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Mark Pagel

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MOTHERHOOD

Sarah Blaffer Hrdy

Evolutionary biology has come a long way as far as mothers are concerned. Nineteenth-century evolutionists like Herbert Spencer correctly observed that mammalian females ovulate, gestate, bear young, and lactate. They then concluded (incorrectly) that the diversion of so much energy into reproduction inevitably led to “an earlier arrest of evolution in women than in men” (Spencer, 1873). Females were thought of as unvarying breeding machines, designed to bear as many young as they could and to selflessly commit to nurturing each one. The absence of variation between females supposedly limited the opportunity for natural selection to operate on the female sex, which is why Charles Darwin and other early evolutionists assumed that women’s intellectual and emotional faculties were inferior to those of men.

An unfortunate byproduct of a century-long delay in correcting wrong assumptions about the female sex was that by the last quarter of the twentieth century, as evolutionary biologists began to recognize the full extent of variation among females and to take selection pressures on females into account, many social scientists, and feminists in particular, had long since closed their minds to evolutionary arguments that they viewed as hopelessly biased. Much of the antagonism characterizing relations between the natural sciences and those in the humanities at the end of the twentieth century—sometimes referred to as the “science wars”—might have been avoided if both sides had been better informed. Evolutionary theory was not the problem here so much as long-standing biases about females that colored starting assumptions. By the last quarter of the twentieth century, however, sociobiologists had begun to incorporate the full range of selection pressures on females—that is, to take female perspectives into account—and to expand evolutionary theory to include both sexes.

Evolutionary paradigms about females began to shift almost imperceptibly from the 1970s onward with the realization that even though Darwinians talk about the origin of species, Darwinian natural selection rarely acts at the level of the group or species. Mothers did not evolve to sacrifice themselves for the benefit of the species, but to translate such reproductive effort as they could muster into progeny who would themselves survive to reproduce. This new view presupposed variable responses from individual mothers, depending on their physical condition and local circumstances.

Prior to this shift, most empirical research on maternal behavior had been by comparative psychologists working with captive animals. Mothers were studied outside of the social and ecological settings in which they evolved, while research protocols relying on “check sheets” preordained what would be noted. Observers counted how often a mother rat, dog, or monkey approached, licked, or suckled her infants. Because food was provided *ad libitum* and no other animals were in the cage besides the infants, little attention was paid to the need for mothers to “make a living,” or to interact with other animals that might either help or hinder infant rearing. There was not much else for mothers to do except nurture young, and if they did do something unexpected (e.g., eat the young), their behavior was dismissed as “abnormal.”

“Maternal behavior” recorded in this narrowly prescribed way provided convenient operational categories that permitted quantification of nurturing behaviors. But the

methods used reinforced prior stereotypes that equated maternal behavior with nurturing. Initial preconceptions shaped the interpretations of primatologists and other field workers when they finally set out (beginning around 1960) to observe mothers in the wild. These early researchers took it for granted that all females become mothers and then instinctively devote themselves to rearing each offspring.

Confronted by an array of challenges and constrained by local history and ecology, different females were likely to respond very differently. There was no one way to be a mother. With sociobiology's recognition of selection at the level of individuals came the belated realization of how much variation there was among mothers, more nearly strategic planners and jugglers than breeding machines. Here was a sex wide open to natural selection.

The Ecology of Motherhood

The reproductive ecologist David Lack was among the first evolutionists to study breeding females as individuals. He recognized that both individual mothers and their circumstances would differ, and that many mothers might well be selected to breed below capacity, or to tolerate brood reduction (e.g., tolerate older, stronger chicks, and eliminate weaker ones), so as to pull at least a few offspring through, or to increase the mother's chances of surviving to breed again, perhaps under better circumstances. This logic paved the way for thinking about maternal behavior in terms of fitness trade-offs made by each female over the course of her life. New models for understanding maternal behavior assumed that mothers traded off reproduction in the present against the possibility of doing better in the future. How one female fares in terms of another in terms of lifetime reproductive success depends on how well a mother handles a series of trade-offs that she encounters over her lifetime. Consider golden hamsters, adapted to irregular rainfall and erratic food supply in arid habitats in the Middle East. In addition to building nests and licking and suckling pups—maternal behaviors in line with early stereotypes—a mother hamster may adjust her litter size by eating a few. Among mice, mothers may cull the smallest pups to enhance litter quality. Occasionally, mother mice, bears, or lions abandon whole litters, if times are tough or if the number born falls below an acceptable threshold.

