Serengeti

Dynamics of an Ecosytem

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Ten Population Changes in Lions and Other Predators

Populations of some large ungulate species have shown a substantial increase during the last two decades (see chap. 4), and one might therefore expect that the numbers of large carnivores have also increased. This study was designed to ascertain the current population trend of lions, for although Schaller (1972) concluded from his three-year study that the Serengeti lion population was stable, subsequent rumours suggested that it might be decreasing.

In order to discover what changes, if any, had occurred between Schaller's study period (1966–69) and our own (1974–77), we reexamined his main study area, about 2500 km^2 of open grasslands and woodlands. We found that there were more lions resident in the area and that they were now found in areas that were not fully occupied before. These changes resulted from at least two factors acting in combination: an increase in rainfall in the dry season (June through October), and an increase in the numbers of resident prey species.

In this chapter, we shall present data in support of these conclusions, and we shall then briefly consider how the same ecological factors may have affected the other carnivores. It is unfortunate that the main Serengeti predator—the spotted hyena—has not been monitored since the termination of Kruuk's study (Kruuk 1972), but a census of predators on the plains conducted in May 1977 has provided some information on the current number of hyenas. Cheetahs and wild dogs, the rarest species, are currently being studied by George Frame and Lory Herbison-Frame, respectively, who have kindly allowed us to quote their preliminary figures.

The Serengeti Lion Population

The social structure of the Serengeti lion population has been described in detail by Schaller (1972) and Bertram (1975; chap. 9 above). The

two basic components of lion society are residents and nomads. The social units of the resident population are prides of two to eleven adult females (presumably related) with their cubs (pl. 30), and groups of one to seven adult males. Males usually attach themselves to a pride and occupy the same range, but large groups (three to seven animals) may maintain a range large enough to span several prides. Resident prides occupy home ranges of 20–300 km^2 in habitats where prey, water, and cover are available throughout the year. Females defend their ranges from female intruders, males from males.

The nomad population is much smaller (perhaps about 20 percent of the total) and consists of individuals (pl. 28) who have emigrated from resident prides. It is normal for subadults, particularly males, to leave their parent pride at two to four years of age and become nomadic; however, some young females are recruited into the parent pride. Nomads are characterized by having no stable range (or an extremely large range), and they wander through the areas occupied by resident lions, whom they avoid as best they can, converging in places where prey is temporarily abundant. Nomads may become resident if conditions permit; thus, females may settle in any suitable area which is not already occupied by a pride, and males may join a group of females if there are no males already present or if they can displace the resident males.

Schaller showed that the main source of recruitment for both the nomadic and resident lions was through cubs born to resident prides. He concluded that the resident prides produced a surplus of 5.5 percent of the population per year and that most of these lions became nomadic and emigrated from the area or died; thus, the lion population remained stable. We conjectured that if conditions improved, much of this "surplus" could survive and a new population level would be reached.

In order to assess trends in the Sergenti lion population, we worked for three years (September 1974 to September 1977) in Schaller's main study area. This area, illustrated in figure 10.1, included the Serengeti plain and a large strip of woodland at the northern and western borders of the plain. Within this area, we attempted to find and identify individually all lions, and to determine whether they were resident or nomadic.

Each lion over one year old was photographed and sketched, so that all lions found could be positively reidentified by the combination of ear notches, vibrissae spot patterns (Pennycuick and Rudnai 1970), and other natural features. This system of individual recognition was also used by Bertram (1975), and his identity cards for three prides in the study area (the Seronera, Masai, and Loliondo prides) enabled us to

