Variable postpartum responsiveness among humans and other primates with “cooperative breeding”: A comparative and evolutionary perspective

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ABSTRACT

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Until recently, evolutionists reconstructing mother–infant bonding among human ancestors relied on nonhuman primate models characterized by exclusively maternal care, overlooking the highly variable responsiveness exhibited by mothers in species with obligate reliance on allomaternal care and provisioning. It is now increasingly recognized that apes as large-brained, slow maturing, and nutritionally dependent for so long as early humans were, could not have evolved unless “alloparents” (group members other than genetic parents), in addition to parents, had helped mothers to care for and provision offspring, a rearing system known as “cooperative breeding.” Here I review situation-dependent maternal responses ranging from highly possessive to permissive, temporarily distancing, rejecting, or infanticidal, documented for a small subset of cooperatively breeding primates. As in many mammals, primate maternal responsiveness is influenced by physical condition, endocrinological priming, prior experience and local environments (especially related to security). But mothers among primates who evolved as cooperative breeders also appear unusually sensitive to cues of social support. In addition to more “sapient” or rational decision-making, humankind’s deep history of cooperative breeding must be considered when trying to understand the extremely variable responsiveness of human mothers.

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Adding allomother
to the maternal mix

In the second half of the twentieth century, Jay Rosenblatt, a psychotherapist interested in human emotions, turned his attention to the physiological underpinnings of maternal responses. His experiments with rats and other laboratory animals ushered in motherhood’s Age of Psychobiological Enlightenment. Ensuing research in his and other laboratories illuminated the roles of hormones acting on the brain during gestation, at birth, and following the onset of lactation priming mothers to nurture newborns. Over time, Rosenblatt and colleagues also documented the roles of infantile cues, local environments and past experiences in eliciting and modulating maternal behaviors most likely to ensure infant survival and well-being (reviewed in Lonstein et al., in press; Fleming et al., 2016-in this issue; Barrett and Fleming, 2011; Numan and Insel, 2003). Their findings complemented the writings of another psychotherapist and psychiatrist, John Bowlby, who relied on animal (especially nonhuman primate) models to inform his ideas about infant-to-mother attachments and the part these powerful relationships play in future psychological development. These early research programs tended to focus on mothers as the main—and as is true for most mammals—the exclusive, nurturers of young.

This central role of mothers was consistent with long-standing evolutionary assumptions about early humankind’s division of labor between man-the-hunter-provider and mother-the-nurturer (Darwin, 1874; Kaplan et al., 2000; Lovejoy, 1981). And why not? Across traditional societies, the continued presence of the mother during the first two years is the single best predictor of infant survival (e.g., Sear and Mace, 2008). Meanwhile, the model organisms selected for study—such as the rats in Rosenblatt’s lab, or the macaques, baboons, chimpanzees and gorillas in the laboratory and field studies that Bowlby selected as templates for early human parenting (1971, 228–229)—fit matrifocal presumptions. So did caretaking in other model organisms, including mice or marmosets, or for that matter, humans, provided these mothers were singly housed in cages, or in the human case spent their days isolated with their infant within walled dwellings rather than in social groups. By century’s end, however, it was increasingly clear that among hominins living by hunting and gathering in African contexts more typical of what Bowlby referred to as humankind’s Environment of Evolutionary Adaptedness, a wider cast of characters, would have been required to insure survival of offspring.

Given the roughly 13 million calories needed to provision human offspring between birth and age 18 or so, when children in foraging societies begin to produce as much as they consume (Kaplan, 1994), children had to be provisioned long past weaning and required more than a mother by herself could provide. Given the vagaries of hunting,
a father by himself also could not provide calories as reliably as growing children need to be fed (O'Connell et al., 1999). Such constraints led to customary sharing such that hunters not only provisioned their own families, but shared with other group members, providing insurance against recurrent shortages critical for long-term survival (Cashdan, 1990; Marlowe, 2010). Mothers helped, not only from fathers but from other male and female allomothers as well (Hrdy, 1999, 2009). Note that the term “alloparent” is only used when paternity is known so researchers can ascertain that a given allomother is “other than” a parent.

Among Africans still living by hunting and gathering when they were first studied, meat and honey brought in by men accounted for some 40% of calories consumed. The majority of the diet came from plant-foods collected by women, with older women past reproductive age contributing disproportionate shares (Hawkes et al., 1989; Hawkes et al., 1998; Marlowe, 2010: Fig. 5.11). Older siblings and cousins sometimes provided gathered food such as berries, but more often they helped with childcare (Crittenden and Marlowe, 2013; Henry, 2000). Even though mothers remained key attachment figures, co-sleeping with their infants at night as in all primates, human infants may be cared for by male and female group members other than their mother 30% or more of the day as well as sometimes being briefly suckled by other lactating women (Hewlett and Winn, 2014; Hrdy, 2009). In this way, infants become attached to multiple allomothers rendering standard measures of attachment security such as Ainsworth’s Strange Situation procedure unusable in hunter-gatherer contexts. Where familiar allomothers are almost always nearby and infants have several attachment figures, they do not object to temporary disappearances by their mother the same way as do infants in the Western samples typically studied by developmental psychologists (Meehan and Hawks, 2013; cf. prescient early critique by Van Ijzendoorn et al., 1992).

Cooperative breeding followed by (even) longer childhoods, bigger brains

New evidence and reassessments of older studies are leading to a paradigm shift among evolutionary anthropologists. It is increasingly assumed that alloparental care and especially provisioning from males and females other than parents, in addition to parents, was essential to keep Pleistocene youngsters safe and fed (Hewlett and Lamb, 2005; Hrdy, 1999, 2009; Burkart et al., 2009; Konner, 2010; Meehan and Crittenden, in press; Trevathan and Rosenberg, in press). Nutritional subsidies provided by allomothers would have been particularly critical around the time of weaning when primates are most vulnerable to malnutrition.

