

BEHAVIORAL ECOLOGY

## At Home on the Range: Prairie Rodents **Yield Their Secrets to a Dogged Observer**

To say that John Hoogland is passionate about prairie dogs is an understatement. Fanatic is more like it. A behavioral ecologist, he has studied these North American colonial rodents for 40 years, spending months at a time sitting in a blind from dawn to dusk recording the activities of each individual in a colony. "Catch 'em. Mark 'em. Watch 'em," is his motto; he rarely does experiments with the animals. "His style is a throwback to the old days of living with your organism and getting to know them really well, and in the process you get insights that are simply not possible otherwise," says Tim Clutton-Brock, a behavioral ecologist at the University of Cambridge in the United Kingdom. "That approach is increasingly rare."

On page 1205, Hoogland, 64, who works at the Appalachian Laboratory of the University of Maryland Center for Environmental Science in Frostburg, describes his latest insight: that young female prairie dogs move out of their territories when their close kin go missing. He finds this tendency in three species, even though long-accepted wisdom holds that relatives tend to disperse to avoid competing with each other. "John has sort of turned this old idea on its ear," says Charles Brown, a behavioral ecologist at the University of Tulsa in Oklahoma. The result helps illuminate how competition and cooperation both play out in the life of a prairie dog and "flies in the face of a lot of mathematical modeling," adds F. Stephen Dobson, a behavioral ecologist at Auburn University in Alabama.

Other researchers have studied mammals for decades, but few have done so with Hoogland's unflagging fervor. Early each spring, he heads to a remote study site, usually in the U.S. Southwest, to catch the animals as they emerge from hibernation. Prairie dogs live in colonies of a dozen to thousands of individuals, sharing burrows with their close relatives. Hoogland stays at the sites for 4 months, until the last pups have started to spend their days above ground and are weaned. To survive sitting still all day in frigid towers at 2600 meters elevation at his current site in New Mexico, he wears 11 layers on his torso, eight pairs of pants, snowmobile boots, and two wool hats. "I usually don't even notice the cold, there's so much

Prairie dog passion. John Hoogland has intensively studied these colonial rodents for 40 years.

going on," he says. But Hoogland repeatedly warns his three or four seasonal undergraduate assistants that in the field, they will be the coldest they have ever been.

The researchers catch pups as they emerge from underground nests, then place permanent tags on their ears and dye a number or unique marking on their flanks to easily identify them from afar. Twice a year, Hoogland sets out 500 live traps for several weeks to recapture and remark the adults.

Hoogland started out in Wyoming in 1974 with black-tailed and white-tailed prairie dogs, two of the five species in North America, trying to assess the costs and benefits of colonial life by looking at differences between small and large colonies. He then spent 15 years observing a 200member black-tailed prairie dog colony at Wind Cave National Park in South Dakota, 7 years watching Gunnison's prairie dogs in Petrified Forest National Park in Arizona, 7 years studying white-tailed prairie dogs in Arapaho National Wildlife Refuge in Colorado, and 11 years with Utah prairie dogs in Bryce Canyon National Park in Utah. Now, he's back with Gunnison's prairie dogs, this time at Valles Caldera National Preserve in New Mexico.

Starting in 1978, Hoogland and his undergraduates discovered that in each prairie dog species studied, a female is receptive to breeding just 1 day a year for about 6 hours. During that time most females try to mate with multiple males. Hoogland's long-term data on reproductive success indicate that polyandrous females are more likely to get pregnant and wean larger litters with offspring that are more likely to live at least a year. But these advantages come at a cost, as the females themselves are less likely to survive to the next mating season, he will report later this year in the Journal of Mammalogy.

Spying on prairie dog romances "is better than watching Grey's Anatomy," the TV show, he says. Males compete intensely with each other, biting and chasing off rivals. Successful suitors go to great lengths to try to keep females from mating a second time. Tracking this prairie dog soap opera, Hoogland has racked up more than 60 papers, several in influential journals, and written two books. "I just wish every biologist in the world could spend 1 day watching prairie dogs during the mating season," Hoogland says. "It would blow them away."