For each mother, life is a series of such "decisions" about how best to allocate resources over her lifetime, although, except among humans, these decisions are not conscious. When is the best time for the body to stop growing and mature, to divert energy otherwise available for body maintenance and continued growth, to reproduce? When should she ovulate a fertile egg? When should she spontaneously abort, as some wild horses and monkeys do when confronted with dangerous social conditions? Juggling somatic versus reproductive effort represents the foremost trade-off in the life of every mother. The second trade-off is between quality and quantity—whether to produce many offspring, investing little in each one, or whether to produce only a few, investing a great deal (Figure 1).

Many resolutions to these recurring trade-offs are determined over the life of a specific individual. Others are the outcome of solutions forged cumulatively by many individuals, over evolutionary time, leading to species differences. For example, a few prosimians such as the Madagascar sifakas still produce litters that mothers stash in nests. But most primates bear single young, widely spaced, heavily invested in by a mother who carries her semicontinuously nursing infant with her.

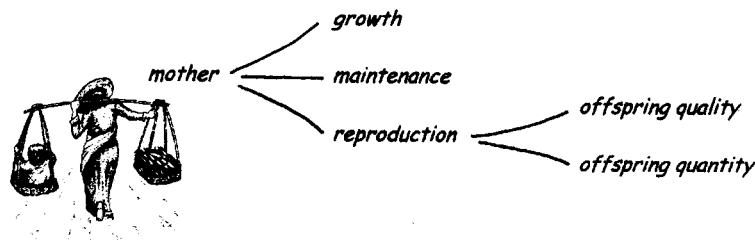


FIGURE 1. Mother's Main "Life History Tradeoffs."
Courtesy of author.

In animals where maternal fecundity or offspring survival is significantly enhanced by large maternal body size, there may be selection on mothers to delay reproduction and keep growing larger. Should a female put all her effort into growing big, then breed in one fecund burst, like the salmon who forage in the ocean, swim upstream, spawn, and die (semelparity)? Or should she bear few offspring, with births spaced at intervals over a long life (iteroparity), the way most primates do?

A survey across species reveals how unusual it is to find the innately self-sacrificing mothers envisioned by Spencer and his predecessors, men who were more nearly moralists than naturalists, projecting onto nature what was essentially wishful thinking. Self-sacrificing mothers exist, but they only evolve as species-typical universals under stringent circumstances. Most often, self-sacrificing mothers are found in highly inbred groups, when mothers are near the end of their reproductive careers, or in semelparous species that breed just once. The prize for what might be called "extreme maternal care" goes to various matrophagous (mother-eating) spiders. After laying her eggs, an Australian social spider (*Diaea ergandros*) continues to store nutrients in a new batch of eggs—odd, oversized eggs, far too large to pass through the mother's oviducts, and lacking genetic instructions. For these eggs are not for laying—they are for eating.

As the spiderlings mature and begin to mill about, the mother becomes strangely subdued. She turns mushy, not in a sentimental, but in a liquefying way. As her tissue melts, it is literally sucked up by the ravenous young, who devour both the mother and the protein-rich eggs dissolving within her.

Antisocial as this cannibalism seems, matrophagy is the key ingredient in the evolution of these spiders' uncharacteristically gregarious lifestyle. By having the bad manners to eat their mother, sated spiderlings are rendered less likely to eat one another, and thus socialize instead. Furthermore, even selfless mothers are not all equal. The more efficient a mother is at capturing prey, the bigger she grows, the more of her there is for her babies to consume, the less inclined her progeny will be to eat one another, the greater their capacity to reap the benefits of a social existence.

