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Article

The Real Females of Human Evolution

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When "woman-the-gatherer" was first proposed as a counter to "man-the-hunter," we were only beginning to understand the many faces of primate females. In ensuing decades we have learned about the skills and talents of female chimpanzees in tool using, hunting, and transmitting behaviors from one generation to the next as teachers, and across space as newcomers to neighboring communities. The perspective of evolutionary time highlights the continuity of female lives from the origin of mammals to the origin of *Homo sapiens*. The combination of behavioral, fossil, and archeological information aid in reconstructing key ingredients acquired by females along the way that contributed to the success of our species.

Real human females have complex lives and multiple roles: as nurturers, teachers, friends, innovators, and carriers of tradition and culture. We are equipped with a large brain, a locomotor system for long-distance walking, more than adequate body fat, strong emotions, late maturity, and a long life. We share an evolutionary history with other real females. How did we acquire all these roles that extend well beyond that of simply mating and birthing the next generation?

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MAMMALIAN FOREMOTHERS

To address this question, we look back in time to almost 200 million years ago, when mammals first appear in the fossil record. With the origin of mammals came a new social bond that appeared between an adult female and her offspring. This bond became the basis for a revolution in social life.

It happened this way. A newborn mammal depends on its mother to provide nourishment by producing milk, which is the source of life for all mammals. Infants come equipped with keen senses of smell and hearing, and the ability to vocalize. In this way, a young mammal identifies its mother, attracts her attention with distress calls, and maintains contact with her; she is its source of food, warmth, and protection. Its very survival depends on her.[1] A mammal mother comes equipped with fat reserves to support her energy requirements during pregnancy and lactation,[2] an emotional brain, and the motivation to respond to, feed, and care for her infant.[1] This mother-infant bond becomes the foundation for the development of other social bonds; it is the building block for success and diversity in mammal societies today.

What was not new was the interaction between an adult female and male during mating. Sexual reproduction had been around a long time, having been established before the origin of mammals.

THE EXTREMES OF SOCIALITY

The complexity of social life correlates with the length of the bond between a female and her young and the time necessary to learn the social rules of the species.[3] To illustrate this principle, we can consider what I call "minimalist" mammals. Elephant seals are a good example. They breed each winter at Ano Nuevo, an island north of Santa Cruz, California.

Why minimalist? Well, here's the deal: Each December, pregnant females (about 500 kg) come ashore, find a place on the beach, and within 24 hours give birth to 45-kg pups. Each mother provides her new pup with rich milk of 55% fat for 3 to 4 weeks. In the process, the female loses almost a third of her body weight, while her rapidly growing pup triples its birth weight.[4] As she weans her pup, the female comes into estrus, mates with several males, and returns to the sea to dive and hunt alone. All of her reproductive obligations are efficiently accomplished in 36 days, just over one month.

A female elephant seal has her first offspring at the age of 4 years. She reproduces each year and has an average life span of 18 years.[4] She does not interact with other elephant seals; there are no social rules to learn. She has the longest bond with

her pup, and the shortest with adult males. The "weaners," now abandoned by their mothers, fend for themselves as they learn to swim, dive, and hunt.

At the other end of the mammal continuum are the "maximalists," the elephants; the gray giants of Africa serve as a good example. Elephants live in herds headed by a matriarch, related females and their offspring that include individuals of various ages that span 3 or 4 generations.[5] From birth, a baby elephant has to move on its own and keep up with the herd. After a 22-month gestation, a female gives birth and nurses her calf for about 4 years. A baby elephant is surrounded by caretakers and teachers, and there is a lot to learn about social relationships. Young males leave the herd at about the age of 10 years; females remain, reproducing at about the age of 15 years. Elephants live for 50-60 years and they have good memories. The older matriarch, wise for her years, shares her knowledge and experience of the world with her group.

So here are contrasting patterns of mother-infant bonds. The elephant seal minimalists nurture their young for one month, then return to a solitary life; the African elephant maximalists nurture their young for 4 years and remain in contact with them throughout life in complex social groups.

THE PRIMATE PATTERN

Where do primate females fit into this continuum? Primate social life builds on the mammalian foundation of the mother-infant bond and expands during development into numerous social relationships played out in social groups with individuals of all ages and both sexes. Compared to other mammals, primate females kick it up a notch. They don't just provide milk and comfort to their young; a primate mother carries her baby until it is weaned, and the infant actively clings to her body. Therefore, a female must be adequately nourished in order to produce milk for her young. She must also have the strength and energy to carry the extra weight of a growing infant.[6,7] The mother becomes the infant's 24/7 "mentor" about complex social and ecological environments. The infant, in turn, must have the strength to grasp with its hands and feet and to hold on to its mother as she climbs and leaps through the forest canopy and runs along branches or on the ground.

