

Serengeti II

*Dynamics, Management, and
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Ecology, Demography, and Behavior of Lions
in Two Contrasting Habitats: Ngorongoro
Crater and the Serengeti Plains

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African lions have been studied in a wide variety of habitats. Previous comparisons between populations have primarily focused on the effects of prey availability on broad measures of lion ecology and demography (see Van Orsdol, Hanby, and Bygott 1985). These studies have shown that population density, cub survival, and dispersal rates of subadults are all highest where prey is most abundant (Van Orsdol, Hanby, and Bygott 1985; Hanby and Bygott 1987; Pusey and Packer 1987; Packer et al. 1988). In this chapter we present a detailed comparison of two groups of lions living in adjacent areas that differ strikingly in prey availability. We document the seasonal food intake rates in both habitats and their effects on demographic parameters. We also examine how ecological factors influence lion foraging, ranging, parental behavior, and social behavior.

Study Sites

The Ngorongoro Crater is an extinct volcanic caldera located at the western edge of the Gregory Rift in northern Tanzania. The Crater Highlands are the source of the volcanic soil that formed the Serengeti plains immediately to the west (Sinclair and Norton-Griffiths 1979). The Highlands also act as a barrier to the moisture in the prevailing winds off the Indian Ocean. Consequently, the Crater is flanked by dense forest to the north, east, and south but by arid land to the west. The 250 km² Crater is thus a natural island of savanna habitat: the Crater floor is primarily open grassland, and the combination of rich soil, plentiful rainfall, and wet season flooding sustains a remarkable abundance of nonmigratory plains herbivores. The surrounding areas support far lower densities of these species over most of the year.

The Serengeti plains are open rolling grasslands to the west of the Ngorongoro Crater. Our study area includes a 1,700 km² section of the

plains from the Seronera River near the center of Serengeti National Park to the southern and eastern park boundary. Large herbivores dominate the 25,000 km² Serengeti ecosystem, and migratory wildebeest, zebra, and gazelle move over the entire area. These herds are common on the plains from late November until late May each year, then move to the north and west, where they remain for most of the dry season. The Crater Highlands create a rain shadow over the plains, and rainfall is more strictly seasonal on the plains than elsewhere in the Serengeti (Sinclair and Norton-Griffiths 1979).

Lion Social Organization

Lions live in stable social groups ("prides") that typically contain 2–9 adult females (range: 1–16), their dependent young, and a coalition of 2–6 adult males (range 1–9) that has entered the pride from elsewhere (Packer et al. 1988). Prides are territorial and often occupy the same range for generations. Births tend to be synchronous within a pride (Bertram 1975); cubs born less than 1 year apart constitute a "cohort." Prides are maintained by the recruitment of daughters, although some cohorts of young females leave their natal pride to form a new pride nearby. All young males eventually leave their natal pride (Hanby and Bygott 1987; Pusey and Packer 1987), and breeding males generally remain in the same pride for only 2 or 3 years (Bygott, Bertram, and Hanby 1979; Pusey and Packer 1994).

METHODS

Lions in the two areas have been studied continuously since the 1960s (Schaller 1972; Bertram 1975; Elliott and Cowan 1978; Hanby and Bygott 1979; Packer et al. 1988, 1991). All animals are individually recognized by natural markings (Packer and Pusey 1993). Most of the data in this chapter were collected by J. P. H. and J. D. B. between 1974 and 1978. Ecological conditions have varied dramatically on the Serengeti plains over the past 25 years (Sinclair and Norton-Griffiths 1979); by focusing on a narrow time span we aim to present a comprehensive picture of these lions under a specific set of circumstances. However, we also include data collected between 1966 and 1990 for certain analyses and also refer to long-term data that have been presented elsewhere.

Demographic and ranging data in this chapter were collected on eight prides on the Serengeti plains and five in the Crater between September 1974 and February 1978. Between June 1976 and July 1977, intensive behavioral observations were made on one representative pride from each habitat. These prides were closely matched in size and composition (table 15.1) and were representative of the prides in their respective habitats.

Table 15.1 Composition of main study prides.

Habitat	Pride name	Average		Total number of					
		Pride size	FEQ ^a	Adults		Subadults		Cubs	
				Males	Females	Males	Females	1-2 yrs.	< 1 yr.
Crater	Gorigor	20	15	1+2 ^b	6	0	2	12	0-6
Plains	Sametu	19	15	1	8	1	2	5	3-9

^aFEQ = female equivalents = total weight of lions/weight of average adult female.

^bOne male from a coalition of three associated regularly with the Gorigor pride; the other two males associated primarily with a neighboring pride.

