

MONOGAMOUS MAMMALS: Variations on a Scheme

Monogamy—a mammalian rarity—appears to have two variations in mammals never before thought to be monogamous

BY MICHELLE GALLER RIEGEL

Monogamous mammals are hard to find. But even though it is not a common mammalian lifestyle, monogamy does exist. And depending on which kind of mammal you happen to be observing—humans and their quasi-polygamous monogamy or their distant relations—the variations on the theme of monogamy are surprising and fascinating.

The choreography for the diverse mammalian mating strategies is inspired by that from which the class gets its name—the mammary glands. These most important of the skin glands separate mammals from the other vertebrates by allowing the female to nurture the young with products from her body, independently of all other species members. She becomes a movable feast, providing her young with all their nutritional requirements. She is indispensable for the rearing of her young.

“Until recently,” reported mammalogist Devra G. Kleiman of the National Zoological Park in Washington at a recent Smithsonian Institution symposium, “the importance of this basic difference between mammals and other vertebrates, and observations of the difference between the male’s contribution to rearing the offspring in some mammals, has not been sufficiently emphasized when discussing the evolution of breeding systems.” Males do not have functioning mammary glands, and so it is impossible for them to figure in child rearing at any level approaching the female’s involvement. Viewing the male solely from a biological standpoint then, his function, in the simpler breeding arrangements, is to fertilize the eggs. So a very basic scenario in a mammalian reproductive system—common among the morphologically less evolved—requires only a relatively short interaction between the male and female, ending in insemination, egg fertilization and birth. This is followed by a short nursing period and the female’s tolerance toward the young. The male, at this point, may not be accorded even this basic tolerance, and in some situations is even thrown out.

Not all animal social systems hold the male in so little esteem. Among some fish and bird species, polyandry (the female mates successively with different males) is the male’s entree into acceptance. In birds, the female might find the

nest of several receptive males choice sites to raise families. She deposits eggs in each nest, and from there on, the male incubates the clutch and plays both mother and father to the newly hatched brood while *she* protects the surrounding territory. In the freshwater darter, however, the male fish is the rearing agent, while the female produces the egg clutches, tends and defends them. All told, polyandry is unknown in mammals. However, the scheme in which males monopolize a group of females during one mating season and fertilize each (polygyny) is common in mammals and some birds.

The system wherein one female mates with one male during a rearing cycle has previously sufficed as the simple definition of monogamy, Kleiman says, but she sees the reality as more diverse. “Among mammals, there is variability in the expression of this [monogamous] social and reproductive system,” she says.

She describes definite distinctions between what she has termed *facultative* and *obligate* monogamy. “The variability arises from the amount of parental investment by males, the quality of the relationship between a pair, and the mechanism and timing of dispersal of maturing offspring. The crucial point,” she emphasizes, “is the amount of paternal investment in rearing the young. Most of the species that I consider to be facultatively monogamous have not previously been considered to be monogamous at all, but rather solitary.”

The elephant shrew, for example, named for the shape of its nose rather than for its size, which is tiny, gives a vivid portrayal of facultative monogamy in action. This feisty little *Macroscelididae* resides in the deserts, bushlands and tropical rain forests of Africa. The female of this insect-eating, cursorial (adapted to running) species is larger and more aggressive than her mate. Since building safe nests is not part of their repertoire, elephant shrews rely on flight over fight as their protection from predation. In