The importance of allomaternal provisioning was magnified in the case of young hominins simultaneously surviving, growing, and also building and maintaining increasingly large brains (Iler and van Schaik, 2012). The significance of provisioning past weaning is underscored by scans of developing human brains indicating that energy demands to support synapse formation peaks between 4 and 5 years, after most hunter–gathering children begin to be, or are, weaned and when, in many cases, their mother would be pregnant with or nursing a subsequent infant (Kuzawa et al., 2014). All apes take a long time to mature, but escalating demands from this unusually greedy organ consuming glucose at a rate up to 66% of resting metabolism, required even more extreme trade-offs with somatic growth. Thus youngsters in the line leading to the genus Homo began growing up even more slowly than other apes, further extending “childhood” and increasing the need for nutritional subsidies from male and female group members other than the mother (Kuzawa et al., 2014).

I have conservatively estimated that cooperative breeding began to emerge with Homo erectus around two million years ago (Hrdy, 2009). Paleontologists such as Jeremy De Silva (2011, in press) hypothesize that selection pressures favoring shared care and provisioning were underway even earlier, perhaps with australopiths some three million years ago. The evolutionary chronology remains murky. But so far as sequence goes, logic dictates that shared care and provisioning of young must have begun to emerge before (or co-evolved with?), the doubling of brain sizes between australopiths and H. erectus (from ca. 450 to ~900 cm³). That is, cooperative breeding must have preceded the evolution of hyper-long childhoods and the tripling of brain size to 1350 cm³ of gray matter that characterize “anatomically modern humans” (at least by 200,000 years ago) and before “behaviorally modern” humans’ capacities for symbolic thought and sophisticated language over the past 150,000 years (Fig. 1).

Breeding systems in which alloparents in addition to parents help to care for and provision offspring are uncommon but scarcely unique. Cooperative breeding has evolved many times across insect, avian and mammalian taxa. Among vertebrates, cooperative breeding has been studied longest among birds. Well known for biparental nest-building, egg tending and care of nestlings (Lynn, 2016-in this issue; Angelier et al., 2015-in this issue), alloparents in addition to parents are observed to tend and provision chicks in some nine percent of 10,000 avian species (Cockburn, 2006). Longitudinal studies of cooperatively breeding birds with known individuals and data on lifetime reproductive success have yielded rich troves of data against which to test Hamilton’s Rule and other theories that explain why individuals might evolve so as to help care for someone else’s offspring (Koenig and Dickinson, 2004). Since such theories can be applied to cooperation and conflict within families generally, the term has been extended to humans as well (Emlen, 1995). It is important to note that the descriptor “cooperative” notwithstanding “cooperative breeding” does not imply absence of conflict. There can be considerable competition between mothers for allomaternal assistance; between sibs for resources; between males for mates, even indirect competition between infants for succor. Nor does shared care and provisioning of young by themselves explain cooperation in other domains.

Cooperative breeding evolves through various routes. Typically, high within-group genetic relatedness is required to get it started but the threshold for shared care of infants is already set low among primates. Typically new infants are magnetically attractive to at least some other group members and rudimentary forms of alloparental caretaking are documented for a slim majority of species of the several hundred species in this highly social order (Hrdy, 2009).

Even in primate species without full-fledged cooperative breeding (i.e. extensive alloparental care plus provisioning), mothers may allow other group members to hold and carry their young resulting in considerable “parenting practice” and sensitization prior to actual parenthood. For example among infant-sharing langur monkeys (Semnopithecus entellus) females remain for life in natal groups composed of overlapping generations of matrilineal kin accompanied by one or more males who enter from outside the group. Since diets are composed largely of leaves, there is little inter-individual competition for food; dominance relations among females on average related as closely as second cousins, tend to be relaxed. Thus pre- and post-reproductive females are available to protect and/or carry young born to other females and mothers permit them to. Mothers need not (as among extremely hierarchical macaques) fear that their infant will fail to be returned, or as among chimpanzees fear that an unrelated female will harm (even cannibalize) her infant. Langur mothers tolerate other females taking their infants as early as the first day of life and allomothers carry them up to 50% of daytime (Hrdy, 1977: Ch. 7).

Nulliparous juvenile and subadult females are especially attracted to new babies, take them most frequently, try hardest to pacify them so as to keep them from complaining and attracting competing caretakers, and keep hold of borrowed babies for the most minutes (Fig. 2). Nulliparous are presumably gaining valuable caretaking experience. Allomothers may also be experientially priming themselves for subsequent parenthood (cf. Storey and Ziegler, 2015-in this issue). In addition to juvenile and subadult females, the second most motivated category
of langur allomother includes adult females in the late stages of pregnancy, followed by mothers who have just given birth and who briefly take and inspect a second infant in addition to their own. Like Rosenblatt’s rats, these langurs are presumably hormonally primed to be especially attracted to babies (Hrdy, 1977: Tables 7.5 and 7.9).

**Difficulties defining solicitous vs. “abusive” care**

Depending on their own reproductive state, langur allomothers exhibit varying levels of interest and solicitude. In contrast to either inexperienced or very pregnant females, experienced parous females will take and inspect infants but soon tire of them. Desperately clinging infants may be forcibly pushed away, held upside down to inspect their genitals, even pressed against the ground, or sat upon, resulting in piteous complaints prompting retrieval by either the mother or another allomother. Brutal as parous allomothers appear (Fig. 3), no injury to borrowed charges has been observed. Even an infant left on the ground will be picked up by either the mother or another allomother within two minutes.