Each pride was observed continuously for 4 consecutive days around the full moon during alternate months. These “4-day follows” were made by remaining with those animals that lagged farthest behind while the pride hunted or traveled. No night vision equipment or radiotelemetry was employed. Observations were made on the largest subgroup if the pride split up temporarily. To compensate for slight differences in pride composition, several results are presented in terms of “female equivalents” (FEQ: Bertram 1973), which are simply the combined weight of all pride members divided by the weight of a typical adult female. For example, adult males are about 50% heavier than females, so one male contributes 1.5 female equivalents to the pride total.

The Serengeti pride was also followed in September 1977, but this observation period is included only in certain analyses. The pride remained in much smaller subgroups during this time, so these observations could not be compared with the remaining data. Group size has an important effect on individual food intake rate during the dry season in the Serengeti (Packer, Scheel, and Pusey 1990).

During the 4-day follows, the activity of each lion was recorded at 15-minute intervals and behaviors were recorded by event sampling (Altmann 1974). The quantity of meat eaten by each foraging group was estimated from the age, sex, and species of prey and the proportion of the carcass that was actually consumed by the lions (see Ledger 1968; Sachs 1967). The distance traveled by each pride was measured with a car odometer. Statistical analyses of all data from the 4-day follows provide a single average from each follow, and each follow is considered to be statistically independent.

Herbivore biomass was calculated following the method of Coe, Cumming, and Phillipson (1976). Biomass was measured at six locations in the Serengeti study area each month from April 1975 to October 1977, and at three locations in the Crater pride range on six occasions between January 1974 and February 1978.

Ground transect counts of hyenas were performed in the Crater and Serengeti in 1977. A total of thirty-nine fixed-width transects, spaced 2.5

km apart, were driven over 3,000 km² of the eastern Serengeti plains in May 1977 (for details see Serengeti Research Institute 1977). Twenty-four fixed-width transects, spaced 0.7 km apart, were driven over the entire Crater floor in August 1977.

RESULTS AND DISCUSSION

Prey Abundance

Serengeti Plains. The annual migration of large herbivores in the Serengeti results in marked seasonal changes in herbivore biomass on the plains. Attracted by short grass on nutrient-rich soil, large herds of wildebeest, zebra, and gazelle remain on the plains during the wet season (Sinclair and Norton-Griffiths 1979; McNaughton 1990). The average herbivore biomass during the wet season in this study was over 20,000 kg/km², and was composed mostly of migratory species (table 15.2). However, because these species move around the plains in response to local rainfall, prey availability during the wet season was highly variable within the Sametu pride range.

At the beginning of the dry season, the herds move to the Serengeti woodlands. The average dry season biomass on the plains during this study dropped to less than 1,000 kg/km² (table 15.2). Most of the dry season biomass consisted of Grant's and Thomson's gazelle; the remainder included topi, kongoni, warthog, ostrich, and the occasional wildebeest, eland, giraffe, and oryx.

Ngorongoro Crater. Over the entire Crater floor, prey biomass is almost constant throughout the year: the prey biomass on the Crater floor averaged 11,693 kg/km² in the wet season versus 12,000 kg/km² in the dry season. The large herbivores do show seasonal movements across the Crater floor, but these are much less pronounced than in the Serengeti ecosystem.

Several permanent streams flow through the Gorigor pride range, and

Table 15.2 Herbivore biomass on the Serengeti plains and in the Ngorongoro Crater.

Habitat	Season	Biomass (kg/km ²)		No. of surveys	% of biomass			
		Mean	SD		Wildebeest	Zebra	Gazelle	Other
Plains	Wet	20,167	18,627	19	41%	13%	43%	3%
	Dry	970	1,326	18	4%	3%	82%	11%
Crater	Wet	8,400	2,617	3	31%	49%	10%	10%
	Dry	15,660	932	3	44%	48%	5%	3%

Note: On the plains prey biomass is significantly higher in the wet season than the dry season ($P < .001$), but prey abundance is also more variable in the wet season than in the dry ($P < .001$). Within the Crater, biomass is slightly higher in the dry season ($P = .10$). Across habitats, prey biomass is lowest in the Serengeti dry season ($P < .01$) and most variable in the Serengeti wet season ($P < .01$).

thus prey biomass on this part of the Crater floor was nearly twice as high in the dry season as in the wet season. Even in the "low" season, however, prey biomass was over eight times higher in the Gorigor pride range than on the Serengeti plains (table 15.2). During both seasons, at least 80% of the biomass in the Gorigor range was composed of wildebeest and zebra. Buffalo, eland, kongoni, and gazelle made up most of the remainder.

