Costly and Cute

Helpless Infants and Human Evolution

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CHAPTER NINE

Of Marmosets, Men, and the
Transformative Power of Babies

SARAH B. HRDY

A survey across some 64,000 species of mammals, birds, reptiles, and mostly fish in the vertebrate subphylum, focusing only on that minority with any parental care at all, would reveal fathers as likely as mothers to be involved. With the emergence 200 million years ago of mammals, this class of vertebrates embarked on a different evolutionary trajectory. Gestating mothers’ certainty of maternity together with their offspring’s reliance on milk led to the evolution of females being peculiarly responsive to signals of need from nearby infants.

Rising levels of estrogen and prolactin, peaking near the end of pregnancy, along with declining progesterone, act on maternal brains to diminish aversive responses and to increase attraction to infantile cues. During pregnancy, receptors to oxytocin and opioids in maternal brains are upregulated, promoting the formation of emotional bonds with the tiny aliens emerging from their bodies (Decety and Svetlova 2012:5–7; Rilling 2013). Over time, through suckling and intimate contact, these ties grow stronger still (Konner 2010). Among humankind’s closest great ape relations, mothers alone carry and nurture new infants. But in over half the other species in the primate order, caretaking is shared by others, providing novel evolutionary opportunities for the latent nurturing potentials in males to become expressed and rendered visible to Darwinian social selection (West-Eberhard 2003).

In quite a few primate species, mothers allow others (typically, relatives) to take and carry even very young infants. There may also be brief bouts of allomaternal suckling (HRdy 2009), a common occurrence among traditional humans (Hewlett and Winn 2014). However, provisioning infants with food...
that allomothers can consume themselves is limited to some 20% of primate species (Hrdy 2010). Physiological and emotional thresholds for responding to infantile signals of need (e.g., cries) (Newman 2007) vary with circumstances. Relevant factors include an allomother’s own reproductive status, past experience, and probable relatedness to the mother. Through the repurposing of highly conserved vertebrate potentials, fathers and perhaps other male allomothers not only respond to infants but, like mothers, can over time become neuroendocrinologically transformed by such experiences (Abraham et al. 2014; Gettler 2014 and chapter 8, this volume; Rilling 2013).

In line with an ongoing paradigm shift in evolutionary anthropology, the care and provisioning of immatures by male and female allomothers (prereproductive, reproductive, and/or postreproductive group members, mostly but not always kin) are now viewed as essential among Pleistocene ancestors rearing slow-maturing young who remained nutritionally dependent on others for years after weaning (Burkart et al. 2009; Hawkes and Paine 2006; Hawkes et al. 1998; Hewlett and Lamb 2005; Hill and Hurtado 2009; Hrdy 1999; Konner 2010; Meehan and Crittenden 2016; Meehan and Hawks 2013). Twenty-first-century research on the developmental trajectories of human brain growth reveals energy demands peaking around 4–5 years, after the age when youngsters would have been weaned and by which time their mothers might be nursing another infant (Kuzawa et al. 2014). Kuzawa and colleagues argued that the massive increases in brain size between australopiths and *Homo sapiens* needed to be accompanied by slower growth, increasingly long childhoods, and, with these, more sustained allomaternal subsidies (see also Isler and van Schaik 2012).

Elsewhere (Hrdy 1999) I have documented unusually contingent levels of maternal commitment, which coevolved in cooperatively breeding hominins as mothers juggled demands from current and future offspring and in the process became increasingly sensitive to cues of social support. In monogamous primates with biparental care, paternal assistance is almost as obligate as maternal investment. But among cooperative breeders (any species with alloparental care as well as parental care and provisioning of offspring), paternal nurture varies along a continuum from fathers highly motivated to care and provide for offspring, at one extreme, to uninvolved fathers, at the other (Hrdy 2008, 2009).

Given how much help mothers need, such facultative fathering seems paradoxical. But compared with infants’ obligate need for mother’s milk, male provisioning of peri- and post-weaning offspring callitrichines, and especially hunter-gatherers. Fathers are freer to adjust their reproductive options and with alternates. For example, even if a human father does not rely on the aper mother’s single-minded commitment to appeal at birth (Hrdy 1999). Infants meanwhile also ingratiating themselves with course of development, hominin infants better assessing the thoughts and feelings (Hrdy 2009, 2016).

In this chapter I explore the dynamic responsiveness to infant signals and commitment elicited from male allomothers to their reproductive enterprise. I hypothesize or adjustments between strategizing paternal Darwinian social selection to promote nurturing potentials present in males.

None of us can go back in time to observatively aloof males into nurturing so prosocially and generously as to volunteer for others. However, there is at hand a possible way into this exercise by the work
provisioning of perinatal and post-weaning offspring among cooperatively breeding callitrichines, and especially hunter-gatherers, represents a more fungible commodity. Fathers are freer to adjust their investment in line with alternative reproductive options and with alternative sources of provisioning and care. For example, even if a human father defects or dies, compensatory nurture from alloparents might pull his offspring through (Hrdy 2008; Sear and Mace 2008).

In other apes, infants arrive widely spaced and, once weaned, provision themselves. Mothers can afford single-minded dedication to each infant until the arrival of the next. By contrast, among modern humans and probably also earlier hominins, infants tend to be more closely spaced and take far longer to mature. Since earlier hominin mothers gave birth to a new infant before an older child was nutritionally independent—their staggered “as-if litters” with multiple dependents vying for investment—her new infant could no longer rely on the ape mother’s single-minded dedication. These hominin infants had to appeal at birth (Hrdy 1999). Infants needed to monitor and engage mothers while also ingratiating themselves with other potential caretakers. Over the course of development, hominin infants were conditioned to become more other-regarding, resulting in neurologically novel ape phenotypes. Over successive generations these novel ape phenotypes were subjected to Darwinian social selection (sensu West-Eberhard) favoring the survival of youngsters better at assessing the thoughts and feelings of others and eliciting their succor (Hrdy 2009, 2016).

In this chapter I explore the dynamic interactions between the more contingent responsiveness to infant signals among mothers and the facultative commitment elicited from male allomothers, often possible fathers, supporting their reproductive enterprise. I hypothesize that the ensuing “negotiations” or adjustments between strategizing parents reconfigured opportunities for Darwinian social selection to promote and elaborate the highly conserved nurturing potentials present in males.

None of us can go back in time to observe the processes transforming comparatively aloof ape males into nurturers who under some conditions behave so prosocially and generously as to volunteer prized commodities like meat to others. However, there is at hand a potentially informative comparison with other cooperatively breeding primates: marmosets and tamarins belonging to the subfamily Callitrichiinae (figure 9.1). I have been inspired to imagine my way into this exercise by the work of Judith Burkart (Burkart et al. 2007;
intimate exposure to infants affects males. Infants need and familiarity will be more pronounced than in humans.

Rationale for Comparing Cooperative Breeding and Callitrichines

In spite of obvious differences between New World monkeys and their far larger, primate-related, longer-lived hominin relatives in reproductive physiology, callitrichines have remarkably similar modes of rearing young. Cooperative breeders share a distinctive combination of features with no other extant ape. These include rearing infants being contingent on social support, an extended period of peri- and post-weaning dependency and callitrichine responses to immature, extremely “unprimate” behaviors more common in apes.

An anthropoid mother long ago opted to co-integrate with other mammals, they utilize less energy and lactate longer, resulting in longer infancy and infant-mother bonds. Primarily folivorous/frugivorous hominoids stretch out for four or more years, and are Challenged by anthropocene habitat loss, a slow reproductive pace spells extinction, reminiscent of the “demographic dice” of ancestral apes moving out onto Plio-Pleistocene landscapes with a line of bipedal and increasingly omnivorous species to produce offspring who were weaned later, and even slower maturing (DeSilva, chapter 17). This is rendered feasible by allomaternality provided by a challenging highly variable Pleistocene climate (Magill et al. 2013; Potts 1996; Wells 2007). Development of young permitted at least some population growth.
intimate exposure to infants affects males in other great apes. My prediction is that infantile need and familiarity will matter, but that the effects will be less pronounced than in humans.

Rationale for Comparing Cooperatively Breeding Homininae and Callitrichinae

In spite of obvious differences between small-bodied, tiny-brained, arboreal New World monkeys and their far larger, brainier, terrestrial, more visually oriented, longer-lived hominin relations, and in spite of marked differences in reproductive physiologies, callitrichines and humans have converged on remarkably similar modes of rearing young. These distantly related cooperative breeders share a distinctive combination of traits found in few primates and no other extant ape. These include maternal responsiveness to infant cues being contingent on social support, and variable or facultative paternal care, which is often accompanied by the direct or indirect provisioning of immatures with highly nutritious and preferred animal prey during prolonged periods of peri- and post-weaning dependence. Comparisons between human and callitrichine responses to immatures permit the exploration of how such extremely "unprimateline" behaviors may be linked.

Anthropoid mothers long ago opted for life in the slow lane. Compared with other mammals, they utilize less energy per day, take longer to gestate, and lactate longer, resulting in longer intervals between births (Charnov and Berrigan 1993; Konner 2010: chap. 2; Pontzer et al. 2014). In the case of primarily folivorous/frugivorous hominoid apes, the intervals between births stretch out for four or more years, and as long as eight among orangutans. Challenged by anthropocene habitat loss and ongoing climate change, such a slow reproductive pace spells extinction for today's great apes, a predicament reminiscent of the "demographic dilemma" Lovejoy (1981) postulated for ancestral apes moving out onto Plio-Pleistocene savannas. But at some point, a line of bipedal and increasingly omnivorous apes switched lanes, starting to produce offspring who were weaned earlier even though they were costlier and even slower maturing (DeSilva, chapter 4, this volume). This switch was rendered feasible by allomaternal provisioning, which buffered immatures challenged by highly variable Pleistocene rainfall and fluctuating resources (Magill et al. 2013; Potts 1996; Wells 2012c). The allomaternal provisioning of young permitted at least some populations to bounce back after local
population crashes and also migrate into new habitats. Although allomaternal provisioning is widely accepted as a defining feature of cooperative breeding, it is not known how the routine sharing of such highly valued resources as animal prey got under way in an ape.