Langur infants do not like being pulled from their mother and complain loudly. Nevertheless, infant-sharing is typical for all but a few species in the sub-family Colobinae and over half of the several hundred species in the order Primates exhibit at least some allomaternal care. Mothers who allow their infants to be taken are neither neglectful nor abusive. Rather, they are preoccupied with staying fed and benefit from having group members whose intentions are sufficiently benign that a mother can temporarily entrust care of her infant to others. In this respect it is worth noting that the handful of non-infant-sharing exceptions within the sub-family colobinae are all species where females move between groups and so (like chimpanzees) rarely have
matrilineal kin nearby (Hrdy, 2009). It takes two conditions for shared care to emerge. The normal possessiveness and extreme protectiveness of a new mother has to be relaxed, and she has to feel sufficient trust or tolerant of nearby group members to allow another individual access to her new infant. Obviously it would be interesting to know more about neuroendocrinological status of postpartum primates with and without trusted associates nearby, but I know of no relevant research.

As Drury et al. (2016-in this issue) emphasize, and the langur cases discussed above illustrate, caution is called for when applying a culturally laden term like “abuse” to nonhuman animals. A lot depends on who is doing what to whom, why, and especially on whether or not the “abused” infant is harmed. One species’ “negative early caregiving” is another creature’s normal. Furthermore, in environments where it is as challenging to avoid being eaten as it is to stay fed, mothers who reject their infants or leave a vocalizing infant unattended, would be unlikely to remain mothers for long. Unless that rejecting mother learned from that experience to be more attentive with subsequent infants, heritable traits leading to maternal neglect would be selected against and disappear form the population’s gene pool. When a mother forcibly restrains her infant, she is less likely to be abusing it than protecting her infant from some perceived threat. Nor can infant complaints be taken as reliable indicators of maternal “abuse.” Infants protest when mothers deem it too dangerous for them to move about or at weaning, when tantrums may be accompanied by rough but non-injurious punishments (e.g., slapping).

Primate mothers closely resemble other mammals among whom steroid hormones during gestation, peptide hormones after birth, and neurological systems all collaborate to render it rewarding for mothers to taste, smell, and remain close to their babies and bond to them (Feldman et al., 2010; Jenkins et al., 2016-in this issue; Lonstein et al., in press; Numan and Insel, 2003; Pryce et al., 1993). Under natural conditions in the wild it takes dire circumstances for an experienced anthropoid mother to abandon her infant and they are even less likely to do so than parous mothers among many nonprimate mammalian species. Rare exceptions include a mother gorilla with twins who became ill, or a langur mother who found herself subject to chronic stalking by an infanticidal male (reviewed in Hrdy, 1999). Ape mothers in particular stand out for single-minded, highly protective possessiveness, remaining in continuous skin-to-skin contact with their baby for months after birth. It is against this primate background that the extremely variable responsiveness of human mothers seems unusual. For comparable variability we must turn to other primates with shared care and provisioning.

From shared care to full-fledged cooperative breeding

Since langurs are leaf-eaters, there would be little advantage to allomaternal provisioning and they do not share food. Among primates generally, shared care is fairly common, but provisioning the offspring of other primates either via allomaternal suckling or actual delivery of food to nearly weaned immatures is very unusual. Animal prey in particular is highly prized among those apes that consume it, and it is difficult to explain how voluntary delivery and offering of prey to others ever became established in the hominin line (Hrdy, in press-b). Nevertheless, such provisioning must have been essential to permit the evolution of the larger brains and longer childhoods in the line of apes leading to the genus Homo.

Today, the best documented cases of provisioning among still extant primates are found among phylogenetically very distant New World monkeys, monogamous species in the genus Aotus (Fernandez-Duque et al., 2009) and the many species in the subfamily Callitrichidae where the majority of calories consumed by just-weaned young are provided by fathers and other allomothers (Burkart and Finkenwirth, 2015; Rapaport, 2006) as is also the case among human hunter-gatherers. Once underway, with alloparental provisioning as well as obligate care embedded in the life history of a particular species, cooperative breeding plays out in various ways. In the case of cooperative breeders characterized by rigid female dominance hierarchies as marmosets and tamarins are, millions of years of cooperative breeding have led to the evolution of some highly derived and quite surprising, physiological adaptations. Dominant female have been selected so as to eliminate infants born to subordinates thereby increasing the number of helpers available for their own offspring.

As predicted by Rosenblatt’s work, there tends to be a correlation between urinary estradiol levels during pregnancy and post-partum infant-directed behaviors (such as licking and carrying) among callitrichids (e.g. red-bellied tamarins, Saguinus laibatus, Pryce et al., 1993). Nevertheless, there are circumstances when pregnant callitrichids respond quite differently. Instead of extremely pregnant females finding babies especially attractive and seeking to nurture them, some marmoset and tamarin females in the late stages of pregnancy actually find infants aversive. Even experienced multiparous marmosets who previously successfully reared young exhibit longer latencies to approach during late pregnancy (Saltzman and Abbott, 2005).

Some dominant females in the later stages of pregnancy even attack and bite to death infants born to subordinates. This risk probably explains why subordinate females avoid reproduction in the vicinity of potentially infanticidial alphas—sometimes their own mother (Digby, 2001; Digby and Saltzman, 2009; Saltzman and Abbott, 2005, 2015; Rapaport, 2006).
see also Clutton-Brock, in press for similar cases among other cooperatively breeding mammals). In spite of such risks, subordinate female common marmoset mothers are known to discriminate based on infantile attributes and will continue to carry the corpse of a dead baby for days as this young langur monkey mother is doing (S.B. Hrdy/AnthroPhoto).

Across vertebrates, alloparental care combined with provisioning has most often evolved among highly social species already characterized by altricial, fairly slow maturing, young under ecological conditions which make it especially challenging to keep recently fledged or weaned offspring provided with palatable foods. Such conditions include extreme fluctuations in rainfall or difficult-to-extract or process food requiring adult provisioning (Hrdy, 2009; Jetz and Rubenstein, 2011). As it happens, such conditions pertained in areas of early Pleistocene Africa 1.8 million or so years ago, areas where early hominin remains are found today (Magill et al., 2013; O’Connell et al., 2002; Potts, 1996).