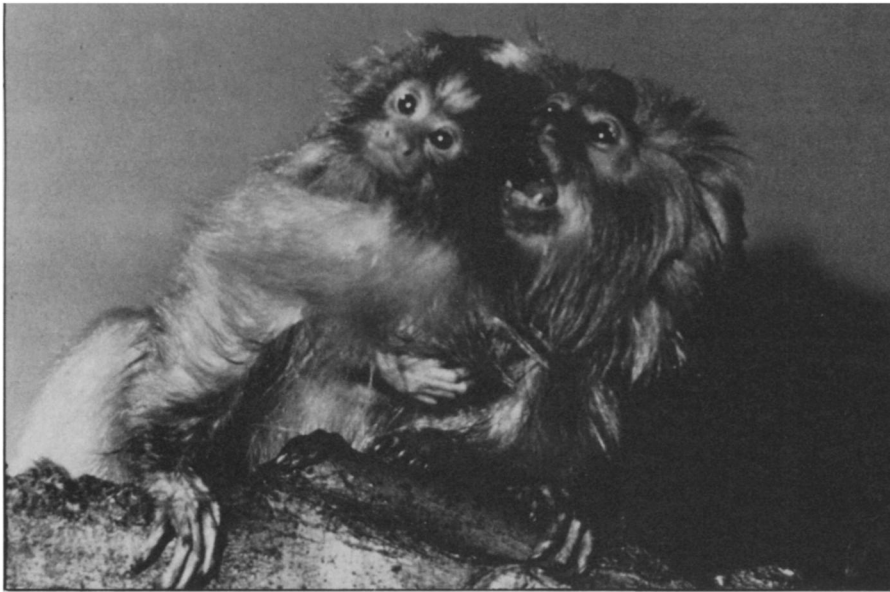
order to flee successfully, a complicated maze of escape routes is scrupulously built and maintained, mainly by the male.

Their connubial cooperation is notable by a complete lack of it; they neither sleep nor rest together, are almost never at the same place at the same time. And mutual grooming or elaborate courtships are pretty much absent. If the female happens to come across a mound of succulent termites, she polishes them off without giving her mate a second thought. Yet, intruders of the same sex are vigorously banished from their joint territory, resulting in less potential for sexual relations outside of the pair. So, the social interactions between them are definitely not effusive. As for reproductive cooperation, aside from the actual mating from which one or two offspring are born in a state of advanced development, the male spends almost as little time interacting with his progeny as he has with his mate. He provides a favorable environment where the young can safely reach maturity, but he does not feed them or socialize with them, aside from some perfunctory “checking them out.”

So, this plan in which there is little direct paternal care, exclusivity in mating characterized by aggression against those of the same sex, and dominance by the female, is facultative monogamy. “It is also the least recognized form of monogamy in nature because the pair do not necessarily remain together during the conduct of the [territory] maintenance activities,” says Kleiman. “Mammals exhibiting facultative monogamy are often [mistakenly] considered to be polygamous. No one was looking closely,” she continues. “After Galen Rathbun made several studies and found that elephant shrews were pair-bonded [the reproductive unit], we began to examine the patterns of paternal care more closely.”

If one looks an evolutionary step or two beyond facultative monogamy—for example, at several species of Canid—the degrees of obligate monogamy become clear. “Monogamy is not a unitary phenomenon,” Kleiman explains, “but, rather, there are two extremes with gradations in between.”

At the simplest extreme of the obligate monogamy continuum is the South American crab-eating fox (*Cerdocyon thous*). The male and female hunt



