

V

THE NEUROBIOLOGY OF PATERNAL CARE



26

COOPERATIVE BREEDING AND THE PARADOX OF FACULTATIVE FATHERING

SARAH BLAFFER HRDY

Department of Anthropology, University of California Davis, CA, USA

INTRODUCTION: PRIMATE MALE-INFANT INVOLVEMENT

Across the vast majority of the world's 5,400 species of mammals, fathers do remarkably little beyond stake out territories, compete with other males and mate with females – a lot of *sturm* and *drung* punctuated by bellowing, barking, roaring and other spectacular audiovisual displays, but once competitors are routed and the progenitor chosen, its “wham, bam and thank you m’am” and the male is off. In this respect, males belonging to the Order Primates stand out as paragons of paternal responsibility. In most primates, males remain year-round with the females they mated with. There is no unitary explanation, but among the main reasons why primate males tend to stick around after mating are protection against predation (a major source of *adult* mortality) and protecting unweaned young from infanticide by rival male (a major source of *infant* mortality) (Hrdy, 1979; Palombit, 2000; Paul *et al.*, 2000). A population of savanna baboons studied at Moremi in Botswana provides a case in point. Over a 10-year period, 34% or more of infant mortality at Moremi was due to infanticide by adult males (Palombit *et al.*, 1997).

All primates share a deep evolutionary legacy of positive and negative male involvement with infants. Under some conditions, prolonged exposure of males to cues from helpless infants produced opportunities for

Natural Selection to favor even more costly and exclusive care directed at infants likely to share genes with them by common descent. In a handful of cases, predispositions to paternal care evolved to the extremes that we see in monogamous titi monkeys (*Callicebus molloch*). As early as the first 3 weeks of life, males carry infants 90% of daytime, more than nursing mothers (Figure 26.1; Wright, 1984). Infants return the favor by actually preferring their fathers over mothers, becoming more agitated (as measured by elevated adrenocortical activity) when separated from their father than from their mother (Hoffman *et al.*, 1995). I know of only one other genus of mammal, the genus *Aotus*, another monogamous South American monkey with biparental care, where fathers rather than mothers are the primary attachment figures (Wolovich *et al.*, 2007).

Given this broad if sporadic primate-wide background of male involvement with infants, as well as the sporadic occurrence of shared care by females-other-than-the mother in many species, it is striking how *little* allomaternal care goes on among our closest primate relations, the Great Apes. Mothers refuse to allow any allomaternal access for the first 6 months or longer, no matter how eager the other group members are to take the infant. Unless the mother is incapacitated, direct male care is rarely observed. Orangutan and chimpanzee fathers, spend little time in the vicinity of mother's and infants. Gorilla silverbacks have

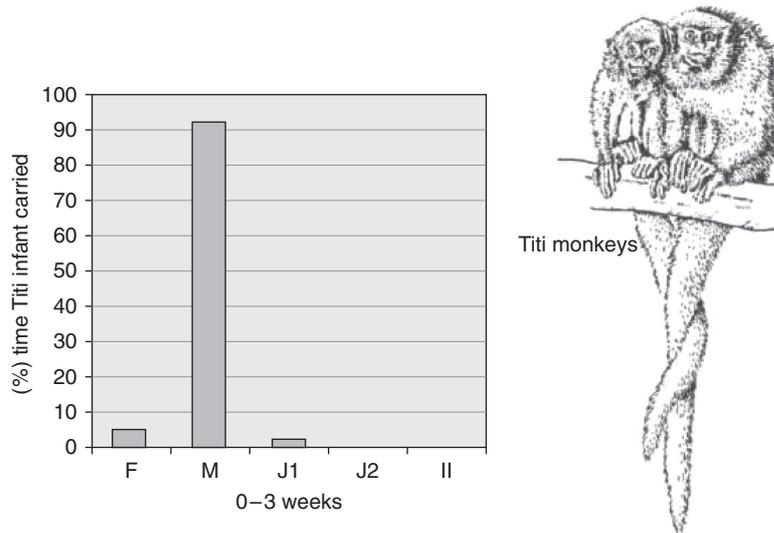


FIGURE 26.1 Percent of time each member of a wild group of titi monkeys (*Callicebus moloch*) in Peru carried the infant during the first 3 weeks after birth. F, adult female; M, adult male; J1, year-old juvenile; J2, 2-year old juvenile; II, independent. (Source: Adapted from Wright, 1984: figure 1.)

a high probability of paternity of infants born in their harems, and are unusually protective, so reliably protective that new mothers, and in time, infants themselves, strive to stay close to them. But still, there is no direct care, nothing like carrying or provisioning of infants in any of the Great Apes comparable to what Jeff French sees in his marmosets (see Chapter 30).

THE HUMAN CASE

As in other apes, highly vulnerable, immobile infants born to nomadic foragers, human infants are virtually always held by someone. But there is one important difference: That someone is not necessarily the mother. Among the !Kung San, when these Kalahari people were still living as nomadic hunter-gatherers a newborn might be handed over by a new mother to her mother right after birth, and the grandmother might thereupon massage the newborn and gently shape his skull with her hands (e.g., see Hrdy, 1999; figure 7.9) Among the Hadza, still living as hunters and gatherers in Tanzania, as among the !Kung, “the baby” right from its birth “is likely to be surrounded by relatives, old adult and young... and is carried by them...” (Blurton Jones *et al.*, 1992). According to Marlowe (2005), a Hadza newborn is held by others 85% of the period just after birth.

