Life at the Top: Animals Pay The High Price of Dominance

Bar-Dot, the dominant female in a pack of dwarf mongooses in Tanzania's Serengeti National Park, has been keeping subordinate animals in line for at least 5 years, carefully watched by behavioral ecologists Scott and Nancy Creel. Day after day, Bar-Dot rushes over to other females who are acting up, bares her teeth, and threatens the others into deferring to her. It's a tough job, but there are perks: She's first in line for any food, and has the sole right to reproduce. And her subordinates should be the ones who get stressed out—at least that's what the textbooks say.

Yet according to the Creels, of Rockefeller University, those textbooks are wrong. In this week's issue of *Nature*, the scientists, with Steven L. Monfort, an endocrinologist at the Smithsonian Institution's Conservation Research Center, report that Bar-Dot and the other dominant female mongooses in 14 packs had the highest levels of cortisol, a stress-related hormone, of all pack members. And they've found precisely the same effect among both male and female wild dogs in Tanzania's Selous National Park. These results, along with recent studies of female baboons by other researchers, show that dominance can exact a high price. In the baboons, the cost seems to be a higher miscarriage rate; in the dogs and mongooses, chronic stress is thought to lead to a shorter life-span for the alpha animals.

Biologists are getting this glimpse of the costs of dominance because for the first time, they are studying hormone levels in several free-ranging rather than captive species of mammals by analyzing urine and fecal samples. "For a long time the dogma has been that the subordinates are the ones that are most stressed," explains John C. Wingfield, a comparative endocrinologist at the University of Washington, Seattle, who has studied pecking orders in wild birds and found patterns similar to those seen by the Creels. "But much of that has been based on captive studies of rats, mice, and primates; whereas the beauty of these [the Creels'] data is that they're from the field—and all of a sudden, things start to be very different." Some scientists do, however, have a few reservations about the accuracy of the testing methods.

The older idea that subordinates are the ones who suffer from chronically high stress grew out of the research of J. J. Christian and Seymour Levine, who worked with captive colonies of rodents and primates beginning in the 1950s and '60s. They found that subordinates, with higher levels of cortisol, suffered from ill health and reproductive failure. Cortisol and other glucocorticoids, secreted as part of an animal's "flight or fight" response, cause severe health problems if pumped out over the long haul, says Stanford University neurobiologist Robert Sapolsky, who has observed stress effects in subordinate wild male baboons. "They put all of the body's long-term processes—tissue repair, immunity, digestion, reproduction—on hold," Sapolsky explains.

PHOTOS BY S. AND N. CREEL

Stressing out. Dominant wild dogs (*above*) and dwarf mongooses (*animal at far right*) have high stress hormone levels.

The finding of high stress levels in subordinates provided an explanation for the evolution of dominance, because it meant that the more aggressive animals stood a better chance of reproducing. And that was the pattern the Creels expected to find in their wild dog and mongoose populations as well, because fertile, subordinate individuals (who receive most of the aggression) in these groups rarely reproduce. "We thought that stress could be a factor" in suppressing the subordinates' reproduction, says Nancy Creel.

From long-term observations, the Creels could identify the dominant and subordinate animals. In studying the dogs, the researchers followed individuals around and collected their fresh droppings for later hormonal analysis. For the dwarf mongooses, the Creels trained the animals to urinate on a rubber sandal at a specific time each day. Both methods allowed them to collect the large number of samples (740 for the mongooses; 216 for the wild dogs) needed to establish basal stress hormone levels for each species, and to observe how individual animals deviated from the norm.

Contrary to their expectations, the Creels found higher glucocorticoid levels in the alpha males and females. "Their high glucocorticoid levels are probably a result of their aggressive behavior," Scott Creel notes. Top dogs and mongooses have to assert their rank daily. And birds do it too. Wingfield has shown that in territorial birds such as the red-winged blackbird, dominant males with large areas to guard have higher levels of corticosterone and testosterone than the males lacking territories.

Just what this means for the dominant animals' health, however, is not clear. Alpha female baboons do have higher miscarriage rates, according to studies by behavioral ecologist Sam Wasser of the University of Washington and Center for Wildlife Conservation, but he hasn't measured their stress hormone levels. But in the birds, dogs, and mongooses, high stress hormones don't keep dominant animals from having babies. "All we can say right now is that, contrary to expectation, the higher glucocorticoid levels are not affecting the dominant animals' reproduction. So they must be paying the price in another way—perhaps in a shorter life span," says Scott Creel. That might still allow the dominants to leave behind more young in their short lives than the subordinates do in their longer ones—an area the Creels now plan to investigate.

Some researchers do worry about the methodology—that hormonal levels drawn from feces and urine will never be as precise as those taken directly from an animal's blood. "There are so many difficulties in putting together an accurate measure. Were the samples collected at the same time every day? Do the animals pool the same amount of steroids in their urine in the same way?" says Sapolsky. "These can all confound the picture." But Wingfield and others say that given the large sample size, most of this "background noise" should be filtered out.

Most importantly, he and other researchers suspect that field biologists will now see a variety of relationships between hormones and behavior in mammals—dependent not only on the individual's place in a hierarchy, but on particular populations and species. "We're realizing that hormonal levels are more and more situation-dependent," says Jeanne Altmann, a behavioral ecologist at the University of Chicago, who is studying stress hormones in free-ranging baboons with Sapolsky. "It may be that we have to examine a lot of particularities before we reach the generalities."

–Virginia Morell