What everyone needs in the [new] millennium is access to the Internet and a grandmother.

—Anonymous (cited in Farmer 2000)

If allomaternal assistance is so beneficial for maternal fitness, why don't all mother apes solicit help? It can't be lack of interest by prospective allomothers—most primates are fascinated by babies. As we just saw, the neural underpinnings for kindenschema are in place, and apes are no exception. Rather, the main obstacle to shared care is the mother's lack of trust in her surroundings and reluctance to allow anyone else to hold her infant. Mother apes in the wild are obsessively anxious about their babies. Frankly, if I were a mother chimpanzee, I would be too.

Primatewide, mothers have to worry about strange males, and in both chimpanzees and gorillas, infanticide by males is a major source of infant mortality. But because females typically leave their natal kin to
Great Ape mothers are notoriously possessive. When Flo, one of Jane Goodall’s Gombe chimpanzees, gave birth to the infant Flint, his older sister Fifi (on the left) was not allowed to take him, although she was obviously interested and eager to do so. In this photograph, Fifi appears to be eying her brother with what looks to me like resigned yearning. (Hugo van Lawick/Jane Goodall Institute)

breed in other communities, they have to worry about unrelated and potentially infanticidal females as well. This is especially true of highly omnivorous common chimpanzees, who eat baby gazelles and colobus monkeys when they can get them. Baby chimpanzees are a no less delectable source of proteins and lipids. Furthermore, because chimpanzees’ primary diet is ripe fruit, elimination of a rival mother’s infant means greater access to a finite local resource for the killer’s own line.¹

Provided they can be dispatched with impunity, baby chimpanzees are fair game. Fortunately for mothers, rival females are rarely any bigger than they are, and few are willing to take the risks males do. The stakes don’t warrant it. Elimination of a nursing infant provides a male one of his few chances to inseminate a fertile female, but infanticidal females merely gain a meal or eliminate a tiny rival who might never grow up anyway—scarcely worth the risk of being wounded by his protective mother. Not surprisingly, the first observations of infanticide by chimpanzee females targeted babies of mothers with some disability that hampered retaliation—illness, a paralyzed wrist, extreme subordination.² Infants of strange females attempting to immigrate into the community are especially vulnerable because community females may gang up on her.
One February day in 2006 a team of primatologists studying chimpanzees in the Budongo forest of Uganda noticed an unfamiliar female moving in from another community. Young adult females usually migrate earlier in their reproductive careers, but this new arrival was already a mother, carrying a week-old infant. The pair was attacked by six resident females. Five had infants of their own, clinging tight to their mothers as they charged. Screaming and bleeding, the strange female was no match for this xenophobic consortium. As her attackers caught hold and pounded on her back, she crouched low to the ground, shielding her baby. Three community males approached, also screaming, noisily ricocheting off tree trunks, but none attacked. One old male actually looked as though he was trying to pry a resident female off, but to no avail. The alpha female wrested the baby away, only to lose it to another female who snatched it from her and delivered a lethal, neck-spanning bite.\(^3\)

Given the company chimpanzees keep, it is understandable that a mother would be reluctant to allow even a well-intentioned older sibling to hold her baby. Caring and attentive as a sister would be, she might not be sufficiently experienced or imposing to ward off a more dominant adult. If ape mothers insist on carrying babies everywhere, it is not because they instinctively seek continuous tactile contact with babies; it is because the available alternatives are not safe enough.

I vividly recall the incident that first brought home this realization. I was watching a group of bonobos at a zoo in the Netherlands. The apes were in their winter quarters—several indoor cages connected by open doors. The only other person around was my host, a young scientist who had just provided sugar cane, a favorite food. The dominant female and the rest of the group were in a connecting cage, some distance away from a mother and baby. Apparently feeling quite safe, the mother actually set her baby down so she could use both hands to eat.

Something similar was observed among common chimpanzees in a zoo in Singapore. The mother even allowed cagemates to carry her 3-month-old infant.\(^4\) But I know of only one published account, described by its author as “an unusual incident,” in which a wild ape mother voluntarily permitted another female to not only hold but actually adopt her newborn infant. This involved a 13-year-old Gombe chimpanzee named Gaia who happened to be living in the same community as her own mother when she gave birth for the first time. As females from a more dominant matriline approached and tried to inspect the
baby, the grandmother (Gremlin) took the baby from her inexperienced
daughter and “turned her back toward them” in a protective mode.
Thereafter, the grandmother retained the baby, nursing him along with
her own two-year-old son right up until Gaia’s baby died at age five
months.\(^5\)

There are more than a dozen cases of wild chimpanzee orphans be-
ing adopted by another group member (usually a close relative). What
was so unprecedented about this case was that the mother was still alive.
All other reported lapses in maternal possessiveness involve new mothers
under more protected conditions. Particularly telling is the case of the
chimpanzee Ai who allowed Tetsuro Matsuzawa, her unusually reliable
friend, access to her new baby, access such as no scientist had ever before
been voluntarily permitted. In another instance, an inexperienced mother
gorilla at the San Diego Zoo allowed her own mother to carry her baby.

Ordinarily, a wild gorilla would have left her natal group long before
she gave birth for the first time, and as in the Gombe case, it was unusual
for this 11-year-old female to be living with her mother. Having lost her
first infant, this new mother was still inexperienced and, like many first-
time primate mothers, seemed unsure what to do. She left the neonate
on the floor. As Masayuki Nakamichi, a Japanese primatologist then
working in San Diego, apprehensively watched, the grandmother came
over, picked up the baby, and held it out near her daughter’s face, as if
demonstrating what needed doing. The grandmother then handed the
baby to its mother, who eventually learned to care for it.\(^6\)

In this rare photo, the grandmother
held the newborn under the face of
her daughter for 15 seconds (shown
here) before gently pushing the
baby gorilla toward its young and
inexperienced mother, who finally
took it. (Masayuki Nakamichi from Na-
kamichi et al. 2004:76)

With the exception of the Gombe case, which was more nearly a con-
cerned grandmother taking protective custody of a baby from an inexpe-
rienced and inept daughter, all the other exceptions to exclusive mater-
nal care of newborns in Great Apes occurred in captivity without predators or potentially infanticidal conspecifics lurking nearby. Even more importantly, I suspect, in all cases the mothers were in unusual company, alone with a familiar, competent, trusted adult. Such admittedly rare incidents nevertheless reveal something important. Sufficiently confident of their physical and social surroundings, even gorilla, chimpanzee, or bonobo mothers will share care.

So why do hunter-gatherers differ from other apes in this respect, by *routinely* sharing care? Might there be neurochemical differences that encourage postpartum women to be more trusting than other apes? Different monkey species in the genus *Macaca* range from the highly aggressive and rigidly hierarchical rhesus and pigtail macaques, among whom mothers never voluntarily allow access to their infants for fear that the dominant female would kidnap the infant and not give it back, to the unusually tolerant and far less competitive Barbary and Tonkean macaques, who freely share care. These species-specific behavioral differences are correlated with neurophysiological differences. Highly possessive rhesus and pigtailed macaque mothers are reported to have reduced serotonin activity compared with the more tolerant, infant-sharing Barbary and Tonkean macaques.⁷

Since both birth and lactation coincide with higher-than-usual levels of the tolerance-and-trust-promoting neurotransmitter oxytocin, it would be particularly interesting to know if there are physiological differences between human mothers and other apes in how they respond to neuropeptides like oxytocin in the postpartum period. Might such differences affect receptors to such “affiliative” and trust-promoting hormones?⁸ Complete sequences of all ape genomes may one day make possible the kind of comparisons already being done with closely related species of social insects. At present so little is known about the comparative neurobiology of maternal behavior in apes that we can neither confirm nor rule out physiological differences postpartum. No one knows, for example, why nonhuman ape mothers often feel compelled to eat the placenta right after birth, while women (even more omnivorous than other apes) eschew this potent dose of extra hormones. Might women already be more responsive to oxytocin, less anxious about social contacts postpartum, and therefore less in need of a nurture-promoting cocktail?

Research from other mammals reveals that adults dosed with oxyto-
cin do indeed become more trusting and affiliative. Voles exposed to higher levels of oxytocin in early infancy exhibit greater propensity to bond with others and behave in more nurturing ways later in life. Furthermore, a species such as prairie voles in which parents rely on others to help care for their young has more oxytocin receptors in certain brain regions than does a closely related species that does not form pair bonds or tolerate alloparental care. Whereas prairie vole mothers readily accept help, other vole mothers attack anyone who approaches their young.

