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Coupling up might have been the best move our ancestors ever made

By Blake Edgar

IN BRIEF

Even in societies where polygamy is permitted, monogamy is by far the most common human mating arrangement. In this regard, we are unusual animals: fewer than 10 percent of mammals form exclusive sexual relationships.

How humans got this way has been the subject of scientific debate for decades, and it is still an open question. But new research is clarifying matters.

We now know that the first hominins, which emerged more than seven million years ago, might have been monogamous. Humans stayed (mostly) monogamous for good reason: it helped them evolve into the bigbrained world conquerors they are today.

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AMMALS ARE NOT BIG ON MONOGAMY. IN FEWER THAN 10 PERCENT of species is it common for two individuals to mate exclusively. The primate wing of the group is only slightly more prone to pairing off. Although 15 to 29 percent of primate species favor living together as couples, far fewer commit to monogamy as humans know it—an exclusive sexual partnership between two individuals.

Humans obviously have an imperfect track record. People have affairs, get divorced and, in some cultures, marry multiple mates. In fact, polygamy appears in most of the world's societies. Yet even where polygamy is permitted, it is the minority arrangement. Most human societies are organized around the assumption that a large fraction of the population will pair off into enduring, sexually exclusive couples. And monogamy seems to have done our species good. "Pair bonds," as scientists call monogamous relationships, were a crucial adaptation that arose in an archaic forebear that became central to human social systems and our evolutionary success. "We have a very big advantage over many other species by having pair bonds," says University of Montreal anthropologist Bernard Chapais.

The monogamous couple also forms the basis for something uniquely human—the vast, complex social networks in which we live. Other primate young establish kinship links only through their mother; humans trace kinship from both parents, broadening each generation's family ties. Among humans, social networks extend to include other families and even unrelated groups in widening ripples of relationships. In Chapais's view, such group ties, along with monogamy, constitute "two of the most consequential features of human society."

Scientists have struggled for decades to understand the origins and implications of human monogamy. Basic questions such as when we started to pair up for life, why it was advantageous and how coupling might have spurred our success as a

species remain unresolved and contentious, but new research has brought us closer to solving the mystery.

THE ORIGINS OF COUPLING

IT IS ENTIRELY POSSIBLE that our most distant ancestors were monogamous. Fossil evidence, says anthropologist C. Owen Lovejoy of Kent State University, suggests that monogamy predates even *Ardipithecus ramidus*, the species best known from a 4.4-million-year-old partial female skeleton, nicknamed "Ardi," discovered in the Middle Awash region of Ethiopia. In Lovejoy's hypothesis, soon after the split from the last common ancestor between the great ape and human evolutionary branches more than seven million years ago, our predecessors adopted a transformative trio of behaviors: carrying food in arms freed by bipedal posture, forming pair bonds and concealing external signals of female ovulation. Evolving together, these innovations gave hominins, the tribe that emerged when early humans diverged from chimpanzees, a reproductive edge over apes.

According to this hypothesis, an ancestral polygamous mating system was replaced by pair bonding when lower-ranked hominin males diverted energy from fighting one another toward finding food to bring females as an incentive to mate. Females preferred reliable providers to aggressive competitors and bonded with the better foragers. Eventually females lost the skin swelling or other signs of sexual receptivity that would have attracted different males while their partners were off gathering food.



SILVERBACK male mountain gorilla (at right) leads his troop in Rwanda. Gorillas, which are polygamous, live in small groups consisting of one dominant male, multiple female mates and their offspring.

For evidence, Lovejoy points to *Ar. ramidus*'s teeth. Compared with living and fossil apes, *Ar. ramidus* shows a stark reduction in the differences between male and female canine-tooth size. Evolution has honed the daggerlike canines of many male primates into formidable weapons used to fight for access to mates. Not so for early hominins. Picture the canines in a male gorilla's gaping jaws; now peer inside your own mouth. Humans of both sexes have small, stubby canines—an unthreatening trait unique to hominins, including the earliest *Ardipithecus* specimens.

A rough correlation also exists between mating behavior in primates and sexual dimorphism—that is, differences in body mass and size between males and females of the same species. The more dimorphic a primate species is, the more likely it is that males fight over females. At one extreme, polygamous gorilla males grow to be more than twice as massive as females. At the opposite extreme, both male and female gibbons, which are mainly monogamous, are nearly equal in mass. Humans lie closer to gibbons on the dimorphism spectrum: human males can be up to 20 percent more massive than females.

There is only so much we can make of the fossil record, though.