Hunting and Food Intake Rates

The seasonal patterns of food intake rates differed between the two habitats (table 15.3). In the Crater, the individual food intake rate (kg/FEQ/day) was virtually constant over the year. However, food intake rates in the Serengeti plains pride approached those of the Crater pride only when the migratory herds were abundant on the plains. During the "poor season" on the plains, the individual food intake rate was lower than during either season in the Crater ($U = 0$, $n_1 = 3$, $n_2 = 6$, $P < .05$, two-tailed, Mann-Whitney U test).

In both habitats, 15 of 17 kills (88%) were made at night. Most of the prey captured were middle-sized herbivores (adult weight = 100–200 kg: topi, wildebeest, kongoni, and zebra): 11 of 16 (69%) in the Crater; 13 of 17 (76%) on the plains. Note that during the dry season on the Serengeti plains most of the herbivore biomass consisted of gazelle (see table 15.2). Although gazelle form a large part of the lions' diet in the Serengeti woodlands (see Scheel and Packer, chap. 14), they are only rarely captured on the plains (table 15.3). Thus the plains lions suffered not only an overall loss in prey biomass in the dry season, but also a virtual absence of preferred prey.

Both prides acquired a similar proportion of carcasses by scavenging: 5 of 22 (22%) carcasses in the Crater versus 3 of 20 (15%) on the plains. However, there was a striking contrast between the two prides in the proportion of meat acquired by scavenging: 21% in the Crater versus 1% on the plains. At least three and possibly four of the scavenged carcasses in the Crater were acquired from spotted hyenas (the fifth was scavenged from other lions); whereas only one Serengeti meal was taken from hyenas, and the other two were stolen from jackals and vultures respectively.

Lions and hyenas show similar prey preferences (Kruuk 1972; Schaller 1972). Data collected in 1977 show that hyenas were considerably more abundant in the Crater than on the Serengeti plains. Transect counts of spotted hyenas in the two habitats provided estimates (with 95% confidence limits) of 451 ± 176 hyenas ($1.8/\text{km}^2$) in the 250 km^2 Crater versus $3,393 \pm 814$ ($1.1/\text{km}^2$) in the wet season and 852 ± 409 ($0.3/\text{km}^2$) in the dry season on the $3,000 \text{ km}^2$ Serengeti plains. Because of the closer proximity of the two carnivore species in the Crater, it is not

Table 15.3 Hunting and feeding during 4-day follows.

Date	Seasonal prey avail.	Total number of hunts	Prey killed	Meal scavenged	Group food intake (kg)	Lion group size (FEQ ^a)	Kg food/FEQ ^a /day
CRATER							
June 1976	Good	14	3 wildebeest 1 reedbuck 1 unknown		399	12.6	7.9
August 1976	Good	11	1 yearling wildebeest 1 zebra		203	12.1	4.2
October 1976	Good	7	2 zebra 1 reedbuck	1 zebra	442	14.1	7.8
		<i>Average = 11 ± 3</i>			<i>348 ± 104</i>	<i>12.9 ± 0.8</i>	<i>6.6 ± 1.7</i>
December 1976	Poor	12	4 young zebra		464	14.7	7.9
February 1977	Poor	11	1 Grant's gazelle 1 goose	2 wildebeest 1 zebra	221	15.2	3.6
April 1977	Poor	3	1 eland	1 eland	480	15.3	7.8
		<i>Average = 9 ± 4</i>			<i>388 ± 118</i>	<i>15.0 ± 0.3</i>	<i>6.4 ± 2.0</i>
PLAINS							
January 1977	Good	9	1 topi 3 wildebeest 1 young Grant's gazelle	1 Thomson's gazelle	471	13.8	8.5
March 1977	Good	21	2 young zebra 1 hare		141	12.9	2.7
May 1977	Good	18	2 young zebra 1 wildebeest		273	13.1	5.2
		<i>Average = 16 ± 5</i>			<i>295 ± 135</i>	<i>13.2 ± 0.4</i>	<i>5.5 ± 2.4</i>
September 1976	Poor	14	1 topi 1 warthog 1 young kongoni	1 hare 1 unknown	162	13.0	3.1
November 1976	Poor	12	1 topi 1 warthog		126	12.7	2.5
July 1977	Poor	13	1 wildebeest		133	13.3	2.5
		<i>Average = 13 ± 1</i>			<i>140 ± 16</i>	<i>13.0 ± 0.2</i>	<i>2.7 ± 0.3</i>

^aFEQ = female equivalent = total weight of lions/weight of average adult female.

surprising that the Crater lions were able to acquire a larger proportion of meat by scavenging.