It is entirely possible that neurological differences between humans and other apes affect how these mothers behave after giving birth. But I know of no studies showing this. Furthermore, even if differences could be documented, we would still need to explain how infant sharing became common enough for natural selection to act on and favor a subset of mother apes whose underlying physiologies inclined them to be more tolerant of others postpartum. Rather than dwell on what we do not yet know about the comparative physiology of apes and humans, let's turn to what the ethological evidence tells us to expect from mothers under various circumstances.

In order for a hyperprotective Pleistocene hominin to voluntarily allow access to her infant, she would have to be in the company of others who were competent and trusted, perhaps her own mother—a full-grown and experienced caregiver familiar from birth. Until recently, most evolutionists took for granted that hominin females had no such candidate around. Now new evidence forces us to reassess this assumption and to consider whether it was not only possible but likely that early hominin mothers gave birth in the vicinity of matrilineal kin. This new way of thinking about the company kept by Pleistocene mothers completely alters the theoretical feasibility of shared care in an ape.

In this chapter, I describe new findings about both Great Ape and hunter-gatherer residence patterns, showing that these creatures were more flexible than previously assumed and that it was not impossible for ancestral apes to give birth near matrilineal kin. In the case of Pleistocene foragers, there is reason to believe that they were not only living under circumstances where alloparental care was feasible but also where food sharing was increasingly important for survival and successful childrearing. I conclude by discussing the different qualifications and variable availability of different kinds of caretakers—older siblings, cousins, co-mothers, fathers, possible fathers, and especially grandmothers,
whose impact on child survival has only recently begun to be studied but is already yielding some surprising twists.

**ON THE IMPORTANCE OF GIVING BIRTH NEAR KIN**

Primate social organization is famously variable. But across species, two generalizations hold up remarkably well. First, females who live among kin are better able to defend their interests than those who leave their natal groups to forage and breed among nonkin. Second, mothers are most prone to share infants when they feel confident that they can readily get them back unharmed.

Until recently, however, it was taken for granted that, like other apes, hominin females left their natal groups to give birth for the first time in another community, to rear young among unrelated, possibly rival, females who were unlikely to be supportive. Just suggesting that early humans lived in matrilocal settings was viewed by evolutionists as some heretical throwback to outmoded views about matriarchal stages in human evolution, bringing to mind advocates for Mother Right or Goddess Cults. There were two reasons for discounting such views. The first had to do with entrenched assumptions about the patrilocal tendencies of all hominid apes—Great Apes, australopithecines, and humans alike. The second reason was a tendency to project onto early Paleolithic ancestors patriarchal attributes from later time periods.

By “patriarchal” I mean a society with patrilocal residence patterns, patrilineal inheritance, and social institutions biased toward patrilineal interests. By this definition, few tropical gathering-and-hunting societies that have not yet adopted horticulture are patriarchal. Yet somehow, patrilocal living arrangements, and even patriarchal elaborations correlated with patrilocality, are routinely assumed to be human universals and are projected back in time onto our early Pleistocene ancestors. The supposed antiquity of patrilocality was further bolstered by comparisons with the African Great Apes, since both gorillas and chimpanzees exhibit marked patrilocal tendencies, with females migrating out to breed among nonkin. Given such entrenched assumptions, it was difficult to imagine hominins ever being sufficiently matrilocal to evolve shared care.

The preeminence of the man-the-hunter/sex-contract paradigm, with its accompanying stereotypes about nuclear families and maternal
caregiving, was another obvious obstacle. So too was the habit among mammal researchers of assuming that cooperative breeding meant that a single dominant female would monopolize the group’s reproduction. Since marmosetlike reproductive suppression has never been reported for hunter-gatherers, this criterion if applied excluded early humans. But the most persistent barrier to thinking humans might have evolved with shared care had to do with residence patterns.

Three widely accepted lines of evidence pointed to male philopatry as a hominid universal. First, behavioral evidence from the African Great Apes initially suggested that females always left their natal group to breed. Second, apart from the special sex-induced alliances in bonobos, none of the Great Apes exhibited the strong female-female social bonds typical of matriloc al species. Third, and most impressive, George Peter Murdock’s classic cross-cultural compilations seemed to document a prevalence of patrilocality in humans as well. Murdock’s analyses of ethnographic information on 862 representative cultures from around the world, expressly coded for use in the Human Relations Area Files and in his Ethnographic Atlas, indicated that the vast majority of human cultures were patrilocal. This included hunter-gatherer societies, 62 percent of which, according to Murdock’s information, were patrilocal. Therefore, it seemed both logical and parsimonious to assume that the common ancestors of apes and humans also lived in male kin groups.

Evolutionists had little incentive to challenge this received wisdom. Assumptions about the universality of patrilocal residence patterns were consistent with other widely accepted assumptions about naturally dominant males and “men in groups” who forged alliances with fathers and brothers to hunt and to protect their mates and natal territories. Furthermore, having men stay put while exchanging their daughters and sisters with other groups seemed like an adaptive way for fathers and brothers to avoid excessive inbreeding while simultaneously forging alliances with other groups—critical building blocks for early human social organization. At the time, sisters and daughters were viewed as essentially passive pawns in largely male-orchestrated transactions.

Patrilocal residence became an integral feature of hominid family life as reconstructed by physical anthropologists in the twentieth century. The resulting assumptions were subsequently incorporated wholesale into early sociobiology and evolutionary psychology. By the early 1980s a few anthropologists were pointing out that female interests and
strategies were being overlooked. By the late 1980s, human behavioral ecologists studying foraging peoples were specifically asking why postreproductive women worked so hard. And by the 1990s, Kristen Hawkes and colleagues were arguing that assistance from maternal grandmothers had played a critical role in early hominin evolution—a hypothesis initially met with considerable skepticism. The main objection was that even if their older matrilineal kin survived long enough to be helpful (which many doubted), older women would not have lived near daughters (and new mothers) who needed their help.

A Hadza boy is shown sitting with his great-grandmother and her sister (on the right). Classically “hard-working” Hadza grandmothers energetically sharpen their digging sticks in preparation for a gathering expedition. When a mother has a new baby, as this boy’s mother did, Hawkes and company found that their older children’s nutritional status was correlated with how much time older kinswomen spent foraging. (James O’Connell)

Biologists and anthropologists alike—who in the early years were mostly male—had long taken for granted that the function of women was to bear and rear a man’s children. From this perspective, women past childbearing age were deemed irrelevant and of no theoretical interest. This prejudice surfaced occasionally in ethnographic descriptions of old women as “physically quite revolting” or “nuisances.” They were depicted as objects of ridicule—“old hags” whose behavior was obviously not worth studying. Such accounts took for granted that in our evolutionary past, postmenopausal females would have been too decrepit or short-lived to be of use. Demographic and archaeological evidence suggesting otherwise was discounted.

Yet careful demographic analysis revealed that a forager who sur-
Hunter-gatherer women who survive to middle age have a reasonable chance of surviving past reproductive age. Like this !Kung grandmother, they continue to interact lovingly with children and grandchildren. (Peabody Museum/ Marshall Expedition image 2001.29.414)

...vived to age 15 had about a 60 percent chance of living to 45. And those who made it to 45 had a good chance of surviving into old age. Consider the !Kung during the period when they still lived as hunter-gatherers. The average life expectancy was only 30. But for those who survived childhood, the odds improved. Of the girls who survived to age 15, the majority (62.5 percent) survived to age 45. About 8 percent of the population lived on to 60 or older. Today, there is a remarkable convergence among demographic anthropologists, evolutionary-minded historians, and human biologists who study life history patterns across primates that the bodies of *Homo sapiens* are "designed" to last about 72 years.

Once behavioral ecologists recognized that substantial numbers of women were living long lives, efficiently gathering and processing food for decades after menopause, it became important to explain why creatures who could no longer directly contribute to the gene pool of the next generation would do so. In early versions of "the grandmother hypothesis," evolutionary biologists George Williams and William Hamil-
ton proposed that postreproductive lifespans are favored when the mother's continued survival enhances the survival of her last-born offspring. A “prudent” mother could not afford to die before her last child was independent. Struck by how especially hardworking old females were, Hawkes proposed an alternative version of the grandmother hypothesis, arguing that the reason women lived longer than other apes after they ceased to ovulate had to do with their impact on grandchildren. But even with compelling evidence for the longevity and industry of grandmothers, a seemingly insurmountable obstacle remained: Even if she were still alive, a hunter-gatherer woman’s mother was unlikely to live in the same group as her daughter—or so it was thought.27

THE ALVAREZ CORRECTIVE

Not until near the end of the twentieth century did accumulating information from long-term studies of Great Apes in the wild prompt primatologists to reassess their assumptions about residence patterns. These field observations revealed that the breeding systems of chimpanzees and gorillas were more flexible, and the apes themselves more opportunistic, than previously supposed.