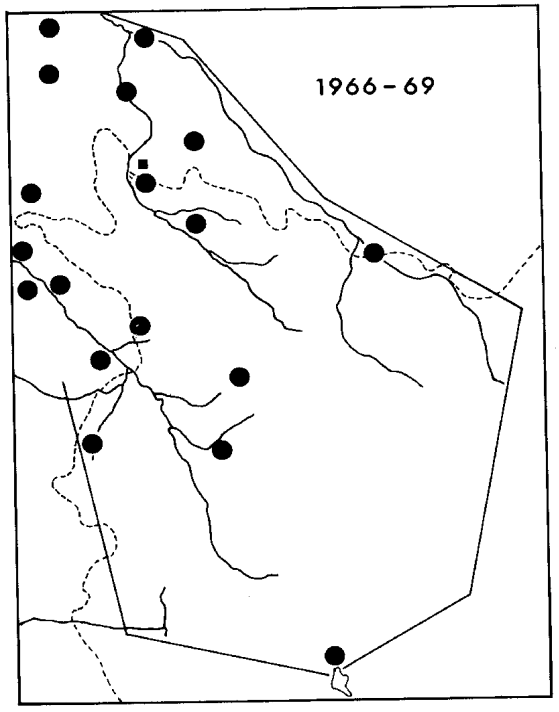

Figure 10.1 Position of resident prides (*solid circles*) on the plains and surrounding woodlands 1966–69 (after Schaller 1972). *Solid line* indicates study area boundary; *broken line,* edge of plains. Seronera is shown by the square.

recognize members of those prides without difficulty. Schaller had marked all the other prides in the study area by ear-tagging an adult female in each pride, but, unfortunately, all the marked lions had lost their ear-tags or died by the time our study began. We could not, therefore, be certain which of the prides we found corresponded to those which Schaller had named, although, in some cases, reasonable guesses could be made on the basis of geographical location. However, the overall numbers and distribution of the resident prides in the study area could still be compared with Schaller's data for the same area, ten years earlier.

Changes in the Resident Population

Prides. The distribution of resident prides in Schaller's study period and our own are shown in figures 10.1 and 10.2, respectively. There are now more resident prides; we found a minimum of twenty-four distinct prides, where Schaller found eighteen (an increase of 33 percent). We actually found twenty-eight different groups, but we did not see some of these often enough to be able to state definitely whether or not they were separate prides or just subgroups. Note that most of the "new" prides were found on the plains, an area in which Schaller found very few prides living throughout the year.

While the absolute number of prides has increased over the ten-year period, mean pride size has also increased from fifteen to nineteen. Figure

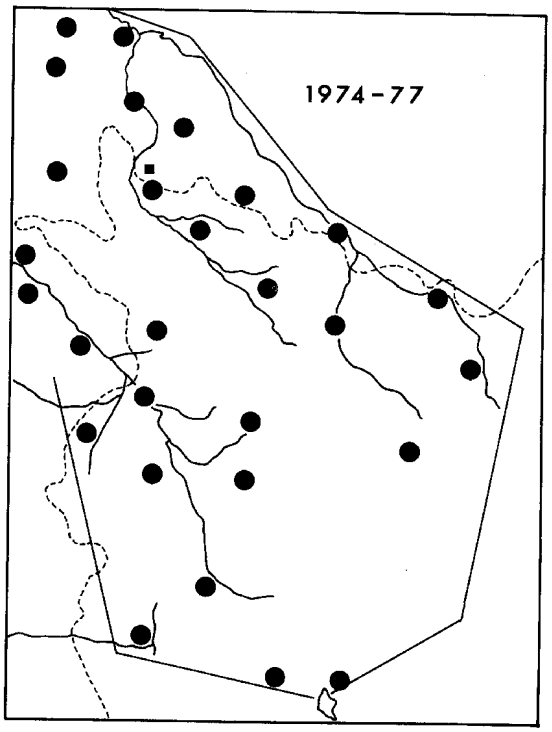

Figure 10.2 Resident prides, 1974–77, in the same area as that shown in fig. 10.1.

10.3 shows that the mean number of adults and cubs per pride has not changed significantly, the increase being mainly due to subadults.