Like humans, the phylogenetically distant callitrichine males also voluntarily share animal prey with others. Like humans, these New World monkeys are adapted to boom-and-bust ecologies and readily colonize new habitats. Like humans, tamarin and marmoset mothers exhibit extraordinarily flexible breeding behavior. Females mate with one or several males, sometimes including extra-group males, in groups containing one to several breeding females (Digby and Ferrari 1994; Goldizen 1988; Hilário and Ferrari 2009; Smith et al. 2001). Like humans, callitrichines produce costly babies at unusually (for their taxon) rapid rates. Relative to maternal body size, no anthropoid primate has a longer gestation period or higher birth mass (Digby et al. 2011; Tardif et al. 2013). The callitrichines’ shift toward smaller size accompanied by multiple relatively large young probably occurred after substantial allomaternal (including paternal) assistance was already available, rather than the other way around (Dunbar 1995; Goldizen 1990; Harris et al. 2014). It is unlikely that allomaternal provisioning could have evolved if these tiny monkeys had not (like hominins) already been adept extractive foragers adapted to fluctuating food supplies—both voracious hunters (arthropods, lizards, nestling birds) and reliable harvesters of plant foods, in the callitrichine case mostly fruits, seeds, and exudates (Garber 1997).

Callitrichine twins weigh up to 20% of the mother’s weight, yet birth in one season rarely diminishes maternal fertility in the next. The more offspring _Leontopithecus rosalia_ mothers produce one season, the more they bear the next (Bales et al. 2001). This is feasible because males carry the infants and help to provision them. In some cases, these allmoms provide nutritious prey between the (relatively early) onset of weaning and the youngsters’ attainment of the strength and the hunting, gathering, and processing skills essential for nutritional independence. Provisioning peaks around 12 weeks after birth. At 16 weeks, allmoms still provide up to 90% of solid foods (Hoage 1982; Rapaport 2011). Not surprisingly, offspring survival is correlated with the number of male helpers (Bales et al. 2000; Culot et al. 2011; Garber 1997). Over evolutionary time, therefore, selection should have favored maternal sensitivity to available help.

Contingent Commitment

Almost from the first discovery of mothers struck by their peculiar combination of rejecting mothers. The first published illegitimacy by primatology’s first-ever description, decades later, French zoologist M. Siret curiously unmoored by infantile signals.

It seemed that the mother cared less... When seen neglecting her charges thirsty... with a cry... After sucking [the twin] heri herself of them. She would free herself upon her back and tearing them away. Each time the father came to the rescue of his back. Once when one of the young fell, below, the [colony proprietor] thinking it had picked it up. At this intrusion the father laid upon his lordship, and shrieked until the young to the floor where he found the offspring and placed it on his back... (translated in Hershkovitz 1977:551)

Under pressure to reduce the metabolic mothers in cooperatively breeding and (Saguinus, _Callicebus, Aotus_ ) reduce their biting their hands and feet (Hoffman et al. 2013:378; Cooper 1964, cited in Hershkovitz, 1977). Fathers come to the rescue, complaining cages (e.g., Eppl 1970:66). Even parous cages who cease to move or vocalize, sometimes primatologists accustomed to the obsessiveness and ape mothers, such nonchalance, partly surprising. Old World monkeys born missing parents picked up, carried, and suckled (Berkson dead infants continue to be carried for da
Contingent Commitment in Callitrichine Mothers

Almost from the first discovery of marmosets, European naturalists were struck by their peculiar combination of attentive fathers and nonchalant, even rejecting mothers. The first published illustration of marmosets was accompanied by primatology’s first-ever description of male care (Edwards 1758). Two decades later, French zoologist M. Siret described a marmoset mother that was curiously unmoved by infantile signals of need.

It seemed that the mother cared less for the twins than did the father. When seen neglecting her charges the mother was warned by the father with a cry . . . After suckling the twins the mother made every effort to rid herself of them. She would free herself by kicking them off or by rolling on her back and tearing them away as they scurried to her underside. Each time the father came to the rescue and invited the twins to mount his back. Once when one of the young fell from a perch and lay stunned below, the [colony proprietor] thinking it dead reached into the cage and picked it up. At this intrusion the father became furious, threw himself upon his lordship, and shrieked until the master of the house returned the young to the floor where he found it. The father then picked up his offspring and placed it on his back where it recovered. (Siret 1778:453, translated in Hershkovitz 1977:551)

Under pressure to reduce the metabolic costs of carrying and nursing babies, mothers in cooperatively breeding and biparental care genera (e.g., Callithrix, Saguinus, Callicebus, Aotus) reduce their load by scraping infants off, sometimes biting their hands and feet (Hoffman et al. 1995:422; Huck and Fernandez-Duque 2013:378; Cooper 1964, cited in Hershkovitz 1977:788; Ross et al. 2005). Unless fathers come to the rescue, complaining neonates may be left on the floors of cages (e.g., Epplle 1970:66). Even parous callitrichine mothers may ignore infants who cease to move or vocalize, sometimes abandoning still-vocalizing ones. For primatologists accustomed to the obsessive protectiveness of Old World monkey and ape mothers, such nonchalance, particularly in experienced mothers, is surprising. Old World monkeys born missing limbs or with cerebral palsy are still picked up, carried, and suckled (Berkson 1974; Turner et al. 2005). Comatose or dead infants continue to be carried for days.
Tiny arboreal monkeys are difficult to observe in the wild, thus most reports of abandonment come from captivity (Bardi et al. 2001; Epplé 1970:66; Johnson et al. 1991; Rothe 1975:316–317). Interpreting the high frequencies of maternal rejections in callithrichines is therefore complicated because even monkey and ape species never observed to reject infants in the wild may do so in captivity. Yet even compared to other captive primates, there is an unusually high incidence of rejections among these monkeys dependent on allomaternal assistance. Furthermore, rejections are also reported from the wild, which represents a marked contrast with experienced mothers in other monkeys and apes, who virtually never reject or abandon, and never wound, their own infants. In the far fewer hours during which tamarins and titi monkeys have been observed in the wild, there are multiple reports of females biting infants to death. In three cases (detailed below) the mother almost certainly killed her own infant. These represent the only known cases from nature in which a mother was sufficiently unmoved by infant signals of distress as to not only push her baby away but to actually kill it. All of these incidents occurred in species with obligate (or nearly obligate) dependence on allomaternal care and provisioning.

Although uncommon, infanticide is widely reported for primates (Hrdy 1979; van Schaik and Janson 2000), witnessed in 56 populations in 35 different species and inferred in 16 more (Palombit 2012). Almost always, the killer is a male or female other than the victim’s own parent. Under unfavorable conditions, primate mothers may spontaneously abort prior to birth (e.g., Roberts et al. 2012), display lower investment after it (e.g., Fairbanks and Hinde 2013), or rebuff infants to facilitate early weaning (Altmann 1980), but the outright rejection of full-term infants is rare. Exceptions involve captive, socially deprived mothers; mothers under extreme duress (e.g., repeated stalking by an infanticidal male); or inexperienced young mothers inadequately tending firstborns (e.g., Schino and Troisi 2005). No primate fieldworker has ever reported a mother killing her own infant except in species with obligate allomaternal care.

Female infanticide is particularly common among cooperatively breeding callithrichines, with many cases reported in captivity, nine well-documented cases among wild populations (Bezerra et al. 2007; Cézar et al. 2011:table 1; DIGBY and Saltzman 2009; TIRADO-HERRERA et al. 2000), and one case in monogamous biparental care, *Callithrix nigrifrons* (Cézar et al. 2008). In seven of the ten wild cases, the female killed another female’s infant, but in the

*Callithrix* and two tamarin cases, living to death by their own mothers, unhappily.

In field primatology’s first report of infanticide (Cézar et al. 2000), a saddle-back tamarin (*Saguinus mystax*) containing several males and a second female, the infant was dropped several times on the males, until when once again reunified, the infant moved its arms and legs. Further pushing to the brain case” (155). After the corpse was found, the baby’s brain had been entirely detached tamarin (*S. mystax*), who had died during periods when four or five males were present. This mother also was not certain about her baby. Although the infant was very young, it was not certain that her son (Cézar et al. 2001:182). In the third case, *Callithrix nigrifrons* gave birth to a healthy son and mate until the third day. When the young infant began to bite his face, eventually dropped him (Rough et al. 2008). Under duress, other males function at their infants or abandon whole litters (Cézar et al. 2001). Males go to extraordinary lengths to socially protective when danger threatens. Maternal care have wild-living mothers attack their own infants.