The Art of Iteroparity

Few mammals breed in one semelparous burst the way social spiders do. Most are iteroparous, breeding sequentially over a long life. Mother mammals produce litters of variable size, or—as in most primates—single young, spaced at intervals of variable duration over her lifetime. An iteroparous mother who overshoots the optimal clutch size for her circumstances, or who breeds too fast, may lose her entire brood to star-

vation, or end up so weak (through maternal depletion) that she does not breed the next season when conditions improve. Worse, she may succumb herself, which, if she is a mammal, means her offspring die with her.

Mothers then must engage in a perilous balancing act, allocating time and energy between making a living, resting, producing young, and rearing them. In social mammals, successful rearing of young often depends on the mother's social status, and her ability to elicit tolerance or actual assistance from other group members, activities which take time, energy, and connections. Jeanne Altmann's classic monograph *Baboon Mothers and Infants* (1980) chronicled tight maternal time budgets among mothers living on the arid Amboseli plains of Kenya. Baboon mothers spend 70 percent of daytime just staying fed. Costs of reproduction are high. For example, the death rate among adult females without infants was 0.08 per year; for mothers with infants, the rate was 0.15—nearly twice as high. These primate mothers are under heavy selection pressure to adjust reproductive effort to their circumstances.

Environmentally Sensitive Feedback Loops

All reproduction is costly, but for most mammals, lactation is the costliest phase. Typically, it is more advantageous for infants than for mothers to prolong this “free meal,” leading to mother–offspring conflict over when to wean. [See Parent–Offspring Conflict.] Theoretically, then, it would not be prudent for mothers to rely on infant demand alone to set the stopping point for lactational amenorrhea, because it will be in the infant's interest to demand more milk (and also to delay conception of sibling competitors) than it might be optimal for the mother to deliver. Evidence from primates conforms to this theoretical expectation. Intensity of suckling by infants turns out to be an important factor delaying the next conception, but not the only one. Resumption of cycling and subsequent fertile ovulations also depend on the mother's nutritional condition, workload, and energy budget.

Ongoing research among primates is helping to unravel the complex and dynamic system that governs ovarian functioning. This environmentally sensitive feedback loop, involving the hypothalamus, pituitary, and ovaries, is best, albeit still not completely, understood for humans (Ellison, 2001). Right after birth, a rapid rise in circulating levels of the hormone prolactin signals onset of milk production. Thereafter, sucking on the nipples by the baby signals the hypothalamus, lowering secretion of dopamine and triggering increased prolactin secretion. Continued sucking on the nipples causes prolactin levels to spike higher, increasing fifteen-fold above prenursing levels, before returning to base level in about three hours—unless the baby sucks again. In women whose infants nurse frequently, prolactin levels remain continually elevated, suppressing ovulation. On average, eighty minutes of suckling per day spread over a minimum of six bouts should suppress menstrual cycling for eighteen months. But this is not the whole story. It takes far more suckling to suppress ovulation in a sedentary mother (who may menstruate again several months after birth) than in one who is walking long distances carrying heavy loads. In women nutritionally depleted by recent food shortages or from breast feeding the last baby, ovarian cycling may resume but without the production of fertile eggs.

Maternal Effects

Although most models in evolutionary biology focus on genes contributed by parents to their offspring, what a mother is and does, the bodily resources she can impart, the

social status she has achieved, and the territory she defends will be critical for infant prospects, with important evolutionary consequences. These maternal effects constitute all the nongenetic influences of the mother's phenotype or local environment on the phenotypes of her offspring.

Biologically, the development of each individual begins as a maternal effect, for the maternal germ cell has already begun dividing prior to contact with sperm. Subsequently, one of these cells continues as the oocyte, whereas others become "nurse cells," manufacturing nutrients and hormones that will be transmitted through the cytoplasm and shape the continuing course of development (West Eberhard, in press).