Cub survival. In 1966–68, Schaller recorded only ten subadults in fourteen prides, while in 1975–77, we found seventy-one subadults in fifteen prides in the same area (the new plains prides were excluded from this analysis). This difference (statistically significant by sign test, or "*t*" test, at $P < 0.01$) implies either that cub survival has increased significantly during the past few years, or that more cubs are allowed to remain with the pride into subadulthood. Both factors are probably operating.

Increased cub survival is clearly shown by continuous data on the reproductive history of the Seronera and Masai prides, collected by Schaller, Bertram, L. H. Frame (pers. comm.), and ourselves. The sur-

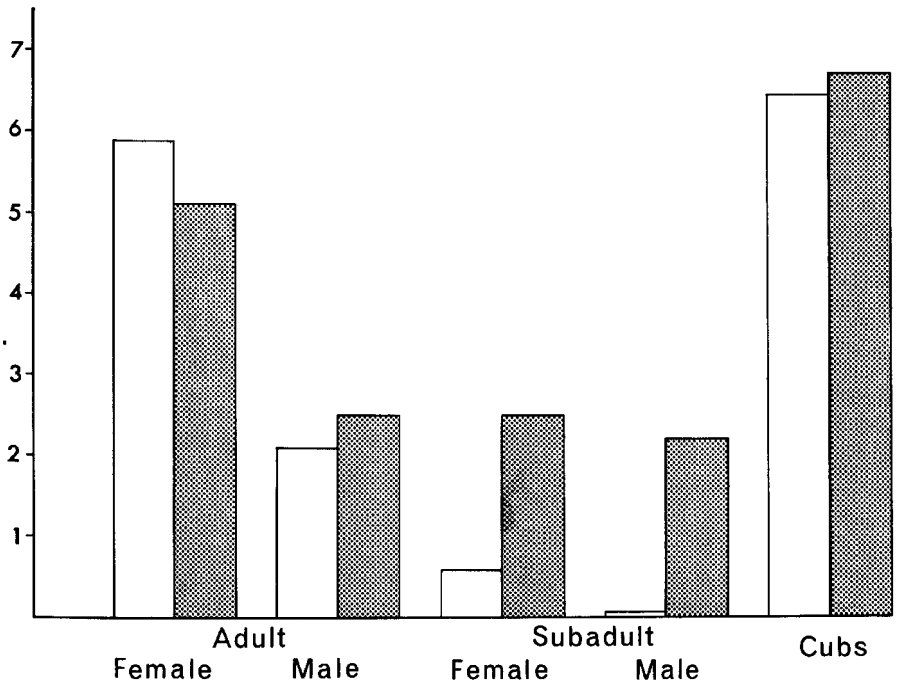

Figure 10.3 The mean number of individuals per pride in the same fourteen prides, for different age and sex classes. *Open column,* 1966–68; *stippled column,* 1975–77.