Thus the Crater lions achieved higher rates of food intake throughout the year than did the plains lions during the dry season, and a considerable proportion of the meat consumed by Crater lions was obtained by scavenging. In both habitats, lions hunted mostly at night, and the two prides focused on prey of similar size.

Lion Density and Reproduction

Over a variety of measures of prey availability, "poor season" prey biomass correlates most closely with lion density across habitats (Van Orsdol, Hanby, and Bygott 1985). From our data, it is clear that lions on the plains had a difficult time acquiring adequate food during the poor season. Schaller (1972) and Packer, Scheel, and Pusey (1990) estimate that a female lion requires 5.0–8.5 kg of meat each day. Lions in the plains pride were unable to achieve these levels during any of the poor season 4-day follows (see table 15.3).

Lion population density increased on the Serengeti plains between Schaller's (1972) study in the late 1960s and the mid-1970s (Hanby and Bygott 1979; also see below). This increase may have resulted from improved prey availability during the poor season. Schaller's only dry season prey count on the plains indicated a prey biomass of only 131 kg/km². Poor season prey abundance subsequently increased for two reasons (Sinclair and Norton-Griffiths 1979; Hanby and Bygott 1979; Packer et al. 1988). First, the Serengeti herbivore populations increased continuously from the early 1960s through the 1970s after the eradication of rinderpest. Second, favorable rainfall patterns throughout the 1970s resulted in a higher population of resident species and a more continuous presence of migratory species on the plains.

Over the course of our study in the mid-1970s, an average of 119 lions were resident in eight prides in the 1,700 km² study area on the Serengeti plains. An additional 50 or so nomadic lions were also present each year when the migratory herds were on the plains, making the total density on the plains 0.1 lions/km². On the 250 km² Crater floor, an average of 97 lions were resident in five prides with an additional 5 nomads present (0.4 lions/km²). The Crater population, however, contained a somewhat higher proportion of immatures (61% vs. 48% on the plains, see below). Thus the biomass of lions in the Crater was about 3.3 times higher per km² than on the plains.

Interbirth interval and age at first reproduction are similar in the two habitats (Packer et al. 1988). During this study there was no difference in litter size between the two populations (fig. 15.1). In contrast, survival of cubs to 3 years of age was over twice as high in the Crater as on the

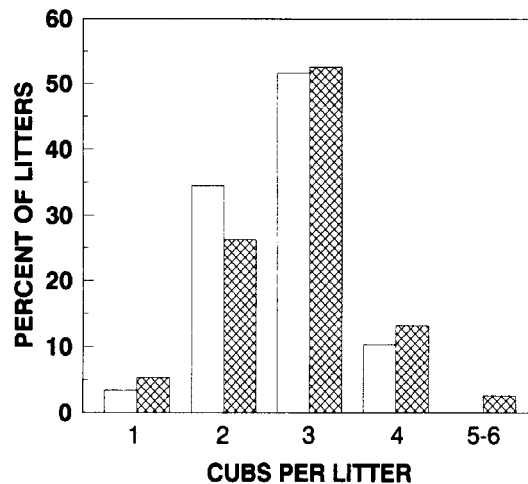


Figure 15.1 Distribution of litter sizes in the Crater (open bars; $N = 28$, mean = 2.8) and the plains (hatched bars; $N = 38$, mean = 2.7) for cubs born between 1974 and 1977.

Serengeti plains, and most mortality on the plains was concentrated in the first 12 months (fig. 15.2). Although female reproductive rates are consistently higher in the Crater (Packer et al. 1988), pride size there is similar to that of Serengeti plains prides (fig. 15.3) because of higher dispersal rates by subadults (Hanby and Bygott 1987; Pusey and Packer 1987) and higher mortality of adult females in the Crater (Packer et al. 1988).

Ranging, Denning, and Territoriality

Over a 3-year period, the mean range size of the five Crater prides was 45 km² compared with 200 km² for the six most frequently observed plains prides. The Crater pride ranges showed very little overlap (also see Elliott and Cowan 1978). In contrast, the Serengeti prides shifted their ranges each year with the arrival of the migration (see also Schaller 1972), with the result that there was considerable overlap between prides in their annual ranges. A detailed analysis of long-term ranging patterns in the two habitats will be presented elsewhere.

Data from the 4-day follows reveal differences in the daily ranging patterns of the two study prides (fig. 15.4). The average distance traveled over a 24-hour period was only about two-thirds as far for the Crater pride as for the plains pride. Although it might seem that this difference was due solely to the greater abundance of prey in the Crater, distance traveled *within* each habitat did not vary with prey abundance: Crater lions traveled only slightly (but not significantly) farther in the poor season than in the good season, and the plains pride traveled similar distances over both seasons.