Experiments with *Callimico goeldii* (they produce singleton young, are solitary) reveal mothers surprisingly quick to abandon their infants*. Callimico fathers are interested in the wild it is usually day 11 before male transfer is the first transfer is later still, around day 6. The pet ferret was experimented introduced to their baby closer and moving away, six days over to the fathers days earlier than their own (Anzenberger 2005). The experimenters
It is difficult to observe in the wild, thus most captive primates (Bardi et al. 2001; Epplle 1970:66; 1971). Interpreting the high frequencies of maternal infanticide is therefore complicated because even in captivity to reject infants in the wild may do so. Under captivity, these monkeys dependent on allomaternal care and are also reported from the wild, which experienced mothers in other monkeys for abandon, and never wounded, their own offspring. Although tamarins and titi monkeys have multiple reports of females biting infants (see below) the mother almost certainly killed only known cases from nature in which they infant signals of distress as to not only kill it. All of these incidents occurred in auditory dependence on allomaternal care and

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...the mother with her own parent. Under unfamiliarity, may spontaneously abort prior to birth or investment after it (e.g., Fairbanks and Hrdy 1980), but reasons to leave the infant is rare. Exceptions involve captive, under extreme duress (e.g., repeated stalking). Experienced young mothers inadequately (Traniello 1995). No primate fieldworker has known infant except in species with obligate

...common among cooperatively breeding species. In captivity, nine well-documented cases (Cárdenas et al. 2000; Culot et al. 2011:table 1; Escalante et al. 2007; Fernández 1994; Fernández et al. 1994), and one case in Callithrix bicolor (Cárdenas et al. 2008). In the case, another female’s infant, but in the

...Callithrix bicolor...two tamarin cases, living babies were almost certainly bitten to death by their own mothers, unheard-of behavior for anthropoid primates.

In field primatology, the first report of maternal infanticide (Tirado-Herrera et al. 2000), a saddle-back tamarin (Saguinus fuscicollis) gave birth in a group containing several males and a second pregnant female. On its first day of life, the infant was dropped several times only to be retrieved, usually by one of the males, unless when once again reunited with its mother, she “took a vertical position on a [tree] trunk, gripped the infant, and bit into its face. The infant moved its arms and legs. Further bites were directed to the face and to the brain case” (155). After the corpse fell to the ground, it was determined that the baby’s brain had been entirely consumed. In the second case, a moustached tamarin (S. mystax), who had successfully reared three sets of twins during periods when four or five males were on hand to help, gave birth when there was a second breeding female in the group, but only two or three males were present. This mother was observed biting and eating the head of her baby. Although the infanticide was observed shortly before, observers could not be absolutely certain that her son was still alive when she began biting (Culot et al. 2011:182). In the third case, a black-fronted titi mother (Callithrix nigrifrons) gave birth to a healthy son, who was then carried mostly by her mate until the third day. When the vocalizing infant was returned to her, she began to bite his face, eventually dropping the corpse to the ground (Cárdenas et al. 2008). Under duress, other mammals are known to kill or cannibalize their infants. Abandon whole litters (e.g., Hoogland 1994), but most primate mothers do not go to extraordinary lengths to keep their babies safe, becoming especially protective when danger threatens. Only in primates with obligate allomaternal care have wild-living mothers been observed to deliberately wound their own infants.

Experiments with Callithrix goeldii (marmoset-like monkeys that, although they produce singleton young, are sometimes classified with Callithrichidae) reveal mothers surprisingly quick to put their own safety ahead of their infants’. Callithrix fathers are interested in their infants right from birth, but in the wild it is usually day 11 before mothers allow them access. In captivity, the first transfer is later still, around day 27. But when a “predator” (someone’s pet ferret) was experimentally introduced near their cages, instead of holding their baby closer and moving away, six of seven mothers turned their infants over to the fathers earlier than they ordinarily would have (Schradin and Anzenberger 2005). The experimenters hypothesized that mothers sought to
protect their infants in this way. But since *Callimico* males are nearly the same size as the females and little better at defending young against predators than the mother would be, her behavior is better explained by an urgent desire for unencumbered escape.

**Have Callitrichines Evolved Neural Overrides to Maternal Commitment?**

Although uncommon, maternal infanticide is widely documented for humans in both the ethnographic and historical records (Hrdy 1999), but it is not known to occur among wild primates. Only among those New World monkeys with extensive allomaternal (including paternal) involvement do we find mothers sufficiently unmoved by *Kindchenschema* as to pass infants off when danger threatens or deliberately mutilate or kill one, even focusing on the vocalizing face. Obviously, the survival of any mammalian species depends on mothers being motivated to care for offspring. Usually mothers, especially primate mothers, are. Nevertheless, systematic analyses of the circumstances surrounding a large sample of callitrichines' rejections reported for a breeding colony in the United States suggest a method to this seeming madness.

Massimo Bardi and colleagues (2001) used stepwise multiple regression to evaluate factors affecting survival to 1 year for 1,093 *Saguinus oedipus* born between 1984 and 1993 at the New England Primate Research Center. Fifty percent (546) were rejected while an additional 12% (134) were killed before they could be removed and hand reared. In 89% of these cases, termination of the mother’s investment ended within 3 days of birth. Infanticide in these instances could not be attributed to pathological individuals since virtually all parents that abused or rejected offspring had on other occasions successfully reared them. Interestingly, the postpartum timing of these rejections echoes the timing of infanticides among traditional and modern human societies (Hrdy 1999:chaps. 12–14). Of 3,312 infanticides recorded by the US Centers for Disease Control between 1989 and 1998, 82.6% of cases occurred on the first day, and the incidents peaked in the first week, with mothers almost certainly present and implicated (Paulozzi 2002; see also Overpeck et al. 1998).

Since mothers are the major caretakers right after birth, it is assumed that the callitrichine mothers are primarily responsible for the “decisions” to reject (Bardi et al. 2001:167). But mothers need paternal willingness to help, or to tolerate the Bardi sample, the single most important availability of helpers. When older siblings were accepted, compared with 17.2% when in poor health and those bearing triplets. The rates of rejection were also higher with experienced (39.5%) mothers and for older ones. These trends parallel maternally (reviewed in Hrdy 1999). Thus it is without prior caretaking experience rendered mothers to mutilate babies they inexperienced mothers who abused in nearly double (15.2%), suggesting that more or incompetence.

Firsthand observations of maternal death some of the mutilated, often headless, infants were bitten by mothers. Quite possibly, recategorization as “prey,” inviting the consumption in contrast with other primate mothers, when dead vary for days, leads me to suspect a loss of bonding mechanisms in postpartum. Why some marmoset mothers fail to deal and unfamiliar infants matched for age and attentioned responsiveness would facilitate recipient allomaternal support. Possibly, mothers need to “poll” the available assistance.

Callitrichine males (especially probable to infant cues (Sánchez et al. 2014), often not coming home but returning to their mothers in good condition are especially responsive to higher prolactin levels (Ziegler et al. 2018). Paternity is valuable feedback for a mother to know if she may be discovered by other paternal involvement, the father information that is worth having sooner
since *Callimico* males are nearly the same in size as those of the *Saguinus* species and are nearly the same age as the females, it is difficult to explain why they would not be willing to help their offspring. It is possible that maternal behavior in *Callimico* is more influenced by the physical characteristics of the offspring rather than by the behavioral characteristics of the females.

**Evolved Neural Overrides to Commitment?**

Infanticide is widely documented for humans and certain non-human primates (Hrdy 1999), but it is not known if this behavior is found among those New World monkeys with parental care. In the *Saguinus oedipus* species, the most common cause of death is infanticide, which is often committed by the mother. However, infanticide is not always observed, and in some cases, it may be the result of a neurological or psychological disorder. In the *Saguinus oedipus* species, the rate of infanticide is significantly higher among parasitic females than among males. This may be due to the fact that parasitic females are more likely to have a history of infanticide in their mothers or fathers.

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(Bardi et al. 2001:167). But mothers might also be responding to signals of paternal willingness to help, or to the availability of male help generally. In the Bardi sample, the single most important predictor of rejection was the availability of helpers. When older siblings were available, 54.9% of infants were accepted, compared with 17.2% when older siblings were absent. Mothers in poor health and those bearing triplets were more likely to abuse infants. The rates of rejection were also higher for inexperienced (64.1%) compared with experienced (39.5%) mothers and for younger parents of either sex than for older ones. These trends parallel maternal competence in primates generally (reviewed in Hrdy 1999). Thus it is surprising that the tamarin mothers without prior caretaking experience were less likely, than experienced mothers to mutilate babies they rejected. Compared with the 8.2% of inexperienced mothers who abused infants, the rate for parous females was nearly double (15.2%), suggesting that mutilations were not due to inexperience or incompetence.

Firsthand observations of maternal rejections raise the possibility that some of the mutilated, often headless, infants found on the floors of breeding cages were bitten by mothers. Quite possibly, a nonresponsive infant is simply classified as “prey,” inviting the consumption of its delectable brain. But the contrast with other primate mothers, who remain protectors of their offspring, leads me to suspect some neurological dampening of bonding mechanisms in postpartum callitrichines. This might help explain why some marmoset mothers fail to discriminate between their own infant and unfamiliar infants matched for age (Saltzman and Abbott 2005). Damaged responsiveness would facilitate rejection under conditions with insufficient allomaternal support. Possibly, maternal distancing even helps mothers to “poll” the available assistance.

Callitrichine males (especially probable progenitors) are highly responsive to infant cues (Sánchez et al. 2014), often retrieving rejected babies and carrying them to their mothers’ hearts and higher prolactin levels (Ziegler et al. 2004a). Gauging her mate’s responsiveness is valuable feedback for a mother to have so that some maternal rejections may be strategic rather than terminal. If she repeats or escalates rejection and no other allomaternal intervention, the father too may terminate his investment, information that is worth having sooner rather than later.
Some Highly Derived Specializations for Ensuring the Availability of Caretakers

Obviously, callitrichine mothers do not conceive and gestate babies in order to discard them. Abandonment is a last resort. Under most circumstances, mothers proactively line up allomaternal assistance in advance by mating polyandrously with several males. Not only do females mate throughout the cycle (as human women also do), but callitrichines ovulate again shortly after birth, while lactating. To inseminate her, a male needs to be nearby in the postpartum period and will thus be exposed to stimuli from her newborns. Furthermore, tamarin fathers may join mothers in consuming the placenta, ingesting an extra cocktail of nurture-promoting hormones, a predilection also documented in other mammals with obligate male care ( Gregg and Wynne-Edwards 2005 ).