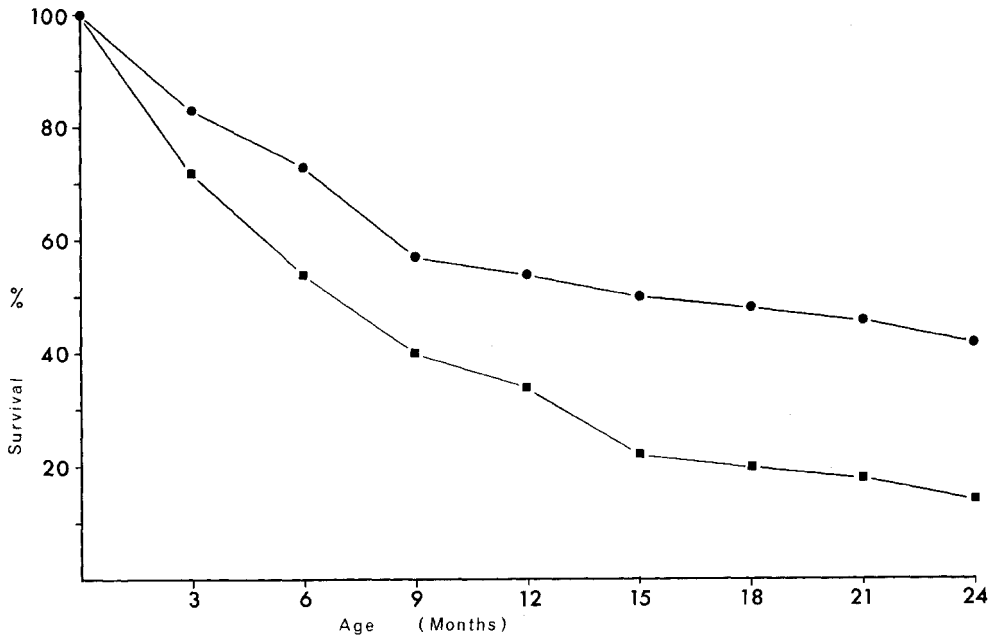

Figure 10.4 Survival of cubs in the combined Seronera and Masai prides. One hundred twenty-seven cubs born in 1971–75 (*circles*) have a 44% chance of surviving to two years of age. Eighty-seven cubs born in 1966–70 (*squares*) have a 14% chance of surviving to two years of age.

vivorship curves in figure 10.4 show a threefold increase in the proportion of cubs surviving to subadulthood (that is, to two years of age). Once a cub reaches two years of age, the probability of its death decreases considerably. Schaller calculated an annual mortality of 5.5 percent for all lions over two years old. We have no direct evidence that the mortality of subadults is any lower now than it was in the past, but we agree with Schaller's conclusion that mortality must be higher for nomads than for residents, and if subadults can remain for longer with their prides, their chances of survival are presumably improved.

Formation of new prides. When subadults leave their parent pride and become nomadic, littermates of the same sex tend to stay together as a stable group. Male groups may eventually succeed in attaching themselves to established prides and becoming resident breeding males, and female groups, under the right conditions, are capable of establishing new prides.

We have found that new prides may be formed in two ways: (1) a group of subadult females may leave the parent pride and settle in an adjacent area, or (2) one or a few nomadic females, of any age, may settle in a suitable area and build up a pride by recruitment of their offspring.

Five of the eight new prides we have found in the study area appear to have been formed in the first way, and in three of these cases, we have been able to trace the parent pride through photographic records. In all three instances, the females left their prides as subadults and took up residence at the periphery of their mothers' range, attracted new males, and began to breed. The age structure of two other prides implies the same process of formation.

Three other new prides were probably formed in the same way, by a "founder female" who recruited her daughters. These prides, though small, contained females of several different ages, and, in each case, the oldest female had obviously been ear-notched or tagged by Schaller. Only one of these presumed founder females could be positively identified by Schaller (pers. comm.), who gave us a list of his sightings of her. These data showed how she initially wandered as a nomad all over the plains, with a variety of companions, then in 1968 began rearing cubs in the northeastern plains. Seven years later we found her still in that area, with two middle-aged female companions and three cubs.

The formation of both these types of pride would seem to be a response to improved environmental conditions. In the first case, improved cub survival in a resident pride results in a large group of subadults; in the second case, a solitary female nomad at last succeeds in rearing some daughters to maturity.

Changes in Nomad Numbers

Schaller (1972) estimated the numbers of nomadic lions on the plains during each wet season; his estimates varied from 267 in 1967 to 123 in 1969 (mean = 185). We identified on average only sixty-eight nomads per wet season during 1974–77, which appears to be a substantial decrease. The sex ratio also seems to have changed; Schaller recorded an average ratio of eighty-eight males to one hundred females among plains nomads,

that is, 53 percent of adults and subadults were females. We found that only 17 percent of nomads were females.