What is the advantage of this "costly system" that taxes a female primate energetically? Whether pregnant or carrying an infant, a primate female travels and forages for food with a social group, gains safety and protection from group living and, perhaps most important, maintains social relationships with other females and males during all phases of her reproduction. Males have little direct interaction with the young, though they contribute to the stability and safety of the social group.

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CHIMPANZEES: OUR LIVING RELATIVES

Coming nearer to ourselves and our living relatives are chimpanzees. They resemble elephants in having a long infant dependency and a long life. But, like other primates, chimpanzee mothers carry and nurse and tutor their young for as long as 4-5 years.

Our understanding of primate females took a giant leap forward when Jane Goodall, initially sponsored by Louis Leakey, undertook her study at Gombe in Tanzania in 1960.[8] Goodall met female chimpanzee Flo, who exemplified to Goodall a patient and confident mother and a matriarch surrounded with her offspring; Flint, Fifi, Figan, and Faben. Fifi was barely a teenager when Goodall first met her. Old Flo, who lived to about the age of 50 years, became a grandmother when her daughter Fifi gave birth to her first offspring, Fanni. Through the decades, Fifi also became a matriarch.

One of Goodall's landmark discoveries was that wild chimpanzees without any human intervention use tools that they create from various organic materials. At the time of her discoveries, anthropologists assumed that making and using tools was unique to the human species and required a large brain and well-developed cognitive abilities. Louis Leakey, who had dug up many stone tools of ancient human relatives at Olduvai Gorge, was particularly excited by this discovery because skill with using tools narrowed the gap between chimpanzees and humans. For instance, chimpanzees use crumpled leaves as sponges and grass stems to probe and extract termites from inside a mound. Goodall noted that a young chimpanzees early in life attempts to select an appropriate tool and copies the moves of its mother. It takes almost five years for a young chimpanzee to master effective termite-fishing. Goodall described two young females as "champion termite fishers."[8]

FEMALE TOOL-USING SKILL AND ITS TRANSMISSION

The talent of female chimpanzees in using tools became well documented in studies by Christophe and Hedwige Boesch in the Tai Forest, Ivory Coast.[9] There, chimpanzees use wooden or stone hammers together with a solid surface, which they use as an anvil, to crack open several different species of hard-shelled nuts. This creative use of hammers and anvils enables the chimpanzees to exploit a rich and nutritious food source. When the nuts are in season,

chimps can feast on an extra 3,500 kilocalories a day.[9]

An individual chimpanzee achieves some success at nut-cracking by the age of 10 years. This first level of skill is measured by the number of hits it takes to open one nut. The second level of skill is the number of nuts processed per minute. Here, females are superior to males. The reason for this sex difference is apparently social: Males favor social activity over cracking nuts.[10]

Exactly how might this difference come about? In a study over four years, Elizabeth Lonsdorf and colleagues[11] investigated how young chimpanzees learn. They videotaped 14 young chimpanzees with their mothers during termite fishing. They found that young females spent more time watching their mothers fish for termites, whereas males spent significantly more time playing. Females start to fish for termites at a younger age, are more proficient than males once they acquire the skill, and use a technique similar to that of their mothers, whereas males do not.

When female chimpanzees reach adolescence, they leave home and transfer into a new community. In so doing, they take along knowledge and skills acquired while growing up. An example of what can happen was demonstrated in a field experiment with chimpanzees in Guinea, West Africa, by Tetsuro Matsuzawa.[12] There, at Bossou, chimpanzees use hammers and anvils to crack open oil-palm nuts, rather than the coula or panda nuts that are opened at Tai. Matsuzawa put out coula nuts, which were unfamiliar to them, to see what would happen. Most of the chimpanzees ignored them. Only one older female, who presumably had transferred from Mt. Nimba, a nearby community, immediately recognized the nuts and began cracking them. Two juveniles watched her and did the same. So this female, drawing on her early experience in her home community, was able to disseminate her knowledge to her adoptive community.

Female skill and knowledge make them bearers of tradition through time as models for their offspring and across space, as newcomers into a neighboring community. The continuity that females provide in tool use and other skills is an underappreciated dimension of the role of females in human evolution.