Callitrichine mothers can produce twins or triplets sired by different fathers, and placental fusion permits the transfer of cells, possibly even germ cells, between multiply sired siblings in utero ( Ross et al. 2007; Sweeney et al. 2012 ). Thus researchers can rarely know which male or males sired which offspring. Interestingly, chimeric infants known to carry DNA from more than one father are more attractive to and more often carried by male allomothers compared to non-chimeric young. Mothers, however, carry chimeras less ( Ross et al. 2007 ), possibly because they count on males to compensate. Callitrichine mothers also increase the availability of babysitters by eliminating the offspring of rival mothers ( Digby 2000 ). Over generations, the threat of infanticide led to selection on females to suppress their own ovulation when in the presence of a more dominant female. Imposing this threat requires a pregnant or postpartum female to override the special responsiveness to signals of infant distress that ordinarily emerges during mammalian pregnancy ( Numan and Insel 2003; Barrett and Fleming 2011 ).

Across mammals, including humans, postpartum mothers exhibit diminished responsiveness when stressed. But an increased aversion to babies in pregnant females is one of the stranger overrides to maternal responsiveness on record. Even multiparous marmosets that have successfully raised young and that were attracted to infants early in pregnancy exhibit longer latencies to approaching infants during late pregnancy. Experiments reveal that some pregnant marmosets are so averse to infants that they reflexively attack them ( Saltzman and Abbott 2005 ). Of the seven wild females that bit another female's infant to death, five were pregnant ( Cuello et al. 2006 )—considering all ten cases (including mammalian mothers with brains preferred—a risky appetite for infanticide ( Bezerra et al. 2007 ). My suspicion is that pregnancy is a highly derived trait that could systems already predisposed to override.

A Common Overall Strategy with Major Variations

Callitrichine and human mothers have proactively line up allomaternal assistance for their infants. Some forager whose new infant is born before contact before lactation is more readily making neglect or abuse less likely ( Strange 1971 ). Nevertheless, having evolved as they have, humans presumably never evolved such extreme measures as postpartum estrus, and except in rare cases bear chimeric offspring. Nor is there an overall pregnancy-related baby aversion or the like.

It may be relevant that callitrichine mothers may go beyond increasing males’ exposure to infants, spending far more energy. Males prepare for their weight prior to birth, starting to “show” ( Ziegler et al. 2004a ), and, as mentioned before, expend far more energy. Males prepared for the onset of lactation, mothers are on a “high” of sorts, incentivized to nurture and far less inclined to infanticide, or so their fathers are ( Hrdy 1999 ).

Among humans, neither mother nor father can lower thresholds for nurturing infants. Their mixing of male and female parental care is a highly derived condition, and it is perhaps only in humans that the biological aspects of its display become so intricately mixed. Mothers who are particularly well-prepared to care for their infants can lose interest or simply move on to more pressing matters, while fathers, who may never have been much interested in the first place, are at least primed to help.

What does this rationalization of nurture have to do with the many other humans who do not participate? For them, the cost of helping is too high. If fathers are not engaged in helping, the overall爸爸s may not be, if doing so were to be.”
Specializations for Ensuring the Reproductive Success of Caretakers

...not conceive and gestate babies in order to rear them as a last resort. Under most circumstances, however, females mate throughout the year, at which point callitrichines ovulate again shortly after giving birth. Thus, a male needs to be nearby in the weeks following parturition to ensure that females are exposed to stimuli from her newborns. Males often join mothers in consuming the placenta, a behavior thought to increase progesterone-promoting hormones, a predilection for desert rats with obligate male care (Gregg and Hrdy 1988). In such cases, it is possible that twins or triplets sired by different males might be produced, assuming there is the transfer of cells, possibly even germ cells, from one male to another in utero (Ross et al. 2003; Sweeney et al. 2007). This phenomenon, known as chimerism, has been observed in rodents and is thought to confer advantages in hybrid environments. Mothers, however, carry chimeric embryos or fetuses in their uteri, which may not develop further, a phenomenon known as embryonic or fetal resorption.

Callitrichines have evolved mechanisms to suppress their own ovulation when they are not the primary female. Imposing this threat requires a significant amount of time and energy, which in turn may have evolved to reduce the special responsiveness to signals that emerge during mammalian pregnancy (Hrdy 2011).

In humans, postpartum mothers exhibit diminishing interest in their newborns after the first few days. But an increased aversion to babies in the first year of life overrides maternal responsiveness. Mothers who have successfully raised young infants exhibit longer latencies of maternal responsiveness. Experiments reveal that some women actually avoid their newborns, a phenomenon known as the “baby blues,” where mothers prefer the company of their own mother over their newborn baby. This may be a survival mechanism, where wild females that bit another female’s infant to death, five were pregnant (Culot et al. 2011:table 1). Furthermore, considering all ten cases (including maternal ones), four involved cannibalism with brains preferred—a risky appetite for pregnant or just-delivered mothers (Bezerra et al. 2007). My suspicion is that this aversion to infants during pregnancy is a highly derived trait that could only evolve in primates with neural systems already predisposed to override maternal responses to infantile cues.

A Common Overall Strategy with Major Human-Callitrichine Differences

Callitrichine and human mothers have converged on a similar decision rule: proactively line up allomaternship, but if that fails, bail out. A human forager whose new infant is born before an older child is sufficiently independent or who finds herself short on allomaternal support will terminate the bond and, if necessary, leave her infant behind to live. The result is a failure to produce offspring. However, humans presumably never evolved such highly derived callitrichine adaptations as postpartum estrus, and the behavior of the lamar in the human is not known. Nor is there any evidence from foraging or captive societies that pregnancy-related baby aversion or the murder of babies born to other women.

It may be relevant that callitrichine infants are relatively less costly for a mother to produce than are human infants. Rejection of callitrichine mothers may go beyond increasing males’ exposure to infantile magic and move into the realm of “extortion”: “Help me, or I’m bailing out.” After all, a callitrichine mother might produce twins or triplets as often as twice a year. Even already pregnant with the next batch, a tamarin mother loses little weight during lactation (Bales et al. 2002). Measured in weight loss, caring callitrichine fathers expend far more energy. Males prepare by gaining up to 15% of their body weight prior to birth, starting to “show” even before their pregnant mates do (Ziegler et al. 2004a), and, as mentioned, tamarin fathers further prime themselves by consuming the placenta. Among humans, by contrast, each newborn represents a tremendous energetic and opportunity cost, especially with the onset of lactation, when mothers require a “mammary leach,” endocrinologically incentivized to nurture and far less inclined to abandon an infant than the father is (Hrdy 1999).

Among humans, neither mother nor father consumes the placenta. But when a mother can lower thresholds for nurturing responses in nearby allomothers by
allowing trusted candidates to hold her baby right after birth, something no other ape does. Nevertheless, if they are short on social support, both callitrichine and human mothers may reduce or terminate their investment right after birth. Women also exhibit some specializations of their own. Never having evolved the physiological equipment for truly partible paternity, human mothers in many parts of the world use culturally generated fictions about paternity to line up extra provisioners. Sexual partners in addition to a woman’s husband who believe they are possible progenitors help to provision her and her offspring (Beckerman et al. 1998; Hrdy 2000; Walker et al. 2010). Prolonged lifespans also make available experienced, hardworking, postreproductive kinwomen to help care for and provision offspring (Hawkes et al. 1998; Hawkes and Coxworth 2013).

Refining What Counts as “Cute”

With the accelerating relevance of culture among behaviorally modern humans, conditional emotional responsiveness may have provided windows of opportunity for mothers to consciously discriminate between infants kept versus those abandoned by using real (physical defects, prematurity) or more arbitrary (culturally invented) criteria relevant to the child’s prospects. Over time, millions of women have eliminated perfectly healthy infants born the “wrong” sex so as to try again for the preferred sex (reviewed in Daly and Wilson 1995; Hrdy 1999:chap. 10). The topic is sensitive and understudied, but I am convinced that preferences for well-timed, robust offspring, those most likely to survive and mature into healthy adults, have characterized humans long enough that unconscious as well as conscious biases have shaped maternal responses. (See Swamy et al. 2008 for the long-term implications of low birth weight; Frodi et al. 1978 for aversion to the cries of premature babies; Glocker et al. 2009 for preferences for plumper, full-term-looking baby faces; Leckman et al. 1999; Mann 1992; Overpeck et al. 1998 for maternal responses to cues correlated with prematurity; Barden et al. 1989 for maternal aversion to babies born with facial disfigurements.) Whether callitrichines ever discriminate based on infant attributes is unknown.

Thermoregulation and especially the need to fuel costly brains would have favored fatter newborns in the line leading to the genus Homo (Kuzawa 1998). As increasingly discriminating mothers came to associate full-term, plump neonates with healthier outcomes, selection would also have favored babies born looking full term and robust, since this trait likely also had appeal to mothers. One result was the other-sex preference for both a narrow birth canal (Trevathan and Rose 1994) and the combined outcome of such selection pressures, which increased the four times the body fat of other apes (e.g., gibbons) born to their mothers, “I’m a good bet; keep me, my father’s retrenchment’s most portentous effects were

Paternal Care in Cooperative Facultative Groups

Paternal care is essential for infant survival in cooperatively breeding species of Callithrix and Aotus. Among cooperatively breeding tamarins, Leontopithecus rosalia, paternally provided care increased as the mother’s titrate increased even as the mother’s titrate constant (Bales et al. 2002:454). Anthropologist Courtney Meehan (2000) found that mothers among Central African foragers. Among the Hadza, patrilineal kin provided care, permitting the father to do little. When the baby was more than 10 weeks old, however, patrilineal kin proved less helpful; the more the mother held her baby, the less the father contributed, and vice versa (figure 9.2).

