

Book Reviews

The Natural History of Lions

The Serengeti Lion. A Study of Predator-Prey Relations. GEORGE B. SCHALLER. Drawings by Richard Keane. University of Chicago Press, Chicago, 1972. xiv, 480 pp. \$12.50. Wildlife Behavior and Ecology.

In the zoocentric human mind the lion has long occupied an exalted position: king of beasts, symbol of the sun, even animal god. The Egyptian pharaoh Rameses II took lions with him into battle, and kings from Amenhotep II to Saint Louis have traditionally hunted them for sport. Now *Panthera leo* has been made the overdue subject of an intensive zoological study. For three years, from 1966 into 1969, George Schaller followed lion prides over the grasslands of Tanzania's Serengeti Park, "a boundless region with horizons so wide that one can see clouds between the legs of an ostrich," where heat waves at noon transform "distant granite boulders into visions of castles and zebra into lean Giacometti sculptures." Schaller logged 149,000 kilometers of travel while keeping the lions under observation for a total of 2900 hours. Few animal populations have been studied so long in the wild. One sees in Schaller's book the beginning of a new level of resolution, in which some free-ranging individuals are traced from birth through socialization, parturition, and death, and their idiosyncrasies and personal alliances recorded in clinical detail.

The core of a lion pride is a closed sisterhood of several adult females, related to each other at least as closely as cousins and associated for most or all of their lives within fixed territories passed from one generation to the next. The degree of cooperation that lionesses display is one of the most extreme recorded for mammal species other than man. The lionesses often

stalk prey by fanning out and then rushing simultaneously from different directions. Their cubs are maintained in something approaching a crèche: each lactating female prefers to nurse her own cubs but will permit those of other pride members to suckle. A single cub may wander to three, four, or five nursing females in succession in order to obtain a meal. The adult males, in contrast, exist as partial parasites on the females. Young males almost invariably leave the prides in which they are born, wandering in a nomadic existence either singly or in groups. (A minority of the young females also become nomads.) When the opportunity presents itself they attach themselves to a new pride, sometimes by aggressively displacing the resident males. Male bands both inside and outside the prides are typically brothers, or at least individuals who have been associated through much of their lives. The pride males permit the females to lead them from one place to another, and they depend on them to hunt and kill most of the prey. Once an animal is downed, the males move in and use their superior size to push the lionesses and cubs aside and to eat their fill. Males also respond more aggressively to strangers, especially to other males who attempt to intrude into the pride domain.

What is the significance of this peculiar social structure, in a group of mammals (the cat family Felidae) otherwise celebrated for its solitary habits? Schaller convincingly argues that the prides evolved primarily because group hunting is a superior means of catching large mammals in open woodlands and grasslands. His data show that several lions stalking together are generally twice as successful at catching prey as are solitary lions. They are also able to bring down certain exceptionally large and dangerous prey, particularly giraffes and

adult male buffaloes, that are virtually inaccessible to single individuals. Schaller further found that cubs are better protected from leopards or nomadic lions when their mother belongs to a group. For both of these reasons, pride lionesses are far more successful in rearing litters to maturity than those living alone.

Lions sometimes kill other lions. Schaller observed several fights between males that ended fatally. He also recorded a case of the killing and cannibalism of cubs after one of the protector males died and the territory was invaded by several other prides. Less severe fighting is more frequent, and it also results in injuries and infections that ultimately shorten the lives of many individuals. I have been impressed how often such behavior becomes apparent as the observation time devoted to a species passes the thousand-hour mark. Murder has been now observed frequently enough in gulls, hyenas, hippopotamuses, langurs, macaques, and some other vertebrates to suggest that it is both widespread and, Konrad Lorenz and some other popular writers to the contrary notwithstanding, far more common and hence "normal" in these species than in man. In fact, if some imaginary Martian zoologist visiting Earth were to observe man as simply one more species over a very long period of time, he might conclude that we are among the more pacific mammals as measured by serious assaults or murders per individual per unit time, even when our episodic wars are averaged in. If the visitor were to be confined to Schaller's 2900 hours and one randomly picked human population comparable in size to the Serengeti lions, he would probably see nothing more than some play fighting—nearly limited to juveniles—and an angry verbal exchange or two between adults. Another cherished notion of our own wickedness starting to crumble is that man alone kills more prey than he needs to eat. The Serengeti lions, like the hyenas described by Hans Kruuk in his excellent companion book *The Spotted Hyena* (University of Chicago Press, 1972), sometimes kill wantonly if it is convenient for them to do so. As Schaller concludes, "the lion's hunting and killing patterns may function independently of hunger."

An important goal of the Serengeti study was the assessment of the effect of lions on the great herds of ante-

lopes and other ungulates for which the region is famous. Although Schaller's data are rich, the pattern he sees, like that emerging from so many other mammalian studies, remains complex and ambiguous. Lions appear to depress the population of some species below the carrying capacity of the grasslands, at least temporarily, and they are very effective in trimming off aged and disabled animals. But the importance of their role as population regulators cannot yet be measured quantitatively relative to disease, food supply, and other key factors.