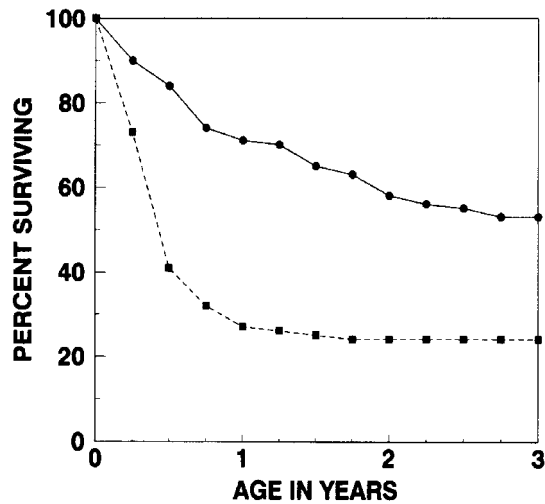


Figure 15.2 Cub survival for cubs born in the Crater (solid line and circles, $N = 109$ cubs) and the plains (dashed line and squares, $N = 142$ cubs) between 1974 and 1977. Treating each litter as statistically independent, a significantly higher proportion of Crater cubs survive to 1 year of age than do cubs on the plains (chi-square = 17.77, $N = 101$ litters, $P < .01$).

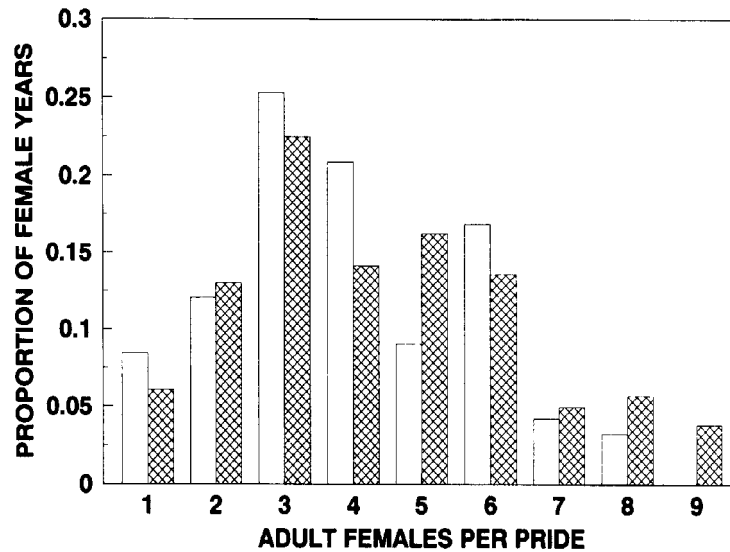


Figure 15.3 Proportion of females that have resided in prides of different sizes in the Ngorongoro Crater between 1963 and 1990 (open bars, $N = 498$ female years) and on the Serengeti plains between 1966 and 1990 (hatched bars, $N = 707$ female years). The distribution of pride sizes is measured in terms of the sizes experienced by individual females (see Pusey and Packer 1987). The proportion of females in each pride size is the proportion of "female years" in which prides of that size existed within each study area. Thus a pride that comprised two females for 5 years and three females for 2 years would contribute $2 \times 5 = 10$ female years to the pride size of two and 6 female years to the size of three.

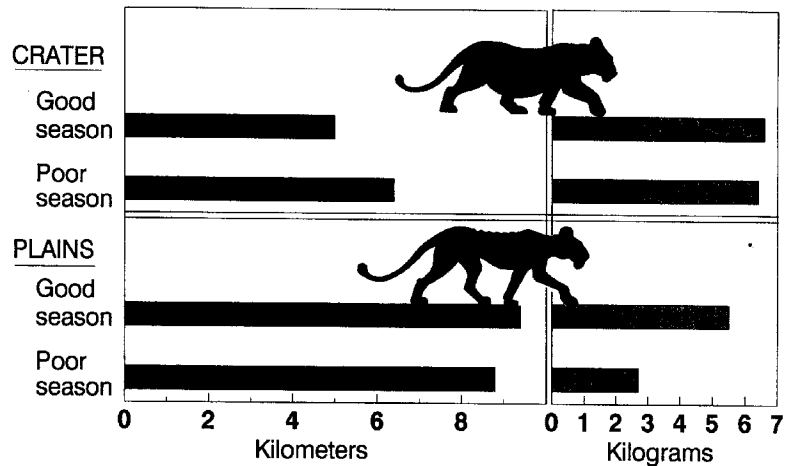


Figure 15.4 Average distance lions traveled per day in each habitat (solid bars) and their average food intake rates (shaded bars) in different seasons. The Serengeti lions traveled significantly farther than the Crater lions ($U = 4$, $n_1 = 6$ 4-day follows in the Crater, $n_2 = 7$ follows in the Serengeti, $P < .02$), but there was no significant effect of season within or between the two habitats. Food intake rate varied significantly between seasons in the Serengeti, but not in the Crater (see table 15.3).