Those who assume that such well-calibrated paternal care can only be explained by uniquely sophisticated humans (e.g., Driscoll 2001) can forget the opportunistic calibrations of parental care (Bales et al. 2002), which lack patrilineal perspective (e.g., Burkart and Heske 2004). Fathers as well as mothers were more li
mother baby right after birth, something no other species do. They are short on social support, both culturally and biologically, so they do not specialize on their own. Never having a truly partible paternity, human mothers often feel they generated fictions about paternity to partners in addition to a woman’s husband or father help to provision her and her offspring (Walker et al. 2010). Prolonged lifespans also help in reproductive kinswomen to help their offspring (Hawkes et al. 1998; Hawkes and Coxworth 2002).

Counts as “Cute”

Interest in the cultural definitions of culture among behaviorally modern humans. Cultural readiness may have provided windows for cultural differences to discriminate between infants kept alive (physical defects, prematurity) or more culturally relevant to the child’s prospects. Over time, the criteria of healthy infants born as well as their plumper, full-term-looking baby faces; their aversion to the cries of premature babies; their plumpness and plumper, full-term-looking baby faces; whether callitrichines ever discriminate known. 1

The need to fuel costly brains would have something to do with the genus Homo (Kuzawa 1998). Fathers came to associate full-term, plump offspring: selection would also have favored babies born looking full term and robust, since such babies would be more likely to appeal to mothers. One result was the otherwise maladaptive-seeming accumulation of white adipose tissue just prior to passage through a bipedal mother’s narrow birth canal (Trevathan and Rosenberg, introduction, this volume). The combined outcome of such selection pressures was human neonates born with four times the body fat of other apes (15% versus 4%), newborns advertising to their mothers, “I’m a good bet; keep me” (Hrdy 1999: chap. 20). Maternal retenchment’s most portentous effects, however, may operate on fathers.

Paternal Care in Cooperative Breeders Even More Facultative than Maternal Care

Paternal care is essential for infant survival among monogamous New World Calliebus and Aotus. Among cooperatively breeding Callitrichinae, however, infant survival is correlated with the total number of adult males in the group because, as in humans, paternal shortfalls can sometimes be compensated for by alloparents (Gettler 2014; Hrdy 2008). In one well-studied group of wild tamarins, Leontopithecus rosalia, paternal effort varied inversely with how many other males were present. Short on alloparental help, paternal participation increased even as the mother’s time spent carrying the infant remained constant (Bales et al. 2002: 454).

Anthropologist Courtney Meehan (2005) documented a similar dynamic among Central African foragers. Among the Aka, residence patterns are typically flexible, and people move between groups. During periods when parents resided matrilocal, the mother’s kin engaged in much direct childcare, permitting the father to do little. When parents moved to be near his family, however, patrilineal kin proved less helpful. Yet, with little change in how much the mother held her baby, the total time infants were held remained more or less constant because fathers compensated by doing exponentially more (figure 9.2).

Those who assume that such well-calibrated adjustments to parental investment can only be explained by uniquely “practical reasoning” in cognitively sophisticated humans (e.g., Driscoll 2005: 287) should consider the similarly opportunistic calibrations of parental care reported for tiny-brained callitrichines (Bales et al. 2002), which lack anything like sapient-grade foresight or perspective (e.g., Burkart and Heschl 2007). Among captive marmosets, fathers as well as mothers were more likely to push 6- to 9-week-old infants
Aka Allomothers

Figure 9.2. Aka babies were held by allomother for roughly the same amount of time in matrilocal and patrilocal settings, but in a matrilocal setting with matrilinear kin offering to help care for a mother’s infant, the father engaged in relatively little direct care, even less than the combined care from other male alloparents. However, in patrilocal settings with less allopaparental assistance on offer, fathers cared far more. Adapted from a diagram provided by Courtney Meehan, reproduced here with permission.

off if experienced alloparents were on hand (Fite et al. 2005). Similarly, as group size (and the availability of alternate care) increases, a wild tamarin male reduces his invitations to infants to climb aboard. Indeed, reproductive males may benefit from additional help even more than mothers do since allopaparental participation reduces the father’s energetic expenditures while also enhancing the group’s defense, potentially extending a given male’s reproductive tenure in the group (Bales et al. 2000:fig. 1 and elsewhere).

Although early evolutionary psychologists were convinced that primate males would only nurture infants whose paternity they could be certain of (e.g., Symons 1982), it has become increasingly clear that fathers as well as mothers may benefit when mothers mate polyandrously if offspring possibly a male’s own thereby garner extra provisioning (Beckerman et al. 1998; Diaz-Munoz et al. 2014; Eliasson and Jorgensen 2014; Hrdy 2009; Starkweather and Hames 2012; Walker et al. 2010). Among hunter-gatherers such as the Hadza, fathers are reported to put more effort into hunting than do unmarried, childless men (Wood and Marlowe 2013). Clearly, probable genetic relatedness matters. Yet even when men manage to channel resources to their own families, more than half the meat men bring back gets distributed to other group members (Hawkes et al. 2010; Hawkes et al. 2016). Infants of fed mothers resume ovulation sooner (Hawkes et al. 2016). Patrilocal camp not only enhances the well-being of infants but also increases the availability of fertile females, extending the viability of the community upon which it relies.

Why Would Male Apes Share?

Regardless of just how closely chimpanzee and bonobo care resemble those of humankind’s last common chimpanzees still provide the insights into their sociocognitive capacities. Experiments suggest that when food is presented by the incentive before them and display the inclinations of nearby others, rarely engaging in consistent exchanges (Yamamoto and Tanaka 2010; Hrdy 2011). In the wild, successful hunters may benefit by other adults, but almost never give additional assistance of mother-to-infant transfers (rarely meat), there is no increase in allotable life stage when youngsters are most a (Achermann 2000). Although less well-researched, the common chimpanzees are more tolerant and “xenophilic” (Hrdy 2013). Even bonobo males are rarely reported to share.

In contrast to either species of chimpanzee, a male bonobo, with marmoset breeders more likely to carry delivering food to another adult (Hrdy 2013). Experiments by Judith Burkart revealed that marmosets with infants 53% of all food items they collected, whereas infant food items are 10–16 weeks of age. The more food item, the more likely it was to be delivered. Interestingly, as in Marlowe’s Hadza study, marmosets tried harder to provision food items obtained compared to food items obtained earlier. Among wild tamarins (Leontopithecus),
Of Marmosets, Men, and Babies

percentage of high-investment care in a patrilocentric setting

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Why Would Male Apes Voluntarily Share Food?

Regardless of just how closely chimpanzee breeding systems do or do not resemble those of humankind’s last common ancestor with other apes, common chimpanzees still provide the best-studied proxies for estimating their sociocognitive capacities. Experiments on the “altruism” of Pan troglodytes suggest that when food is presented, chimpanzees are “overwhelmed” by the incentive before them and display little interest in the mental states or desires of nearby others, rarely engaging in spontaneous sharing or reciprocal exchanges (Yamamoto and Tanaka 2009). Chimpanzees will respond to persistent solicitations, but rarely initiate voluntary donations (see esp. Silk et al. 2013). In the wild, successful hunters may proffer scraps after persistent begging by other adults, but almost never give any food to youngsters. With the exception of mother-to-infant transfers (rarely involving commodities so prized as meat), there is no increase in allomaternal provisioning around weaning, the life stage when youngsters are most at risk of starving (Boesch and Boesch-Achermann 2000). Although less well studied, bonobos are genetically as closely related to humans as common chimpanzees are, and bonobos are both more tolerant and “xenophilic” (Hare 2014; Hare et al. 2007). Nevertheless, even bonobo males are rarely reported by fieldworkers to offer food to others.

In contrast to either species of chimpanzee, callitrichines readily volunteer food, with marmoset breeders more willing than nonbreeders to pull in a tray delivering food to another adult (Burkart et al. 2007; Martin and Burkart 2013). Experiments by Judith Burkart reveal that adult Callithrix jacchus share with infants 53% of all food items they obtain, with provisioning peaking when youngsters are 10–16 weeks of age. The more difficult it was to obtain a food item, the more likely it was to be delivered to a nearby begging immature. Interestingly, as in Marlowe’s Hadza sample mentioned above, breeding male marmosets tried harder to provision than did nonbreeding helpers (offering 61% of food items obtained compared to 46%) (Burkart and Finkenwirth 2015).

Among wild tamarins (Leontopithecus rosalia) as well, allomothers (usually

Sarah B. Hrdy
male) were four times more likely to share animal prey than (less coveted) vegetable foods. Amazingly, the hunter himself refrained from eating any meat. Seventy-one percent of the time, the male allomother accompanied his gift with a special call designating “animal prey” (Rapaport 2006:217–218).

Callitrichine food transfers seem calibrated both to meet infant nutritional needs and to selectively transfer information. Lab experiments confirm that adult male tamarins monitor emerging competence in juveniles, ceasing to respond to their begging once immatures learn to operate a food-delivery apparatus for themselves (Humle and Snowdon 2008). The delivery of novel fruit or prey that youngsters have not previously encountered is accompanied by special staccato food calls (Rapaport and Brown 2008). Humans aside (“Here, sweetie, try this”), callitrichines are the only primates known to accompany gifts with context-specific vocalizations. Once “mentors” locate potential prey, they vocalize, luring 4- to 12-month-olds to that location. Novices then set about foraging for themselves, learning where to search and, through trial and error, how to hunt.