These front row seats to prairie dog biol-

ogy demanded sacrifices both personal and professional, however. After a postdoc at the University of Minnesota, Hoogland spent 6 years as an assistant professor at Princeton University but failed to get tenure. "They really wanted me to be on campus for more of each year, but my research was going so well that I wouldn't give up on the prairie dogs," he says.

He quickly landed at the University of Maryland satellite lab in Frostburg, where he can spend 5 months away at his field sites. But the center is hundreds of kilometers away from the main campus, and Hoogland has only one Ph.D. student, from the Princeton days, in his pedigree.

To keep his family together, Hoogland's wife, Judy, home-schooled their four children. The kids grew up watching prairie dogs with their dad and with open spaces as their playground. "We were like gypsies, leaving [home] each spring," Hoogland says.

His 1985 finding that closely related lactating females will kill their relative's newborn pups, presumably to eliminate competition, drives home the value of such dedication. This was "a gargantuan surprise," Hoogland recalls, as most of the time, related prairie dog females seem to help each other out. The team witnessed infanticide only once every 300 hours of observation. But Hoogland has many thousands of such hours under his belt and spent a season with a backhoe to dig out burrows to find dead pups. He was able to document that more than one-third of litters have some or all of its members killed by other prairie dogs. The finding demonstrates that fierce competition lurks beneath

the prairie dogs' communal life (*Science*, 29 November 1985, p. 1037).

Hoogland can thank his wife for his latest surprise. Among prairie dogs, young males often leave their birthing ground while females stay put, forming a family unit called a clan with the mother, her daughters, sisters, and sometimes cousins. But a few exceptional females left their territories, and these sparked Judy's curiosity. "I said it's so rare, it's not worth looking at," Hoogland recalls. But she wore him down.

When Hoogland did the analysis in blacktailed prairie dogs, he found that females with no mother, sisters, or brothers nearby







**Hoogland's world.** By marking prairie dogs on their flanks (*top*) and watching them in all sorts of weather from towers (*middle*), Hoogland has gleaned insights into these animals' family dynamics (*bottom*).

were 12.5 times more likely to move away than females with a close relative around. In Gunnison's prairie dogs, such dispersal was 5.5 times more likely, and in Utah prairie dogs, 2.5 times, he reports.

The results are very convincing because Hoogland has such a large sample size—the data were drawn from recorded movements of 744 males and 907 females from 1093 litters—says Dirk Van Vuren, a behavioral ecologist at the University of California, Davis. And the findings were unexpected. "This [result] is contrary to the predictions made by two of behavioral ecology's superstars," Hoogland says.

In 1977, William Donald Hamilton and Robert May argued that close kin disperse to avoid competing with one another. They used mathematical models to evaluate the effect of relatedness on animal behavior and predicted that if two sisters stayed in the same place, for example, competition for resources would lower the fitness of both. In theory, one sister should leave. Research in scores of species, including mice, wasps, and lizards, has supported this idea.

Instead, Hoogland finds that "cooperation with other kin can counterbalance the amount of competition that close relatives have," Dobson comments. That counterbalance may help explain family groups in other animals, such as wolves, dolphins, and primates. Prairie dogs are indeed cooperative: They sound off to warn each other of approaching predators, and once the young emerge from nests, females nurse them irrespective of parentage. When the services provided by their close kin disappear, young females may leave to seek out territories with more food where cooperation is not as crucial to their survival or reproductive success, Hoogland suggests. Alternatively, the absence of kin may simply signal that the area is no longer a good place to live.

Prairie dog researcher Con Slobodchikoff, a behavioral ecologist who is now officially retired from Northern Arizona University in Flagstaff, is hesitant about these results, however. He suggests that genetic data would help guarantee that individuals sharing a territory really are closely related. But Hoogland thinks that his observations are enough to establish kinship.

Clutton-Brock is satisfied with Hoogland's observational approach. "There's a big push throughout science to focus on experimental results," he explains. Hoogland's work "shows how top level science can be done without experimenting."

Analyzing the effects of competition and cooperation in prairie dogs may help explain the behavior of other species, too, adds Ana Davidson, a conservation ecologist at Stony Brook University in New York. "Uncovering all these exciting insights into the world of the prairie dog is teaching us a lot about social behavior of animals in general."

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