If they could do so and still be safe and find enough fruit to eat, some females (like Gremlin’s daughter Gaia) did remain in their natal place. Fifi, daughter of Jane Goodall’s famous chimpanzee matriarch Old Flo, provides a case in point. Born to a locally dominant mother, Fifi remained in Flo’s relatively secure and food-rich home range, within her mother and brothers’ sphere of influence. Advantaged by this legacy, Fifi went on to produce nine offspring, the all-time record for a wild chimpanzee, and almost all of them survived. In 2004 when Fifi together with her last infant daughter disappeared and were presumed dead, a few of her older daughters and all of her sons still resided at Gombe in the same community as their mother and grandmother. Several of Flo’s daughters and some of her granddaughters continue to live in their natal place, enjoying what sociobiologists refer to as “the benefits of philopatry.”

In addition to these field studies, new DNA evidence revealed that co-resident males who jointly defended their community against neighboring males were not necessarily close kin. Thus, even though females were more likely than males to migrate, community males—even males
who were close allies—were on average no more closely related to one another than females were.\(^{29}\) Gorillas too were turning out to be more flexible, with both sexes routinely transferring between groups, often more than once.\(^{30}\) Then came a reanalysis of the ethnographic evidence for hunter-gatherers which suggested that they too were more flexible in their residence patterns than previously assumed.

Undeniably, Murdock’s early efforts to make cross-cultural comparisons more evidence-based and amenable to statistical analysis represented a tremendous advance. From the 1960s onward, he and his followers strove to lay empirical foundations for “the science of human behavior.” But the devil was in the details, in translating complex, often very incomplete published records into simple codes that accurately reflected the complex realities of people’s residence decisions. When the University of Utah anthropologist Helen Alvarez went back to the original ethnographies for a painstaking reexamination of how Murdock had determined hunter-gatherer residence patterns, her reassessment came as a shock.

Murdock had set up strict criteria for assigning each culture to a particular residence category. For example, a specified proportion of couples had to conform to particular residence rules in order to be assigned as either patrilocal, bilocal (or what Murdock called “ambilocal”), with residence established optionally near parents of either husband or wife and perhaps alternating over time, or matrilocal (“uxorilocal” in Murdock’s terminology). Yet as Alvarez reread the ethnographies, she realized that the numerical census data needed to meet Murdock’s criteria were rarely there. His exacting, explicit specifications notwithstanding, residence patterns were often assigned on the basis of hunches. When Alvarez recoded the ethnographies, this time using only the 48 hunter-gatherer societies for which empirical evidence on residence patterns was actually available, she found that only 6 of the 48 (12.5 percent) were patrilocal. The majority, 26 of 48 (54 percent), were bilocal.\(^{31}\)

Notwithstanding dogmatic pronouncements about how humans “tend to be patrilocal” because “in traditional societies sons stay near their families and daughters move away,” this underlying assumption about human nature is not supported by evidence from people actually living as hunter-gatherers.\(^{32}\) Rather than being naturally patrilocal, most hunter-gatherer societies have remarkably flexible and opportunistic res-
idence patterns as couples move between the woman’s natal group and the man’s. Furthermore, various customs increase the likelihood women will have matrilineal kin nearby when they first give birth. The same pattern we saw among the !Kung can also be found a continent away, among such bilocal foragers as the Pomo Indians of northern California: “The married couple kept moving from one family to the other . . . [but] when a child was expected they always went to live with the wife’s family.”

Even among unequivocally patrilocal peoples such as the Maidu foragers of northern California, the ethnographer specifically noted that “before residing permanently in the husband’s village, the married couple lived for a time with the wife’s family, and the new husband rendered service to them by providing food.” Murdock along with early ethnographers even had a name for it: “matri-patrilocal.”

IF DAUGHTERS HAD MOTHERS NEARBY AFTER ALL . . .

In less than a decade, the starting assumptions of evolutionary-minded anthropologists studying societies who still subsist (at least partly) by gathering and hunting have changed. Fieldworkers take seriously the proposal that humans evolved as cooperative breeders and so include information on available alloparents in their censuses and record the effects of their presence on child survival. Thus, when Brooke Scelza and Rebecca Bliege Bird recently went back to study the Mardu, a traditionally patrilineal and patrilocal people who still actively hunt and gather wild foods in the Western Desert of Australia—albeit these days with trucks and government food subsidies—the researchers specifically asked women how much they were able to rely on matrilineal kin to help rear their children. Following the lead of researchers working in Africa among Aka and Hadza, they also wanted to know how grandmothers and sisters strategized so as to be nearby when help was needed.

Even though the Mardu are, like many Australian Aborigines, traditionally patrilocal, women still manage to line up matrilineal assistance. In particular, women will urge their husbands to take a kinswoman as their second or third wife. As in earlier times, sororal polygyny (when the man marries his wife’s sister) was a preferred form of marriage. Marriage to the wife’s cousin was also common. Fifty-one percent of women were
in polygynous unions with co-wives who were close relatives. Usually, polygynous marriage with more than one wife favors the husband’s reproductive interests. Several wives bear him children, but competition between wives for limited family resources can undermine child well-being. Rivalry is less pronounced when wives are related. In line with this logic, elsewhere in Australia, among the Aborigines of Arnhem Land, child survival to age five was significantly higher for polygynous families where co-wives were close relatives. In search of social support and help, Aboriginal wives actively lobby husbands to marry their sisters, and in the interests of harmony (and perhaps child well-being) men oblige.

Among the Mardu, 68 percent of polygynously married women were in sororal unions. Mardu mothers also obtained help from their own mothers, who often relocated to be near daughters of childbearing age, especially if the daughter was monogamously married and lacked an older co-wife to advise and help her. Mothers were especially eager to join a daughter if she was married to the same man as her sister. Traditionally patrilocal or not, half of married Mardu women ages 14 to 40 have a mother in the same group. Between footloose mothers-in-law and related co-wives, average degree of relatedness between females in a Mardu band is high, with women related to each other on average as closely as cousins and having an 11 percent chance of sharing genes by common descent. This average degree of relatedness turns out to be virtually the same as that found among infant-sharing matrilocal monkeys like langurs.

Did ancestral hunter-gatherers likewise have matrilineal kin nearby? We cannot know for sure, but post-Alvarez, long-standing barriers against thinking this was possible have disappeared. Instead of some highly conserved tendency, the cross-cultural prevalence of patrilocal residence patterns looks less like an evolved human universal than a more recent adaptation to post-Pleistocene conditions, as hunters moved into northern climes where women could no longer gather wild plants year-round or as groups settled into circumscribed areas. In the Middle East, people began to herd livestock and became increasingly dependent on growing crops, storing the surplus, and accumulating property. As group sizes along with population densities increased, people adjusted their behavior to these new demographic, dietary, epidemiological, and social realities.
For settled people, shorter birth intervals and faster population growth, along with the accumulation of resources and the emergence of social stratification, brought with them the need to protect livestock and cultivable land as well as wives and children. Protecting such valuable resources became a higher priority than maintaining cordial and reciprocal exchange with neighbors. As outside invasions became more routine, men needed allies they could count on. Who better to rely on than close male kin? Increasingly, men sought to remain near fathers and brothers, obtaining wives from other groups. Only in the past 10,000 or so years has interclan warfare become an integral part of human lives, necessitating patrilocal residence patterns and in the process changing the way that children are reared.

As in all primates, mothers without support from matrilineal kin lost some of their autonomy. The reproductive interests of patriline increasingly took priority. With both patrilocal living arrangements and shorter birth intervals, the alloparents at hand were more likely to be older siblings of the current infant than maternal grandmothers or great aunts, with mixed results for children, not always good.

**GENETIC EVIDENCE ABOUT RESIDENCE IN THE RECENT PAST**

Based on genetic evidence from the past few thousand years, after the introduction of herding, horticulture, and social stratification, we know that women in many parts of the world were marrying out and moving between groups. But so far, genes cannot tell us much about residence patterns during the Paleolithic when our ancestors still lived exclusively by gathering and hunting. Let me explain.

Analyses of non-recombining portions of the Y chromosome, which is passed only from fathers to sons, as well as comparative frequencies of mitochondrial DNA, which is passed exclusively from mothers to both daughters and sons, reveal that in the past five thousand years or so women were more likely to move between populations than men were. If residence was patrilocal, we would also expect reproductive behavior to have been more tightly regulated, since men living in patrilocal clans tend to guard their mates from outsiders. Such reproductive control could explain why gene flow between patrilocal populations was largely confined to women.³⁸
Consider an admittedly extreme but very telling case involving the recent migration of people between Africa and the Middle East. While there was little male-mediated gene flow from sub-Saharan Africa into the area around Yemen about 2,500 years ago, as evidenced by Y-chromosome data, mitochondrial DNA indicates a tremendous influx of fertile women of African origin around this time. This genetic information, combined with historical accounts, means that captured or enslaved African women bore children to Middle Eastern Arab men. African men either were not taken to the new location or, if taken, left no surviving offspring. Conquests yielding access to women are starkly inscribed in genetic records from other parts of the world as well. The most famous case involves genetic evidence from a particular haplotype on the Y chromosome that points to a rapid spread of genes from one particular male lineage linked to Genghis Khan. It is consistent with the dates of his army's conquests across Asia from the Pacific to the Caspian Sea.

