



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



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ABSTRACT

This article is part of a Special Issue “Parental Care”.

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 allomothers 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,

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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 received help 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 time 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; Trevathen 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 (Isler 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-gatherer 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 australopithecines 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 australopithecines 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). Nulliparae 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

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