Lions drink after every meal, and females keep their cubs hidden in dense brush until they are 2 months old. The distribution of water and cover probably had an important influence on the contrasting movements of the two prides. The Crater pride's range included open grassland, *Acacia* forest, lakeshore, freshwater streams, bushy hillside, and brush-covered mounds. Thus adequate cover was available over most of the pride's range, and no part of the range was more than 2 km from fresh water at any time of year.

The plains pride's range was by contrast featureless and harsh. Rocky outcrops (kopjes) and alkaline marshes provided cover, shade, or den sites in only four locations. One female traveled 20 km in 12 hours between her cubs' den and the remainder of her pride. In the wet season, water could be found in rock clefts, water holes, and low-lying areas on the plains. But in the driest months, water was available only in two marshes located 10 km apart.

The long distances traveled by the plains pride probably contributed to the higher mortality of its cubs (see fig. 15.2). Once cubs are old enough to leave their dens, they join the other cubs in the pride to form a stable "crèche," thus spending more time with their mothers (Packer, Scheel, and Pusey 1990). By this age, cubs feed on meat and must be able to range widely. Mothers give cubs access to kills, no matter how thin they are themselves, but they do not carry their cubs to kills, nor do they carry kills to their cubs. When prey is scarce on the plains, weakened cubs are often unable to keep up and may be abandoned (Packer and Pusey 1984). Most cub mortality on the plains occurs in the dry season, whereas

there is no seasonality in cub mortality in the Crater (Packer et al. 1988). Thus, although the Serengeti pride traveled as far in the wet season as in the dry season, the cubs were less able to cope with long-distance travel when food was scarce and water was widely scattered.

Lions are intolerant of same-sex intruders within their territories. Although ranges in the Serengeti often overlap, members of adjacent prides usually remain several kilometers apart. The *annual* overlap results from *seasonal* shifts in ranges due to the changing distribution of prey. Interpride encounters usually end in aggression, with the larger group chasing the smaller (Packer, Scheel, and Pusey 1990). Roaring and marking play conspicuous roles in the territorial behavior of lions, although these behaviors also function in long-range communication between pride-mates (Schaller 1972; Rudnai 1974; McComb et al. 1993; Grinnell, Packer, and Pusey 1995).

Males roared and marked more frequently than females, and both behaviors were broadly correlated with prey availability (table 15.4). Females in both habitats roared more in the good season than in the poor season, and males marked more in the good season.

Although there was no difference in the mean frequency of roaring between the two habitats, the Serengeti lions showed significantly higher variance in roaring behavior than the Crater lions (table 15.4). This may have been due to the fact that Serengeti lions frequently readjust their territorial boundaries over the course of a year and are often widely separated from their neighbors. The need to announce their location to their rivals may therefore be more intermittent than in the Crater.

Overall, these results suggest that roaring and marking within each habitat are most frequent when prey is most abundant. These are the conditions in which intruder pressure from nomadic lions is highest (Schaller 1972).

Activity Patterns and Social Behavior

Lions in the two habitats showed striking similarities in their activity patterns (fig. 15.5). In spite of very different physical habitats and prey abundance, lions in both habitats spent about 80% of their time sleeping, lying down, or sitting.

A detailed analysis of social behavior suggests that prey availability may affect frequency of social behavior in both habitats. Within each habitat, the frequency of social interactions was higher in the good season (fig. 15.6). The seasonal decrease in social interaction on the plains could be due to the energetic consequences of lower food intake when prey are scarce. However, a similar seasonal decrease was found in the Crater even though food intake rates there do not vary over the year (see table 15.3). This finding suggests that social interaction is correlated with changes in prey availability per se rather than with food intake. Lions may need to

Table 15.4 Frequency of roaring and marking (event/individual/hour).

