



NEW BIOLOGICAL BOOKS

The aim of this department is to give the reader brief indications of the character, the content, and the value of new books in the various fields of Biology. In addition, there will occasionally appear one longer critical review of a book of special significance. Authors and publishers of biological books should bear in mind that THE QUARTERLY REVIEW OF BIOLOGY can notice in this department only such books as come to the office of the editor. All material for notice in this department should be addressed to The Editors, THE QUARTERLY REVIEW OF BIOLOGY, Division of Biological Sciences, State University of New York, Stony Brook, N.Y. 11790, U.S.A.

THE SOCIABLE "*Leo serengeti*"

BY HELMUT K. BUECHNER

National Zoological Park, Smithsonian Institution,
Washington, D.C. 20009

A Review of

THE SERENGETI LION. *A Study of Predator-Prey Relations. Wildlife Behavior and Ecology Series.*

By George B. Schaller; drawings by Richard Keane.
University of Chicago Press, Chicago and London.

\$12.50. xiii + 480 p. + 21 pl.; ill.; index. 1972.

In this superb book, George Schaller provides some remarkable and long-awaited insights into the social organization and behavior of the African lion, with just the right balance of pertinent information about its associated predators to give a well-rounded impression of the impact of predation on the vast ungulate herds in the Serengeti National Park. The three-year study was based on 156 tagged lions and 60 recognized by natural markings. Although the data and interpretations apply primarily to the Serengeti, the study is so thoroughly and carefully executed that the observations and conclusions have far-reaching implications, in the broadest sense, including also a better understanding of human behavior, since man "has lived ecologically as a social carnivore for some two million years . . ." (p. 10).

The lion is the most sociable of the cats, living in prides of 1 to 4 adult males, a core of several related lionesses, and a number of subadults and cubs, averaging about 15 individuals which are scattered singly or in groups within a pride area. Schaller distinguished members of the pride on the basis of peaceful interactions during encounters. Some difficulty was experienced in determining the nature of territoriality, especially from the viewpoint of defense

of boundaries and exclusive use; but in regard to attachment to an area, notably the focus of activity, and its defense against members of other prides, as well as recognition and respect for proprietary rights, it seems that territoriality is quite well defined in the lion.

Aggression, directed almost always against members of the same sex, is ritualized and fatalities rarely occur. In an exceptional case one of two adult males of the Seronera pride was killed by a male from the neighboring Masai pride; the second male disappeared, and three Masai males gradually took charge of the Seronera pride over a period of several months.

Subdivision into prides is linked to availability of prey, not only in the leanest season, but also in the most critical period in a series of years. Besides the prides, which are stable, closed social systems, lions also live in open groups as nomads. All males and some females become nomads as subadults. Reassortment of genetic material among the separate inbreeding prides is accomplished through the nomad system, which provides new males for prides, and through frequent copulation of pride females with nomads and males of other prides.

Schaller estimated 1,600 to 2,000 resident lions and 400 nomads in the ecological unit, which extends beyond the borders of the park, or one lion per 10.6 to 12.7 sq. km. The social and reproductive interactions among known individuals were concentrated mostly on two large prides in the Seronera area. Here 18 lionesses reared 17 young to the age

of 1 to 2 years, about 23 per cent of the potential total for the three years of observation. The length of estrus varied from 1 to 14 days in one lioness, and up to 22 days in another; the intervals between estrus were also highly variable, with an average of 34.5 days for 17 intervals. Sexual activity (not always with observed copulation) was seen 40 times, only 8 of which led to conception and birth. On 5 occasions the lioness was already pregnant, having conceived 3 to 8 weeks earlier. The average litter size was 2.3 for cubs less than a year old. The presence of one estrous lioness stimulated others, and the synchronization was striking. Cub starvation and abandonment during periods of prey scarcity seemed to be one of the main mechanisms in numerical regulation.

In the study area the rate of increase was at least 5 per cent annually; pride size remained stable as a result of the emigration of subadults which became nomads, many of which moved outside the park, where they were subject to high mortality from poaching.