Such reproductively skewed patterns contrast with those from matrilocal societies, which tend to be more relaxed about who breeds with whom. Routinely, both sexes move around, although men usually move somewhat more. Over the past 10,000 years or so, matrilocal and matrilineal societies have increasingly given way to pressures from expansionist, patrilineal neighbors and invaders so that patterns of conquest are widely documented across Europe, Africa, Asia, and South America.

Genes tell us a surprising amount about patterns of conquest. They even tell us when people started to live in cities, rely on milk products, or suffer from various diseases. They can shed light on when dogs and cats began to be domesticated. Comparing the genetic histories of lice that live in body hair with lice that cling to garments even allows us to make an educated guess at when humans started wearing clothes. But genetic evidence tells us almost nothing about the residence patterns of men and women prior to a few thousand years ago, with one possible exception.

In 2000 scientists working on the Human Genome Project reported that genes involved in sperm production turn out to have evolved at an unusually fast rate compared with other genes. This curious finding suggests that there may have been selection pressure on our hominin ancestors to produce quantities of competitive sperm, a trait critical for the reproductive success of males in primates where females mate with more
than one male. Polyandrous matings would not be at all consistent with females being captured or exchanged between patrilineal clans, where reproductive access to women is closely guarded. However, occasional polyandrous matings are perfectly consistent with the more flexible breeding combinations (alternately monogamous, polyandrous, and polygynous) found in cooperative breeders.

Even if this admittedly speculative interpretation concerning sperm-related genes holds up, genetic evidence still does not tell us whether or not matrilineal kin were on hand to help mothers rear their children among African Homo erectus 1.8 million years ago. What it does do, though, is remind us how much evolution has gone on since humans last shared a common ancestor with gorillas (whose females mate with a single alpha male and where sperm competition is virtually nonexistent) and with chimpanzees and bonobos (whose females mate with many males and where sperm competition plays an important role in reproductive fitness). Each species of ape differs from every other, and none of them breed like women do today.

Chimpanzee females advertise ovulation with large red swellings around the time of ovulation, and they only copulate around midcycle. Bonobos, by contrast, exhibit swellings that last for weeks and copulate with multiple partners throughout most of their cycle. Gorillas, orangutans, and women do not advertise ovulation with conspicuous swellings at all. In other words, reproductive traits like the sexual swellings of chimpanzees can evolve quite fast, and 5–10 million years have elapsed since humans last shared a common ancestor with primarily patrilocl African Great Apes. This is the main reason I agree with Alvarez that as far as residence patterns are concerned, the best we can do is extrapolate from people who still lived as nomadic foragers when first described.

Granted, the residence patterns of modern hunter-gatherers may or may not resemble those of the first anatomically modern humans. As humans became behaviorally modern—armed with higher-caliber tools and weapons, with fire to cook food, and with language to communicate—their subsistence strategies would likely have diverged from those of the earliest Pleistocene hunter-gatherers. Their lifeways would have been altered further still by contacts with post-Neolithic herders and neighboring farmers, not to mention anthropologists. Yet ethnographic evidence about these people reveals the sorts of behaviors, customs, and
strategic maneuvering by parents and alloparents that make it feasible for highly mobile foraging peoples to survive and rear unusually costly and slow-maturing children. This is the basis for arguing that in order to successfully reproduce, foragers needed to be, and were, opportunistic and flexible in their mating and residence patterns.

If correct, Helen Alvarez’s revised interpretation of hunter-gatherer residence patterns removes the last barrier for taking seriously the hypothesis that maternal grandmothers and other matrilineal kin helped early hominin mothers rear their young. But even if a mother had older matrilineal kin nearby to help, would they want to?

ON THE ALTRUISM OF AGING FEMALES

As they age, female primates behave differently from younger females. If they are still breeding, mothers spend more time in direct contact with infants and wean them later than younger mothers do. In general, older mothers are more committed to these last installments on their lifetime reproductive success. In addition to their aging ovaries, such heavier investment may be one reason why older mothers experience longer intervals between births. For female primates at or near the end of their reproductive careers, this tendency to “give of themselves” may also lead them to audaciously defend offspring born to female kin.

As with most Old World monkeys, the maximum lifespan for a langur is around 30 years. As they approach this age, females become less active in troop affairs, avoid competition with other animals, and—even in those matrilocal species with routine infant-sharing—rarely take infants just to carry them around. In an emergency, however, these same socially marginalized old matrons become the most active in defending the group’s feeding grounds from neighboring groups. They are also the most daring in defending infants attacked by infanticidal males. Among langurs, sooty mangabeys, and savanna baboons, it is these 20- to 30-year-olds who take bigger risks to defend an endangered infant than the victim’s own mother does.

Such episodes are uncommon, but the heroics are unforgettable. Some time ago, scientists observing baboons at Moremi, Botswana, watched as a new male arrived in the troop. Shortly after, he attacked an infant sired by his predecessor. The newcomer chased the seven-month-
old female, knocked her down, and dragged her along the ground, then threw her six feet into the air. Nearby group members vocalized and rushed forward but were rebuffed by the male, who resumed his attack on the stunned infant, “biting her in the head, the groin and below the navel.” At this point, several females rushed to intervene. The defenders included both the infant’s mother and her mother, who in spite of being older, smaller, and weighing much less than the muscular young male, was the most audacious. “The grandmother attacked . . . with particular persistence,” prompting retaliation from the male, who inflicted a deep cut on the crown of the old female’s head. Despite her wound, the grandmother continued to harass the male, managing to temporarily hold him off before he renewed his attack, once again dragging the infant and biting her in the stomach and ribs. Twenty-two minutes later, the baby was dead.47

Another instance of matrilineal heroics involved the langur monkeys I studied at Mount Abu in Rajasthan. A usurping male had been stalking a young mother and her infant for several days. After each abortive attempt, the male would give up for a time, then resume. To evade him, the mother retreated onto the flimsy outer branches of a jacaranda tree when suddenly the infant (but not his mother) fell. The male, who had been riveted to the pair, immediately bounded to the ground and was the first to reach the fallen infant. He was pursued seconds later by the two oldest females in the group. After a fierce struggle, they managed to retrieve the superficially injured infant and return him to his mother. Then the oldest of the two, a solitary female I called Sol because she spent so much time on the margins of the group, continued to harass the male.

This female had ceased to menstruate and no longer bore offspring. She spent her days foraging on the outskirts of the troop and never attempted to take and hold babies. Her main contact with other females was to give way when they displaced her from a feeding position. To all appearances Sol was just biding her time until she died. Yet the striking thing was how abruptly Sol could transform herself into a super-hero. I was a young woman myself, 26 years old and still childless when I watched, astounded, as again and again this worn-toothed old female fought with a male twice her weight and armed with dagger-sharp canine teeth.

In general, monkeys are cautious about escalating aggression, warily
(Top) After retrieving the slightly wounded infant from the male, a grimacing Sol continued to punish the male, slapping at his face and pulling the hairs on his face with one hand while fending off his bites with the other. To me this postmenopausal old female was signaling: “Attack this baby one more time, and it is going to cost you.” (Bottom) Nevertheless, four days later, the male was able to grab the infant again (his body can be seen swinging from the male’s muzzle like a rag), and Sol together with another old female charged to the rescue. Although they succeeded in getting the baby back, he was horribly wounded, with cuts in his head and deep wounds in his groin. (S. B. Hrdy/AnthroPhoto)

sizing up the opposition in advance so as to avoid being wounded. I marveled at Sol’s audacity. Based on what is known about the breeding structure of langur groups, she was almost certainly either a grandmother or great-aunt to the infant she defended.48 It was her extraordinary selflessness that first inspired my interest in the evolutionary importance of old females.