Sex	Season	Habitat	
		Plains	Crater
Roaring			
Males	Good	0.76 ± 0.01 (N = 2)	0.12 ± 0.07 (N = 3)
	Poor	0.26 ± 0.23 (N = 2)	0.08 ± 0.03 (N = 3)
Females	Good	0.27 ± 0.22 (N = 3)	0.08 ± 0.04 (N = 3)
	Poor	0 (N = 4)	0.04 ± 0.02 (N = 3)
Marking			
Males	Good	0.29 ± 0.24	0.18 ± 0.09
	Poor	0	0.03 ± 0.02
Females	Good	0	0.01 ± 0.01
	Poor	0.10 ± 0.17	0

Note: Across all conditions, males roar and mark significantly more often than females (roaring: $T = 1$, $n = 10$ 4-day follows when both males and females were present, $P < .01$, Wilcoxon signed ranks test; marking: $T = 3$, $P < .01$). Across habitats, females roar more during the "good" season than during the "poor" season ($U = 6.5$, $n_1 = 6$, $n_2 = 7$, $P < .05$); and males mark more during the "good" season ($U = 0$, $n_1 = 5$, $n_2 = 5$, $P < .01$). Differences in the variance in roaring frequency between the two habitats are significant for both males and females ($P < .01$). N , number of 4-day follows; sample sizes for marking behavior are the same as for roaring.

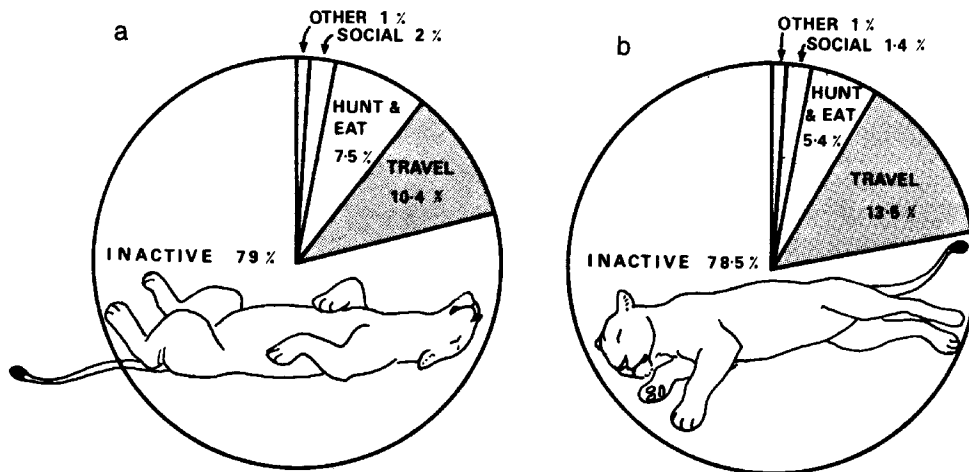


Figure 15.5 Pie charts of lion activity during the 4-day follows. A = Crater, B = plains. Data include all seven 4-day follows on the plains pride and are not separated by season because activity patterns did not vary seasonally (except for social behavior; see text and fig. 15.6). "Inactive" includes sleeping, lying, and sitting. "Other" includes marking, patrolling, roaring, self-grooming, and defecation/urination.

take more care to remain hidden from their prey when food is scarce and therefore may engage in lower levels of conspicuous activity.

CONCLUSION

Lions on the Serengeti plains clearly lead a harder life than their Crater counterparts do: food supplies are more ephemeral, water is scarcer, and denning sites are widely scattered. Cub mortality on the plains is highly seasonal and far higher than in the Crater. Moreover, most of our data

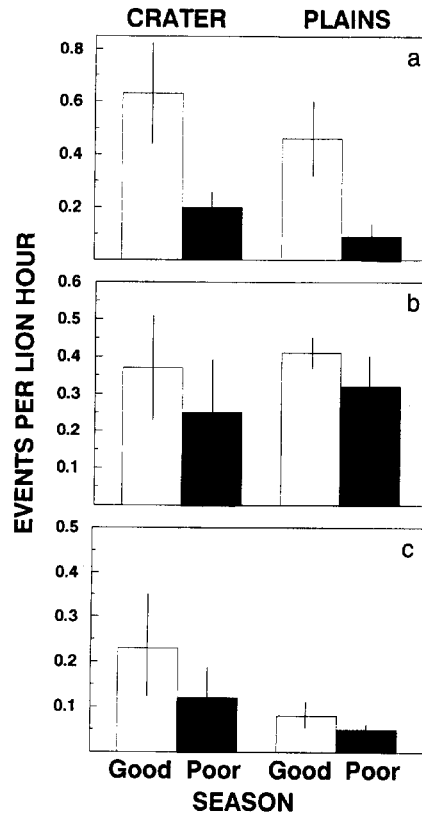


Figure 15.6 Frequency of social behavior during 4-day follows. Data include all seven 4-day follows on the plains pride. Play (*a*) includes mock fighting and hunting behavior. Affiliative behavior (*b*) involves licking, grooming, and head rubbing. Hostile behavior (*c*) involves growling, snarling, biting, swatting, and chasing another lion. None of the differences within or between habitats are statistically significant; however, lions in both habitats engaged in significantly more play in the “good” season than in the “poor” season ($U = 5.5$, $n_1 = 6$, $n_2 = 7$, $P < .025$). Data from the Crater are based on 4,056 lion hours; from the plains, on 6,610 lion hours.