For mammals, the mother is the most important feature of the environment during the most perilous phases of any animal's existence in utero and right after birth. The mother provides food, security, and, in the case of creatures like primates that carry their young, mobility. Her fortunes, the social and ecological niche she has constructed for herself, as well as her ability to cope with her world—its scarcities, predators, and pathogens, as well as the conspecifics in it—influence the survival chances, and sometimes future reproductive prospects, of her infants. For example, the mother's bodily resources may determine offspring condition and size at birth, which, in humans at least, have long-term implications for brain development and later health. After birth, immatures confront pathogens with immunological defenses imparted in mother's milk.

In most mammals, direct maternal investment ends at weaning. Among some, most notably humans, direct investment in offspring continues as long as the mother lives. Typically, one or both parents continue to provision children through a long period of juvenile and adolescent partial dependency. Continued parental involvement in education, negotiating marriages, and setting up homesteads extends beyond their own life spans, especially if resources are transmitted across generations, as in the transfer of customary rights or other inheritances. Some of the most stunning maternal effects are produced by information about the world communicated by the mother early in life. Such information can be transmitted chemically (e.g., molecules in mother's milk can affect subsequent food choices), through observation, or, in the human case, through linguistically transmitted memes.

For many animals, maternally acquired social statuses or territories not only contribute to the survival of the offspring but also may pass to one or more offspring after death, generation after generation, with profound implications for the relative reproductive success of different matriline, as has been demonstrated for humans and some other primates, such as cercopithecine monkeys and chimpanzees. "Old Flo," for example, the chimp mother made famous in *National Geographic* films about the primatologist Jane Goodall, had a number of sons and daughters, one of whom, Fifi, inherited her mother's secure, food-rich territory in the center of the Gombe Stream community. Flo's daughter Fifi produced seven surviving offspring, a record number for a wild chimp. Fifi's firstborn daughter in turn remained near her mother. Advantaged by her matriline's safe and productive larder and by a network of well-placed kin (brothers and uncles who were dominant males in the community), this wild chimp matured at the unusually early age of eight.

It is still common in Western society to equate "maternal instincts" with a desire to bear offspring, and many people still equate ambition with being a "bad mother." They are overlooking our primate heritage. There need never have been selection on ape females to "want" to bear children. Rather, there was selection on females to

strive for local status and for access to the necessary resources that would allow them to keep such infants as they did bear alive. For any early hominid plump and mature enough to ovulate, pregnancy followed as a consequence of intercourse, not necessarily from a conscious desire for children per se. Hence, we should not be surprised that among modern women—who for the first time in our evolutionary history can consciously choose whether or not to become pregnant—many opt to delay conception, or even to forgo childbearing altogether, in order to strive for status or greater security.

The Optimal Number of Mates

In some cases, maternal effects have more to do with males than with material resources. As Darwin pointed out, female choice of mates is of extraordinary evolutionary importance because offspring may inherit their father's advantageous traits. [See Cryptic Female Choice.] Less often considered, however, are the nongenetic consequences of a mother's mating choices. Should she mate once or many times? With one male or many?

If the female is monandrous and her mate is as well, the father's reproductive success is equivalent to the mother's. Confronted with an infant who needs his help, such a father—certain of paternity and lacking other parenting options—should be predisposed to provide it. This is the case among titi monkeys (*Callicebus molloch*). In these monogamous South American monkeys, the father carries the infant 93 percent of the time (based on observations during the first two weeks of life), returning the baby to its mother only to nurse. Interestingly, the mother is more stressed by being separated from her mate than by being separated from her baby. Because it is the father who does the carrying, motherhood in titi monkeys has more to do with giving birth, lactating, and driving away rival females, who might divert her mate's attentions from their offspring, than with infant care.