Since then, systematic observations across species have shown that the presence of a mother makes her daughter more secure. Across the
very hierarchical cercopithecine Old World monkeys, among vervets, baboons, and macaques where a female’s rank is inherited from her mother, having a grandmother nearby has a significant impact on the childrearing success of younger kin. This is so even if the grandmother is still fertile and preoccupied by her own infants. Just her quotidian presence results in modest improvements to her daughter’s or her grandchild’s security. In the case of vervet monkeys, a young mother foraging with her own mother nearby will allow an older infant to wander about more freely than at other times. The independence permitted a two-month-old vervet with his or her maternal grandmother present was comparable to that of a three-month-old who did not have a grandmother’s support. 49

Modest differences add up, especially in the case of young and inexperienced mothers. When vervet matriarchs were experimentally removed, their absence was correlated with a marked decline in survival and fertility of daughters between the ages of four and six years. Vervet females were less likely to be threatened or attacked by competing females and were more effective at keeping their babies alive if their own mother was in the same group. Similarly, Japanese macaque females who have a postreproductive mother nearby give birth for the first time at earlier ages, and give birth again after a shorter interval than do females without a mother present. 50 Since females of higher rank give birth at a younger age and produce more offspring who reach adulthood, over many generations the cumulative effects of mother-supported rank are potentially enormous.

When an older female has more than one daughter in the troop, she spends more time near the youngest or least experienced daughter, the one who most benefits from her support. 51 In the langur case, aging females with little potential for directly contributing to the next generation’s gene pool (that is, females whose reproductive value was low) were much more willing to defend the offspring of their kin, with whom they shared some genes. 52 The objection might be raised that valiant old females like Sol or the Moremi baboon grandmother were just defending a group member the way any adult female would. 53 But no other adult females present, not even the infants’ own mothers, took anything like the risks their elders did.

The strongest evidence for the generalization that primate mothers breed more successfully with social support comes from Amboseli ba-
boons. In five different groups, the mothers with the highest rates of infant survival were the most socially integrated. The most successful females all had a half-dozen or so close female associates.\textsuperscript{54} Taking into account the fact that “giving impulses” go up with age, it is easy to see why young females would benefit from remaining in their natal groups to take advantage of such selfless allies.\textsuperscript{55}

Yet only a minority of mother apes have matrilineal kin nearby. Most social mammals, and the majority of monkeys, are matrilocal, but not Great Apes—even though their residence patterns are somewhat more flexible than previously assumed. However, if we accept Alvarez’s corrective, hunter-gatherer mothers (who among other things have different dietary needs than other apes) depart from the Great Ape pattern, and in this respect more nearly resemble Old World monkeys.

So what changed in the line leading to \textit{Homo sapiens} to make it more advantageous and more possible for daughters to be near their mothers when they breed? What tipped the cost/benefit balance among early hominins in favor of young females remaining near kin? Or, alternatively, what made it possible for old females to relocate to be near female relatives who needed them? And what so increased the benefits of having aging kin nearby that natural selection began to favor longer postmenopausal lifespans? For these things to happen, three conditions had to be met.

First, great-aunts and grandmothers needed sufficient freedom of movement so they could live near kin or move to be where they were needed—that is, they had to have the \textit{opportunity} to help. Second, old primate females needed some \textit{motive} for their increasing helpfulness or altruism on behalf of kin. Finally, these old matriarchs had to find some \textit{means} to help—something useful they could do to enhance the reproductive success of younger kin, something so chronically useful that it outweighed the extra pressure that females past breeding age put on local resources.

\textbf{IT’S TIME TO TALK ABOUT FOOD}

What little we know about australopithecines suggests that although they walked on two legs, these tiny-brained 80-pound apes were built a lot like chimpanzees. By 2.5 million years ago, \textit{Homo habilis} was starting
to look more human, walking upright and using tools. No one knows for sure what led some of these creatures to evolve into heavier, larger-bodied, longer-legged, longer-faced, and larger-brained *Homo erectus*. Various factors were involved, as we will see in the next chapter, but one thing seems clear. Whatever else was going on, *Homo erectus* had found new ways to find, process, and digest the food needed to support both their larger bodies and, especially, their energetically more expensive larger brains. To date, the most plausible scenario is one set forth by anthropologists James O'Connell, Kristen Hawkes, and Nicholas Blurton Jones. According to their version of the grandmother hypothesis, new opportunities to help kin generated selection pressures favoring longer lifespans among postmenopausal women. But what were the new opportunities?

O'Connell and colleagues propose that long-term trends toward a cooler, drier climate at the end of the Pliocene pressured the precursors of *Homo erectus* to seek new ways to supplement their primary diet of fruit. By around two million years ago, game was increasingly important, but its availability was unpredictable. A division of labor between men who hunted and women who gathered also became more critical. O'Connell and others suggest that when neither meat nor more nutritious plant foods like nuts were available, our ancestors fell back on large underground tubers that plants in dry areas use to stockpile carbohydrates.

These storage organs occur throughout the savanna but are protected by a deep layer of sun-baked earth and are hard to extract. Savanna-dwelling baboons access shallower rhizomes and corms, and chimpanzees in the only population ever to be studied in a savanna habitat use pieces of wood to dig out shallower tubers, suggesting that australopithecines may have done so as well. But it takes special equipment to dig out the larger, deeply buried tubers. This is why, except for a few burrowing mammals like mole rats equipped with shovel-shaped incisors, humans are the only primates who exploit this widely available but difficult-to-access food source.

Tubers are not only hard to extract, they can be fibrous and difficult to digest, hardly ideal food for children. Like nuts, they need to be pre-masticated or processed in some other way. To eat them, weaned youngsters would have to depend on older providers. Nevertheless, evidence is
increasing that starchy tubers were an important fallback food among our ancestors. A 2007 report in *Nature Genetics* revealed that people like the Hadza who rely on roots and tubers have accumulated extra copies of a gene positively correlated with salivary amylase enzymes useful for the digestion of starch. Such copies are absent in Siberian Yakut herders and others with little starch in their diets. Tellingly, three times more copies of these genes are found in foragers who rely on starchy tubers than among chimpanzees, who, except for rare savanna populations, do not eat them.  

Not only do savanna-dwelling foragers have salivary juices specifically adapted for digesting starch, but African *Homo erectus* possessed the right teeth for the job. Isotopic analysis of their flat, thickly enameled molars yields results consistent with a diet containing underground roots. Once *Homo erectus* developed the use of fire, perhaps as early as 800,000 years ago, roasting tough, fibrous tubers would have rendered them more digestible and more useful still.  

Even before cooking, the addition of tubers to the other plant foods gathered by women would have provided new incentives for food sharing between hunters and gatherers, as well as new opportunities for postreproductive women willing to enhance the survival of kin. For women who knew where to look and who were willing to walk long distances, dig into hard earth, and carry their bounty back to camp, tubers provided a widely available if not particularly palatable source of calories when other foods were in short supply.  

The experience and diligence of old women would have been useful in other contexts as well. In many parts of Africa today, tree nuts provide a protein-rich staple for chimpanzees and humans alike. But perfecting the art of cracking their hard outer shells can take years. Furthermore, if every gatherer is a botanist—expert at identifying which plants are edible versus poisonous and predicting their availability—older women are the PhDs. Paula Ivey Henry describes one old Efe woman's uncanny ability to locate medicinal plants and vegetable foods rarely used except during famines. Her own children had all died, yet this wizened old woman spent hours in the forest collecting fish, shellfish, nuts, fruits, and roots too scarce or hard to locate at that time of year for other women to bother with or even remember.

The significance of ethnobotanical knowledge for the well-being of
children in parts of the world where most people are perpetually undernourished is only beginning to be studied. In 2007 a team of American and Spanish anthropologists working among Tsimane forager-horticulturalists in Amazonian Bolivia reported a significant correlation between how much mothers knew about the diversity and uses of local plants and the nutritional status and health of their children. The effects were independent of other measures like household income or years of schooling. Although the researchers did not report how mothers acquired their special knowledge, most likely it was transmitted woman-to-woman.

Other forms of traditional knowledge—about environmental hazards, diseases, or people in distant communities—are less likely to be gender-specific. Across primates, aged females and, when they are still around, aged males provide vital reservoirs for intergenerationally transmitted knowledge. Whether Hamadryas baboons or foragers, it is the oldest group members who remember where to find water in drought years when all the usual sources have dried up. But with the exception of humans, information and skills are primarily transmitted through demonstration rather than through teaching or the intentional sharing of knowledge. When suffering from diarrhea, for example, chimpanzees seek out a particular plant that hinders intestinal parasites. But as far as I know, chimpanzees only medicate themselves. It was the skilled utilization of new food sources and technologies in the genus Homo, combined with the increased importance of sharing and teaching, that opened up new possibilities for kin-directed assistance between generations and for altering the cost/benefit ratio of keeping older group members around.

THE MORPHING OF GRANDMOTHERS

We have come a long way since the days when evolutionists and anthropologists alike ignored females past reproductive age. Today, the presence or absence of postmenopausal women, their longevity, their efficiency, along with their dedication to kin have become legitimate research topics. The new significance accorded postreproductive females was very much in evidence in 2002, when I attended the first-of-its-kind international symposium on “the psychological, social, and reproductive
significance of the second half of life” at the Hanse Institute for Advanced Study in Delmenhorst, Germany.