Among Mbuti pygmies in Central Africa, “the mother emerges and presents the child to the camp...” whereupon “she hands the (baby) to a few of her closest friends and family, not just for them to look at him but for them to hold him close to their bodies...” (Turnbull, 1965; quote from Turnbull, 1978: p. 172). As far away as the Pacific among Phillippine foragers like the Agta, “The infant is eagerly passed from person to person until all in attendance have had an opportunity to snuggle, nuzzle, sniff and admire the newborn... Thereafter he enjoys constant cuddling, carrying, loving, sniffing and affectionate genital stimulation...” (Peterson, 1978; cited in Hewlett, 1991a).

Worldwide, such accounts are typical for hunter-gatherers. When anthropologist Ivey (2000) asked Central African Efé pygmy mothers “who cares for infants?” people immediately replied “We all do” which is literally true since infants are passed around right from the first day of life. Efé infants average 14 different caretakers and by 4 months of age are being carried by allomothers more time than by their own mothers. However, group members are not equally likely to care. When matched by age and sex with other group members, Ivey found that female allomothers are disproportionately older, sisters, aunts and grandmothers. Male allomothers are brothers, cousins and fathers – with grandfathers doing surprisingly little.

In addition to being held and carried by multiple caretakers, long before weaning, as early as 4 months, infants begin to receive treats like honey sweetened saliva, the first installments on several decades of allomaternal supplementation. In all apes breastfeeding goes on for years. Nevertheless, non-human ape infants are nursed for far longer than humans in hunting and gathering societies are. Intervals between births average 60–100 months compared to the 36–48 month intervals typical for nomadic foraging peoples (Knott, 2001). The reason humans can afford much shorter birth intervals, has to do with all the shared care and provisioning that goes on. Whereas other apes, once weaned provision themselves, human children remain dependent and rely on handouts from others for many years to come. As in many other cooperatively breeding birds and some cooperatively breeding mammals, humans have unusually long periods of “post-fledging” or “post-weaning” dependence, what in humans is known as “childhood” (Hrdy, 2005).

Many of us have had occasion to marvel at how much kids today cost. But keep in mind that ever since the Paleolithic and all through the Neolithic, human offspring have always taken a long time and cost a great deal to rear. Whether in foraging or horticultural societies, it takes on the order of 13 million calories to rear a human from birth to maturity, and most foragers will be 19 years or older before they begin to produce as much food as they consume, which means that the mother will bear other infants long before older children are independent. This is why, when Bob Bridges asked me to give a “Father’s Day” talk, what came to my mind was this glaring human paradox: men and women mate to produce the costliest and slowest maturing young in all mammalhood, and yet compared to a titi monkey where a male’s top priority in all the world is to hold and carry young born to his mate, men’s priorities are nothing like so single-minded. Having a father hard-wired to help is not something a human mother can count on.

VARIABILITY IN PATERNAL CARE

Across cultures there is more variation in paternal care in humans than in all 275 species of other primates put together. Routinely, rates of male care are higher in hunter-gatherers than in herding, horticultural/farming or modern post-industrial societies. But even within foraging

societies, male involvement ranges from relatively low levels of caretaking among the South African !Kung, to the highest ever reported – infants held by dads 22% of the time – among Central African Aka pygmies. The Aka are net hunters and husbands and wives both participate, taking children with them on expeditions into the forest, where even very young infants remain in ear-shot of their fathers most of the time (Hewlett, 1991a, b).

Contrast this with an average of 50 min per day found among fathers in the United States, up from 20 min a few decades ago (Sayer *et al.*, 2003). Cross-culturally there are also major differences in types of interactions (Lamb *et al.*, 1987; Hewlett & Lamb, 2005). Whereas American and European fathers compress a great deal of hyper-stimulating play into brief periods they spend with infants, in 264 h of systematic observation of father–infant interactions among Aka pygmies, Hewlett reported only one instance of “vigorous” play. Hunter-gatherer style paternal care tends to be soothing, affectionate and custodial and under some ecological conditions, absolutely critical for child survival.

Even more striking than stylistic differences in male care is the variation in paternal commitment between the “Mrs. Doubtfires” of the world who go to great lengths to stay near children (more often found in art than life), and fathers who are more remote, invest little or nothing at all in children at any age. Worldwide, 10–25% of households with children are headed by women. In countries like Botswana, Swaziland, Barbados and Grenada some 40% of households contain children with no father present, while in Zimbabwe, Norway, Germany and the United States, the proportion is closer to 30%. It is difficult to get accurate statistics for men who sire children without knowing or acknowledging it at all. But according to one recent survey in Chile, 42% of children born out of wedlock were receiving no support at all from fathers 6 years later (Engle & Breaux, 1998). In the United States, close to half of all children whose parents divorce lose touch with their fathers shortly after, and by 10 years up to 75% have lost touch (Dominus, 2005). Indeed, according to one survey by the Children’s Defense Fund, Americans are 16 times more likely to repay used car loans than pay child support, the delinquency rate for the former being only 3%, compared to the 49% delinquency rate on child support (Associated Press, 1994).