As youngsters mature and learn to process more plant foods for themselves, the proportion of animal prey delivered actually increases. This counterintuitive result suggests that male provisioning really does function to promote faster growth and earlier weaning, buffering youngsters from starvation around this vulnerable time. Rapaport and colleagues (2013) have even hypothesized that inclusive fitness benefits from male provisioning might explain the overproduction of sons that has been documented for various tamarin species (Hershkovitz 1977:table 89B). Whether provisioning by opening hard-to-open fruits (Garber 1997), by teaching young to forage in the forest for themselves (Rapaport 2011), or by pulling in trays of food for others in captive experiments (Burkart et al. 2007; Cronin et al. 2011), callitrichines tend to be remarkably prosocial, generous where food is concerned (Burkart et al. 2014) as well as rescuing infants from danger (e.g., Graetz 1968).

Among human foragers, energetically rich foods (meat and honey) obtained by males also are routinely shared. But even leaving aside language and culture, there are major differences. In particular, callitrichines lack sex-defined divisions of labor in either infant care or hunting. Callitrichines’ prey are small, located in circumscribed geographic ranges, caught on the fly in one hand or extracted from tree holes by nimble fingers, so the young are nearby, and male hunters hand prey directly to immatures (Brown et al. 2004). Among humans, by contrast, captured prey are divided and prepared by other group members.

Rarely do men directly offer meat to kin and even non-kin (Burkart et al. 2014). The division of labor accompanied kinship relationships between groups of unrelated individuals (Burkart et al. 2014). How do humans acquire other forms of unpredictable resources (Cashore and Smith 1995)? Maturing, intelligent apes already do. How might the labor (e.g., Boesch and Boesch-Achermann 2000; van Lawick-Goodall 1968) be divided among the group members? How might they socialize with each other? How might they ensure that they get their share? How might they function as a group to solve problems and share resources? Even when they eat together, do they share equally? How do they negotiate sharing and allocation of food? How do they resolve disputes over the division of labor? How do they ensure that all group members are rewarded fairly for their contributions?

Setting the Stage

Food sharing among primates ranges from voluntary and frequent. Humans engage in such “donative intent,” spontaneous and frequent sharing of food to kin and even non-kin (Burkart et al. 2014). The division of labor accompanies kinship relationships between groups of unrelated individuals (Burkart et al. 2014). How is this division of labor achieved?

Relatively few primates hunt, but the hunting of protein and lipids is highly risky to the males, who are the only apes really interested in hunting. It is not surprising that hunting is only in human apes does meat predominate in the diet. Given how self-centered great apes are, it is surprising that they do not share most of their food more often.
Rarely do men directly offer meat to immatures. Instead, when asked, ethnographers recall men “helping a young child eat soupy stuff from a gourd” or “fathers helping kids eat small fish with bones” (R. Hames discussing Amazonian hunter-horticulturalists, pers. comm., 2014); New Guinea highlander men delivering premasticated food via kiss-feeding (I. Eibl-Eibesfeldt’s photo archives); and Hadza men sharing bits of cooked meat or highly desired honey (A. Crittenden, pers. comm., 2014).!Kung children begging food from fathers are rarely rebuffed (Konner 2010:462). The only quantitative data come from Courtney Meehan and Jessica Collins (pers. comm., 2014). Of 78 Aka children between birth and 4 years of age, six were given food by their fathers while four received food from other men. Such instances sound more like demonstrations of affection than routine provisioning yet nevertheless appear symptomatic of high levels of tolerance and nurturing intent.

**Setting the Stage for Male Tolerance**

Food sharing among primates ranges from nonexistent to “tolerated theft” to voluntary and frequent. Humans and callitrichines fall at the extreme end of such “donative intent,” spontaneously proffering food, including meat, to kin and even non-kin (Burkart et al. 2009). Once established, the routine division of labor accompanied by food sharing and long-term exchange relationships between groups allowed human foragers to lower the risks of unpredictable resources (Cashdan 1990; Wiessner 1982). Among slow-maturing, intelligent apes already characterized by incipient divisions of labor (e.g., Boesch and Boesch-Achermann 2000; McGrew 1979 for chimpanzees), behaviorally modern *Homo sapiens’* increased recourse to cultural solutions (including language) made it increasingly possible to reduce starvation risks through pooling and sharing resources (Cashdan 1990; Kramer and Ellison 2010; Wiessner 1982). Such exchanges generate their own hyper-social sequelae, which are beyond the scope of this chapter. But how does voluntary sharing get started?

Relatively few primates hunt, but among species that do, meat’s concentration of protein and lipids is highly prized. Wrestling meat from a possessor risks aggressive retaliation. Humans and chimpanzees, typically males, are the only apes really interested in hunting (e.g., McGrew 1979; Marlowe 2010), but only in human apes does meat constitute an important part of the diet. Given how self-centered great ape males tend to be, and how little caretaking
beyond generalized protection they do, how did apes in the line leading to the genus *Homo* become sufficiently tolerant as to allow others to partake of prized commodities?

In tracing the origins of hominin male tolerance, it is worth keeping in mind how dangerous to infants males can be. Infanticide by males is widespread among primates, rodents, and other animals. Tolerance-producing mechanisms were essential to reduce the likelihood of males harming offspring possibly their own. In some house mouse strains, ejaculation during mating activates a time-delayed neural inhibition of infanticidal responses beginning 3 weeks (the mouse gestation period) later, and spontaneously reemerging 2 months after ejaculation, long enough for offspring possibly the male’s own to be weaned (Perrigo and vom Saal 1994). In other mice, testosterone implants in virgin, castrated males were enough to switch their response to neonates from tolerant to infanticidal (Perrigo and vom Saal 1994:372). Among mammals, including nonhuman primates, most infanticidal males only attack infants cared for by females they have not mated with (Hrdy 1977).

Male mice encountering stray pups either ignore or attack (and possibly cannibalize) them, but repeated exposure to pup after pup elicits tolerance, even nurture. It has been discovered that immature mice secrete a pheromone from the lacrimal gland that, when released in the tears of 2- to 3-week-old mice, inhibits sexual activity in adult males (Ferrero et al. 2013). In species where males find themselves in proximity to infants likely to be close kin, neural overrides to the attack impulses would be essential fail-safes, especially if accompanied by thresholds for responding to infantile cues sufficiently low to promote nurture under the right circumstances.

Not only do males become more tolerant and affiliative after intimate exposure to infants, but with or without recent histories of direct male care, primate males appear preadapted to recognize, look out for, and behave affiliatively toward possibly related youngsters (Fox et al. 2014; Hrdy 1979). For example, polygynously mating male baboons preferentially respond to distress calls from mothers with infants only possibly their own (Palombit 2000) as do Barbary macaque males (Small 1991). Even ordinarily aloof, promiscuously mating male chimpanzees care for orphans likely to be relatives (Boesch and Boesch-Achermann 2000; Goodall 1986). My speculation is that the neuropeptides and other hormones enlisted by natural selection here are “recycled” from molecules and neural circuits already on hand because they promoted maternal nurture. Whatever the physiological basis, it behooves primate mothers to seek to remain near males with infanticidal tendencies (Hrdy 1979).

Initially, maternal preferences might be particularly strong near those males—males predisposed to protect rather than harm the infant rather than infanticidal (Hrdy 1979). However, phylogenetically ancient, higher primate species of which humans are a part may have reemerged in the evolution of a species brain that is deceptively similar to that of our closest living relatives (e.g., West-Eberhard 2003; Whiten and Young 2014). As Gettelman and Whiten (2014) suggested, female intimate contact with infants is correlated not with being in a courtship situation but with being in a situation in which the infant requests close female contact. Presumably, such tolerance extends to other males, possibly even nonfamilial males, that beggars get some food. For example, begging youngsters were more likely to be fed by mothers remaining close to previous mates in the expectation that someone else might return to take the infant in the event that the mother’s next consorting mate is not capable of caring for it (Ferrar et al. 2013; Small 1991).

In the first phylogenetically controlled experiment with cotton-top tamarins, Jaeggi and van Schaik (1997) observed that offspring in the conspecific group who had been carrying infants on their back when she was fed as a child were more likely to return to the mother to be fed (Jaeggi and van Schaik 1997). Presumably, success obtaining food also increases the likelihood of obtaining and keeping infants. Youngsters and their mothers to be able to cooperate and maximize the benefits of close social contact most likely to occur when the available resources are relatively abundant.

Within proleptic societies, the capacity to provide additional food beyond those available within the family group (Roitblat 2011; see also O’Connell et al. 1999 for evidence regarding capacities among slow-maturing apes).
how did apes in the line leading to the human lineage ever get on with males to the point as to allow others to partake of prized resources? Thus, to consider the matter of male tolerance, it is worth keeping in mind that it can be. Infanticide by males is widespread among other animals. Tolerance-producing strategies may reduce the likelihood of males harming offspring when they are not of the same strain, as observations of infanticidal responses beginning many years later, and spontaneously reemerging again for offspring possibly the male's (Saal 1994). In other mice, testosterone levels were found to be sufficient to switch their response to that of a female (Perrigo and Saal 1994:372). Among apes, most infanticidal males only attack males not mated with (Hrdy 1977).

Mothers either ignore or attack (and possibly even attack) pup after pup eliciting tolerance, but immature mice secrete a pheromone released in the tears of 2- to 3-week-old male rats (Ferrero et al. 2013). In species in which infants are close kin, it would be essential to have permanent members of infantile cues sufficiently low to ensure the survival of the infant. The tolerant and affiliative after intimate contact with the mother is a recent history of direct male care, which in turn, leads to, and behaves affiliatively (Fox et al. 2014; Hrdy 1979). For baboons, preferentially respond to distress in the presence of their own (Palombit 2000) as well. Even ordinarily aloof, promiscuously mating males are likely to be relatives (Boesch and Boesch-Horn 1986). My speculation is that the neurochemical mechanisms underlying these findings are probably natural selection here are "recycled" in that they already exist because they promoted maternal behavior, and it behooves primate mothers to seek to remain near males with whom they mated (Altman 1980; Hrdy 1979).