Throughout the last quarter of the twentieth century, sociobiologists, many of us women, had worked hard to expand evolutionary theory to include selection pressures on both sexes. Along with other field-workers, I had also been studying the contributions to infants’ well-being of both mothers and allo- mothers, old females included. But this meeting was the first time that researchers from around the world convened specifically to discuss the impact of grandmothers. Well past menopause myself, yearning for grandchildren, I was anything but a disinterested participant.

Kristen Hawkes was there, along with Ruth Mace, who two years previously had reported that the presence of a maternal grandmother halved child mortality among the Mandinka. The German primatologist Andreas Paul summarized accumulating evidence that menopause can no longer be considered uniquely human and that other primates, if they live long enough, may also cease to menstruate before they die, and also exhibit strong impulses to help younger kin. What is unusual about humans, Paul stressed, is not that follicles in a woman’s ovaries peter out around age 40 but how long women go on living afterward. Just why this might be useful was explained by the anthropologist Donna Leonetti as she described what she and colleagues were learning about Khasi tribal peoples from Meghalaya in northeast India.

The Khasi are among the few matrilineal peoples to retain their traditional way of life. Daughters, especially the youngest daughter, continue living with their mothers after they begin to bear children, and this residence pattern pays off in higher child survival. Twelve percent of Khasi mothers had lost one or more children before the age of ten, but the chances of a child dying were 74 percent greater if no grandmother lived with them.

A young woman who does not happen to reside matrilocally may nevertheless return to her mother around the time of first birth. The Bavarian medical anthropologist Wulf Schiefenhövel stressed the value of such customs. Not only is support at hand during childbirth, but if the mother dies before her children are independent, or choose not to rear her children, matrilineal kin are available to help. Among the Trobriand Islanders Schiefenhövel studied, 27 percent of children, especially first-
borns, end up being fostered out shortly after weaning and are reared by allomothers. In about a third of these cases, the adopter was their grandmother.\textsuperscript{72}

For society after society, grandmothers have been shown to influence the reproductive success of kin. For European and North American farming communities where written records were available, the increased lifetime reproductive success of mothers with a grandmother to help could be traced over several generations.\textsuperscript{73} Birth and death records for 500 Finnish women and 2,400 Canadian women leading hardscrabble peasant lives and destined to lose 40 percent of all infants born to them revealed that if these mothers had their own mother still living in the same community they lost significantly fewer children. In both samples, numbers of surviving grandchildren depended on how much longer the woman herself survived after the birth of her last child. Postreproductive women gained roughly two extra grandchildren for every ten years they survived past completion of their childbearing.\textsuperscript{74} But these effects were significant only in the case of the first three grandchildren. This suggested that either mothers were gaining valuable experience or else help from older children compensated for the increasing frailty or absence of a grandmother.

News about hardworking postmenopausal women among the Hadza and the stunning impact of grandmothers on child survival among Mandinka horticulturalists (discussed in Chapter 3) spread fast among anthropologists. Researchers working in highland Peru, Senegal, rural Ethiopia, northeasternmost India, and the deserts of Western Australia began to ask new questions. Others scoured archives in Europe, North America, and Japan. All confirmed the importance of postmenopausal altruists.\textsuperscript{75} Wherever populations were characterized by high average rates of child mortality, grandmothers—if available—made a difference to child survival.

Galvanized by the new findings, Rebecca Sear and Ruth Mace set out to review evidence for 28 traditional societies where we already had fairly good demographic information. In all of them, death of the mother in the first two years proved catastrophic, presumably because substitutes for mother’s milk and maternal care were so inadequate. But the lethal impact of losing one’s mother decreased with the child’s age, and in five societies a motherless child who survived to age two had as good a chance
or reaching adulthood as a child whose mother had not died. Since two-year-olds were still far from independent, other caregivers had to be stepping in. And no single class of caregivers made a bigger difference than grandmothers. Their presence was correlated with higher child survival in every one of the twelve societies for which relevant data had been recorded.\(^7\)

**WHEN AND EXACTLY HOW DO GRANDMOTHERS HELP?**

Overall, grandmothers were turning out to be the most reliably beneficial of all alloparents. Under some ecological conditions, for example in foraging societies where game is short, their presence had an even bigger impact on child survival than the father’s did. At other times grandmothers proved most useful when mothers were young, inexperienced, or lacked older children to help out.\(^7\) Children’s age was also a factor since, statistically, children benefited most from having a grandmother present around the age of weaning.\(^7\) Whereas some youngsters are nonchalant about the end of nursing and may even wean themselves, more often little monkeys and apes (including human ones) find rejection from the mother’s breast quite stressful. Not only do youngsters lose access to the emotional comfort of sucking there, but they have to compete for available food with larger group members, and may suffer pangs of jealousy if they see a younger sibling nestling where they want to be. It is no wonder that weaning sometimes feels like a death sentence. To some already malnourished and immunologically challenged toddlers, it may actually be one.\(^7\)

Recollecting her earliest years, the !Kung woman Nisa recalled how jealous she felt when her newborn brother displaced her at her mother’s breast. Tension between Nisa and her mother erupted whenever he nursed, so what did she do? “I went to the village where mother’s mother lived and told myself I would eat with her. When I arrived at her hut, grandma roasted [food], and I ate and ate and ate. I slept beside her and lived there for a while.” Later, her grandmother returned Nisa to her parents, making a point of scolding her adult daughter in front of Nisa for punishing instead of being nice to her. Nisa was comforted by knowing that she had such an influential ally.\(^8\)

Kindly old grannies are a long-standing cultural stereotype. Yet re-
searchers have only begun to zero in on the stress-reducing component of their benevolence. In 2006, seventeen years after he had first gone to Trinidad to find out whether alloparental affected maternal reproductive success, Mark Flinn was still doing research there and published a paper describing the physiological benefits of having supportive alloparents. As predicted, a traumatic social event—such as being threatened or witnessing a fight between parents—led to increases in salivary cortisol levels by anywhere from 100 percent to 2000 percent. But the negative effects of early social trauma (as measured by cortisol levels) was moderated for children with alloparental support, including children with a grandmother on hand.81

Such demographic circumstances are crucial. The more inexperienced the mother or the fewer older children around to help (her own or perhaps their cousins), the more a grandmother or great-aunt matters.82 Fortuitously, the same high child mortality rates that make grandmaternal contributions so critical also make it likely that postmenopausal women will have few direct descendants vying for their help. Grandmothers can also distribute themselves and channel contributions according to those who need their help the most.83 But demographics aside, it also matters whose mother a grandmother was.

MOTHER’S MOTHER VS. MOTHER-IN-LAW

Clearly grandmothers have a range of beneficial effects, even in some cases dramatically reducing child mortality. However, the type of effect she has may vary depending on whether the nearby grandmother happens to be the mother’s mother or the father’s. Across traditional societies, the presence of a maternal grandmother is more likely to be correlated with the enhanced well-being of grandchildren, whereas the presence of the father’s mother is more likely to be correlated with increased maternal fecundity, earlier reproduction, and shorter intervals between birth.84 Such increased maternal fecundity may be a boon for her mate’s reproductive success, but it will not necessarily enhance the well-being of children born in rapid succession and forced to compete for family resources with more siblings. Furthermore, the benevolence of every grandmother is far from guaranteed. Under some circumstances her ministrations prove downright detrimental.
We need only turn to case studies from some of humanity’s more stratified and highly patriarchal societies to find grandmaternal interventions reminiscent of murderous marmoset and meerkat “grandmothers from hell.” For example, long-standing preferences for particular family configurations in some parts of the world, especially a preference for sons, may result in a paternal grandmother taking the initiative to dispatch an unwanted granddaughter. I am still haunted by a photograph sent to me once by a colleague depicting a pair of brother-sister twins born to a Pakistani mother. The much-desired son, who had remained with his mother to breastfeed, was healthy and robust, while the daughter, who had been taken at birth by the paternal grandmother and bottlefed with a lethal mixture of powdered milk and unboiled water, was limp and emaciated. Shortly after the photograph was taken, the little girl died from chronic diarrhea and malnutrition.\^{85}

Another case of what is better termed a mother-in-law than a grandmother effect can be found in Eckart Voland and Jan Beise’s reconstruction of eighteenth- and nineteenth-century families from Germany’s Krummhörn region. As expected, child survival rates were higher if the postreproductive caregiver was the wife’s mother.\^{86} If the husband’s mother lived in the house, the most salient effect was her daughter-in-law’s shorter intervals between births and higher overall fertility. Although one might expect this higher fertility to result in higher overall reproductive success, it did not. Having a live-in mother-in-law turned out to be correlated with a significantly higher rate of stillbirths and neonatal mortality.\^{87} According to Voland and Beise, these poor outcomes may have been artifacts of pregnant wives living in a dour Calvinist community, separated from their own families and under the oppressive and presumably highly stressful surveillance of their husband’s mother.