{AQ1}

Nor is there is anything particularly modern or evolutionarily novel about absent fathers. When Marlowe (2005) censused Hadza hunter-gatherers still living in the traditional way in southwestern Tanzania, only 36% of children had fathers in their same group. A hemisphere away, among Yanamamo tribes people the chance of a 10-year old child having both a father and a mother still living in the same group were one in three (Chagnon, 1992: p. 177), about the same as among the Aka (Hewlett, 1991a), while among Ongee foragers in the Andaman Islands *none* of the 15-year olds in the sample were still living with either natural parent (Hewlett, 1991a: pp. 19–20).

Even when fathers are around, hunting and fishing are notoriously unreliable ways to stay fed. Hunters may go for days without bringing back meat, in part because hunters prefer big splash prey to small game. Thus specialists on hunter-gatherer ecology and archeology like O'Connell *et al.*, (2002) point out that even though "meat represents a sizable fraction of their families' *annual* caloric intake, it is not acquired reliably enough to satisfy the *daily* nutritional needs of their children." To compensate, women became specialists in tapping more reliable food sources, like nuts, berries, insect grubs and underground tubers, and as among all foraging people, Plio-Pleistocene hominids had to have set up elaborate networks for sharing – a tremendously important part of their lives. Gaps between what children needed and what a mother could supply were potentially met by a range of group members. When he was alive, on hand, and able to, the mother's mate was critically important. Otherwise, child survival often depended on a mother's other male kin or lovers, or post-reproductive helpers. Assistance by older offspring also freed mothers to forage more efficiently. Unrelated group members such as pre-reproductives fostered in from other groups, who like modern *au paires* "pay their keep" by helping, also play roles (Hrды, 1999: Chapter 11).

THE IMPORTANCE OF ALLOMATERNAL CARE

We've known for a long time that outside of the Great Apes a lot of allomaternal assistance goes on in primates, especially shared care of infants by young females who eagerly

practice with borrowed babies among these langurs, leaf monkeys and proboscis monkeys (reviewed in Hrды, 1999). Furthermore, as females approach the end of their reproductive lives, in female philopatric species where aging females live among close matrilineal kin, old females may become especially dedicated in defending immature kin (Hrды & Hrды, 1976; Paul, 2005). Allomaternal defense of infants as well as allomaternal assistance caring for them means that wherever allomothers are available and mothers are willing to give up infants (presumably under conditions where they deem it safe to do so), there is a correlation between allomaternal care and enhanced maternal reproductive success. By the late 1990s, it was becoming apparent that the same correlation between allomaternal assistance and maternal reproductive success that was reported for some other primates, was going to hold for humans as well, especially those in populations with high rates of infant mortality (Hrды, 1999, 2005 and references therein).

Humans fit the general primate pattern but with an important difference. In the human case, food sharing as well as shared knowledge about resources means that there is so much more that post-menopausal women can do to help kin on a daily basis. The anthropologist Kristen Hawkes first called attention to how hard post-reproductive females worked in hunter-gatherer societies and showed that the presence of older matrilineal kin was correlated with child survival, especially during periods of food shortage. Hawkes *et al.* (1998) have hypothesized that the reason post-menopausal women go on living for decades, rather than for just a year or two after menopause like other primates, is because of what old females can contribute to the survival of matrilineal descendants.

Across a wide range of traditional human societies – African hunter-gatherers, South Asian rice farmers, German peasants and West African horticulturalists, the availability of older matrilineal kin is correlated with faster child growth rates, shorter maternal birth intervals and increased child survival (summarized in Figure 26.2 and references therein; see also Voland *et al.*, 2005). The case of West African Mandinka horticulturalists is especially interesting. Based on a large data set on maternal health and child well-being collected in the middle of the last century, it was known that 40% of infants born (883 of 2,294) died before age five. But no one thought to look at

{AQ2}

Presence of older matrilineal
Kinswomen correlated with:

- Faster child growth rates
 - Hadza hunter-gatherers (Hawkes *et al.*, 1998)
 - West African horticulturalists (Sear *et al.*, 2000)
- Shorter maternal birth intervals
 - South Asian swidden agriculturalists (Leonetti, 2002)
- Increased child survival
 - 18th century German peasants (Voland & Beise, 2001)
 - West African horticulturalists (Sear *et al.*, 2002)
- Increased lifetime reproductive success for mother
 - 18th and 19th century Finnish peasants (Lahdenperä *et al.*, 2004)

{AQ8}

FIGURE 26.2 Summary of recent studies documenting that the presence of older matrilineal kin is correlated with faster child growth; shorter inter-birth intervals; increased child survival; and/or increased maternal reproductive success over her lifetime.

allomaternal effects on these high mortality rates until 2000 when Sear and Mace reanalyzed the initial Gambian data set (Sear *et al.*, 2000). They found that the presence of a father had *no* detectable impact on infant survival in the first 2 years of life, though if the father died and the mother remarried, the presence of a step-father turned out to be somewhat detrimental for the survival chances of older children. What did matter very much in this Mandinka case was having a maternal grandmother. Presence of a maternal grandmother was correlated with a halving of the mortality rate from 40% dying before age five, down to 20% (Sear *et al.*, 2002). To my knowledge, these sorts of significant effects from allomothers have only been reported in populations with infant mortality rates in the range of 40% or higher, that is, comparable to those found in wild primates and many foraging societies.