When male care is neither so costly nor so exclusive as in the titi case, even males less than certain of paternity may protect or provision offspring, or, at least, refrain from harming offspring possibly their own. Hence, in species in which infanticide by strange males is a problem, as is the case with many primates, females solicit and mate with multiple males, possible, as a tactic to confuse paternity. [See Infanticide.]

To date, the best evidence for how mothers increase survival of offspring by manipulating information about paternity, comes from birds, especially dunnocks (*Prunella modularis*), studied by ornithologist Nick Davies. Dunnock females typically mate polyandrously, males (if they can) polygynously. Alpha and beta males calibrate mouthfuls of food carried back to nestlings in proportion to how often they managed to copulate with the mother when she was last fertile. Consistent with the hypothesis that it behooves mothers to thus manipulate information about paternity in this species, DNA fingerprinting reveals that provisioning males are often but not always genetic progenitors of the infants that they feed. Among *Prunella collaris*, a close relative of dunnocks with a similar breeding system, fertile females exhibit primatelike red swellings in the cloacal region, presumably for the same reason as in baboons and chimps—to attract males and to increase a mother's chances of drawing multiple males into the web of possible paternity. Among dunnocks, langur monkeys, and humans, where the behavior of males has a critical impact on infant survival, effects of maternal mating decisions extend beyond genes to include the ways that a mother's

recent sexual history affects the behavior of males likely to be in the vicinity of her infants.

Mothers and Allomothers

In addition to fathers and possible fathers, mothers living in social groups may elicit assistance from a range of other group members. Individuals other than the parents who help rear offspring are known as alloparents, from the Greek prefix *allo* ("other than") (Wilson, 1975). However, without DNA tests, it is often impossible to identify fathers, so it is more accurate to talk about assistance by individuals other than the mother, or allomothers. One of the surprises of the postsociobiology era has been the realization of both how common and how evolutionarily important allomaternal assistance can be.

For example, in a number of primates, including vervet monkeys and most species belonging to the Colobine subfamily, mothers are less possessive of their infants than are other Old World monkeys. Mothers in these infant-sharing species permit other females in the group to hold and carry their infants, thus freeing the mother to forage more efficiently. A comparative analysis across primates by John Mitani and David Watts revealed that mothers in infant-sharing species give birth after shorter intervals. The anthropologist Barry Hewlett has done a similar analysis for humans living in hunter-gatherer societies, among whom there is great variation in how much mothers rely on other group members for help with child care and provisioning. For humans, as among other cooperatively breeding animals, the availability of such assistance alters the terms of maternal fitness trade-offs, because mothers with help reproduce faster without excessive maternal depletion or offspring mortality (see Hrdy, 1999, for review).

Allomaternal assistance, ranging from moderate to extensive, is widespread in nature, now documented for a diverse array of insects, birds, and mammals, always with similar outcomes: divisions of labor permit animals to subsist and breed in habitats previously not available to them, and cooperative breeding allows mothers to breed faster, rear larger young, or more young, or rear young that (as in humans) mature slowly and remain dependent on adults for nutritional subsidies for a very long time. The cooperatively breeding Florida scrub jay provides a classic example of how cooperative breeding allows animals to move into habitats that would not be available without a division of labor. These jays can breed in relict patches of stunted forest where other jays can not successfully breed because young, pre-reproductive helpers serve as lookouts while parents forage. This extra assistance and division of labor helps parents defend their young against relentless predation from snakes and raptors in this highly exposed habitat (Woolfenden and Fitzpatrick, 1990). A shift toward cooperative breeding among Pleistocene humans may have been critical for withstanding periodic food shortage and enabled populations of *Homo ergaster* to expand. Hawkes and colleagues (1998) stressed prolongation of the human life span long past menopause, which would have made available a particularly well-qualified class of alloparents, postreproductive group members who were both experienced and had no better reproductive option than to help provision the offspring of kin. The maternal ancestors of modern humans must have been gambling on having such help. Otherwise, how could there have been selection on the earliest human mothers to produce slow maturing young so beyond any woman's means to rear by herself?