Clearly the impact of paternal grandmothers on the survival of grandchildren is not as uniformly beneficial as is that of the maternal grandmother. Several authors attribute reported differences in solicitude to the level of uncertainty that surrounds paternity. If “it is a wise child who knows his own father,” it will take an even wiser, unusually well-informed grandmother to distinguish her son’s child. A paternal grandmother may feel less emotionally committed to grandchildren to whom she might or might not be related.\^{88} It is also possible, of course, that the two women simply do not like each other.
Whatever the reasons, opposing effects from paternal versus maternal grandmothers similar to those reported for German peasants have also been documented for patrilineal societies in mid-twentieth-century West Africa and eighteenth- to nineteenth-century Quebec. Rice-growing peasants from seventeenth- to nineteenth-century Tokugawa, Japan, also conform to this pattern, albeit with extra twists. It was very unusual in this patrilocal, patrilineal, extremely patriarchal society for a mother to be living with her daughter, but a few did, and the maternal grandmother’s presence was correlated with increased survival rates for both her grandsons and granddaughters. More commonly, it was the father’s mother in the household, and although her presence had no effect on granddaughters, it was detrimental to the survival of grandsons. One possibility is that in this rigidly patrilineal system, paternal grandmothers had a stake in reducing the number of heirs competing to inherit the land.

Different roles played by grandmothers depend on a range of factors—residence patterns for sure, but also local subsistence conditions, the family’s socioeconomic status, family composition, and inheritance patterns—which will obviously be more important for settled people than among hunter-gatherers who have few possessions. Leonetti and her coworkers have undertaken the first study aimed at teasing apart such factors. They are comparing childcare patterns among the mother-centered Khasi community in the northeastern Indian state of Meghalaya with those in a patrilineal and patrilocal Bengali community in the neighboring state of Assam. Among these patriarchal Bengalis, men monitor and seek to control women’s movements, and mothers and their children alike suffer from a lack of direct access to resources.

Owing to the importance of patrilineally inherited farmland, female chastity is a matter of tremendous concern to Bengalis. Wives are under chronic surveillance, with the father’s mother in her stereotypical role as watchdog, and (as in the case of the eighteenth-century German peasants) her presence is correlated with shorter intervals between births and an overall increase in the number of children born (some women have as many as eleven children). Nevertheless (and this diverges from the German case), the paternal grandmother’s presence is more helpful than harmful in keeping infants alive, even though the fast reproductive pace probably takes a toll on their mothers.
In contrast to Bengali mothers, Khasi mothers own property, have considerably more freedom of movement, and benefit from having matrilineal kin nearby. Maternal grandmothers in particular attach high priority to keeping the mother and her children as well-nourished and healthy as possible. Not surprisingly, the grandmother's labor is positively correlated with how much children weigh, which is on average significantly more than Bengali children of the same ages. Even though the socioeconomic status of the two groups is roughly similar (with no one being that well off), on average Khasi mothers are taller, better nourished, and weigh more than their Bengali counterparts, who by and large are fed less well in childhood and all through adulthood. Among 2,666 Khasi infants in this study, those with maternal grandmothers present as opposed to absent were more likely to survive to age ten.

Are maternal kin invariably good news then? Not necessarily. Even within matrilocal societies, growing population density can increase competition between kin for matrilineally inherited resources. This appears to be the case in parts of contemporary Malawi, where having the mother's mother or sisters around actually proves detrimental to child survival. In the case of Malawi, I suspect that this situation is due to the decreasing availability of farmland women need to support their families. In the terminology of Sherman's eusocial continuum, such competition increases the degree of reproductive skew, since mothers with access to more land can rear more young. This speculation is consistent with the fact that the correlation between nearby matrilineal kin and child mortality was confined to girls and most pronounced in families that had heritable land. This 2008 study from Malawi is important, reminding us how much we still have to learn about humans as cooperative breeders.

PATRIARCHAL COMPLICATIONS SINCE THE PLEISTOCENE

Patrilineal concerns are one reason why the impact of the husband's mother on the well-being of grandchildren can be so variable. Universally, people in traditional societies want children, but residence patterns, family compositions, values, and priorities regarding children differ. Whereas people with matrilineal/matrilocal histories award high priority to maternal interests, those in patrilineal, and especially full-
fledged patriarchal, societies where property is passed from fathers to sons are more concerned with ensuring the husband’s paternity and preserving patrilineal access to resources, even when this entails practices detrimental to the well-being of mothers (and children too), such as sequestering women or sewing up their vaginas (infibulation).

Through time, a fixation with chastity can take on a symbolic and institutional life of its own, so that tremendous mental energy and effort gets channeled into policing and controlling female sexuality and convincing women that it is essential for their own and their children’s sake to be “good” (that is, chaste, dutiful, submissive, and self-sacrificing) mothers. It’s not that men and their mothers in these societies don’t care about children. They do, often desiring lots of them, especially several sons (an heir plus a spare). But preservation of the patriline and patrilineal institutions still takes priority, even to the point of depriving children of grandmothers. Consider the once widely practiced South Asian custom of suttee. When a man died, it was his widow’s “sacred duty” to burn herself alive. Her suicide forestalled diversion of resources for her continued support as well as eliminating risks that she might dishonor the patriline by taking up with another man. However, suttee was not just hard on virtuous widows. It deprived dependent children of grandmothers and great-aunts, as well as mothers.

**WHAT ABOUT GRAMPS?**

Even among foragers like the Efe, where lots of hands-on male care can be found, grandfathers spend surprisingly little time holding babies. Fathers, cousins, and older brothers spend more than twice as long babysitting as grandfathers do (also more than five times more than uncles). Among the Hadza, grandfathers are far less likely than grandmothers to even be in the same camps as their grandchildren. In Sear and Mace’s 2008 overview, the proximity of grandfathers had little detectable impact on the survival of their grandchildren. Does this mean grandfathers don’t matter?

Certainly as they age, most men continue to be interested in what happens to their descendants. In patrilineal societies, older men take a special (if not particularly hands-on) interest in sons and grandsons, while in matrilineal societies uncles (mother’s brothers) are especially
important mentors. In societies like our own, where intergenerational transmission of property is both very important and unusually well-documented, men go to more trouble than women do to channel wealth down the generations to blood descendants, to keep property “in the family.”100 In hunter-gatherer societies, property does not have anything like the same importance, but social relationships are no less complex—or prone to generate discord. Respected middle-aged and older men, aging fathers, grandfathers, and uncles help relatives broker disputes between rivals or co-wives, increase the likelihood that groups retain the use of waterholes, and perhaps most importantly help arrange suitable matches and influence group recruitment and retention.

As Polly Wiessner has shown for the !Kung, the combined hunting, healing, and political skills of “elder statesmen” diffuse tensions, promote solidarity, attract useful group members, and otherwise promote the group’s solidarity and continued access to resources. The impact of a respected man can persist long after he passes his prime. In a follow-up study tracing the fates of different Bushmen families, Wiessner found that a man skilled in setting up long-term *nxaro* relationships and in other ways could keep his group together in the same area almost twice as long as less-gifted elders could. As she put it, “Thirty-four years later, the wives of men who excelled in these activities had an 84% chance of living with their mature, married children as opposed to the 34% chance of women married to less skilled men.”101 Whether or not old men continue to reproduce themselves, or even whether or not they are actually the progenitors of children born to younger wives, such elder statesmen have kin in the groups whose long-term interests they promote.102 Such men are not so much uninterested in children as they are uninvolved in childcare.

There are few primate analogues for the stabilizing influence of postprime men. With physical decline, nonhuman primate males tend to become marginalized or are driven out of the group altogether. The closest parallel might be a silverback male gorilla accompanied by a younger black-backed male apprentice in his same group. Even after the older male has passed his prime, the silverback continues to play a protective role, and the presence of multiple males in the group increases infant survival.103

In gerontocratic human breeding systems, where old men not only
control the marriage options of younger men but monopolize younger women themselves (think Aboriginal Australia), old “silverbacks” continue to exercise influence. This led Frank Marlowe to hypothesize that selection favoring longevity might have operated even more strongly on these old patriarchs than on grandmothers (the “patriarchs hypothesis”). Bear in mind, however, that uniquely human ideologies promoting respect for elders long after they have lost their physical edge probably required language. If lifespans were already longer by the time humans acquired language (a proposition I will examine in the next chapter), this brings us back to grandmothers.