Because hunter-gather sample sizes are almost invariably tiny, the best documentation for this “grandmother effect” comes from archival records kept for pre-industrial European communities such as these 18th and 19th century Finnish farmers where presence of the mother’s mother turns out to have been significantly correlated with that woman’s enhanced fertility as well as child survival, resulting in significantly higher lifetime reproductive success for these women who have a grandmother on hand to help (Lahdenperä *et al.*, 2004).

Since 2000, there has been an explosion of research documenting the reproductive impact of post-reproductive kin on daughters’ reproductive

success (reviewed in Voland *et al.*, 2005) – provided kinswomen live long enough, or live close-by, which are noteworthy “ifs.” In a sample of Aka pygmy infants studied by anthropologist Courtney Meehan, only one in two Aka infants had either maternal or paternal grandmothers present. In another, comparable sample of Efé infants, only one in four did (Ivey, 2000). Such demographic profiles are consistent with estimates calculated on the basis of archeological from now vanished Paleolithic nomads living under a range of circumstances. The higher the mortality risk, the less either a mother or her slow-maturing children can afford to depend on any specific family composition, and the more important it becomes for other kin, fathers, collateral kin and older siblings, to compensate, relocating if necessary, pitching in as needed.

MATERNAL BET-HEDGING

In environments with high adult mortality and/or extremely unpredictable resources, mothers need to hedge their bets against a shortage of allomaternal assistance. In disparate areas of the world, in parts of North and South America, Africa, Asia and the ancient Near East, one way mothers manage this is by lining up “extra” fathers. Customs and belief systems that function to help mothers pull this off vary tremendously and have become a special interest of mine. I only have time today to talk about the subset of these cases known as “partible paternity” belief systems.

Across a broad swath of forager-horticulturalist Amazonian societies, from the Canela of Brazil in the East, the Matis of Peru in the West, northwards to the Bari of Venezuela or Wayana of French Guyana, southward down to the Takana of Bolivia or the Aché of Paraguay, (also Arawete, Kalina, Kuikuru, Mehinaku,) people subscribe to a convenient folk wisdom about “partible paternity” (Beckerman & Valentine, 2002). A woman believes that semen from each of however many men she had sex with in the preceding 10 months contributed to the growth of the fetus developing inside her body. Fortunately, men believe this as well, and bring gifts of food to women they have mated with during their pregnancy. After birth, such “possible” fathers continue to provision children (e.g., see Hill & Magdalena Hurtado, 1996 for the Aché; Beckerman *et al.*, 1998 for the Bari).

Marriage patterns tend to be quite flexible. Among the Aché for example, the majority of marriages at any given time are monogamous, but these are dynamic unions that fluctuate through time, passing through polygynous or polyandrous phases. Sixty percent (11 of 18) of Aché men spent some time in a polyandrous marriage (one woman, several men) and most women have children with two or more fathers (Hill & Magdalena Hurtado, 1996). Odds are, a woman’s official husband *will* be the genetic-father of any child she bears, but not necessarily. This combined with the belief in partible paternity is probably why uncertain paternity does not upset men as much as it might husbands from a more gene-focused society.

“Extra” fathers are socially recognized and may be invited or expected to observe the same dietary restrictions at the time of birth that the mother’s official husband is. As a courtesy to the husband, “extra” fathers are expected to be discreet (Pollock, 2002), but in some partible paternity societies it is not only socially acceptable for a husband to permit real brothers or fictive “clan brothers” to have sex with his wife, but polyandrous liaisons during public ceremonies may actually be encouraged as reported for the Canela of Brazil (Crocker & Crocker, 1994).

For several of these societies, we have data on how extra fathers impact child survival (Hill & Magdalena Hurtado, 1996; Beckerman *et al.*, 1998). For example, 80% of 194 Bari children with a secondary possible father in addition to their primary father survived to

age 15, compared to only 64% of 628 children without a second father participating (Beckerman *et al.*, 1998). The optimal number of “fathers” turns out to be two. Clearly mothers and children benefit from extra fathers, but because of high levels of child mortality, husbands benefit as well since they have a better than average chance of being the progenitor or at least a relative of the progenitor.

Obviously, women cannot *actually* produce multiple young sired by different fathers as is the case in litters born to mother lions, prairie dogs and wild dogs. Nor did women evolve to produce chimeric young, combining several gene lines within a single individual the way *Calithrix kuhli* can (Ross *et al.*, 2007) so that several males are super-closely related to the young they care for. But humans can rely on these cultural constructs to line up extra fathers, producing in our species the same functional outcomes other animals end up with through conventional evolution.