FIGURE 2. Among Cooperatively Breeding Tamarins, Allomaternal Assistance Permits a Rapid Pace of Reproduction.

On left, a golden lion tamarin mother passes the twins to one of her former mates to carry, below right, a pre-reproductive helper catches a beetle for the nearly weaned young to eat. Drawing by Sarah Landry.

In cooperative breeders generally, mothers have been selected to behave so as to increase the availability of allomaternal assistance by remaining near kin, by mating with several males, by eliminating offspring sired by rival females, or by delaying reproduction until such assistance is available. Among cooperatively breeding Callitrichid primates (tamarins and marmosets), mothers give birth to single, twin, or triplet offspring, as often as twice a year. The combined weight of twins may weigh up to 20 percent of the mother's body weight—a staggering reproductive load. Fortunately, allomothers carry the infant much of the time, when the mother is not actually suckling them. The allomother in charge of carrying the infants is usually the male, or one of several males, with whom the mother mated. Other males and immatures—often siblings of the infant—catch insects to supplement their diet around the time of weaning. For three species, *Saguinus mystax*, *Callithrix jacchus*, and *Leontopithecus rosalia*, the golden lion tamarins (Figure 2), a correlation is observed between infant survival and the number of adult males in the group helping to care for them. Learning how powerfully allomaternal assistance affects a mother primate's reproductive success changes the questions sociobiologists ask about maternal behavior. Instead of assuming that mothers always care for babies, the question now arises: why don't mothers delegate care more often? The answer is that reliable, willing, competent alloparents are in short supply, and, for most primates, using allomothers is not a safe option.

Allomaternal and Maternal Commitment (Ultimate Causation)

In 1963, William D. Hamilton sought to explain at a theoretical level why nonreproductive workers in social insects devote themselves to caring for the offspring of the queen. He devised a simple equation to explain the altruism of these allomothers, known as Hamilton's rule:

$$c < rb$$

Altruistic caretaking should evolve whenever the cost to the provider (c), is less than the fitness benefits (b) obtained by helping another individual related by r , a term

designating the proportion of genes these two individuals share by common descent. In many of the cooperative breeders, including wild dogs, wolves, hyenas, dingos, dwarf mongooses, and marmosets, as well as in some of the wasps and other social insects, the breeding female—always socially dominant over other females in her group—may kill such infants as a subordinate bears (Digby, 2000). Thus, in species where offspring are too costly for a mother to rear by herself, the dominant female essentially alters potential payoffs to subordinate females from becoming mothers. Under these circumstances, subordinate females make the best of adverse circumstances by delaying reproduction, suppressing their own ovulation. In cooperatively breeding canids such as wolves, subordinate females do ovulate, but instead of becoming pregnant, they undergo pseudopregnancy, swelling up as if the female were pregnant and beginning to produce milk, which is then available for the dominant female's litter.

Callitrichids exhibit full-fledged cooperative breeding. Help from allomothers means that mothers can sustain a heavy reproductive load. However, mothers are thus dependent on help, and their dependency explains why—compared to other primates—maternal commitment in tamarins is unusually sensitive to social circumstances, compared to the social systems of most other primates, in which mothers care for offspring by themselves. If the tamarin mother's mate disappears, or if there are no pre-reproductive tamarins in the group to help, the cost of caretaking exceeds the potential payoff or benefit to the mother from bearing young, so that in a high proportion of such cases, the mother abandons her infants in the first seventy-two hours after birth. Human mothers, whose own highly dependent and often (for an ape) closely spaced offspring require assistance to rear, are similarly sensitive to social support.

Even though all mothers are related to their offspring by roughly the same amount, variation in the cost of caretaking and in the potential payoff means that Hamilton's rule can be insightfully employed to explain the ultimate causation of maternal commitment among mothers as well as allomothers. The proximate causation of nurturing behaviors can also be quite similar for both mothers and allomothers, although for various reasons the threshold for initially responding to infant cues is almost invariably lower in the mother than in fathers or other allomothers.