Paleoanthropologist J. Michael Plavcan of the University of Arkansas urges caution in making the leap from fossilized bones to social behavior in hominins. Consider *Australopithecus afarensis*, the species to which "Lucy" belonged, which lived between 3.9 million and three million years ago. Like *Ardipithecus*, *A. afarensis* had small canines, but its skeleton displays a level of dimorphism between that of modern chimpanzees and gorillas. "You have [a level of] body-size dimorphism suggesting that [*A. afarensis*] males were competing for females and [a] loss of canine dimorphism that suggests they weren't," Plavcan says. "It's a puzzle."

Many anthropologists also dispute Lovejoy's conclusion that monogamy nurtured by males providing food for their mates and offspring has been a hominin strategy for millions of years. Last year in the journal *Evolutionary Anthropology*, Chapais argued that the unique features of human family and social structure (monogamy, kinship ties through both parents and expanding social circles) emerged in a stepwise sequence. Before the first step, Chapais said, both male and female hominins were, like chimpanzees, promiscuous with partners. Then came a transition to polygamy, which is found in gorillas. But keeping

many mates is hard work. It involves a lot of fighting other males and guarding females. Monogamy might have emerged as the best way to reduce the effort of polygamy.

Chapais declines to speculate about when this shift happened and what species were involved. But other researchers are homing in on the period between two million and 1.5 million years ago, after the origin of our genus Homo and coincident with physical changes that show up in Homo erectus, most likely the first hominin species to successfully migrate beyond Africa. H. erectus possessed a much larger body, proportioned more like that of a modern human, than its predecessors. Roughly twice the size of Lucy's species, H. erectus also seems to be less sexually dimorphic than australopithecines and the earliest members of Homo. Limited fossil evidence suggests that H. erectus females started to approach the physical stature of males and to have a similar degree of dimorphism as in modern humans, which together could suggest that H. erectus had a less competitive way of life than its ancestors. Because primates with similar body sizes tend to be monogamous, this change could signal a shift toward more exclusive mating behavior.

A STRATEGIC PARTNERSHIP

IF SCIENTISTS CANNOT AGREE on when humans became monogamous, we can hardly expect them to agree on why it happened. In 2013 two independent research teams published separate statistical studies of existing literature to determine which behaviors could have been drivers of monogamy. Both studies aimed to determine the best explanation for monogamy from three persistent hypotheses, generally known as female spacing, infanticide avoidance and male parental care.

The female-spacing hypothesis posits that monogamy arises after females begin to establish larger territories to gain more access to limited food resources and, in the process, put more distance between one another. With females farther apart, males have a harder time finding and keeping multiple mates. Settling down with a single partner makes life easier, reducing a male's risk of being injured while patrolling his territory and enabling him to ensure that his mate's offspring are his own.

Zoologists Dieter Lukas and Tim Clutton-Brock, both at the University of Cambridge, found evidence for this idea in a statistical analysis of 2,545 species of mammals. They described their findings in a paper published in *Science*. The data indicated to them that mammals started out solitary, but then one species or another switched to monogamy 61 different times during their evolutionary history. Monogamy most frequently emerged in carnivores and primates, suggesting that species will tend toward mating in pairs when its females require a rich but rare diet (such as protein-rich carcasses or ripe fruits) that can usually be obtained only by searching a large area. Their findings provided the strongest statistical support for the conclusion that increasingly scattered, solitary females drove males to solicit single partners.

Lukas acknowledges that although the hypothesis may work for nonhumans, it might not be so apt for humans: it is difficult to reconcile the inherent sociality of humans with a hypothesis that depends on a low density of available females. It may be that our ancestors were too social for females to have been scattered across the savanna like other mammals. But the theory could potentially hold for humans if monogamy arose



AZARA'S OWL MONKEYS of South America are fully monogamous, with the father handling much of the child care.

in hominins before our tendency to dwell in groups did.

The second leading hypothesis holds that monogamy originated from the threat of lethal violence toward offspring. If a rival male challenged or supplanted a dominant male in a community, the usurper could kill infants that he had not sired. Mothers would stop lactating and start ovulating again, giving the marauding male a chance to spread his genes. To prevent infanticide, a female would select a male ally who could defend her and her baby.

Anthropologist Kit Opie of University College London cites evidence for the infanticide-avoidance hypothesis in a study published in the *Proceedings of the National Academy of Sciences USA*. Opie and his colleagues ran computer simulations of primate evolutionary history for 230 primate species; they then applied what is called a Bayesian statistical analysis to determine which of the three prominent hypotheses for the origin of monogamy had the highest probability of being correct. They identified a significant correlation between monogamy in primates and each of the three hypothetical triggers, but only an increase in the threat of infanticide consistently preceded the appearance of monogamy in multiple primate lineages.