CIRCUMSTANCES FAVORABLE TO ELICITING MALE CARE

The point here is not that genetic relatedness does not matter, or that sexual jealousy is eliminated. Rather the point here is more is that *eliciting male nurture is more complicated than a man being certain of his paternity*. People like the Aka, who are far more monogamous than the Aché or the Bari, ensure childcare in other ways (Hewlett, 1989). Proximity to infants is a key factor. Men have a lot of leisure time and spend it in camp with prolonged opportunities for intimate interactions (Hewlett, 1992). Over time, cues eliciting nurture in humans have taken on a life of their own, including selection on babies to be irresistible, broadcasting the infantile equivalent of sex appeal (Hrdy, 1999). To understand male care, we need to take into account a range of factors in addition to genetic relatedness. These include belief systems, time in proximity, exposure to infant cues, the man’s relationships with the mother and his recent and past experience with children (Fleming *et al.*, 2002; Fleming, 2005). We also need to take into account *residence patterns*. Who else is around can be very important. Recently, in one of the first studies of its kind, Meehan (2005) set out to learn precisely how important.

{AQ3}

Like most foragers, Aka pygmies in Meehan's study move around over the course of their lives. It is customary for a husband to come live for a time with his wife and her family where he hunts on behalf of his wife and her kin for a period of years (known as "bride service") until after one or more children have been born. Thereafter, the couple may stay or move with their children back to his people, or to another group altogether. This pattern of remaining near the wife's kin, living "matrilocally," until after children are born means that inexperienced young mothers are likely to be among their own kin when they give birth for the first time, an especially vulnerable time (Hrdy, 1999).

Aka mothers specifically say they prefer to live matrilocally because they have more kin to help. Indeed, mothers residing matrilocally received nearly 5 times more alloparental care than mothers living patrilocally, not counting care by the infant's own older siblings which did not vary with place of residence. Nevertheless, the amount of time the baby was held did not differ in matrilocal and patrilocal settings even though the baby had fewer alloparents eager to help, and even though the mother herself held the baby about the same amount of time. How could this be? The answer was the father, who engaged in 20

times more care in the patrilocal setting, so that fathers' contribution to what Meehan termed "high investment allomaternal care" rose from 2.6% in the matrilocal setting to 62% in the patrilocal setting (Marlowe, 2005 for Hadza foragers; see Figure 26.3; Meehan, 2005).

In other words, foragers are characterized by a highly flexible breeding system that can involve monogamy, polygyny, even polyandry, or any combination thereof, along with proactive and strategic maneuvering by alloparents. Human mothers and their infants are opportunistic and resourceful in eliciting care, and allomothers are flexible about providing it, relocating, adjusting, juggling and compensating in strategic ways.

This flexibility is the hallmark of the human family and provides the key to resolving the paradox of facultative fathering. Paternal care could be less than obligate, and early hominid mothers could overshoot their capabilities to provide because if a father turned out to be an indifferent nurturer, or if he disappeared altogether, his offspring might still pull through, permitting a non-investing "cad" to enjoy his cake and fitness too. Cynical as all this sounds, this model of the family based on cooperative breeding is consistent with a growing body of empirical evidence – most of it collected since the year 2000.

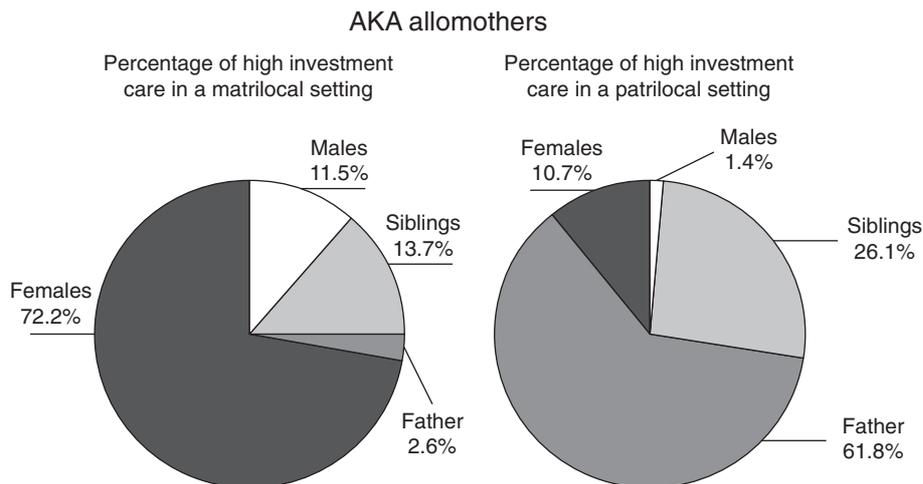


FIGURE 26.3 In Meehan's study of allomaternal childcare among Aka foragers, fathers engaged in more care in patrilocal settings where mothers tended to have fewer matrilineal kinswomen to rely on. (Source: Adapted from Meehan, 2005 and from data courtesy of C. Meehan.)

FLEXIBILITY OF HUMAN FAMILIES

Until recently, most anthropological reconstructions of humankind's "Environments of Evolutionary Adaptedness" took "Man the Hunter and his Sex Contract" for granted. It was simply assumed that "monogamous pair-bonding and nuclear families were dominant throughout human history in hunter-gatherer societies..." where monandrous mothers cared for infants in exchange for meat provided by a father certain of his paternity (Lovejoy, 1981). Supposedly, the "most straightforward explanation of the trend toward monogamy (being) that smart female hominids went to work on chimpanzee like hominid-males and – step by step, mate selection by mate selection – shaped them up into loving husbands and fathers with true family values..." (Lawrence & Nohria, 2002: p. 182). No mention was made of what happened when dads failed to adequately provide or of whom else might be involved.