Figure 1. Tumbo, a Fongoli chimp, was the first chimp observed hunting with tools, and has been a prolific hunter. Photo: Joshua Marshak. (Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.)

FEMALES AS HUNTERS WITH TOOLS AND AS SHARERS

Much more ink has been spilled vaunting the hunting prowess and running skills of males than recognizing females' skills and activities. Male chimpanzees often hunt in groups and cooperate in tracking monkeys through the forest canopy.[13] The chases are dramatic and the excitement is high as they make the kill and begin sharing the spoils. The events make for gripping film footage. Consequently, in the public mind, only male chimpanzees have become associated with action, hunting, and sharing meat. However, female chimpanzees do capture and eat small animals.[8,14,15] Female orangutans also kill and eat slow lorises, small prosimian primates,[16] and gibbons eat flying squirrels and birds.[17] Female chimpanzees even use tools in the hunt.

Some years ago, a short paper reported on a single observation of an adolescent female chimpanzee from Mahale, Tanzania. She was seen using a modified branch to rouse, capture, and eat a squirrel hiding in a narrow tree hole.[18] It turns out that the behavior of this adolescent female was not a fluke. Years later, at her study site at Fongoli, Senegal, Jill Pruetz discovered that chimpanzees fashion sticks, on average 70 cm long, into little spears. They bite off the end of a stick to make a sharp point, then jam it into hollows of trees to kill sleeping bushbabies (Fig. 1). And it is predominantly females, particularly adolescent females, that hunt this way, doing so almost three times as often as males.[19] This hunting behavior is habitual, having been observed about 200 times, often with females sharing the meat.[20] In addition to the exciting findings from Fongoli, other new information on ape and human relationships, chimpanzee ecology and behavior, and early hominid fossils reinvigorate our speculations about human evolution.

CHIMPANZEE-HUMAN RELATIONSHIPS: NEW GENOMIC EVIDENCE

Since the 1960s, studies on proteins, mitrochondrial DNA, and nuclear DNA have all pointed to a fairly recent divergence of ape and human lineages around 5 million years ago.[21] A later estimate for chimpanzee-human divergence based on 36 nuclear genes yields about the same time, 5.4 mya.[22] Today, whole genomes consisting of billions of

base pairs are available. In announcing the gorilla genome, a separation date of 3.7 million years is given for chimpanzee-human, and 5.9 million years for gorillas.[23] Such recent separation shows that chimpanzees and humans are more closely related than are African and Asian elephants[24] or dogs and foxes.[25]

Ever since Goodall's observations, anthropologists have remarked on how much chimpanzee behavior resembles our own. We should not be surprised; after all, we are closely related. Chimpanzee anatomy and behavior have long been emphasized as a baseline for the common ancestor of apes and humans.[26–29] Using chimpanzees for a model in this type of analysis has also been criticized.[30,31] However, the consistency and preponderance of the molecular data support the reliance on chimpanzees as a model for the common ancestor and among ape species as the most useful comparison with early hominid anatomy.

SAVANNA CHIMPANZEES

The long-term studies of chimpanzees at Fongoli, Senegal, are of interest not only because they challenge the stereotype of male hunting and meat sharing, but also because these chimpanzees live in a savanna environment. This mosaic of woodland, grassland, bamboo, and gallery forest more closely approximates the environment of early hominids[32] than do more forested chimpanzee habitats. Compared to other chimpanzee populations, Fongoli chimpanzees have a larger home range, more cohesive social groups,[33] and share plant food more often.[34]

At one time, baboon behavior was proposed as a model for early hominids, in recognition of the challenges faced in a savanna-mosaic environment.[35] However, chimpanzees in more open habitats point up possible parallels with early hominids in use of digging tools for exploiting underground plants[36] and in creative use of caves for thermoregulation.[37] The anatomy and physiology of early hominids may have developed for more effective exploitation of the savanna mosaic.[38] The combination of genetic relatedness and a comparable habitat makes chimpanzees a compelling case, indeed, for use as a starting point in evaluating early hominid challenges.