There are several possible reasons for a decrease in nomads on the plains: (1) nomad mortality may have increased (for example, from poaching or starvation); (2) more nomads may now remain in the woodlands during wet seasons; (3) fewer subadults may leave their prides; (4) more subadult females may be forming new prides. An increase in mortality so heavily biased against females seems unlikely. One would expect females to be better able to support themselves than males (see Schaller 1972), while snaring and hunting might be biased against males, since they are more mobile than females. It is conceivable that more nomads are staying in the woodlands, particularly since several large subadult groups (whose members we knew individually) left their prides in the woodlands but were never seen on the plains. But alternatives 3 and 4 could explain the proportional reduction of female nomads, and fit well with the observed data.

During the wet season of 1976–77, our sightings of nomads, plus the new plains prides, totaled 141 individuals; this is a minimum figure but well within the confidence limits of Schaller's estimates of plains nomads in 1968 and 1969. Of the adults and subadults within this sample, 49 percent were females, which more closely approaches Schaller's nomad sex ratio.

Thus, the number of nomads using the plains during the wet season may have decreased because many females and some males, who would formerly have become nomads, now stay on the plains throughout the year in resident prides. These prides live in areas which used to attract nomads during the wet season during Schaller's study. These new resident lions are territorial and tend to keep nomads out of their ranges; thus, to the casual observer, there may appear to be fewer lions in the area.

Climatic Changes and Prey Availability

The formation of new prides and the improvement in cub survival in established prides are presumably due to an increase in the availability of food. It would be naive to assume that the big increase in the population of wildebeest (the species most frequently eaten by lions) was responsible for the increase in lions, because most of the Serengeti wildebeest are migratory and most of the lions are resident. Any resident pride will have access to migratory prey for only a few months in every year, and

must subsist at other times on resident herbivore species. Schaller considered that the major factor limiting the size of the resident lion population was the availability of prey during the leanest time of year; this is the wet season in the northern and western woodlands, when the migratory species (wildebeest, zebra, Thomson's gazelle, and eland) have moved out to the plains, but in our study area on and around the plains, there is least prey during the dry season. If more lions can now survive in this area than formerly, we might expect resident prey to have increased since Schaller's study.

Unfortunately, there are few data on the resident ungulate populations that span the past ten years and include the numbers on the plains. Buffalo have shown a continual increase (see chap. 4) but are only available to lions living in the woodlands or at their edge. Their increase may well have benefited lions in these areas; Schaller found that only 2.4 percent of 545 ungulates eaten by the Seronera and Masai prides during 1966–69 were buffalo, whereas during our study, 20 percent of 101 ungulates eaten by the same prides were buffalo (pl. 30). Our sample is smaller and less systematic, but supports the hypothesis that buffalo now form a greater part of the lions' diet.

Schaller (1972) presents data on the total numbers of resident prey in the Masai pride's home range. Utilizing his data, we found that in 1966–67, the mean biomass of resident prey in that area was about 300 kg/km^2. Our own systematic monthly sample counts from specified points within the same area in 1976–77 gave a figure of 600 kg/km^2. A comparison of the two methods showed that the sample counts underestimated the actual biomass, so resident prey had at least doubled. The increase is mostly due to buffalo, giraffe, topi, and warthog. It is noteworthy that during this ten-year period, the number of adult females in the Masai pride increased from six to sixteen.

Reliable quantitative data on the numbers of ungulates on the plains during the dry seasons have been difficult to obtain. Norton-Griffiths (pers. comm.) calculated a mean biomass minimum of 99 kg/km^2 for resident ungulate species on the plains during the dry season of 1972. Most observers (for example, Schaller 1972; Kruuk 1972; R. M. Bradley and A. R. E. Sinclair, pers. comm.) agree that toward the end of the 1960s there were very few ungulates or large carnivores on the short-grass plains during the dry seasons. Schaller conducted one prey count approximately in the center of the plains in October 1966 and found a prey biomass of 131 kg/km^2. Our sample counts of prey at the Gol Kopjes, where a resident lion pride now lives, showed a mean biomass of 950 kg/km^2 in

the dry season of 1975, and 850 kg/km² in 1976. However, in July of both years, prey biomass in this area fell as low as 25 kg/km². Although the overall availability of prey may have increased enough to support a resident pride, this area is still a marginal habitat subject to large fluctuations in prey availability.