Today however, human behavioral ecologists and sociobiologists attempting to reconstruct the deep history of the human family are increasingly taking the role of alloparents into account. There has been a paradigm shift from models based on a sex contract between man, the hunter and his nurturing mate toward a model based on cooperative breeding (Hrdy, 1999, 2005) that draws on a rich sociobiological literature to explain the evolution of shared care in other cooperatively breeding birds and mammals (Emlen, 1995; Solomon & French, 1997; Koenig & Dickinson, 2004). We continue to assume that our hunter-gatherer ancestors lived in small, intimate family units, but the composition of these families fluctuated through time, and we now take for granted that alloparental assistance was critical for successful childrearing. The highly idealized "nuclear family" (father, mother and their children) was typically just a temporary phase, often a less than optimal phase at that, since by themselves two parents would so rarely have been able to meet the needs of children. In reconstructing the Pleistocene family, the key descriptors I use are "kin-based," child-centered, opportunistic, mobile and very, very flexible. Alloparental safety nets provided the conditions in which highly facultative paternal commitment could evolve.

No one has a machine to travel back through time to observe childcare among African

hominids 1.7 million years ago. Reconstructions based on ethnographic evidence from hunter-gatherers and comparative evidence from other primates are admittedly speculative. The best source of information we have about parental brains in early hominids remains the brains of extant humans, along with comparative data on the behavior and neurophysiologies of well-studied cooperatively breeding mammals like marmosets, tamarins, meerkats and voles, creatures who without benefit of a giant neocortex, language or symbolic culture still manage to make highly strategic decisions in regards to allocating care (Emlen, 1995; Bales *et al.*, 2002; Russell *et al.*, 2003; Fite *et al.*, 2005). However, we can not hope to understand the evolution of paternal brains without understanding *alloparental* brains as well. Why do allomothers help? Why does the "donative intent" of grandmothers run so high? Why are human mothers so tolerant of allomothers right after birth, while other apes are not? And how do males in non-cooperatively breeding primates, like chimpanzees, respond to infant cues? Are male responses to infants the same, or different from those Jeff French describes for the cooperatively breeding mammals they study?

A decade ago, in a paper on social and endocrine factors in alloparental behavior among voles, Sue Carter and Lucille Roberts proposed that some cooperative breeders might have "a distinct mechanism for alloparental behavior which is independent of other activation mechanisms for parental behaviors" (Roberts *et al.*, 1998, 1866). Even if the evolutionary origins of such behaviors *were* ultimately parental, I think there has been so much selection over time, that Lucille and Sue have to be right, and that in the human case there may be a number of such mechanisms, most of them age- and experience-dependent and highly facultative as Alison Fleming's work with humans is already beginning to suggest. To say then that these are exciting times to be studying the underpinnings of male nurture puts it mildly. There is a vast, nearly infinitely expandable, highly sustainable and as yet untapped human resource out there.

{AQ4}

ACKNOWLEDGMENTS

Thanks to Matthew Gibbons for his assistances adapting this lecture for publication here.

