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Rebranding the Hyena

Researchers unravel the private life of this weird, wonderful carnivore

John Pickrell

In the movie *The Lion King*, hyenas are the villains. They're portrayed as slobbering, mangy, stupid scavengers always ready to do someone else's dirty work. It's entertaining, but the caricature perpetuates wrong ideas about these social carnivores, bemoans zoologist Kay Holekamp. She should know. For the past 14 years, she has followed the soap opera played out by a clan of around 70 spotted hyenas in the Talek area of Kenya's Masai Mara National Reserve, and she's out to set the record straight.

The truth of the matter, Holekamp exclaims, is that the spotted hyena (*Crocuta crocuta*) is highly intelligent, with mental abilities and social skills to match many a primate. These hyenas are also superb predators, feeding mostly on fresh meat. Their hunting skill equals that of lions or cheetahs. Moreover, Holekamp continues, "once you've seen a female delicately carrying babies in those great bone-crushing jaws, you realize what wonderful mothers they are."

Holekamp and her colleagues at Michigan State University in East Lansing have a deep affection for hyenas. They've given the animals names of U.S. presidents, ancient gods and goddesses and goodies, such as Hot Dog, Moon Pie, and Jujubee. The zoologists have been monitoring the Talek clan from dawn until dusk since 1988. At any one time, several members of Holekamp's team are stationed in Kenya.

In their jeep, the researchers follow the hyenas. The scientists collect data on behavior and interactions and take blood samples. They have used the information to investigate topics ranging from immunology to conservation. Recent studies focus on social structure and how it passes between generations, mating preferences, variation in reproductive success, and the evolution of intelligence

The study by Holekamp and her colleagues "is without a doubt one of the best long-term studies on a social carnivore," says Marc Bekoff, a behavioral ecologist at the University of Colorado at Boulder. "They ask really neat questions . . . and in terms of breadth, [their work] is the best you can get."

Evolutionary oddity

Hyenas, which are more closely related to cats than to dogs, come in four species. Only the spotted hyena lives in a clan with a rigid hierarchy. It's by far the most prevalent hyena and, in fact, the most abundant large African carnivore?outnumbering the lion many times over.



FEARSOME YAWN. Hyenas have incredibly powerful teeth and jaws. Researchers say that a hungry pack can reduce a 450-kilogram zebra to a pile of hooves in less than 25 minutes.

Engh

Spotted hyenas are unique in many ways. They live in large clans whose members occupy a common territory. The Talek clan's homeland covers 65 square kilometers, equivalent to the area of a medium-size city. The clan is a loose entity in which animals travel, forage, and rest in fluid subgroups that can change composition by the day or even hour. In the rigidly structured clan, high-ranking animals enjoy the best access to food. Within a clan's related female lineages, rank is passed from a mother to her cubs.

The spotted hyena differs from most mammals—with the exception of lemurs—in that the females are the dominant sex. They outrank males and are the more aggressive gender.

This female dominance comes by way of a rare degree of masculinization. Female hyenas, which are often larger than males, have higher concentrations of the typically male hormone androstenedione in early life and are host to some bizarre genital morphology. The hyena clitoris is an elongated structure that resembles the male's penis. The females urinate, mate, and give birth through this highly elastic pseudopenis.

The reversal of gender roles in the spotted hyena raises compelling questions, not the least of which is, How do males fare in a mating game where the females call the shots?

In many mammal societies, the reproductive success of males is tightly tied to rank. Male carnivores from polar bears to meerkats attempt to defeat each other in competitions. Victors attain a higher rank and tend to father more offspring. Does this behavioral dynamic hold true in spotted hyena clans?

To answer this question, Holekamp and her colleagues examined a behavioral pattern common among mammals. Female hyenas remain in the clan of their birth, while even high-ranking males between 2 and 5 years of age say goodbye to home. Life is tough for a lone hyena, and many perish, but with luck, the male is accepted into a new clan.

The immigrant male enters at the back of the hierarchical queue. Even a top-ranking male with easy access to food in his original clan is forced to feed on scraps in his new clan.

"We wanted to know why they would leave such a great situation" for one that was uncertain at best, says Anne Engh, also of Michigan State.

Could it be that the highest-ranking male hyenas don't have the reproductive advantage described in other mammals? Engh wondered. She and her coworkers examined DNA to determine the paternity of all Talek cubs born between 1988 and 1999. The team compared the number of cubs sired by young, sexually mature males who hadn't yet left home with that by immigrant males.

The researchers found that an astonishing 97 percent of cubs are fathered by immigrant males, even though they are outranked by the younger native males. This is a powerful confirmation that absolute rank is not the major factor in defining reproductive success, the researchers say. The tenure of the immigrant does matter, however. The longer he stays with a new clan, the more likely a hyena is to father offspring. The findings are reported in the March *Behavioral Ecology*.

Female hyenas have the reproductive ball in their court, partly because their strange genital morphology gives them a rare sexual power—it's impossible for a male to force them to mate. To complete the difficult task of penetrating the pseudopenis, the male needs the female's cooperation. As a consequence, male success becomes completely dependent on the whims of females.

"Spotted hyenas stand in marked contrast to virtually all other [promiscuous, group-living] mammals," Holekamp adds. "Large size and aggressiveness appear not to do male hyenas much good."



EASY DOES IT. Notwithstanding the status they enjoyed at home, immigrant males, such as this new recruit to Talek, are forced to adopt a submissive posture to even tiny cubs in a new clan.
Holekamp

Lucky in love?

Although female choice plays a domineering role in hyena mating, males can also be picky, even if they're the mate-and-run type.