Although relatively recent by the standards of cooperative breeding’s far longer evolutionary history among marmosets and tamarins, two to three million years is sufficient for Darwinian selection to have begun to shape responses of all involved, mothers, fathers, alloparents and infants. Elsewhere I have explored cooperative breeding’s implications for the unusually variable expression of paternal commitment within and between human societies (Hrdy, 2008, 2009). I have also examined how the need to appeal to, and elicit succor from, allomother’s as well as mothers would have affected infant development, generating novel ape phenotypes which over evolutionary time would have been subjected to novel selection pressures favoring those immature apes best at monitoring the thoughts and feelings of others and ingratiating themselves with prospective caretakers, resulting in the emergence as early as several million years ago of more “emotionally modern” apes better able to read, and more interested in, the intentions of others (Hrdy, 2009; in press–a). Here I focus on the extreme variability of responsiveness in pregnant females and new mothers, both those with and without prior maternal experiences.

**Human mothers as outliers among hominoid primates**

Nonhuman ape mothers are all characterized by exclusive care of their new infants. They stand out for single-minded dedication to their infants. Poachers are well aware that to capture a baby gorilla or orangutan to sell in local markets, they first must shoot the highly protective mother. Otherwise she is not going to let go. Theirs is a reflexive protectiveness. Similarly, Old World monkey mothers carry and suckle infants no matter what, even those born with palsy or missing limbs (Berkson, 1974; Turner et al., 2005). Both Old World monkey and ape mothers continue to carry for days the desiccating corpses of infants that die (Fig. 4). Exceptions to such reflexive protectiveness among wild primate mothers almost all fall among species with obligate allomaternal care. For example, among cooperatively breeding callitrichids, even experienced mothers who have already successfully reared infants may not only ignore infants who cease to move, but sometimes abandon still vocalizing infants.

Infanticide is widespread among primates and a major source of infant mortality. However, perpetrators virtually always attack the offspring of others, not their own infants (Hausfater and Hrdy, 1984; Parmigiani and vom Saal, 1994; van Schaik and Janson, 2001). Yes, inexperienced first-time monkey and ape mothers may prove incompetent or negligent, and may even abandon infants altogether, especially in captivity or if a primipara lacked opportunities for prior caretaking experiences. Cases of mothers dragging or neglecting infants such as those reported among free-ranging Japanese macaques (e.g., Hiraiwa, 1981; Schino and Troisi, 2005) typically involve first-time young mothers or females who had lost their own mother and so presumably had less exposure to younger sibs. In these respects, human primates are outliers. As in other primates, infanticide is widely documented across both traditional and modern human societies. But unlike other primates, the likeliest perpetrator is the mother herself, usually in the hours or days right after birth. With the exception of cases summarized below, all involving species with obligate allomaternal care, I know of no other instances from nature where an experienced nonhuman primate mother inflicted injury on her own infant.

As in all mammals, new human mothers are acutely sensitive to the sight, smells and vocalizations of newborns. Yet unlike their self-sacrificingly dedicated Great Ape relations, there are a range of circumstances where postpartum mothers, including even experienced mothers, seem peculiarly insensitive to infantile appeal (kindchenchema) or infantile signals of distress, voluntarily abandoning or even killing their own infants (Drury et al., 2016-in this issue; Overpeck et al., 1998; Resnick, 1970).

![Fig. 4. Old World monkey and non-human ape mothers are not known to discriminate based on infantile attributes and will continue to carry the corpse of a dead baby for days as this young langur monkey mother is doing (S.B. Hrdy/AnthroPhoto).](image-url)
Maternal rejection of newborn humans is understandably a sensitive topic. Even anthropologists with relevant data can be reluctant to publish them. Nevertheless, numerous historical, sociological, institutional as well as ethnographic sources, testify to the widespread occurrence of postpartum abandonments or infanticide of newborns considered premature or otherwise poorly timed (e.g., born too close to an older sibling; born female when males are preferred, or vice versa, or born defective in various real or culturally arbitrary ways rendering them unlikely to prosper. Space here does not permit review of what is a vast, if largely non-quantitative, often anecdotal or otherwise problematic literature (see Hrdy, 1999: chapters 12–14; regarding scholarly reluctance to publish, see pp. 289–297).

Curiously insensitive, and in the human case, even discriminating, primate mothers

Whether in industrialized societies where infanticide is against the law or in traditional societies where abandonment or infanticide are regarded as lamentable but sometimes necessary, this under-reported and way under-studied phenomena cannot always, or even typically, be dismissed as the result of “deranged” or pathological behavior. Rather, the scale and patterning of maternal abandonment and infanticide among humans (e.g., Badinter, 1981; Bonnet, 1993; Bugos and McCarthy, 1984; Schiefenhövel, 1989; Sheper-Hughes, 1992) raises the possibility of some dampening of maternal responses in postpartum mothers, a dampening that in some cases permits new mothers to discriminate against offspring born at the “wrong” time or possessing the “wrong” attributes, in ways that have not been observed in other anthropoid primates. Such limited ethological evidence as is available also suggests that mothers may sometimes find it aversive rather than rewarding to hear cries from a very low birthweight, premature or sickly-looking infant or to look at a baby with facial disfigurement (Barden et al., 1989; Frodi et al., 1978; Mann, 1992). Such effects may co-occur or be exacerbated in mothers experiencing severe postpartum depression, stress, or anxiety (Agrati and Lonstein, 2016-in this issue; Brummelte and Galea, 2015-in this issue; Lonstein et al., in press; Haim et al., 2016-in this issue).