Eliciting Maternal Commitment (Proximate Causation)

When a virgin rat encounters pups, she may ignore, avoid, or eat them. Only after multiple trials and much exposure is a female conditioned or "primed" to tolerate pups. At that point, she may begin to lick them, crouch over them, even retrieve them in her mouth and consolidate them in a nest. By contrast, a pregnant rat responds within minutes. Furthermore, if a virgin female is injected with blood from a rat who has just given birth—as was done in a now famous 1968 experiment by Joseph Terkel and Jay Rosenblatt—there is a marked reduction in how much time it takes to prime a female to respond in a nurturing way.

A great deal has since been learned about the endocrinological and neural underpinnings of maternal responses. During the last third of pregnancy, a cascade of endocrinological events lowers a mother's threshold for responding to pups in a nurturing way. Prominent in this maternal cocktail are the steroid hormones estrogen and progesterone, manufactured by the placenta and essential to maintaining pregnancy. Be-

cause the placenta is delivered along with the babies, progesterone and, a bit later, estrogen, levels decline around parturition. Hence, by themselves, these hormones do not account for nurturing behavior.

Enter two hormones essential for milk production, prolactin and oxytocin. Prolactin, the mother's work order signaling production of more milk, is a very ancient and versatile molecule also linked to nurturing and protective behavior by males, both in mammals and in birds. Oxytocin however, is a quintessentially mammalian hormone. Oxytocin (from the Greek for "swift birth") evolved in mammals as a muscle contractor that, among other things, promotes the uterine contractions leading to birth as well as contractions in mammary glands causing milk ejection. Present when the mother first greets her emerging offspring right after birth, oxytocin continues to be released whenever a mother nurses. Because oxytocin promotes calm and positive social responses, the effect on the mother can be compared to candlelight and soft music for her first date with tiny strangers that suddenly materialize near her nest. Because high levels of oxytocin are also found in mother's milk, there is also the possibility that this soothing hormone helps make the mother's growing attachment to her infant mutual.

As important as hormones can be in preparing mothers to respond to their infants, they do not act in a deterministic fashion. Hormones both affect and are affected by a mother's behavior and her experience. For example, the act of caring for pups leads to reorganization of neural pathways in a mother's brain, making her more likely to respond more quickly to pups the next time. This is one reason why experienced females tend to be more responsive to pups than first-time mothers. This is especially true in primates, where learning is critical for competent caretaking.

Although hormones like prolactin are frequently considered "maternal" hormones, in fact elevated levels of this hormone can be found in both sexes and have been documented for both avian and primate allomothers engaged in carrying, protecting, or provisioning infants. Recent research on men living with pregnant women revealed that prolactin levels rise near term, as do cortisol levels. The most significant effect was the 30 percent drop in testosterone in men right after birth. The more responsive to infants the men were, the more likely it was that their testosterone levels would continue to drop (Wynne-Edwards and Reburn, 2000). No doubt about it, hormonal changes during pregnancy are more pronounced in mothers than in nearby fathers. The point, however, is that primates of both sexes are to some extent, primable, and proximity to and experience with infants matter. This helps explain why adoptive parents can become so deeply committed at a biological level to the infants that they care for, and why a fully engaged father in close contact with his infant can sometimes be even more committed than a detached mother.

However, given that the mother is invariably present at birth, and already hormonally primed to respond to sensory cues from the infant (olfactory, auditory, and visual), the mother is the likeliest candidate to become most attached to her offspring, and the infant to her. Within days of birth, the human mother learns to recognize her own infant's smell, and by this time too—if she is breast feeding—lactation is under way with all the attendant endocrinological consequences. From this point on, infants have lactating mothers on an endocrinological leash as the bond between a mother and an infant develops during the weeks and months after birth.

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