The biology and behavior of modern primates add some plausibility to the conclusion that infanticide is a spur to monogamy. Primates are uniquely at risk for infanticide: they have big brains that need time to develop, which leaves babies dependent and vulnerable for long periods after birth. And the killing of babies has been observed in more than 50 primate species; it typically involves a male from outside a group attacking an unweaned infant in a bid for dominance or access to females. But there are limits to the evidence: nearly all these species have either promiscuous or polygamous mating systems, so the distribution of infanticide in living primates does not fit the prediction that monogamy should evolve when infanticide is a big threat.

The third hypothesis for why monogamy evolved highlights a male pulling his weight with parental duties. When a baby becomes too costly in terms of calories and energy for a mother to raise on her own, the father who stays with the family and provides food or other forms of care increases his offspring's chances of survival and encourages closer ties with the mother. A related idea, proposed by anthropologist Lee Gettler of the University of Notre Dame, holds that the mere carrying of offspring by fathers fosters monogamy. Mothers have to meet the considerable nutritional demands of nursing infants. Yet for primates and human hunter-gatherers, hauling an infant, especially without the benefit of a sling or other restraint, required an expense of energy comparable to breast-feeding. Carrying by males could have freed females to fulfill their own energetic needs by foraging.

South America's Azara's owl monkey may offer some insight into how paternal care would reinforce monogamy. These monkeys live in small family groups, with an adult male-and-female pair and an infant, plus a juvenile or two. A mother monkey carries a newborn on her thigh just after birth. But the baby's

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father assumes most of the carrying and caretaking—grooming, playing and feeding—from the time the baby is two weeks old. The adult partners literally stay in touch with frequent tail contact, and the male's mere proximity to both the female and his young may promote deeper emotional ties.

Indeed, a study published in March in the *Proceedings of the Royal Society B* presented genetic evidence that Azara's owl monkey pairs remain monogamous—the first genetic confirmation for any nonhuman primate. DNA collected from several study groups revealed that all the females and all but one of the males in 17 pairs were the most likely parents of 35 offspring. "They go all the way and commit to a monogamous relationship in genetic terms," says anthropologist Eduardo Fernandez-Duque, now at Yale University and a co-author of the study. Mating bonds between Azara's owl monkeys last an average of nine years, and monkeys that stay with the same partner achieve greater reproductive success—the end game of evolution under any mating system.

What do the two recent statistical studies have to say about the paternal care hypothesis? Both concluded that paternal care seemed the least likely among the competing hypotheses to trigger monogamous mating—but, Lukas says, "paternal care may still explain why a species *stays* monogamous."

IT TAKES A VILLAGE

A MONOGAMOUS SET OF PARENTS is not enough to raise an ape as smart and social as a human, says anthropologist Sarah Hrdy of the University of California, Davis. A human baby consumes some 13 million calories on its long journey from birth to maturity, a heavy burden for a mother to bear even with a mate helping. This demand might explain why in many societies, human mothers rely on "alloparents" (such as the kin of either parent or other group members) to help provide food and child care. "Human mothers are willing to let others hold their babies right from birth," Hrdy notes. "That's amazing, and it's remarkably unapelike." No ape engages in anything like alloparenting.

Hrdy maintains that cooperative breeding, a social system in which alloparents help care for young, evolved among our ancient ancestors starting with *H. erectus* nearly two million years ago. This species had a much larger body and brain than its ancestors; by one estimate, it took 40 percent more metabolic energy to run an *H. erectus* body relative to previous hominins. If *H. erectus* started down a humanlike path of delayed development and prolonged dependency, cooperative alloparents might have been required to support the energetic demands of raising bigger-brained babies.

Without cooperative breeding, conclude Karin Isler and Carel van Schaik, both at the University of Zurich, early *Homo* would not have broken through the hypothetical "gray ceiling" that constrains an ape's brain to a maximum volume of about 700 cubic centimeters. To pay the energetic cost of having an enlarged brain, an animal must reduce its rate of birth or its rate of growth, or both. But humans have achieved shorter weaning periods and greater reproductive success than a creature with a brain volume ranging from 1,100 to 1,700 cm³ should have been able to. Isler and van Schaik attribute this success to alloparenting, which enabled *H. erectus* to have offspring more frequently while providing those offspring enough energy to grow a large brain.

It was cooperation, then, whether in the form of monogamous pairs, nuclear families or tribes, that enabled humans to succeed when all our fossil ancestors and cousins went extinct. In fact, cooperation may be the greatest skill we have acquired during the past two million years—one that enabled our young genus to survive through periods of environmental change and stress and one that may well determine our geologically young species' future.

MORE TO EXPLORE

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Male Infanticide Leads to Social Monogamy in Primates. Christopher Opie et al. in *Proceedings of the National Academy of Sciences USA*, Vol. 110, No. 33, pages 13,328–13,332; August 13, 2013.

FROM OUR ARCHIVES

Evolution of Human Walking. C. Owen Lovejoy; November 1988.

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