Initially, maternal preferences might involve nothing more than remaining near those males—males predisposed to be tolerant and protective toward their infant—rather than infanticidal (Hrdy 1979). Under the right circumstances, however, phylogenetically ancient, highly conserved male proclivities can reemerge (e.g., West-Eberhard 2003; Wu et al. 2014; Dulac et al. 2014; Rilling and Young 2014). As Gettler (2014 and chapter 8, this volume) explains, intimate contact with infants is correlated with the downregulation of testosterone, predisposing males to be more tolerant toward immatures and others. Presumably, such tolerance extends to the immatures persistently importuning males for animal prey. Elevated oxytocin and prolactin would promote affiliative emotions as well as tolerance (Carter 2014), increasing the likelihood that beggars get some food. For example, when Saito and Nakamura (2011) administered oxytocin into the central nervous system of male marmosets, begging youngsters were more likely to be fed rather than rebuffed. Meanwhile, mothers remaining close to previous mates would find they could minimize care in the expectation that someone else would pick up the protective slack, further increasing males’ exposure to infant signals of need. Since former mates have a stake both in possible offspring’s well-being and in reducing the interval until the mother’s next conception, Darwinian selection should favor lower and lower thresholds of male responsiveness—sometimes including a greater willingness to share food.

In the first phylogenetically controlled examination of food sharing’s evolution among primates, Jaeggi and van Schaik (2011) analyzed data from 68 different species. They concluded that “food sharing among adults only evolved in species already sharing with offspring” (2123). Their phylogenetic analysis is consistent with available natural history. For example, when a tamarin male who has been carrying infants on his back and providing them occasional snacks returns the twins to be nursed, he may tolerate them to remove food from his hands or chew on insects he has caught (e.g., Graetz 1968). Presumably, success obtaining food in this way conditions and emboldens youngsters and their mothers to beg more. The provisioning of young is most likely to occur when the available foods require strength or processing skills beyond those immatures ordinarily possess (Jaeggi and van Schaik 2011; see also O’Connell et al. 1999 for hominins). The elaboration of other-regarding capacities among slow-maturing, long-dependent youngsters that
need to ingratiate themselves with nurturers is one corollary of this mode of child-rearing (Hrdy 2009); the enhanced tolerance among male caretakers is another (Burkart et al. 2009).

**How Cute Babies Catalyze Self-Reinforcing Feedback Loops**

Allomaternal care and provisioning enhance the inclusive fitness of collateral kin and in some cases the direct fitness of fathers through offspring’s survival. A male’s provisioning also increases his mate’s lifetime reproductive outputs by shortening interbirth intervals (e.g., Marlowe 2001). If exposure to infants coincides with the downregulation of testosterone, reducing aggressive inclinations, and with even a slight upregulation of oxytocin—enhanced tolerance, the stage is set for more prosocial responses. Instead of responding with irritation, the possessor of a preferred food item allows another to take it. If tolerated snatchings enhance the survival of offspring likely to be related, there is all the more reason for selection to favor lower and lower thresholds for males responding to signals of infantile need. This becomes, quite literally, a self-reinforcing feedback loop with profound implications for ongoing evolution in the genus Homo.

There is general agreement that scavenging and hunting played important roles in human evolution and that meat was shared. However, debate persists over why men hunted. Some researchers emphasize fathers’ motivations to provision their families (Lovejoy 1981; Kaplan et al. 2000; Wood and Marlowe 2013). Others emphasize sexually selected female preferences for good providers (Darwin 1871; Lancaster and Lancaster 1987; Lawrence and Nohria 2002:182). Still others stress socially selected quests for prestige (Hawkes 1991; Hawkes et al. 2010). While Wood and Marlowe (2013) emphasize that Hadza men with children put more effort into bringing back food for the community, doing so on 41% of days (married men without children: 31%; unmarried men without children: 21%), attempting to channel it to their own relations, Hawkes and colleagues (2014) question whether delivering protein to the mothers of their own children is men’s only, or even primary, motivation for hunting. They point out these hunters’ preference for targeting more elusive and obligately shared but also reputation-enhancing large game rather than smaller prey that would more reliably provision their own families. Any combination of these explanations seems plausible, but I am not qualified to weight them.

Sidestepping these debates, I focus on the relatively efficient tolerant toward others for food was shared, generosity might subsequently be favored for the same reasons, including the punishment of offending behavior (Boehm 2012). Indeed, Hrdy’s and the more tolerant bonobos became “their” condition—the most common context to punish offending males is not when some threat is perceived, but rather when the threat is an infant. Thus I favor the idea that men rendered more tolerant by increased exposure to infants, especially Kindchenschemiziert and already before routine food sharing got started.

**A High-Stakes Coordination Game**

Little is known about the sequence of events in the Pleistocene (Hrdy 2009) and possibly this volume) led to the evolution of full parental care. and both parental and alloparental provisioning, a carefully worked-out scenario for the early primate is for callitrichines (Goldizen 1990).

Goldizen’s model (1990) assumes an environment that encouraged the evolution of the cooperative breeding system (Homo). The hominins were also characterized by parental care (Lovejoy 1981) and Anotinae, not yet knowable. Both Goldizen’s proposals for life and foraging for centric, continuity to the extent over how allomaternal provisioning got started in males hunting to provision needy offspring.
arturers is one corollary of this mode of increased tolerance among male caretakers is

**Self-Reinforcing Feedback Loops**

To enhance the inclusive fitness of collateral fitness of fathers through offsprings' increases his mate's lifetime reproductive interval (e.g., Marlowe 2001). If exposure to a pool of testosterone, reducing aggressiveness, upregulation of oxytocin-enhanced bonding behavior likely to be related, we may expect to favor lower and lower thresholds for social support. This becomes, quite literally, a self-reinforcing process for ongoing evo-

Foraging and hunting played important roles in what was shared. However, debate persists on whether or not it is the emotional component to the social structure (Kaplan et al. 2000; Wood and Marlowe 2012). People engaged in helping behavior are more likely to be related, even if they do not share a direct kinship. This is especially true when the investment is high, as in the case of children: 3% of children are not with the children's own parents. Hawkes and Marlowe (2013) emphasize that Hadza men with children do not engage in hunting for the community, doing so for their children. They allocate it to their own relations, Hawkes and Marlowe (2013) emphasize that Hadza men with children do not engage in hunting for the community, doing so for their children. They allocate it to their own relations, Hawkes and Marlowe (2013) emphasize that Hadza men with children do not engage in hunting for the community, doing so for their children. They allocate it to their own relations, Hawkes and Marlowe (2013) emphasize that Hadza men with children do not engage in hunting for the community, doing so for their children. They allocate it to their own relations, Hawkes and Marlowe (2013) emphasize that Hadza men with children do not engage in hunting for the community, doing so for their children. They allocate it to their own relations, Hawkes and Marlowe (2013) emphasize that Hadza men with children do not engage in hunting for the community, doing so for their children. They allocate it to their own relations, Hawkes and Marlowe (2013) emphasize that Hadza men with children do not engage in hunting for the community, doing so for their children. They allocate it to their own relations, Hawkes and Marlowe (2013) emphasize that Hadza men with children do not engage in hunting for the community, doing so for their children. They allocate it to their own relations, Hawkes and Marlowe (2013) emphasize that Hadza men with children do not engage in hunting for the community, doing so for their children. They allocate it to their own relations, Hawkes and Marlowe (2013) emphasize that Hadza men with children do not engage in hunting for the community, doing so for their children. They allocate it to their own relations, Hawkes and Marlowe (2013) emphasize that Hadza men with children do not engage in hunting for the community, doing so for their children. They allocate it to their own relations, Hawkes and Marlowe (2013) emphasize that Hadza men with children do not engage in hunting for the community, doing so for their children. They allocate it to their own relations, Hawkes and Marlowe (2013) emphasize that Hadza men with children do not engage in hunting for the community, doing so for their children. They allocate it to their own relations, Hawkes and Marlowe (2013) emphasize that Hadza men with children do not engage in hunting for the community, doing so for their children. They allocate it to their own relations, Hawkes and Marlowe (2013) emphasize that Hadza men with children do not engage in hunting for the community, doing so for their children. They allocate it to their own relations, Hawkes and Marlowe (2013) emphasize that Hadza men with children do not engage in hunting for the community, doing so for their children. They allocate it to their own relations, Hawkes and Marlowe (2013) emphasize that Hadza men with children do not engage in hunting for the community, doing so for their children. They allocate it to their own relations, Hawkes and Marlowe (2013) emphasize that Hadza men with children do not engage in hunting for the community, doing so for their children. They allocate it to their own relations, Hawkes and Marlowe (2013) emphasize that Hadza men with children do not engage in hunting for the community, doing so for their children. They allocate it to their

Sidestepping these debates, I focus here on how ape males became sufficiently tolerant toward others for food sharing to occur at all. Once meat was shared, generosity might subsequently be further favored for all sorts of reasons, including the punishment of selfish, aggressive, or self-aggrandizing behavior (Boehm 2012). Indeed, Hare and colleagues (2012) propose that the more tolerant bonobos became “self-domesticated” through selection of disfavoring male aggressiveness. But primate-wide—so presumably a basal condition—the most common context in which group members mob and punish offending males is not when some male behaves selfishly by hoarding a resource for himself, but rather when a male responds inappropriately by threatening an infant. Thus I favor the hypothesis that hominin males were rendered more tolerant by increased exposure to infantile solicitations, essentially “Kindersgenschism” and already preadapted for prosocial responses, before routine food sharing got started.