THE LUCK OF THE DEMOGRAPHIC DRAW

Apart from human females, no other primates, and very few other mammals, take decades to mature before they begin to breed and then live for decades after their ovaries peter out. Among the rare exceptions, short-finned pilot whales and orcas quit breeding around age 40 but live decades longer. Nonhuman female primates who survive long enough to cease menstruating go on to live only a few years afterward, or a decade at most in the case of chimpanzees, who reproduce for the last time around age 42. Even the most long-lived of these females spend only 16–25 percent of their lives as postreproductives, not nearly as long as women, who cease to cycle some time after age 40 and then potentially live on for twice that long. The proposal mentioned in Chapter 6 that menopause might have evolved to produce in humans a sort of “sterile caste” to forestall competition between older and younger breeding females overlooks the fact that what is different about human apes is not cessation of reproduction around age 40—that is, menopause itself—but how long women go on living afterward.

Experienced in childcare, sensitive to infant cues, adept at local subsistence tasks, undistracted by babies of their own or even the possibility of having them, and (like old men as well) repositories of useful knowledge, postmenopausal females are also unusually altruistic. Given the flexibility of forager lifestyles, these ideal allomothers can readily relocate near needy kin—though it is well to keep in mind that the meat a new husband provides members of his wife’s group may also be part of the attraction. Across the societies in the Sear and Mace overview,
grandmothers were second only to mothers, and rivaled only by older siblings, in their beneficial impact on child survival. But postmenopausal allomotheres also have a drawback: the probability they will eventually grow frail.

Nothing guarantees that a postreproductive woman will survive long enough to be of use. In an unusually well-researched thought experiment, anthropologists Jeffrey Kurland and Corey Sparks used archaeological records from late Paleolithic gravesites to compile demographic parameters and then used these to estimate probable lifespans for foragers under a range of ecological conditions. Under good conditions with low mortality, they estimated that a 20-year-old mother would have a roughly 50 percent chance of having a 40-year-old grandmother alive to help her raise her children. As mortality went up, this chance drops to around 25 percent. Using census data from ethnographies, Kristen Hawkes and Nick Blurton Jones came up with lifespan estimates that fell between those two extremes. Their low estimate was consistent with that for a sample of 20 Efe infants—four had surviving grandmothers. At the high end, 7 of 15 Aka infants had either maternal or paternal grandmothers present.108

Fewer than half of Pleistocene mothers would be likely to have had a mother alive or living in the same group when they first gave birth. The chances of a mother having an older sibling still alive were several times higher than that. The chance of her infant having older siblings or cousins, or having either a father, possible fathers, or a would-be father, or some combination thereof would have been higher still. Depending on the circumstances, some combinations would be more beneficial than others, even though—all other things being equal—those with a helpful grandmother would be better off than those without. In the terminology of five card stud poker, where only the very lucky are likely to be dealt a full house or even a matching pair, having a grandmother nearby was like having an ace in the hole. Given equivalently mediocre hands, a grandmother was often the winning card in the Darwinian game of life—but only for those lucky enough to have been dealt one.

The probability of different types of help varied with circumstances. So did the kind of help different allopants provided and how such help
Cousins and older sibs can be good for a snack, but children’s most common allo-maternal contributions are as role models and child-minders (usually with adult supervision not far off). (Peabody Museum/ Marshall Expedition image 2001.29.416)

was weighted. Children make adept berry-pickers and lizard-catchers but lack the upper body strength and long arms to dig out deep tubers.\textsuperscript{109} Nor do they come close to being as practiced and single-minded at tasks like gathering or nut-cracking as old women are. But prereproductive babysitters have the merit of availability. Supervision by a nearby adult would have made older children more usable still, freeing mothers to forage more efficiently. And of course after the Neolithic, with all the chores typical of farming societies, children became productive assets in their own right.\textsuperscript{110}
WHEN GRANDMOTHERS OUTLIVE THEIR USEFULNESS

Helpful as grannies are, a grim final question remains: What happens when they cease to be useful? Medicare, Social Security, and other features of the modern safety net make Westerners some of the only people (and the only primates) where resources routinely flow from the young to the very old. More often in primates, resources flow from grandparents and parents down to breeding adults and their offspring. Inevitably among our ancestors there came a time when even the most helpful old female became too decrepit to provision herself, much less share with others.

In some species, grandmothers voluntarily opt out of competition for food with younger kin, falling in rank, giving way to younger relatives, marginalizing themselves and being marginalized by others. Across human societies, treatment of old people varies from reverence to astonishing callousness. Just as in modern America, where children telephone grandparents more times each month if they possess significant heritable resources, old women in foraging societies are more valued when the food they gather is an important component of the diet. Along with women generally, they are less valued in societies subsisting primarily on game brought in by men.

Customs for coping with decrepitude range from reverse solicitude (the young caring for the old) to voluntary euthanasia (as in traditional Japan), from reverence to marginalization, abandonment, or outright execution. As Kim Hill listened, an old Ache man recalled when as a young man he used to sneak up with his axe behind old women who had become a burden on the group. “I would step on them, then they all died, there by the big river . . . I didn’t used to wait until they were completely dead to bury them. When they were still moving I would [break their backs and necks].” In other words, it may not be purely altruism that motivates an Ache woman my age to work so hard.

THE ART OF MANUFACTURING ALLOMOTHERS

Given the neediness of human children and the vagaries of a hunter-gatherer existence, humans were fortunate to be so flexible, mobile, and well-equipped to consciously strategize. For unlike marmosets, human
children are not chimerically related to several fathers who are also brothers. Nor can they rely on allomothers who are genetically more closely related to them than the helpers are to their own young, the way honeybee grubs can. This is why the special talent human parents have for cultivating future caretaking prospects, even to the point of manufacturing fictive kinship, is so important. The sort of sexual liaisons described in Chapter 5 provide a taste of myriad possible ploys. Once acquired, language and kinship customs equip women with an even wider range of options for manufacturing kin. Humans are expert at forging alliances on their children’s behalf.

Beginning in girlhood, and as they mature, women become increasingly adept at making friends. The roots of such predispositions do not grow out of men’s quest for hunting partners or brothers-in-arms. Whether consciously or not, women seek “sisters” with whom to share care of our children. Even the obsession with being popular and “belonging” so poignantly evident in teenage girls, rendering them both acutely sensitive to what others think and also causing them to be competitive and ruthlessly mean in excluding others, may possibly have much to do with forging bonds which in ancestral environments would have been critical for successful childrearing. From adolescence onward, many girls are more concerned with popularity and belonging than with achievements per se, so much so that their “sense of self becomes . . . organized around being able to make, and then to maintain, affiliations and relationships,” and they dread the rupture of friendships and other social ties.114

Some evolutionary psychologists attribute such tendencies to the innate powerlessness of women in ancestral worlds, where they were carried off from their natal communities to breed among less-than-supportive members of another patriline.115 Others see in the human female’s urge to “tend and befriend” a way to obtain support in times of stress (such as during attack by a saber-tooth tiger).116 But neither of these hypotheses explains why women became so much more affiliative than say chimpanzees, who also usually left home to breed and also had to worry about big cats. These psychologists overlook a key difference between women and other apes. Girls as they matured to breeding age and throughout life needed to line up help from more individuals than just their mates. The bonds themselves became the resource to be protected.
Grandmothers are not the only aged females who forge loving relationships with children. Her dimming eyesight notwithstanding, this 85-year-old Himba woman peers expectantly into the face of her grandson’s four- to five-month-old daughter as she makes a soft grrrrr-sound and gently shakes the baby. The girl looks back tentatively, the more intently as the old woman's forehead touches hers and she begins to rhythmically sing while patting the baby on the back. Meanwhile, the baby looks away from the old woman, to her mother, and back again to her great-grandmother. (I. Eibl-Eibesfeldt/Human Ethology Archives)

Over generations, devices for manufacturing kin have been culturally elaborated and maintained. “It is intriguing to speculate,” Wiessner writes, “that the roots of human kinship systems might lie in cooperative breeding communities where maternal-like care comes from a number of individuals other than the mother, thereby extending concepts of who constitutes family.” Stratagems include honorary naming devices, systems of classificatory kin, as well as customs such as designating “extra fathers.” Females in many species use polyandrous matings to line up possible fathers, while bonobos use sexual gratification as well as grooming and occasional gifts to strengthen social bonds with members of both sexes. No species, however, proves as clever or opportunistic and—once language became part of the species repertoire—so endlessly inventive as humans are in the manufacture of partners to share with and alloparents to rely on. If long-lived grandmothers were humankind’s ace in the hole, all these classificatory kin—distant relatives, godparents, possible fathers, namesakes, trading partners, and other manufactured alloparents—became their wild cards.