The prey species now found on the plains during the dry season include Thomson's and Grant's gazelles, topi, kongoni, and warthog. Warthogs, in particular, seem to be important prey for several plains prides; the lions can stalk them in the daytime, or dig them out of their holes at night. There are no data on the numbers of warthogs on the plains over the past ten years, but G. Frame has notes from 1965 onward that indicate an eastward expansion of warthogs around Olduvai Gorge during the past five years, and, thus, presumably on the short-grass plains as well. R. M. Bradley (pers. comm.), who studied gazelles on the plains during 1970–72, considered that there were virtually no warthogs on the plains at that time. A ground census of the whole plains by transects during May 1977 gave a mean density of 0.76 warthogs/km² (representing about 2000 in our study area), which would suggest an increase.

The greater abundance and wider distribution of prey species suggested a change in the rainfall pattern—in particular, an increase in dry-season rainfall on the plains. Fortunately, this hypothesis could be checked against the Serengeti Ecological Monitoring Programme's rain-gauge data, which covers the entire area and time period under consideration. The mean monthly rainfall for twenty-one rain-gauge stations on the short- and intermediate-grass plains over the last thirteen years is shown in figure 10.5. Wet-season rainfall has been variable with no particular trend, but for the last five years, dry-season rainfall has been higher than for the previous five years. This small increment is sufficient to promote grass growth and, thus, to attract and sustain a greater number of herbivores.

Corresponding increases in dry-season rainfall throughout the park (chap. 4) may account in part for increases in resident herbivores in the woodland areas, and the resulting improvement in cub survival in those areas.

Changes in Other Carnivore Populations

Hyenas

The most important large predator in Serengeti is undoubtedly the spotted hyena (pls. 31, 32), which Kruuk (1972) studied from 1964 to 1968.

Figure 10.5 Mean rainfall from twenty-one stations on the plains. Dry-season rainfall (*solid line*) was highest in the seventies. Wet season rainfall (*broken line*) showed no trend.

He found that Serengeti hyena numbers were much lower than would be expected from the size of the prey populations, and suggested that the limiting factor for the hyena population was the distance that females had to travel from their dens to the concentrations of wildebeest, then main prey. The increase in both the number of wildebeest and the dry-season rainfall (and, hence, resident prey) may now allow hyenas access to a greater food supply than before. From this, one would predict an increase in hyena numbers comparable to the lion increase discussed in the preceding sections.

In order to assess the number of hyenas, the Serengeti Research Institute conducted a census of the plains in May 1977. At this time (the end of the wet season), the wildebeest herds were massed on the plains before migrating into the woodlands, and the density of hyenas was presumably maximal. An area of about 3000 km^2 (bounded by the plains-woodland border, Olduvai Gorge, and the Gol Mountains) was sampled by ground transects (Anon 1977). The resulting estimate for hyenas was 3391 (with 95 percent confidence range of 2560–4122). The lower limit still exceeds

Kruuk's estimate of the wet-season hyena population on the plains (2117) by 21 percent, so we conclude that there are now considerably more hyenas on the plains during the wet season. Kruuk found that the density of hyenas in the woodlands was very low, and we have no evidence that this has changed.

The factors which have caused lions and hyenas to increase in numbers or distribution may also have affected other predators, but apart from cheetah and wild dog, there are no long-term records for other species. Records of the resident leopard population (pl. 34) around Seronera over the past eight years, kept by Bertram and ourselves (unpub. data), show no indication of a change in numbers, but the area concerned is small, and the status of leopards elsewhere in the park is unknown.