In respect to relinquishing care or, under certain circumstances, ceasing altogether to care for babies, human mothers more nearly resemble non-primate litter-bearing mammals than other higher primates. Faced with severe scarcity or when disturbed, mammalian mothers are known to abandon dens or nests, or as in the case of lions, whole litters. Mothers with multiple young may also discriminate between infants based on specific attributes such as a kangaroo mother closely pursued by a predator who jettisons an older joey while retaining a tinier joey latched to her teat or a mother with a large litter who shunts aside a runt (e.g., Hoogland, 1994, for prairie dogs; the author’s personal observation for domestic dogs). Litter-bearing rodents as well may differentially care for young in ways that differentially affects their development (Jenkins et al., 2016-in this issue; Ragan et al., 2016-in this issue).

Over the course of hominin evolution, more closely stacked dependents emerged in concert with allomaternal provisioning which permitted shorter intervals between births of slow maturing young. These “as-if” litters would have produced circumstances where hominin mothers benefit from being able to calibrate investment in line with local conditions but also in line with attributes relevant to one infant’s viability relative to that of a current older, or as yet unborn, sibling. I hypothesize that more discriminative maternal responsiveness at emotional levels not only co-evolved in humans with larger brains, increased foresight and capacities for conscious decision-making and various cultural criteria—a generally accepted premise—but also co-evolved with a dampening of reflexive maternal responsiveness postpartum that facilitated the adjustment of a mother’s level of commitment in line with how much allomaternal support was available.

Apart from humans, the main (and so far only?) primate instances of maternal infanticide known to involve experienced mothers under natural conditions occurred in species with obligate allomaternal care. Every report known to me is summarized below. All occurred either among monogamous species with obligate paternal care or else among monogamous or polyandrous cooperative breeders with alloparental as well as parental care and provisioning. Perhaps because Callitrichidae have relied on allomaternal care and provisioning many millions of years longer than hominins have, the “dampening” processes involved are even more pronounced.

Comparative evidence from long-time cooperative breeders

As Bales and Saltzman (2016-in this issue) and Drury et al. (2016-in this issue) stress, it is important to select ethologically appropriate models. But in the case of social neuroscientists interested in the underpinnings of maternal responses under the range of conditions which characterized human mothers during the course of evolution, this presents special challenges. Neither the often-studied rhesus macaque nor any of our phylogenetically closest Great Ape relations who possess human-like neural structures and nearly identical reproductive physiologies, raise infants the way our hominin ancestors did. But if we turn to other primates with cooperative breeding, they are not only phylogenetically very distant from humans, they have also been cooperative breeders millions of years longer under conditions of within-group breeding competition far more extreme than those among band-level hunter–gatherers. Humans last shared common ancestors with cooperatively breeding New World monkeys in the subfamily Callitrichidae more than 35 million years ago. During much of that time, fast-breeding marmoset and tamarin mothers were producing twins or triplets weighing up to one fifth of their body weight as often as twice a year, in the process becoming neurologically as well as physiologically adapted to allomaternal assistance. I hypothesize that their obligate reliance on allomaternal support was implicated in the evolution in these species of mechanisms for somehow bypassing ordinary neurophysiological sequelae to the hormonal changes accompanying primate gestation.

When late-stage pregnant females encounter infants, instead of responding positively, they attack them. Of seven wild callitrichids observed birthing to death another female’s infant, five were pregnant (Cult et al., 2011: Table 1). These pregnant females ignored visual cues or distress vocalizations that in other contexts signal “cuteness” or elicit care, sometimes targeting the vocalizing face. Even stranger, in primates with obligate allomaternal care, new mothers may sometimes directly attack their own infants. Under pressure to reduce metabolic costs from carrying and nursing babies, tamarin and marmoset mothers in the genera Callithrix and Saguinus, as well as mothers among monogamous, biparental care species in the genera Callicebus and Aotus, pass babies off to others (usually males) after they suckle them. But if babies continue to cling, they may attempt to forcibly scrape babies off, or bite their hands or feet. In extreme cases, mothers may bite off hands in their effort to force clinging babies to let go (Cooper, 1964, cited in Herschkowitz, 1977:788; Hoffman et al., 1995:402; Huck and Fernandez-Duque, 2013:378; Ross et al., 2007). Unless fathers pick them up, complaining neonates may be left on the ground where they fell (e.g., Epelle, 1970:66). Interpreting surprisingly high frequencies of rejected infants among calitrichids is problematic. Because these tiny, arboreal, monkeys are difficult to observe in the forests where they live, most reports of abandonments derive from infants or their corpses, found on the floor of breeding colonies (Bardi et al., 2001; Epelle, 1970:66; Johnson et al., 1991; Rothe, 1975:316–317) and even species of primates not known to reject infants in the wild are known to do so in captivity. But even taking this consideration into account, rates of infant rejection among calitrichids seem unusually high. Furthermore, only among cooperatively
breeding primates have mothers in natural habitats ever been observed to deliberately wound their own infants. In tens of thousands of hours that chimpanzees, baboons, and other primates have been observed in nature, mothers are almost unfailingly protective. Yet in spite of far fewer observation hours, monogamous or cooperatively breeding species with obligate reliance on allomaternal care are the only nonhuman primates where mothers living in natural settings have been observed to deliberately mutilate, and in three cases, almost certainly kill, their own infants. These mothers appear sufficiently inured to infantile signals of distress as to not only push their baby away, but in their effort to unburden themselves, bite it to death.

By now, infanticide (mostly by males but also by females) is reported for more than 50 species of primates (Palombit, 2012). But in these pro-simian, monkey and ape cases individuals attack the offspring of others. The only three exceptions of maternal infanticide from nature involve species with obligate allomaternal care. It’s worth a closer look.

To date there are ten reports of infanticide among wild-living nonhuman primates with either obligate paternal or alloparental care: nine involve cooperatively breeding callithricids (Bezerra et al., 2007; Culot et al., 2011: Table 1; Digby and Saltzman, 2009; Tirado-Herrera et al., 2001) and one involves monogamous biparental-care Callithrix migrifrons (Cásar et al., 2008). In seven of these ten cases, a breeding female killed another female’s infant. But in the Callithrix and two tamarin cases, living babies were almost certainly bitten to death by their own mothers.

