

SQUIRRELS: A WINDOW INTO SOCIAL EVOLUTION

By Richard W. Thorington Jr.

Because animal behavior leaves few traces in the fossil record, how do scientists study its evolution, which has an astonishingly long history?

Jane Waterman, of the University of Central Florida, believes one way is to compare the social behavior of related groups of animals living in different environments. By comparing a unique mating system discovered in ground squirrels in Africa to the more typical mating systems of ground squirrels in North America, Waterman seeks answers to important questions about social behavior's evolution.

For instance, why live in groups? "Most people don't realize that being social incurs many costs," Waterman said. Whenever you live with another member of your species, you run the risk of competing for limited resources, exposure to disease and parasite populations, attracting predators to the group, competition for mates, and social conflict. There have to be benefits to counter these costs, such as more quickly detecting predators, locating food, hunting cooperatively, defending resources, or improving care of young.

The hypothesis Waterman plans to test in southern African ground squirrels is that a harsh, arid environment can delay the dispersal of young from the family unit, which may be what led to social groups in this species in the first place.

What makes Africa's Cape ground squirrels unique is that they are extremely social creatures, but males and females operate within very different social systems. No other species of ground squirrel has all-male groups that band together on a permanent basis. Male Cape ground squirrels live in all-male bands of up to 19 individuals, though they usually

cluster in smaller sub-bands of about four or five individuals.

The size and composition of the sub-bands change daily. The males in each band have a linear dominance hierarchy (also known as a pecking order) determined not by outright aggression but by displacement. The way displacement works and the way hierarchy is maintained is that one male usually jumps away from another, more dominant male.

The most dominant males are the oldest. New animals typically begin at the bottom of the hierarchy and slowly work their way up. Social readjustments appear to be determined by this displacement and by ritualized jumping without contact.

Male bands are very cohesive. Animals spend time in the evening grooming one another and sharing sleeping burrows. Evidence suggests these groups are composed of unrelated males, and Waterman plans to examine DNA from marked individuals to test their genetic relationships.

She has shown that the most dominant males have the greatest mating success, but that does not guarantee the greatest success in siring offspring. There may be sperm competition, in which sperm from one male out-competes sperm from other males within a female's reproductive tract. To test this, Waterman will look at the paternity of offspring in the area of the male band.

Female social groups are smaller than male groups, comprising about five related females and their young, and the adults are cooperative breeders. Although females ovulate according to irregular cycles throughout the year, young females living in larger groups (with two to three adult females) seem to have their cycles suppressed compared to young females in groups with only a single adult female.

All individuals in a group care for their young. They interact directly with the juveniles and mob potential predators. Juveniles survive better in smaller groups,

probably because in larger groups, home range size is larger and the home burrow farther from foraging areas, making it more difficult for young squirrels to escape from predators.

The male and female home ranges overlap. The males move throughout their ranges, approaching almost every female they see. Females usually ignore the males unless they harass them too much, in which case they respond aggressively. On the day a female begins ovulating, males actively seek her, and she copulates with them both above and below ground.

If the benefits of being social outweigh the costs, then what do the ground squirrels gain from this arrangement? For male Cape ground squirrels, social groups may help them defend against predators. The group is better at avoiding predators through enhanced vigilance (with more eyes to watch for predators) and at deterring predators by mobbing them. For small rodents that are active in the day and move about the veldt looking for females, the benefit of grouping to avoid predators must be high.

What about female Cape ground squirrels? Is the same true? Are there significant benefits from cooperative breeding that outweigh the costs of group living?

Most cooperative breeding units among mammals are despotic—only a single female reproduces. By studying a social system in which more than one female is breeding, Waterman can test many hypotheses on behavioral evolution.

Africa's Cape ground squirrel offers a fine model to study social evolution. The all-male groups in this species are not typical because the individuals usually are not closely related to one another. The females offer a paradox because they cooperate to breed.

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