THE FOSSIL RECORD AND LOCOMOTOR EVOLUTION

Much fossil evidence expands our ideas about early hominid behavior and adaptation, and about females' roles in the social complex. Early hominid fossils, the australopithecines, dated between 2 and 4 million years ago, have small brains the size of chimpanzee brains, but, importantly, depart from them in their locomotor system and how they moved around. Indeed, the australopithecines had abandoned a four-legged gait and were habitually walking on two limbs, as has been documented from abundant fossil evidence from sites in Ethiopia, Kenya, and Tanzania, South Africa.[39]

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The famous "Lucy" skeleton (AL 288) shows anatomical adaptations to walking bipedally in its limb proportions, pelvis, and knee joint. The remarkable fossil footprints of Laetoli, Tanzania, discovered by Mary Leakey, confirm what the bones were telling us: They leave no doubt that by 3.5 mya hominids walked on two legs.

Fossil foot and ankle bones from several archeological sites provide the opportunity to compare this part of the locomotor anatomy.[40–43] Each set of bones apparently belongs to a different species and shows distinct differences from the others in shapes of the bones. This evidence suggests that there was more than one anatomical solution for walking effectively on two legs; that is, the bipedal behavior may have been similar but with a different infrastructure. Unfortunately, from fossil bones alone, it is not possible to reconstruct in detail the locomotor repertoire of a species or the frequency of any particular behavior, such as climbing.

If you need to travel several miles during the day to collect and carry food, walking on two legs is a better way to get around on the ground. Chimpanzees, even the savanna-living chimpanzees, rarely travel more than about 3 kilometers, or 1-2 miles each day.[8,44,45] In contrast, women in hunting and gathering societies routinely walk 10-15 kilometers to collect food, and men walk longer distances when tracking animals during hunting. Women take their babies until age 3 on gathering trips, as well as tools and whatever food they collect. Richard Lee calculated that a !Kung woman carries her growing child and walks an estimated 2,500 miles until the child is weaned and somewhat independent.[46]

The fossil record rarely preserves organic material. Almost all of the tools used by chimpanzees are made of branches, twigs, stems, and leaves, as are many tools used by hunter-gatherers. The all-purpose digging sticks of women gatherers, the animal skins used as slings, leaves and ostrich shells used as containers – none of women's "tool kit" would show up in the fossil record.[46] Archeologists rely on the discovery of stone tools, which are not recognized in context until 2.5 million years ago, more than a million years after we have evidence of hominid bones.[47]

SORTING THE SEXES

The fossil record is often fragmentary, and it is not always easy to sort anatomical variation, whether it is due to species differences or sex differences. It is particularly difficult to assign male or female to unassoci-

ated or immature limb and pelvic bones. Hence, estimating the relative body size of each sex and their proportions to each other is conjectural. For example, two fairly complete and famous skeletons exist. From west of Lake Turkana in Kenya, is an immature *Homo erectus* individual, affectionately labeled "Turkana boy," dated to 1.6 mya.[48] The specimen was still growing because the pelvis and most of the long bones are unfused, and the third permanent molars have not yet emerged. This fossil (museum number WT 15000) was thought to be male because he was judged to be tall[49] and "tall" is taken as male.

"Lucy," the australopithecine fossil from Hadar, Ethiopia (AL 288), dated to about 3 million years ago, has a small skeleton and was assumed to be female. The name "Lucy" was assigned when the fossil was initially discovered, before the skeletal elements had been measured or analyzed. The name has stuck, and is a powerful obstacle to thinking of "Lucy" as anything other than female. The configuration of the pelvis is not modern, and there are few other pelvic bones for comparison of the same species and none from the same fossil locale. Still, there is a 50% chance that AL 288 is a female; if so, we don't know the body size of the males or how the two sexes compared in size.[49] Similarly, for the Turkana *Homo erectus*, if male, then the body size of the female remains unknown.

There are few unequivocal ways to assign sex to postcranial fossil bones or to figure out how different in size are females and males from the same species. However, amazing fossil discoveries from Malapa in South Africa are providing new evidence to resolve this sexual dilemma. These remarkable fossil discoveries were recently announced as a cover story in *Science*; named *Australopithecus sediba*, they have been dated to about 2 million years ago.[50]

The fossils consist of not one, but two partial skeletons, preserved together from the same area. One of the individuals is immature; it has only its second permanent molars and several of its long bones were not fused, another indication of its immature state. The other partial skeleton is adult, defined by having all permanent teeth, being somewhat worn, and having all bones fused. The surprise is that the juvenile individual is notably larger than the adult, even though its growth is not yet complete. It is likely that the young individual is male and the adult is a female. It is not often that we can assign sex to fossils with this reasonable level of certainty.