The existence of many firsthand observations of maternal rejections raises the possibility that some of the many dozens of mutilated, often headless or partially cannibalized, infants found on the floor of breeding colonies were also bitten by mothers (Bardi et al., 2001). Quite possibly, a nonresponsive infant gets reclassified as “prey,” inviting consumption. But the contrast with other primate mothers who remain protective of comatose or dead babies for days leads me to suspect some neuro-physiological dampening of bonding mechanisms in postpartum callithricids. 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).

Neural overrides to gestational and postpartum priming?

Clearly, the acute responsiveness to infantile signals of need and distress that ordinarily emerges during mammalian pregnancy and which in some species emerges following previous exposure to infants (Akbari et al., submitted for publication; Drury et al., 2016-in this issue; Lonstein et al., in press; Numan and Insel, 2003) does not always operate. Such responses seem particularly variable among primates with obligate reliance on allomaternal care and provisioning. In field primatology’s first report of maternal infanticide (Tirado-Herrera et al., 2001), a saddle-backed tamarin (Saguinus fuscicolis) gave birth in a group containing several males and a second (pregnant) female. On its first day of life, the mother dropped her infant several times, only to have it retrieved by one of the males, until 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.” The corpse fell to the ground, revealing that the baby’s brain had been entirely consumed. In the second case, a mother mustached tamarin (Saguinus mystax), who had successfully reared three sets of twins at times when four or five males were on hand to help, gave birth when there were only two or three males as well as a second breeding female in the group. This mother as well was observed biting and eating the head of her baby. Her son was vocalizing shortly before, but observers could not be certain he was still alive when the mother began biting (Culot et al., 2011:182). In a third case, a black-fronted titi mother (C. nigrifrons) gave birth to a healthy male carried mostly by her mate until the third day, when, on its being returned to his mother, she began to bite the face of her vocalizing son, eventually dropping the corpse to the ground (Cásar et al., 2008).

Apart from humans, only among these New World monkeys with extensive paternal and/or alloparental involvement do we find primate mothers under natural conditions sufficiently inured to infantile signals of distress as to deliberately injure one, even mutilate a still vocalizing face or preferentially consume the brains—a risky predilection in a mother who, like most mammals, will consume the placenta right after giving birth. Under most conditions such a mother has good reasons to distinguish her neonate from say, the afterbirth.

Obviously these mothers are not conceiving and gestating babies in order to discard or recycle them. Abandonment and cannibalism are last resorts. Faced with insufficient assistance and hence a low likelihood of successfully rearing her infant(s), a cooperatively breeding mother’s best option would be to terminate investment, the sooner the better (cf. the Bruce Effect where spontaneous abortions or reabsorption of fetuses occurs in pregnant mice, langurs or gelada baboons when in the presence of a potentially infantilistic conspecific). Systematic analyses of circumstances surrounding a large sample of captive callithrid infanticides rejects are consistent with this interpretation. Massimo Bardi et al. (2001) used stepwise multiple regression to evaluate factors affecting survival to one year for 1093 Saguinus oedipus born between 1984 and 1993 at the New England Regional Primate Center. Fifty percent (546) were rejected and an additional 12% (134) were killed before they could be removed and hand-reared. In 89% of these cases, termination of investment ended within three days of birth. It is worth noting that the postpartum timing of these rejections echoes the timing of infanticides among both traditional (Hrdy, 1999) and modern human societies. Of 3312 infanticides recorded by the U.S. Centers for Disease Control between 1989 and 1998, the incidence peaked in the first week, with 82.6% of cases occurring on the first day. Thus, mothers were almost certainly present and implicated (Paulozzi, 2002; see also Bonnet, 1993; Overpeck et al., 1998).

Among callithricids, mothers are the major caretakers immediately after birth making it likely that mothers are primarily responsible for these rejections (Bardi et al., 2001:167). Bardi’s further analysis suggests that these mothers were responding to the availability of caretakers or to pre- or postpartum signals of paternal willingness to help. In Bardi’s breeding colony sample the best predictor of maternal rejection was shortage of allomaternal assistance. When older siblings were available 54.9% of infants were accepted, compared with 17.2% when absent. Mothers in poor health and those bearing triplets were more likely to abuse infants. Rates of rejection were also higher for inexperienced (64.1%) compared with experienced mothers (39.5%) and for younger parents of either sex than for older ones. Nevertheless, infanticide in the wild cases cannot be attributed to inexperienced individuals since mothers who abused or rejected offspring were known to have successfully reared young previously. Furthermore it is noteworthy that in Bardi’s sample, the tamarin mothers without prior caretaking experience were less, not more, 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 twice that (15.2%) suggesting that mutilations were due to something other than inexperience or incompetence.

Are callithricid mothers polling available help?

Once established, damenking of maternal responsiveness provides novel evolutionary opportunities. In the case of callithricids, it may have provided opportunities for mothers to elict information about availability of help. Adult male callithrichids, especially progenitors,1

1 The usual uncertainty surrounding primate paternity is especially complicated among callithricids. Not only can twins and triplets be sired by more than one of the several males a polyandrous mother mates with, but the possibility of cells migrating between fetuses in utero can result in chimeric individuals (Ross et al., 2007).
respond to infant vocalizations as readily as mothers do (Sánchez et al., 2014), and sometimes more readily. When mothers push their babies (typically twins) off and they vocalize, it is males who usually retrieve and carry them, eventually returning them to their mother to nurse. Thus rejecting mothers can poll fathers, gaining information about their readiness to retrieve and carry infants. Some information about probable male assistance may already have surfaced prior to birth. Tamarin fathers gain up to 8% of their body weight during a mate’s pregnancy in anticipation of the extra effort they will expend carrying babies (Ziegler et al., 2004). No doubt building up reserves in advance makes energetic sense, but Toni Ziegler’s findings suggest that fathers may also be secondarily signaling to mothers their willingness to stay and to help rear young.