If you have only enough time to read one book about field biology, this is the one I recommend. Schaller continues the best tradition of Fraser Darling, Paul Errington, and Adolf Murie. *The Serengeti Lion* displays a maturing of its author, measured both in deepening insight and a surer touch, since his already excellent works *The Mountain Gorilla* and *The Deer and the Tiger*. Although not a theoretician, Schaller has a strong intuitive feel for the important questions of population ecology and sociobiology, and he has organized his information with reference to some of them without departing from the traditional monographic approach. The organization and illustrations are sound, and the writing is sometimes delightful. Schaller has the master's ability to enliven his scientific report with brief personal anecdotes and expressions of personal emotion that do not lose objectivity or even noticeably digress from the data. We are told, for example, that at no time is the lion's movement "more vitally beautiful than when a lion tautly snakes toward its prey. I found that fleeting hesitation between the end of the stalk and the final explosive rush a moment of almost unbearable tension, a drama in which it was impossible not to participate emotionally, knowing that the death of a being hung in the balance."

Schaller, in fact, seems to be a Victorian who has successfully adapted to modern science. Part of the pleasure I have received from his books, as well as from such similar monographs as Valerius Geist's *Mountain Sheep*, Hans Kummer's *Social Organization of Hamadryas Baboons*, and Hans Kruuk's *The Spotted Hyena*, is the promise they imply that physical adventure has not died in science, that one can still journey to some unknown land and publish one's notebooks for the benefit of a fascinated audience. And this

time there is a difference: the recent emergence of authentic theory in ecology and sociobiology has created a demand for large amounts of new information from experimental and field studies. The gap between theory and factual information is already large and is growing faster, because the latter accumulates more slowly. Schaller's study has shown us how little we knew about one of the most famous of all animal species, and it can be taken as indicative of the opportunity for original discovery that lies immediately ahead in most aspects of field biology.

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Plant Process

Biological Fixation of Atmospheric Nitrogen. E. N. MISHUSTIN and V. K. SHIL'NIKOVA. Translated from the Russian edition (Moscow, 1968) by Alan Crozy. Pennsylvania State University Press, University Park, 1972. x, 420 pp., illus. \$19.50.

During this century six significant books have appeared on biological nitrogen fixation and a comprehensive treatise encompassing inorganic chemistry, biochemistry, biology, agronomy, and ecology is in preparation. The leguminous symbiotic system was emphasized in two early books—*Root Nodule Bacteria and Leguminous Plants* by Fred, Baldwin, and McCoy in 1932 and *The Biochemistry of Symbiotic Nitrogen Fixation* by Wilson in 1940. After a period of dormancy, four books on broader aspects of N_2 fixation appeared within a five-year span—*Nitrogen Fixation in Plants* by Stewart in 1966, *Biological Fixation of Atmospheric Nitrogen* by Mishustin and Shil'nikova in 1968 in Russian and in 1971 in English, *Chemistry and Biochemistry of Nitrogen Fixation* edited by Postgate in 1971, and *Biological Nitrogen Fixation in Natural and Agricultural Habitats* edited by Lie and Mulder in 1971.

There is increasing recognition of the need for additional fixed nitrogen to fill the world requirement for protein and growing concern with the possible deleterious effects of nitrogen compounds in the environment. Renewed consideration is being given to the possibilities of coupling additional atmospheric N_2 more directly to the plant.

This has stimulated an unprecedented number of adventuresome suggestions in the last two or three years. These include N_2 -fixing chloroplasts, domestication of N_2 -fixing rhizosphere or phylloplane associations, genetic engineering, N_2 -fixing *Agrobacterium*, "*Rhizobium cerealis*," protoplast fusion, and bacteriophage transduction. Many of these suggestions have been put forth by people not engaged in N_2 -fixation research. It is obvious that the expanding interest in N_2 fixation is creating a need for books that assemble and evaluate the substantial literature in the field.

Biological Fixation of Atmospheric Nitrogen fills one aspect of this need in that the authors pay "special attention to the utilization of nitrogen fixation in agriculture." The biology and ecology of N_2 -fixing organisms are also emphasized. The Russian literature is compiled and integrated with that of the Western world. Over 2500 references are listed (the chapter on legume symbiosis contains an estimated 1100, requiring 50 pages for tabulation), and even well-read investigators will probably discover unfamiliar information.

A general discussion of the activity of N_2 -fixing organisms introduces the book, and a short discussion of the biochemistry of N_2 fixation and theories of the evolution of biological N_2 fixation concludes it. The part in between is devoted to symbiotic N_2 fixation in legumes and nonlegumes and to asymbiotic N_2 fixation by *Azotobacter*, *Beijerinckia*, *Clostridium*, blue-green algae, and other groups of organisms. The authors' chief concern is with biology. The biochemistry of N_2 fixation has developed so rapidly that most of their chapter on it is so out-of-date as to be useless. Postgate's *Chemistry and Biochemistry of Nitrogen Fixation* provides a more useful, though somewhat selective, account of those aspects.

The discussion of symbiotic N_2 fixation extends from biology to ecology, including evaluation of the effectiveness of inoculation and techniques of production and application of rhizobial inoculum. Evidence for N_2 fixation by various nonlegumes is collected, and the inconclusiveness of information on some systems such as *Mycorrhiza* is indicated.

The review of *Azotobacter* nitrogen fixation is extensive. Of possibly greatest interest is the agronomic effect of *Azotobacter* on higher plants. Azotobacterin, a fertilizer preparation con-