were collected when conditions were unusually benign for the plains lions: successive years with favorable rainfall coupled with a continuous increase in herbivore populations allowed the plains lion population to increase (Hanby and Bygott 1979). These conditions persisted until 1979. Thereafter rainfall returned to a more typical pattern, herbivore populations leveled off, and the plains prides had to rely on even lower levels of prey availability or leave the plains on temporary forays to the woodlands (Packer, Scheel, and Pusey 1990). Cub mortality on the plains subsequently increased (Packer et al. 1988), and the number of adult females resident on the plains reached a peak in the early 1980s (fig. 15.7).

Many of the plains prides originate from Serengeti prides that live along the woodlands/plains boundary. Dispersing groups of young females leave the more crowded parts of the Serengeti to settle in the relatively vacant plains, thus avoiding the more intense intergroup competi-

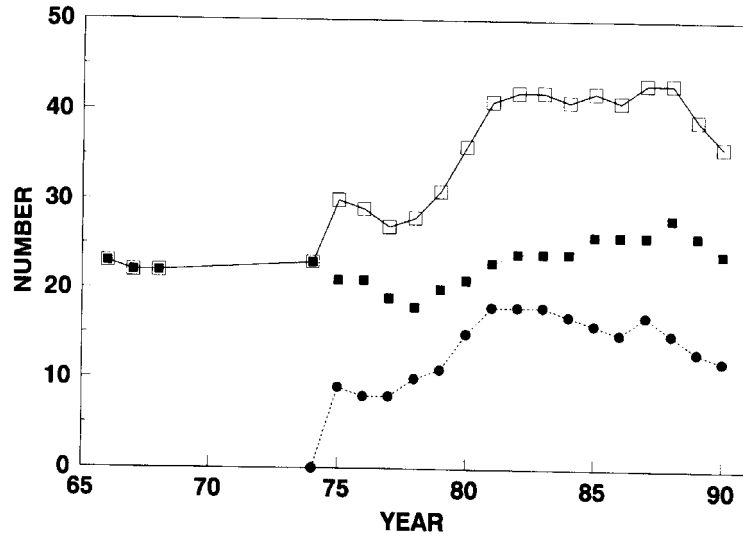


Figure 15.7. Number of adult females (≥ 4 years old) that resided in the eastern part of the Serengeti plains between 1966 and 1990. "Original prides" (solid squares, dotted line) are prides first identified and censused by George Schaller in 1966; "immigrant prides" (solid circles, dashed line) are those that were born in the Serengeti woodlands but dispersed onto the plains. The total number of females living on the plains (open squares, solid line) increased in the late 1970s following the immigration of excess females from the woodlands.

tion in the woodlands (Pusey and Packer 1987; C. Packer et al., unpub.). In fact, most of the increase in resident females on the plains over the past two decades is due to immigration from the woodlands (fig. 15.7). Thus the plains can be viewed as a sink for excess lions from the woodlands.

Like the Serengeti woodlands, the Crater is a net exporter of lions. Crater lions gain access to adequate food each year, and reproductive rates are consistently higher than on the plains (Packer et al. 1988). Competition for space in the Crater is intense: the reproductive rate of the Crater lions is sufficiently high to permit rapid population growth, yet the number of prides on the Crater floor has remained relatively constant (Packer et al. 1991), and pride size in the Crater is comparable to that on the Serengeti plains (see fig. 15.3). A large proportion of subadults born in the Crater disperse and settle in areas (both in the Crater Highlands and in the Serengeti) with far lower prey availability than on the Crater floor (Hanby and Bygott 1987; Pusey and Packer 1987).

Thus the continued presence of lions in suboptimal habitats may be guaranteed only if excess animals from superior habitats are able to travel freely into them. Where large lion populations have been subdivided by the creation of small parks or reserves surrounded by agricultural areas or human habitation, it may be necessary to create corridors between reserves to maintain viable lion populations within each reserve.

Of special relevance to the Serengeti is the fact that most poaching

activity occurs in the northern and western woodlands (see Arcese, Hando, and Campbell, chap. 24; Campbell and Hofer, chap. 25). Although the woodlands lions may be less conspicuous than their photogenic plains counterparts, their numbers are far more important to the long-term viability of the Serengeti lion population.

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