There is a long and fascinating chapter on behavior within the group. Head-rubbing functions as a greeting and signifies peaceful intentions, inhibits aggression, reestablishes friendly relationships after a fight, integrates the activity of the group before a communal endeavor, tightens social bonds, and probably spreads a distinctive odor throughout the group. Lions lick one another to remove blood from the face after a meal, to dry one another after a rain, and apparently for sheer pleasure. As with the house cat, facial expressions are highly developed in the lion, many of which are illustrated by the excellent line drawings of Richard Keane. Both males and females roar, and they respond to the roars of other individuals in relationship to the proximity of the sound. The roar helps lions to find each other, to avoid contact, and to delineate the pride's area. Males mark vegetation with urine mixed with scent from anal glands; they usually rub their faces on foliage before squirting, probably in places where other lions marked previously. Both males and females scrape with the claws of their hind paws and urinate during or immediately after the scraping, but they do not defecate on the scrape. Although a male lion is superior in strength to the female, lionesses retaliate when males harass them, and they initiate most of the aggression. If a female being chased by a male whirls around and hits him, the male is discouraged from further action.

One chapter deals with prey populations and food habits of the lion. Of 1,180 food items eaten in the woodlands and plains combined, lions scavenged 16 per cent; in the plains alone they scavenged about 50 per cent because hyenas were more abundant there, deaths from disease were localized by herd concentrations, and vultures alerted lions to the availability of food. Serengeti lions prey mostly on

wildebeest, zebra, buffalo, and topi. Only the nomads move with the migrating herds. The large, conspicuous mane of the male, "like a moving haystack" (p. 360), makes it difficult for males to kill their own food. Few descriptions of hunting and killing by lions have been published, and one chapter on this topic is filled with new information and captivating illustrations.

Part III (68 pages) of the book includes Schaller's valuable observations on other predators, especially leopards, cheetahs, and wild dogs, in the Serengeti. Each predator has a different social system, which is closely related to the animal's strategy for exploitation of a food resource. Lions are adapted for hunting large prey cooperatively in open terrain. The limited social life of most cats is related primarily to the small prey. Leopards live alone along riverine forest and elsewhere in the areas of their home ranges least frequented by other leopards; and the limited overlap of ranges among males suggests territoriality, for which there seems to be no evidence so far for females. Schaller's observation of cheetah show that "adult females are unsociable, except when in estrus and when they have cubs, but that adult males may form social bonds with others of their sex" (p. 302-303). Adults avoid contact and there is no evidence of territoriality. Their lives are geared to following the movements of Thomson's gazelle and catching them with great bursts of speed. Where prey is abundant hyena clans maintain territories, but when migrating herds move to woodlands, the clans disintegrate and some hyenas commute to prey concentrations, while others become nomadic and follow the prey. The society of the wild dog differs from that of lions and hyenas by being inflexible and not adjusting its size seasonally to the available prey.

In the final two chapters, Schaller provides a very interesting discussion of predator social systems and the dynamics of predation. Ecological separation of the Serengeti predators is incomplete, and interspecific intolerance is evident in the manner in which the predators pursue and kill one another, using bared teeth and vocalizations as in intraspecific aggression. The lion's strategy is to live as residents in the woodlands, as a consequence of which the migratory wildebeest and zebra, favored prey of the lion, are unavailable during the rainy season, when these animals move into the plains. The limitation of food to resident topi, hartebeest, impala, warthog, and waterbuck in the woodlands during the rains largely determines the population level of the lion; but self-limitation of pride size by emigration of subadult females appears to be another major numerical control.

All the large predators in the Serengeti obtain meat by "scavenging animals dead from disease, malnutrition and other causes; by driving predators off their

kill; by capturing newborn young, sick individuals, and other vulnerable prey; and by capturing healthy large mammals" (p. 386). Schaller speculates that primitive man, using these same methods, may have filled an ecological opening for a diurnal social predator, pursuing healthy animals when nothing else was available. The predators remove about 10 percent of the prey biomass, and the lions, based on a 20- to 30-animal killing rate per lion annually, take 40,000 to 72,000 animals per year in the Serengeti ecological unit. Schaller concludes that predators are a major force in keeping ungulate populations depressed

below a level that they would attain if predation did not exist, below a level at which disease, starvation, and other regulatory forces associated with poor nutrition can take effect.

This book lays the scientific foundation for the preservation and management of the lion in the Serengeti. It is also written in such a readable and interesting way that it is likely to catch the attention of society in general as well as that of scientists and conservationists, and for this reason it will play an important role in the future of the African wildlife.