Neither Schaller nor Kruuk considered lions or hyenas to have a limiting effect on their prey in Serengeti, and we have no data that conflict with this view. However, they may well affect other predators. Hyenas and lions are themselves major competitors, in that both are large, common, hunt similar prey, and scavenge from each others' kills, though in the latter situation, lions are usually dominant. In the past, during the dry season on and around the plains, this competition may have been reduced, since lions were then dependent on resident prey within their pride ranges, while the majority of hyenas commuted to areas where migratory prey species were abundant. However, it is possible that some hyenas now take advantage of the increased resident prey populations, a possibility that deserves further study.

Cheetahs

Potentially, hyenas could be serious competitors of cheetahs (pl. 33), since they can easily steal kills from cheetahs. However, cheetahs are much more diurnal than hyenas, and G. Frame (pers. comm.) has found that most cheetah hunts occur at times when hyenas are seldom active. The hunting technique of cheetahs is also fairly unobtrusive; a long stalk in the cover of grass or herbs is followed by a quick chase and concealment of the prey after capture.

The frequency of encounters between the two species could be further reduced because hyenas tend to stay with the wildebeest concentrations, while cheetahs follow the gazelle herds, and these two ungulate species are usually concentrated in different areas at any one time. The reduction in dry-season grass fires over the past ten years (chap. 13) may have benefited cheetahs by providing more cover for stalking and also for safe con-

cealment of cubs. It is perhaps for these several reasons that the Serengeti cheetah population is flourishing. G. Frame estimates that there are at least five hundred in the ecosystem, a large proportion of which are young.

Wild Dogs

The only large predator which is known to have suffered a decrease over the past ten years is the wild dog (pl. 35) living on the plains. (There are no reliable figures for dogs living in the woodlands.) The number of adults living on the plains year-round has declined from around 110 in 1970 (J. R. Malcolm, pers. comm.; Malcolm and van Lawick 1975) to only thirty at present (L. Herbison-Frame, pers. comm). Packs are fewer and smaller, and pup survival is very low.

It is on the plains that wild dogs must compete most directly with other predators, especially hyenas. While single hyenas are effectively driven off by a dog pack, a group of hyenas can easily steal the dogs' kill (pls. 37, 38), and may also kill puppies that are left unattended. One or more adults must stay at a den to guard the young when hyenas are around, thus diminishing the hunting pack and increasing the number of mouths to be fed. Lions will also steal kills from dogs whenever possible, but they are neither as widespread nor as mobile as hyenas. Competition with an increased hyena population on the plains may well have contributed to the high mortality of wild dog pups during the past three years, but shooting and diseases such as distemper have also taken a toll in the past.

Conclusion

Lions and hyenas have increased in numbers on the Serengeti plains and adjacent woodlands, but the main causal factors seem to be different for the two species. The main factor accounting for the improved cub survival and wider distribution of resident lions is an increase in resident prey. The main factor accounting for the increase in hyenas is probably the increase in migratory prey, though they may also have benefited from the increase in resident prey. The cheetah population may have increased for the same reasons that the lion population has. Wild dogs living on the plains have decreased, probably because of disease combined with intense competition with the enlarged hyena population.

A relatively small change in dry-season rainfall has made a large area of Serengeti available to resident herbivores and carnivores during the years 1972–77. Schaller's and Kruuk's studies (of lions and hyenas, re-

spectively) happened to coincide with a run of dry years, and ours with a run of wet years. Fortunately, the existing long-term records of predator populations and rainfall have enabled us to detect, and suggest explanations for, the changes in predator populations. The importance of long-term studies that monitor populations and climate is well illustrated here, and it is easy to see that a reversion to more severe dry seasons might eliminate the resident lion prides on the plains and reduce the reproductive success of other resident prides.

This study would not have been possible without the financial support of the Science Research Council, England, and the New York Zoological Society. Tony Sinclair and the African Wildlife Leadership Foundation have also contributed substantially to the predator counts. We acknowledge our indebtedness to all the scientists and S.R.I. for their generous help in counting predators and their help in other ways too. We particularly want to thank G. Frame, L. Frame, J. Malcolm, A. Sinclair, and M. Norton-Griffiths for contributing data and comments on the manuscript, as well as for support and inspiration.

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