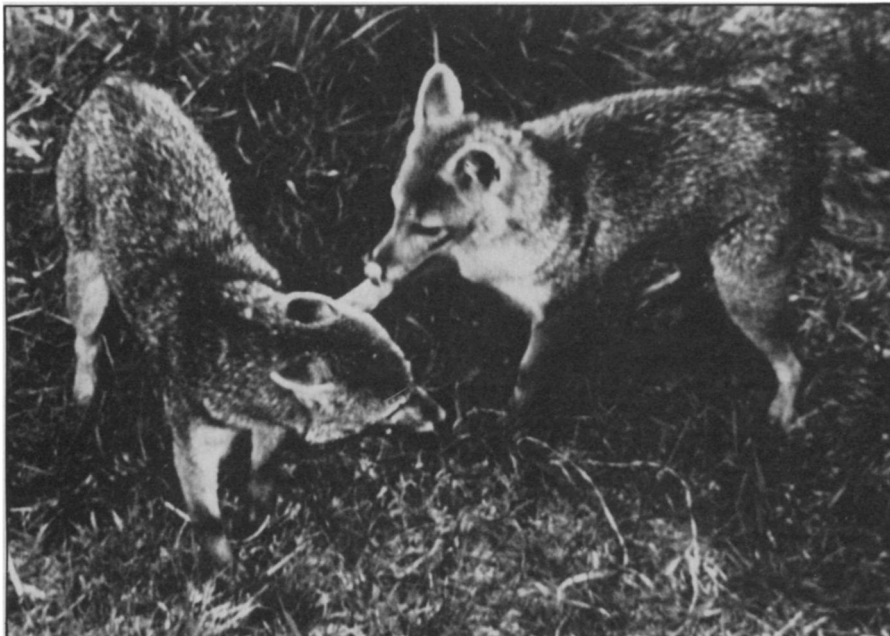
Father lion tamarin carries junior piggyback style, illustrating direct paternal care.

Pat Vosburgh/National Zoo



The elephant shrew's mating scheme involves role separation and little paternal care.

Galen Rathbun/National Zoo



Greeting behavior in the crab-eating fox is part of their obligate-monogamous bond.

Charles Brady/National Zoo

together in a jointly maintained territory, and, in general, appear quite companionable, a relationship which they blatantly display on reunions, through much face licking and tail wagging. She builds the nest for the three to six helpless young, and he drops out of the picture for a while. Like the elephant shrew, he may occasionally check out the young, but, aside from that, the only contact he maintains with his new family is depositing chunks of carrion or some juicy vegetable matter at the mouth of the nest. Not until weaning has substantially progressed does he attempt direct contact with his clan, at which time the family joins in communal foraging forays. But this paternal propinquity lasts only until the pups show that they can hunt independently. It is not clear what causes the breakup of the family, but the pups disperse at this stage, and, consequently, there is no chance for an extended family to form. By the time the female becomes pregnant again, the litter is gone.

The African wild dog (*Lycaon pictus*) and the bush dog (*Speothos venaticus*) further elaborate on this obligate monogamous theme. They are distinguished by the male's increased investment in the care of the juveniles, and also by the use of older offspring from previous litters. This more sophisticated form of obligate monogamy places them up further on the continuum.

Since the wild dogs function in closely linked packs of unrelated adults—except for young litter mates—previous studies have assumed that they were polygamous. But, in fact, their reproductive strategy is a highly evolved form of obligate monogamy. "It is important to think of the social unit involved in the production of young as a means for replication of itself," says mammologist John F. Eisenberg, also with the National Zoo. Only one dominant pair breeds at a time, and the survival outlook for any competitive female and her litter is bleak, as the dominant female guards her status fiercely, to the point of seeking out her rival and threatening her and, in some cases, killing any illegitimate pups.

By utilizing older juveniles in pup-rearing detail an extended family develops which serves a dual purpose. It reduces the potential for adultery since the nonreproductive females are supportive of the dominant female and will ignore and starve out any contender for that status, and the nonreproductive siblings do contribute their genetic material to future litters by aiding in the survival of the present litter. As Eisenberg says: "Related kin could pass on a significant portion of their genotype by exhibiting 'altruistic behavior' toward a relative, if by such behavior they increase the probability of passing on the shared genotype to a level greater than their own probability of reproducing." It is not clear whether the father wild dog plays a role in child rearing that is any different than those of the communal assistants, but that he participates is clear.

The bush dog, also previously thought to be polygamous, is "one of the few monogamous mammals in which the exclusivity of the emotional bond may itself prevent adultery, rather than just within sex aggression," says Kleiman. "If this can be adequately demonstrated, the importance of the emotional bond and its genetic consequences will have been shown."

The male lion tamarin (*Leontopithecus rosalia*), a small, arboreal primate, expends considerable amounts of paternal energy by being his youngster's main source of transportation—he carries them from tree to tree on his back. The tamarin pair shows synchronous behavior similar to that of the foxes and bush dogs. They rest in contact, groom each other and aggression seems to be predominant among the females.