**A High-Stakes Coordination Game with Cute Babies at the Center**

Little is known about the sequence of events that by the beginning of the Pleistocene (Hrdy 2009) and possibly earlier (DeSilva 2011 and chapter 4, this volume) led to the evolution of full-fledged cooperative breeding with both parental and alloparental provisioning of groupmates. To date, the most carefully worked-out scenario for the evolution of cooperative breeding in primates is to callithrichines (Goldizen 1990:fig. 1) rather than hominins. Goldizen’s model (1990) assumes an obligately monogamous starting condition that encouraged the evolution of parental investment, followed by increased fertility (twinning), selection favoring increased alloparental assistance from kin, and increasingly facultative (polyandrous) mating by females. Chimerism and suppressed ovulation emerged later, as highly derived features of this cooperative breeding system (Hrdy 2009). Whether or not the earliest hominins were also characterized by pair bonding, as suggested for Australopithecus afarensis (Lovejoy 1981) and Ardipithecus ramidus (Lovejoy 2009), is not yet knowable. Both Goldizen’s proposal and explanations for pair bonding, including mate guarding, antagonism toward same-sex rivals over resources, and forestall incipience, continue to be debated and bleed into discussions over how allomamternal provisioning got started. Were monogamously paired males hunting to provision needy offspring (Marlowe 2010)? Was alloparental
provisioning initiated with plant foods donated by postreproductive matrilineal kin (Hawkes et al. 1989; Hawkes and Paine 2006), by older siblings or co-suckling co-mothers, or some opportunistic combination thereof (Hrdy 2009)? The reliance on male provisioning among some obligately monogamous primates (e.g., Huck and Fernandez-Duque 2013) is consistent with paternal provisioning arguments, while correlations between female philopatry and shared infant care in anthropoid primates underscore the importance of nearby matrilineal kin (Hawkes et al. 1998; Hrdy 2010). Any resolution must await more and better paleontological evidence. My aim here is to highlight how the increased exposure to infantile signals of need affects males.

Until recently most researchers focused on human maternal responsiveness, leaving the effects of babies on group members other than mothers unexplored. Twenty-first-century experiments using recordings played to parents revealed that yes, mothers respond more readily to mild infant distress (cries of a just waking baby), but fathers responded just as fast if cries signaled real distress (Stallings et al. 2001; Fleming et al. 2002). As with most primates, men tend to be protective of infant group members, with probable fathers especially so. Assuming he is within earshot, if the mother fails to respond, the father eventually will, resulting in his increased exposure to infantile stimuli. Researchers have also discovered the socioendocrinological effects on male allomothers. As mentioned, prolonged proximity to an infant leads to decreased levels of testosterone in men while prolactin and oxytocin are likely to go up; the enhancement of affiliative emotions and social tolerance are likely corollaries (Carter 2014). Any fitness payoffs from increased offspring survival would produce self-reinforcing feedback loops favoring even lower thresholds of male responsiveness.

Humans are not as specifically adapted to cooperative breeding as callitrichines are. Human mothers are not so prone to filter out signals of infant distress and are rarely as rejecting as tamarin mothers. Nevertheless, in both taxa, when mothers fail to respond, the father or other relations may pick up the slack. By ignoring or even rebuffing infants desperate to cling to them, mothers increase males’ exposure to the infantile equivalents of “sex appeal.” Furthermore, as in the cases of both tamarins and some foragers, how much care is required from fathers varies with the amount of alloparental assistance on offer. Just as fathers signal their probable commitment to mothers, fathers need to monitor the intentions of others.

Weeks before birth, in anticipation of the extra exertion required, a marmoset male signals his future commitment; mothers informally poll paternal commitment. Males retrieve the infants. A highly motivated baby whenever the mother pulls away. Thus, if their mates’ responses appeal, intervenes, mothers may terminate their own infant raising approaches, fathers themselves are likely to intervene. Certainly, the infants are doing something embedded in far more complex communication, humans and callitrichines alike. “Coordination game.” The optimal strategy for the father, the other players do. But this coordination strategy, this fine-tuned play, by the needy baby can profoundly alter (sensu Hrdy) the other players.

Human mothers of course also make decisions informed by their age, past reproductive prospects, and specific attributes. If consciously and unconsciously processing even before mate choices are final, take alloparents into account is captured by advice given to a son in search of a wife: The advisor here is not referring to the son but to his prospective wife’s own mother: “Wait. Available alloparents. In worlds without institutionalized social safety nets, how much energy the father himself withholds he may have to forgo in order to ensure survival. Still, today, the most rational and occasionaly overridden, by responses. Consider the case of a mother who cannot be so captivated by an infant that she cannot end up more committed than genetic parents.

Conceptualizing the interactions among care-delegating, occasionally rejecting, and tentative levels of commitment exhibited by fathers changes the way infantile cues are interpreted.
of marmoset male signals his future commitment by gaining weight. After birth, mothers informally poll paternal commitment by monitoring how readily males retrieve the infants. A highly motivated father will persist in retrieving the baby whenever the mother pushes it off, returning it to her to nurse. However, if their mates' responses appear inadequate and no other allomother intervenes, mothers may terminate their investment. I suspect that as weaning approaches, fathers themselves are scanning how readily others provision infants. Certainly, the infants are doing so. In spite of the fact that people are embedded in far more complex communities with very different criteria at issue, humans and callitrichines alike are engaged in what economists call a "coordination game." The optimal strategy for each player depends on what other players do. But this coordination game has a special twist. Cues emitted by the needy baby can profoundly alter the internal motivations (neuroendocrinology) of the other players.

Human mothers of course also make conscious, culturally influenced calculations informed by their age, past experiences, current and future reproductive prospects, and specific attributes of their infant. And both parents consciously and unconsciously process signals of likely social support beginning even before mate choices are finalized. That fathers as well as mothers take alloparents into account is captured by a traditional African proverb, advice given to a son in search of a wife: "First, find yourself a good mother." The advisor here is not referring to the mother of a man's future children, but to his prospective wife's own mother and her kin, the suite of potentially available alloparents. In worlds without safe nurseries, food markets, or institutionalized social safety nets, how much help his mate can command impacts how much energy the father himself will have to expend and what opportunities he may have to forgo in order to ensure that at least some of his offspring survive. Still, today, the most rational parental calculations are colored and occasionally overridden, by responses far older than the human neocortex. Consider the case of a mother who consciously decides to reject but ends up so captivated by an infant that she changes course, or of adoptive parents who end up more committed than genetic parents (Hrdy 1999:chaps. 12–14, 20–21).

Conceptualizing the interactions among cooperative breeders as coordination games provides useful frameworks for interpreting both the behavior of care-delegating, occasionally rejecting, modern mothers and the highly facultative levels of commitment exhibited by human fathers. This perspective also changes the way infantile cues are interpreted. A case in point would be the
discovery by researchers in Israel that men sniffing pads wetted with women's odorless emotional tears instead of a saline control "experienced reduced self-rated sexual arousal, reduced physiological measures of arousal, and reduced levels of testosterone" (Gelstein et al. 2011:226). Some have assumed that this must be nature's way for women to communicate "turn-off" messages to unwanted sexual partners (e.g., Zimmerman 2011). But if one assumes that crying babies long provided the likeliest context for encountering tears, it makes more sense to view reduced sexual arousal in tear-exposed men as another highly conserved neurobiological retention (possibly one further elaborated by millions of years of breeding cooperatively) through which men in intimate proximity to infants become less aggressive, more tolerant, and prone to nurture.

Selection in this coevolving feedback loop falls heaviest on vulnerable immatures. Infants play for higher stakes with the most to lose. But as the currency of fitness, "cute" babies also hold a trump card. Over hundreds of millions of years, selection would have favored myriad sensitivities to the signals babies broadcast. In the primate case, conditional maternal investment opened novel opportunities for others to respond, to be drawn in, and through the resulting experiences, to be transformed. The expression of nurturing potentials in male phenotypes renders highly conserved vertebrate legacies newly visible to natural selection, which has favored lower and lower thresholds for tolerant, affiliative, and perhaps even generous responses in men intimately exposed to babies. Those interested in fostering calmer, gentler societies might do well to keep in mind this transformative power of babies.

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1. Note that “allomother” here refers to a sibling, not the mother, possibly including the "father" is only used when there is sufficient inbreeding; a given male is “other than a parent,” which is tricky.

2. Anecdotal reports suggest that fathers may stay with their mothers because they are more encumbered as carers (pers. comm., 2014).

3. One Saguinus geoffroyi mother abandoned the other (Epple 1970:66), and Mallin (1973) describes partial cannibalism of premature infants against a backdrop of frequent abandonment of those infants.

4. Such experiments, with their resulting data, are promisingly acceptable.
of marmosets, men, and babies

notes

1. note that "allomother" here refers to any female or male group member other than the mother, possibly including the progenitor. the designation "alloparent" is only used when there is sufficient information to be confident that a given male is "other than a parent," which without dna evidence can be tricky.

2. anecdotal reports suggest that fathers are more vulnerable to predation than mothers because they are more encumbered by carrying infants (l. rapaport, pers. comm., 2014).

3. one saginus geoffroyi mother abandoned the twin with a harelip but not the other (epple 1970:66), and mallinson (1965) reported the abandonment and partial cannibalism of premature twins among captive s. nigricollis. but against a backdrop of frequent abandonment in captive tamarins, who knows what these isolated cases mean?

4. such experiments, with their resulting levels of mayhem, are no longer ethically acceptable.

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