REFERENCES

- Associated Press (1994). Parents better at car payments than child support, group says. *Sacramento Bee* June 18, A8.
- Bales, K., French, J., and Dietz, J. (2002). Explaining variation in maternal care in cooperatively breeding mammals. *Anim. Behav.* 63, 453–461.
- Beckerman, S., and Valentine, P. (2002). *Cultures of Multiple Fathers: The Theory and Practice of Partible Paternity in Lowland South America*. University of Florida Press, Gainesville.
- Beckerman, S., Lizarralde, R., Ballew, C., Schroeder, S., Fingelton, C., Garrison, A., and Smith, H. (1998). The Bari partible paternity project: Preliminary results. *Curr. Anthropol.* 39, 164–167.
- Blurton Jones, N., Smith, L., O'Connell, J., Hawkes, K., and Kamuzora, C. (1992). Demography of the Hadza, an increasing and high density population of savanna foragers. *Am. J. Phys. Anthropol.* 89, 159–181.
- Chagnon, N. (1992). *Yanomamo: The Last Days of Eden*. Harcourt Brace & Co., New York.
- Crocker, W., and Crocker, J. (1994). *The Canela: Bonding Through Kinship, Ritual and Sex*. Harcourt Brace & Co., Fort Worth, Texas.
- Dominus, S. (2005). The father's crusade. *New York Times Magazine* May 8.
- Emlen, S. (1995). An evolutionary theory of the family. *Proc. Natl Acad. Sci. USA* 92, 8090–8099.
- Engle, P. L., and Breaux, C. (1998). Fathers' involvement with children: Perspectives from developing countries. *Soc. Pol. Report XII*, 1–21.
- Fite, J., French, J. A., Patera, K. J., Rukstalis, M., and Hopkins, E. (2005). Opportunistic mothers: Marmoset mothers with elevated and diminished energetic constraints reduce their investment in offspring. *J. Hum. Evol.* 49, 122–142.
- Fleming, A. S. (2005). Plasticity of innate behavior: Experiences throughout life affect maternal behavior and its neurobiology. In *Attachment and Bonding: A New Synthesis. Report on 92nd Dahlem Workshop* (C. S. Carter, et al., Ed.), pp. 137–168. The M.I.T. Press, Cambridge.
- Fleming, A. S., Kraemer, G. W., Gonzalez, A., Lovic, V., Rees, S., and Melo, A. (2002). Mothering begets mothering: The transmission of behavior and its neurobiology across generations. *Pharmacol. Biochem. Behav.* 73, 61–75.
- Hawkes, K., O'Connell, J. F., Blurton Jones, N. G., Alvarez, H., and Charnov, E. L. (1998). Grandmothering, menopause and the evolution of human life histories. *Proc. Natl Acad. Sci. USA* 95, 1336–1339.
- Hewlett, B. (1991a). Demography and childcare in preindustrial societies. *J. Anthropol. Res.* 47, 1–37.
- Hewlett, B. (1991b). *Intimate Fathers: The Nature and Context of Aka Pygmy Paternal Infant Care*. University of Michigan Press, Ann Arbor.
- Hewlett, B. (1992). Husband–Wife reciprocity and the father–infant relationship among Aka pygmies. In *Father–Child Relations: Cultural and Biosocial Contexts* (B. Hewlett, Ed.), pp. 153–176. Aldine De Gruyter, Inc., New York.
- Hewlett, B. (1996). *Cultural Contexts of Human Infancy*. Prentice Hall, Englewood Cliffs, N.J. Hewlett and Lamb (Eds.) 2005. {AQ6}
- Hill, K., and Magdalena Hurtado, A. (1996). *Ache Life History: The Ecology and Demography of a Foraging People*. Aldine de Gruyter, Inc., Hawthorne, New York.
- Hoffman, K. A., Mendoza, S., Hennessey, M., and Mason, W. (1995). Responses of infant titi monkeys *Callicebus molloch* to removal of one or both parents: Evidence of paternal attachment. *Dev. Psychobiol.* 28, 399–407.
- Hrdy, S. B. (1976). Care and exploitation of nonhuman primate infants by conspecifics other than the mother. In *Advances in the Study of Behavior* (J. S. Rosenblatt, A. Hinde, E. Shaw, and C. Beer, Eds.), Vol. 6, pp. 101–158. Academic Press, New York. {AQ7}
- Hrdy, S. B. (1979). Infanticide among animals: A review, classification, and examination of the implications for the reproductive strategies of females. *Ethol. Sociobiol.* 1, 13–40.
- Hrdy, S. B. (1999). *Mother Nature: A History of Mothers, Infants and Natural Selection*. Pantheon Inc., New York.
- Hrdy, S. B. (2005). Comes the child before man: how cooperative breeding and prolonged postweaning dependence shaped human potential. In *Hunter-Gatherer Childhoods* (B. S. Hewlett and M. E. Lamb, Eds.), pp. 65–91. AldineTransaction, New Brunswick.
- Hrdy, S. B., and Hrdy, D. B. (1976). Hierarchical relations among female Hanuman langurs. *Science* 193, 913–915.
- Ivey, P. (2000). Cooperative reproduction in Ituri forest hunter-gatherers: Who cares for Efé infants?. *Curr. Anthropol.* 41, 856–866.
- Knott, C. (2001). Female reproductive ecology of the apes: Implications for human Evolution. In *Reproductive Ecology and Human Evolution* (P. Ellison, Ed.), pp. 429–463. Aldine de Gruyter, Hawthorne, NY.
- Koenig, W. D., and Dickinson, J. L. (2004). *Ecology and Evolution of Cooperative Breeding in Birds*. Cambridge University Press, Cambridge.
- Lahdenperä, M., Lummaa, V., Helle, S., Tremblay, M., and Russell, A. F. (2004). Fitness benefits of prolonged post-reproductive lifespan in women. *Nature* 428, 178–181.