The point is, some maternal rejections appear “strategic” rather than terminal. Detailed observations of parental care among wild tamarins (Leontopithecus rosalia) indicate that mothers adjust investment in line with how much others are providing (Bales et al., 2002). This may explain the curious observation that marmoset males, but not mothers, find chimeric infants especially attractive (Ross et al., 2007, for Callithrix kuhlii). Perhaps mothers can afford to “relax” if several males (including progenitors, partial progenitors, or former mates who are possibly progenitors) are going to pick up the slack. In any event, if the mother repeats her rejections and no other allomother intervenes, the father too may terminate investment.

Gauging her mate’s probable responsiveness is valuable feedback for a mother to have sooner rather than later. Males with experience or in good condition are especially responsive as reflected both by behavior and in higher prolactin levels (Storey and Ziegler, 2015-in this issue). Elsewhere, I have speculated that neuroendocrinological changes during maternally imposed exposure of males to infants, along with prolonged intimate contact with infants, might also facilitate the emergence of male provisioning in callitrichids and may perhaps have done so in prehuman (hominin) apes as well (Hrdy, in press-b) (Fig. 5).

A mother is not a mother is not a mother, and certainly not a marmoset

Callitrichids, like early humans, make their living by both hunting for (small) prey and gathering plant foods. In contrast to other Great Apes, but again, like callitrichids, humans are highly adaptable colonizing primates whose potential for rapid reproduction when conditions are good allows them to bounce back after recurrent local population crashes. Yet these tiny-brained, arboreal, squirrel-like monkeys not only occupy different habitats but utterly different sensory worlds than any ape does. Phylogenetically distant callitrichids also have very different reproductive physiologies characterized by postpartum estrus, multiple births, a simplex uterus, partible paternity and chimeric progeny. Nor does anything in the ethological record for band-level human hunter-gatherers indicate callitrichid-like skew in female reproductive success (e.g., Tardif et al., 2013) or suggest that pregnant hunter-gatherers are motivated to harm infants born to group-mates.

So far as humans go, the sort of competition between mothers that would lead to one mother eliminating the offspring of another has only been reported for the more stratified, propertied, human societies such as emerged in the past 20,000 years. Female reproductive competition can be particularly pronounced in post-Neolithic societies where inheritance of land or other resources are at issue. Such cases include exploitation of reproductively disenfranchised slaves or subordinates, or wet-nurses coerced into caring for and even suckling the young of more dominant group members at the expense of their own infants’ survival or reproductive opportunities (reviewed in Hrdy, 1999). However it is unclear how relevant to human neurophysiology such relatively recent customs might be.

Clearly, humans are physiologically and cognitively very, very different from callitrichids, able to consciously assess current dilemmas and to make predictions about the future Yet what human mothers share with these otherwise phylogenetically distant primate relations is an evolutionary legacy of relying on extensive allomaternal care and provisioning in order to rear young, and perhaps because of it (?) a situation-dependent dampening of maternal responsiveness in the postpartum period. It is this respect that humans and callitrichids seem convergent.

Evolved predispositions versus conscious decisions? Or both?

Chimpanzees and other apes are reflexively possessive of their newborns, remaining in protective, skin-to-skin contact with them for months after birth until infants themselves begin to take the initiative to move about. Women’s postpartum responses are far more flexible, more contingent on external cues and varied than in other apes. Almost everywhere new human mothers tolerate the proximity of familiar (and one assumes, trusted) conspecifics and voluntarily allow them to hold their newborns, something no other ape will do. Odder still, under a

Fig. 5. A golden lion tamarin (Leontopithecus rosalia) male passes twin infants back to their mother so they can nurse. Previous mates of the mother, as well as her older offspring, help to care for infants and also capture prey to feed them around the time of weaning. The more male helpers infants have, the better are their survival prospects (drawing by S. Landry, a gift to the author).
range of conditions many mothers through history and prehistory have drastically reduced levels of care for their own offspring (reviewed in Hrdy, 2009: Chapter 3), a level of apparent disinterest sometimes dismissed as pathological or as evidence disproving the existence of any biological basis for maternal “instincts” (Badinter, 1981; Sheper-Hughes, 1992). It was the last quarter of the 20th century before it was recognized that a mother’s lifetime reproductive success can take priority over the well-being of particular offspring so that some of that maternal retrenchment can be considered as adaptive (Hausfater and Hrdy, 1984; Parmigiani and Vom Saal, 1994).

As mammalian mothers go, women exhibit a dearth of “fixed action patterns” post-partum. Although visual and tactile inspections of their newborns are routine, other behaviors are less predictable. Rarely do new mothers lick their babies and (New Agers aside) women never consume placentas as do all but a handful (camelids, many marine mammals) of other mammals. There exists far more intra-specific variation in the breeding systems of nonhuman primates than previously assumed, yet even this variation pales by comparison with the extraordinarily variable and flexible parenting behaviors observed within and between human societies. Furthermore, humans are virtually the only apes where experienced mothers are known to voluntarily abandon or harm their own offspring under natural conditions.