There is not a lot of agreement among paleoanthropologists about how to interpret the source of anatomical variation that we find in the fossils – that is, whether the variation indicates multiple species or denotes sex. But about two things we can be sure: Early hominids lived in social groups having both females and males, and mothers had strong bonds with their offspring. Therefore, in considering the two skeletons from Malapa, South Africa, preserved together for two million years, I see it as not much of a stretch to suppose that what we have here is a mother and her son, probably traveling together, perhaps in the company of other as yet undiscovered individuals.

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We might be able to squeeze even more from the South African fossil record. In a couple of studies, researchers measured isotopic ratios (strontium 86/85) in tooth enamel from fossil hominids and fossils associated with them preserved in the dolomitic cave sites of Sterkfontein, Swartkrans, and Malapa.[51,52] Individuals designated as "local" have a specific isotopic ratio, meaning that they grew up in the area; those having a different ratio are designated as "nonlocal," meaning that they migrated into the area from elsewhere when mature or nearly mature. To test whether the hominids were local or nonlocal, researchers assumed that the smallest teeth were from females and the larger ones from males.[51] The results indicate that the hominids designated as females have a "nonlocal" ratio, along with the large bovids; the hominid males and small animal species like the rodents have the "local" ratio. This finding is of considerable interest because it parallels findings in chimpanzee communities and suggests that adolescent female hominids may have changed communities, whereas male hominids may have remained in their natal group with their mothers.

THE ORIGIN AND EXPANSION OF *HOMO SAPIENS*

Now, fast forward from 2 million years ago to the origin of *Homo sapiens* in Africa some 200,000 years ago. Here, our species diversifies into numerous and variable populations within Africa before expanding to other parts of the world.[53,54] Archeological sites along the southern and eastern African coast dated as far back as 160,000 years ago preserve remains of shellfish and marine resources, and sites dated at 1.5 mya preserve remains of aquatic animals in lake deposits.[55,56] Marine and fresh-water resources may have been crucial for the survival of early *Homo sapiens* populations as they expanded their range along the African coast. It wasn't until 50,000-60,000 years ago that *Homo sapiens* began to leave Africa, perhaps initially hug-

ging the coast past the Arabian Peninsula and along the Indian coastline.[57]

Homo sapiens walked out of Africa on what was by then a tried-and-true locomotor system for effective long-distance walking, honed during the past several million years. Women were now well equipped with adequate fat stores for energy to nurse and carry large-brained and helpless infants.[58] *Homo sapiens* reached Australia between 40,000 and 50,000 years ago, presumably following a coastal route and exploiting marine resources as they continued to expand their range.[53,55,59] Along the northern coast of Australia, aboriginal women collect shellfish that constitute a major portion of the diet; they follow the receding tide that exposes the beds, thereby safely taking their small children with them,[60,61] not unlike the foraging women of the Kalahari. Aboriginal women are also expert hunters who provide for their families.[62] The evidence demonstrates that men's hunting and the importance of meat have been overemphasized. In contrast, the role of women as providers and sharers of resources and their contribution to the success of *Homo sapiens* has been considerably underemphasized.

SUMMARY AND CONCLUSIONS

In summary, the origin of the human lineage from ape ancestors builds on the combined mammalian and primate foundation of infant care, female mobility, and both emotional and social communication. Early hominid females, like other mammals, retained mobility during gestation and, like primates, added on the carrying of dependent young for months and years after birth.

Our story culminates in our species *Homo sapiens*, who appeared in just the last 200,000 years. Until a few thousand years ago, we lived a nomadic way of life, collecting, gathering, hunting our food, moving continually from camp to camp.[46,63] Women continued their central role in nurturing, maintaining friendships, acting as social glue, apprenticing slow-growing infants, provisioning their families, and sharing the cultural richness as part of a multi-generational community.

In closing, I share the following story from Elizabeth Marshall Thomas, who lived with and studied the hunter-gatherers of the Kalahari in southern Africa.[63] The story she tells documents women's strength, their physical and emotional endurance, which has been so important in the evolutionary success of our species.

"In a group of people who fell ill during an epidemic was a young widow with two small children; all three were too sick to follow when the group was forced by lack of food to leave its camp. The other people of the group might have had to abandon the young widow and her children. But her mother was there. This small, rather elderly woman took her daughter on her back, her infant grandchild in a sling across her chest, and her 4 year old grandchild on her hip. She carried them 35 miles, to her people's new camp. They arrived almost a day after the rest of the group, and eventually they all recovered."[64]

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