In an overview of the two patterns of monogamy, says Kleiman, "Paternal care is the crucial difference between the facultative and obligate types of monogamy [in mammals]." Bonds between the dominant pair are strong, kin are nonreproductive in the extended families and cooperation between the breeding pair in getting food and maintaining territory are characteristic of obligate monogamy. Dominance and aggression seem to be the female's domain. That the female is also dependent on familial support for her offsprings' survival is in sharp contrast to the facultatively monogamous elephant shrew, whose major need from her spouse seems to be secure territory in which to rear the youngsters. There is less paternal child-rearing support in the shrew's type of monogamy.

The reasons for these kinds of ecological specializations, say, in the elephant shrew's brand of facultative monogamy, can be understood. According to Kleiman: The species is too small to be highly mobile and, because of its size, can defend only a small area of territory. Resources such as food and shelter are rich but widely scattered, so they are outside of the little creature's turf and so are scarce. The male is too small to defend an area large enough to hold more than one female; the female cannot share a territory with another female, but cannot defend it alone and still care for the offspring. The best thing her mate can do for her and for future generations of little shrews is to defend the common territory, as opposed to the needs of the obligate female who has increased her reproductive burden so much that direct paternal, or kin, assistance is mandatory.

Coming full circle to human mammalian creatures, no clear-cut classifications can be easily made about reproductive strategies. "We do not live according to the realistic demands of our environment and the restrictions of our resources," says Eisenberg. "It is axiomatic that many cultural norms enforced through group ethics were once highly adaptive to a particular economic situation . . . Were we to understand our history completely we would find that the

ethical systems of humans were once rooted in biological necessity."

As the unique and highly mobile tribes of our ancestors settled into more stable lifestyles, intertribal behavior changed. The infant's increasing dependence and its slow maturation rate may have provided the impetus for greater paternal contribution to rearing the children. Kleiman does not think humans started out being monogamous but, she says, "Humans became monogamous because their evolution was dependent on the fact that the females were producing infants that were extremely dependent and would need prolonged parental care. This pushed humans into an obligate monogamous situation. We were expanding range very rapidly," she says. "and so, many culturally imposed sexual taboos designed to reduce infidelity may have resulted, but separating the biological reasons from the cultural reasons for monogamy is very difficult. Monogamy was imposed upon us and has been successful," from a reproductive standpoint.

According to Kleiman, the American middle-class brand of monogamy, as seen in the suburbs, is typically of the facultative or the simple obligate kind, depending on the amount of contact the spouses maintain and on whether their roles are clearly divided. "A typical household can consist of a woman essentially rearing her children alone . . . with the male protecting the home and indirectly providing food through wages received from his job, but having little interaction with the young and a weak emotional bond with his wife," she ventures. The chance for sexual infidelity is great because the man has so absolutely little to do with the woman.

"It is interesting to compare this to a farm family with a more obligate-like lifestyle where there's less sexual role differentiation and perhaps more likelihood of an extended family . . ." says Kleiman. In the West, the extended family, composed of nonreproducing adult offspring with parents, aunts and uncles, is the exception, and this form of obligate monogamy has usually occurred where land was limited and populations expanding. For instance, in Ireland, where the young could not marry without holding land, it was common to postpone any matrimonial plans until the death of the parents.

Says Kleiman, "Man seems to have retained behavior that is more in line with polygamy." Human males are generally larger, more dominant and are encouraged to be the aggressors. There still tends to be great role differentiation, and the extent to which males become directly involved in child-rearing activities seems to stop at the nursery window. None of these traits concur with obligate-monogamous characteristics.

Bertrand Russell sensed this dichotomy of human behavior and in 1929 he wrote in his *Marriage and Morals*: "Uninhibited civilized people, whether men or women, are generally polygamous in their instincts." □

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