Without doubt, the large human neocortex and extensive capacities for culture play important roles. Why lick your baby when you can wipe it clean, bathe it in water or with oil? As discussed, sapient capacities come into play when mothers discriminate between infants based on specific physical attributes or cultural ideals. Given that Homo sapiens parents can consciously calculate future prospects for a given infant, ascribe more or less value to that infant, and respond accordingly (Daly and Wilson, 1980, 1984; Scrimshaw, 1984), it is understandable that some social scientists insist that we first rule out the “consequences of ordinary practical reasoning” (Driscoll, 2005) or cultural constructs (Badinter, 1981; Sheper-Hughes, 1992), as well as social pathology (reviewed in Rees, 2009), before invoking neurobiological adaptations. But as committed as most primate mothers – especially those with prior experience – are, human mothers are not the only primates whose variable responsiveness in the first hours or days after birth includes rejection of infants and in extreme cases, even infanticide. Parallels between humans and other cooperative breeders, including tamarins or marmosets with a mere ten grams of gray matter and no paternal species, paternal behaviors as well. Yet by themselves, hormones rarely determine parental responsiveness (Bales and Saltzman, 2016-in this issue; González-Mariscal et al., 2016-in this issue; Lonstein et al., in press; Lynn, 2016-in this issue; Numan and Insel, 2016-in this issue; Storey and Ziegler, 2015-in this issue; Olazábal & Alsina-Llanes, 2016-in this issue). Parity, past experience, sensitization and learning, along with local conditions, epigenetic and inter-generational effects sometimes going back several generations, sensitize their impacts (reviewed in Barrett and Fleming, 2011; also see Beery et al., 2016-in this issue; Bridges, 2015-in this issue; Lonstein et al., in press; Lynn, 2016-in this issue; Lomanowska and Melo, 2016-in this issue; Mileva-Seitz et al., 2016-in this issue; Stoltenberg and Champagne, 2016-in this issue). When we consider large-brained H. sapiens with all our “later-evolving associative, and mentalizing brain networks,” as described by Ruth Feldman (2016-in this issue), Kim et al. (2016-in this issue), and Pawluski et al. (2016-in this issue), the underlying potentials so essential to our extraordinarily flexible family systems, capacities for coordinated endeavors and culture-generated adaptability to a range of habitats, things become more complicated still. Yet I am convinced that even the most rational calculations by parents are colored and complicated by humankind’s deep history of cooperative breeding.

**Counteracting the overrides even before we understand them**

Patterns revealed by comparisons across species are useful for generating hypotheses and predictions. But the comparative method is rarely sufficient to identify, much less explain, underlying mechanisms. It is my hope that the innovative experimental approaches reviewed in this special issue that have yielded so many insights into the nature of maternal responses that enhance the survival of immature infants will also help us learn how maternal responses come to be so much more conditional among cooperative breeders. Until then though, do evolutionary and comparative perspectives have anything useful to offer?

Although only sporadically practiced among post-industrial people, breast-feeding and co-sleeping are primate universals. Around the world, women in traditional societies still breast-feed and sleep with their babies. As amply shown by articles in this special issue, such intimate contact with infants has neurophysiological effects correlated with maternal responsiveness toward infants (e.g., Meliva-Seitz et al., 2016-in this issue; Jonas and Woodside, 2016-in this issue and other articles in this issue) and is inversely correlated with neglect or abuse (e.g., Strathearn et al., 2009). Anecdotal evidence strongly suggests that intimate contact with nursing infants postpartum can override a mother’s reason-based assessment of future prospects, including her premeditated decision to abandon her infant (Hrdy, 1999:315ff, 454ff). Even absent parturition or breast-feeding, intimate contact with infants has transformative effects on the neurophysiology of both male and female allomothers (Glocker et al., 2009; Kringlebach et al., 2008; Lonstein et al., in press; Stoltenberg and Champagne, 2016-in this issue, and especially Abraham et al., 2014; also summarized by Storey and Ziegler, 2015-in this issue).

But holding her baby close and the establishment of breastfeeding are not foregone post-partum events. For example, human mothers may experience delays, or even dampening in postpartum responsiveness. As in other cooperatively breeding primates, their responses appear shaped by both social context and available support as well as by particular attributes of their infant, something not yet reported for any other primate. In no other primate are mothers known to discriminate on the basis of specific infant attributes (robustness, sex, birth weight, culturally arbitrary traits such as too much or too little hair or other perceived defects). No doubt, culture and rational assessments concerning a child’s future prospects are involved. But another possibility is that the dampening of maternal responsiveness to infant cues postpartum seen in cooperative breeders provided novel opportunities for selection to operate in this realm, but as to how and through which mechanisms, I am not qualified to even guess. I can however provide neuroscientists with several (hopefully testable) predictions. Situation-dependent neural overrides to maternal responsiveness should be situated in more ancient portions of the brain than discriminative solicitude based on specific infant attributes, and these discriminations will not be entirely conscious.

The neurophysiological underpinnings for flexible parental commitment are beginning to be explored in humans but remain completely unstudied in other apes. More research is needed but finding ethical and humane ways of doing so will be a challenge. Based on recent discoveries about the neurophysiological bases of parental responsiveness (e.g., Abraham et al., 2014; Bell et al., 2014, 2015; Cong et al., 2014; Dula et al., 2014, Kim et al., 2016-in this issue; Numan and Young, 2016-in this issue; Pereira and Ferreira, 2016-in this issue; Wu et al., 2014; Tsuneoka et al., 2015), Rosenblatt’s successors in the field of social neuroscience are well positioned to learn why post-partum responses in human mothers, even experienced ones, are so much more contingent than in most other primates. In the meantime comparative and evolutionary perspectives and hypotheses about the evolutionary functions of maternal distancing can at least help us understand why some interventions are proving more effective than others and thus worth pursuing.
In particular, the proposal that a deep hominin legacy of cooperative breeding produced new mothers peculiarly sensitive to their perceptions of available assistance can explain why social support sometimes proves a better predictor of postpartum commitment than economic circumstances (e.g., Bonnet, 1993: 509; Hrdy, 1999: 371ff). It also helps to explain why aversive emotions toward infants postpartum tend to co-occur with feelings of “social isolation” (Bonnet, 1993: 504), why the presence of “doula” during birth can matter so much (Meyer et al., 2001), why the responsiveness of an “at-risk” young mother is enhanced by her grandmother’s presence in the same house (Spieker and Bensley, 1994), or why even such trivial seeming interventions as brief home visits to pre- and post-partum mothers by a supportive social worker prove so beneficial (Eckenrode et al., 2000; Olds et al., 1997).

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