Female animals typically invest more time and energy in pregnancy and parental care, so it pays for them to be selective about mates. However, in species where males also invest heavily in parenting, or where there's a wide range in mate quality, it makes sense for males to be choosy, too.

The quality of hyena mothers varies widely. High-ranking females have greater access to resources than their clanmates do, so they get pregnant earlier and produce more offspring, says Micaela Szykman, formerly of Holekamp's group but now at the Smithsonian Institution Conservation and Research Center in Front Royal, Va. "High-ranking females can produce 6 to 10 times the number of offspring that a low-ranking female produces," she says.



BENEVOLENT BRUTE. A hyena mom from the Talek clan shows her gentle side. Holekamp

Szykman and her Michigan colleagues decided to test whether immigrant males distinguish between females of varying rank and state of fertility. Observers can identify individual hyenas by their constellation-like spot patterns, each as unique as a human fingerprint.

The researchers chronicled how much time immigrant males spent approaching and associating with specific females. Previous research had indicated that males increase chances of mating with a particular female by spending time with her.

The researchers observed 15,353 interactions of males and females between 1988 and 1995. They then created so-called association indices for each possible male-female pair. The higher the score, the more time the couple spent hanging out together. The researchers also turned to the stored blood samples and examined DNA markers to determine the paternity of the cubs. The findings confirmed that male hyenas spend more time with the mothers of their cubs than with other females.

The scientists used the same body of data to identify those females with whom the males initiated the most interactions. The results showed that males know exactly what they are doing. Overall, males preferentially associated with females of high rank and in a fertile reproductive state.

Male rank was also a significant factor. High- and middle-ranking males associate most commonly with top females, while low-ranking males associated more equally with females of all ranks. Szykman and her colleagues reported these findings in the May 2001 *Behavioral Ecology and Sociobiology*.

Even though investing a lot of time with one female can preclude exploring other reproductive opportunities, says Szykman, the investment can pay off by increasing the chances of siring offspring with a first-class mother. "Traditionally, the males of a species dance, and the females choose," adds Szykman, but in hyenas, females vary so much in reproductive success that it makes sense for males to select wisely.

Aping monkeys?

Another puzzling aspect of the spotted hyena's social structure is that it closely resembles that of the socially complex old-world monkeys, a group including baboons and macaques.

These primates also live in permanent social groups which include adult males and multiple lineages of adult females with offspring and have well-established pecking orders. Social status is usually not based on size, strength, or fighting ability, but instead passes from a mother to her offspring.

Scott Creel, an ecologist at Montana State University at Bozeman, says he's often been struck "by the view of anthropologists that [primates] were unique and qualitatively different from the rest of the animal kingdom" Largely due to the work of Holekamp's group, "it's now widely recognized that

'primatelike' social complexity can be found in other species," he says.

Considering the similarities between the monkeys and hyenas, Holekamp and her coworkers wondered whether any of the existing theories about how primates pass their rank from generation to generation could apply to young hyenas.

One theory holds that rank is based on physical characteristics and is therefore genetically inherited. Another suggests that higher-ranking animals preferentially direct unprovoked aggression—a sign of dominance—toward the offspring of lower-ranking females. Yet another theory says that mothers differ in how they defend their offspring when the youngsters are engaged in fights with peers—stepping in more frequently when the opponents are offspring of lower-ranking females. A fourth theory suggests that when youngsters tussle, animals of higher rank provide third-party support to unrelated offspring of equal or higher rank.

Engh and her coworkers tested whether any of these theories applied to hyenas. The scientists counted all instances of antagonistic and submissive behavior expressed by 67 cubs born during an 11-year study and used statistics to correlate the tallies with the eventual rank of each cub.

The researchers found that the first two theories were unlikely to apply to hyenas. Because low-ranking coalitions occasionally overthrow their high-ranking superiors, genetic inheritance of rank doesn't seem to hold true in primates or hyenas, says Engh. And cubs of all ranks appeared to endure similar amounts of harassment.

The two remaining theories are based on adult support during fights among cubs. Both theories appear compatible with the hyena behavior, the researchers reported in the September 2000 *Animal Behaviour*.

High-ranking mothers intervened in fights more frequently and more effectively than their low-ranking counterparts did. Also, most support from unrelated animals was given when cubs behaved aggressively toward lower-born opponents. These two factors also appear to be the most common ones in those primates with hyena-style social structures, the researchers note.

"Maternal-rank inheritance is similar in hyenas and primates not just in appearance, but in the process by which it occurs," concludes Engh.

Holekamp adds that the research hints that cognitive processes in hyenas resemble those documented in primates. So, similar selection pressures have probably guided evolution in both groups.

There's a great deal of detailed information on behavior and life history in primates, but it's important to learn about other complex social mammals, says Susan Alberts, an ecologist at Duke University in Durham, N.C., who studies baboons. Then, interspecies comparisons can be made to answer general questions about the pathways of evolution.

Hyena studies may even reveal something about humanity, says Bekoff. The social structure of the hyena may be surprisingly similar to that of early humans. "Looking to carnivores may teach us about the evolution of sociality in our own species," he suggests.

There's far more to hyenas than their social structures. Engh and Holekamp say that they will soon publish additional evidence of complex mental capabilities shared between primates and social carnivores. Recent research has shown that hyenas are able to recognize third-party relationships, for instance between a mother and her offspring. Holekamp points out that a third-party relationship is an abstract concept, an understanding of which is thought by researchers to indicate highly developed levels of social intelligence.

Hyenas are forever doing things that are unexpected and difficult to explain, says Holekamp. "Each time you think you've got one thing figured out, they throw you a curveball," she notes.

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