

This Week's Citation Classic®

Kruuk H. *The spotted hyena: a study of predation and social behavior.*
Chicago, IL: University of Chicago Press, 1972. 335 p.
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Diverse territorial and group-hunting strategies are adapted to prey ecology and antipredator behavior; social behavior and communication among hyenas relate to social structure. Predation by hyenas can be the dominant mechanism of adjustment of ungulate populations to habitat productivity in African savannahs (here, Serengeti and Ngorongoro); on the other hand, hyena numbers are probably limited by ungulate densities or movements. [This book has been cited in more than 520 publications.]

Hunting Carnivores and Social Strategies

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One of the pipe dreams of the analyst of ecosystems is an understanding of multipredator/multiprey interactions, to achieve a model of that huge complexity that baffles so many field biologists. I think something like that was in the mind of the then director of the Tanganyika National Parks, John Owen, when he asked in 1963 if I could come and study "the ecology of the carnivores" of the Serengeti. There were 24 species.

At the time, I was completing my doctorate with Niko Tinbergen in Oxford, England, on predation on gulls, and there was not that much general scientific interest in the nocturnal carnivores. The reason for the National Parks' concern with predation was a management problem: politicians pressed for game-cropping, for utilization of the larger masses of migratory wildebeest and zebra by the African people. The question was, how would this affect the animals for which the tourists visited the park—the large predators?

I concentrated on just one, a species that, among Africans, was the butt of many jokes; consequently, I was, too. Hyenas are thoroughly mixed up in witchcraft, hated by hunters, despised by ignorants, and subjects of terror tales for children; and I must admit to momentary doubts about what I had let myself in for when,

at an early stage, I found quantities of human hair in their feces. For a long time, I found them almost impossible to study; those were days before radio-location or night-vision equipment. The animals walked over enormous distances (frequently 50 kilometers or more a night, through rough terrain), and their social organization appeared to be chaos.

The breakthrough came when I temporarily left the Serengeti and studied hyenas in the much smaller Ngorongoro crater. It all fell into shape: the clan system of very large groups, discrete ranges, the clear effects of hyenas on wildebeest and zebra, the predator's response to variations in antipredator systems. With that background, one could understand the much more fluid populations in the Serengeti, a quite different social system and ecology in response to the migratory prey. This was many years before "behavioral ecology"; most mammalogists still thought in terms of simple territorial social organizations, of animals with species-specific behavior patterns, with intraspecific variation just a noise in the system and rather a nuisance. The initial observations¹ met with some skepticism; for instance, it took years before it was generally accepted that, in some areas, hyenas are the predators, lions merely the scavengers that come after.

The research was done a quarter of a century ago; how much of it still stands? Studies on the behavior of hyenas have continued, doing much of what I should have done in the first place, disproving or confirming. Within the clan system, a sex-linked dominance order has been found, almost a class system, in which dominance appears to be passed on from mother to daughter.² The role of hyenas as predators in populations of large herbivores has been confirmed in the Kalahari, and comparison among hyena social organizations in different ecosystems uses the enormous intraspecific flexibility to study effects of ecology on social structures and on the evolution of sociality in different hyenids.³ The old Serengeti data still serve as reference points.⁴⁻⁶

1. Kruuk H. Clan system and feeding habits of spotted hyaenas (*Crocuta crocuta* Erxleben). *Nature* 209:1257-8, 1966. (Cited 15 times.)
2. Frank L G. Social organization of the spotted hyaena, *Crocuta crocuta*. II. Dominance and reproduction. *Anim. Behav.* 35:1510-27, 1986. (Cited 5 times.)
3. Mills M G L. *Kalahari hyaenas*. London: Unwin Hyman, 1990. 304 p.
4. Kruuk H. Functional aspects of social hunting in carnivores. (Baerends G, Beer C & Manning A, eds.) *Function and evolution in behaviour*. Oxford, England: Oxford University Press, 1975. p. 119-41. (Cited 40 times.)
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