter would be sufficient to select for sapient brains in worlds where building blocks (e.g., a rudimentary theory of mind) were already in place. Small survival and reproductive advantages from slightly greater intelligence did not have to compensate completely for the enormous costs of delayed maturation (Hrdy 1999:287).

As it happens, delayed maturation is particularly well suited to finance energy-costly brains since both children and their providers can take advantage of food availability to "pay as they go" (Langen 2000; Ricklefs 1984). This argument is similar to that employed by Bird and Bliege Bird (Chapter 6 in this volume), but the perspective used here is broadly comparative across taxa and the focus is on developmental context. The emphasis here is not just on postreproductive kinswomen, but on the ecological release provided by allomothers generally, that is grandmothers, siblings, aunts, uncles, fathers, possible or "would be" fathers, as well as helpful but unrelated opportunists. Which class of allomother mattered most, and at exactly which stage of the child's development, would have varied with circumstances.

Obviously, every human being's childhood is unique, a rich and formative experiences that shapes and educates the person each of us long-lived and clever apes becomes. But if we stand back and examine "childhood" in broad comparative perspective, that allomaternally buffered delay in maturation ceases to look quite so unusual.

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NOTES

1. Note that by the late 1960s, field studies from titi monkeys, vervets, patas monkeys, and langurs were already available, species where infants spent some or much of each day being carried by allomothers.

2. The following passage is typical of the literature: "The latest studies of ancient human family structure report that monogamous pair-bonding and nuclear families were dominant throughout human history in hunter-gatherer societies. . . . The most straightforward explanation of the trend toward monogamy is that smart female hominids went to work on chimpanzee hominid-like males and—step by step, mate-selection by mate-selection—shaped them up into loving husbands and fathers with true family values" (Lawrence and Nohria 2002:182). Echoing longstanding patriarchal presumptions about husbands guaranteed paternity by "coy" and monandrous mates, the authors remind us that women would choose the husband most able to support them. No mention is made of help from any quarter besides this "loving husband."

3. Wiessner hypothesizes that men hunt not just for prized meat, but because meat in camp encourages helpful kin and affines to stick around. This would make hunting a form of parenting effort rather than mating effort (cf. Hawkes 1991). Instead of provisioning mothers and young with meat, these hunter-politicians would be providing their children with helpful alloparental networks. The two hypotheses generate competing predictions that should ultimately be testable.

4. For an interesting parallel consider conditions under which spectacular problem-solving abilities have evolved outside the ape lineage, in an avian line. New Caledonian crows stand out for intelligence among "bird brains" (e.g., Chappell and Kacelnik 2002) almost as much as humans do among apes. As hypothesized here for humans, these geniuses emerged from a lineage of clever crows with a legacy of cooperative breeding.

5. For my money, this creature would have been more bonobo- than chimplike, a creature with female-female bonding; male-mother-infant intimacy; and frequent social exchanges that include food-sharing between allomothers and the infants of friends (Parish 1998 and pers. Com.).