- Lamb, M., Pleck, J. H., Charnov, E. L., and Levine, J. A. (1987). A biosocial perspective on paternal behavior and involvement. In *Parenting Across the Lifespan* (J. B. Lancaster, J. Altmann, A. Rossi, and L. Sherrod, Eds.). Aldine, Hawthorne, NY.
- Lawrence, P. R., and Nohria, N. (2002). *Driven: How Human Nature Shapes Our Choices*. Jossey-Bass, San Francisco.
- Leonetti, D., Nath, D. C., Hemam, N. S., and Neill, D. B. (2002). Cooperative breeding effects among the matrilineal Khasi of N.E. India. *Paper presented at Human Behavior and Evolution Society Meetings*, Rutgers, University, Newark, New Jersey.
- Lovejoy, C. O. (1981). The origin of man. *Science* 211, 341–350.
- Marlowe, F. (2005). Who tends Hadza children? In *Hunter-Gatherer Childhoods* (B. S. Hewlett and M. E. Lamb, Eds.), pp. 177–190. AldineTransaction, New Brunswick.
- Meehan, C. (2005). The effects of residential locality on parental and alloparental investment among the Aka foragers of the Central African Republic. *Hum. Nat.* 16, 58–80.
- O'Connell, J. F., Hawkes, K., Lupo, K. D., and Blurton Jones, N. G. (2002). Male strategies and Plio-Pleistocene archeology. *J. Hum. Evol.* 43, 831–872.
- Palombit, R. A. (2000). Infanticide and the evolution of male–female bonds in animals. In *Infanticide by Males and Its Implications* (C. P. Van Schaik and C. R. Janson, Eds.), pp. 239–268. Cambridge University Press, Cambridge.
- Palombit, R. A., Seyfarth, R. M., and Cheney, D. L. (1997). The adaptive value of “friendships” to female baboons: Experimental and observational evidence. *Anim. Behav.* 54, 599–614.
- Paul, A. (2005). Primate predispositions. In *Grandmotherhood: The Evolutionary Significance of the Second Half of Female Life* (E. Voland, A. Chasiotis, and W. Schiefenhövel, Eds.), pp. 21–37. Rutgers University Press, New Brunswick.
- Paul, A., Preuschoft, S., and Van Schaik, C. P. (2000). The other side of the coin: Infanticide and the evolution of affiliative male–infant interactions in old world Primates. In *Infanticide by Males and Its Implications* (C. P. Van Schaik and C. R. Janson, Eds.), pp. 269–292. Cambridge University Press, Cambridge.
- Peterson, J. T. (1978). *The Ecology of Social Boundaries: The Aka Foragers of the Philippines*. University of Illinois Press, Chicago.
- Pollock, D. (2002). Partible paternity and multiple paternity among the Kulina. In *Cultures of Multiple Fathers: The Culture and Practice of Partible Paternity in Lowland South America* (S. Beckerman and P. Valentine, Eds.), pp. 42–61. University of Florida Press, Gainesville.
- Roberts, R. L., Miller, A. K., Taymans, S. E., and Carter, C. S. (1998). Role of social and endocrine factors in alloparental behavior of prairie voles (*Mircrotus ochrogaster*). *Can. J. Zool.* 76, 1862–1868.
- Ross, C. N., French, J. A., and Orti, G. (2007). Germ-line chimerism and paternal care in Marmosets (*Callithrix kuhlii*). *Proc. Natl Acad. Sci. USA* 104, 6278–6282.
- Russell, A. F., Sharpe, L. L., Brotherton, P. N. M., and Clutton-Brock, T. H. (2003). Cost minimization by helpers in cooperative vertebrates. *Proc. Natl. Acad. Sci. USA* 100, 3333–3338.
- Sayer, L. C., Bianchip, S. M., and Robinson, J. P. (2003). Are parents investing less in children? Trends in mothers' and fathers' time with children. *Am. J. Sociol.* 110, 1–43.
- Sear, R., Mace, R., and McGregor, I. A. (2000). Maternal grandmothers improve the nutritional status and survival of children in rural Gambia. *Proc. Roy. Soc. Lond. B Biol. Sci.* 267, 461–467.
- Sear, R., Steele, F., McGregor, I. A., and Mace, R. (2002). The effects of kin on child mortality in rural Gambia. *Demography* 39, 43–63.
- Solomon, N. G., and French, J. A. (1997). The study of mammalian cooperative breeding. In *Cooperative Breeding in Mammals* (N. G. Solomon and J. A. French, Eds.), pp. 1–10. Cambridge University Press, Cambridge.
- Turnbull, C. (1965). The Mbuti pygmies: An ethnographic survey. *Anthropological Papers of the American Museum of Natural History* 50(3), 141–282.
- Turnbull, C. (1978). The politics of non-aggression. In *Learning Non-Aggression* (A. Montagu, Ed.), pp. 161–221. Oxford University Press, Oxford.
- Voland, E., Chasiotis, A., and Schiefenhövel, W. (2005). *Grandmotherhood: The Evolutionary Significance of the Second Half of Female Life*. Rutgers University Press, New Brunswick, NJ.
- Wolovich, C. K., Perea-Rodriguez, J. P., and Fernandez-Duque, E. (2007). Food sharing as a form of parental care in wild owl monkeys (*Aotus azarai*). *Abstract. Paper presented at the 77th Annual Meeting of the American Association of Physical Anthropologists*, March 28–31, Philadelphia.
- Wright, P. C. (1984). Biparental care in *Aotus trivirgatus* and *Callicebus moloch*. In *Female Primates* (M. Small, Ed.), pp. 59–75. Alan Liss, New York.

Author Queries

- {AQ1} Please note that Hewlett & Lamb, 2005 has not been provided in the reference list.
- {AQ2} Please confirm the reference Hawkes et al. (1998).
- {AQ3} Please note that Hewlett, 1989 has not been provided in the reference list.
- {AQ4} Please note that Roberts et al. 1866 has not been provided in the reference list.
- {AQ5} please provide volume number.
- {AQ6} Please note that Hewlett, 1996 has not been cross referred in th etext.
- {AQ7} Please note that Hrdy (1976) has not been cross referred in the text.
- {AQ8} Please note that the reference Voland & Beise, 2001 in Figure 26.2 has not been provided in the reference list.
Also please confirm the reference Sear et al., 2002 in this figure.