

# Serengeti II

*Dynamics, Management, and  
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## FOURTEEN

### Variation in Predation by Lions: Tracking a Movable Feast

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The Serengeti ecosystem is characterized by the annual migration of wildebeest, zebra, and gazelle. The Serengeti also supports sizable populations of resident ungulates. Even though the migratory species are their most frequent prey, Serengeti lions are territorial except during periods of extreme hardship (Packer, Scheel, and Pusey 1990). Lions must therefore endure wide fluctuations in the local densities of certain prey species, relying on the stable abundance of resident species during the lean season. The influence of local prey abundance can be measured by the predators' functional response (e.g., Holling 1959; Hilborn and Sinclair 1979) and by economic models from foraging theory (e.g., Stephens and Krebs 1986). Foraging theory successfully predicts the prey preferences of hunting lions (Scheel 1993). By preferring wildebeest and zebra during the migration and specializing on warthog and buffalo when the migrants are scarce, lions appear to be risk-sensitive foragers that maximize food intake rate.

The precise timing and pattern of the Serengeti migration is complex and erratic. Thus, local prey densities can vary dramatically on a weekly or even daily basis, and no two years are exactly the same. In addition, the sizes of the Serengeti ungulate populations have changed markedly over the past quarter century. In this chapter, we show that lion predation patterns vary not only with short-term changes in local prey density but also with long-term changes in herbivore population sizes.

#### **METHODS**

##### **Lions and Their Habitats**

Lions in a 2,000 km<sup>2</sup> area of southeastern Serengeti National Park have been studied continuously since 1966 (fig.14.1; Schaller 1972; Bertram 1979; Hanby and Bygott 1979; Packer et al. 1988; Packer, Scheel, and Pusey 1990). Forty-four different prides have occupied this area over the

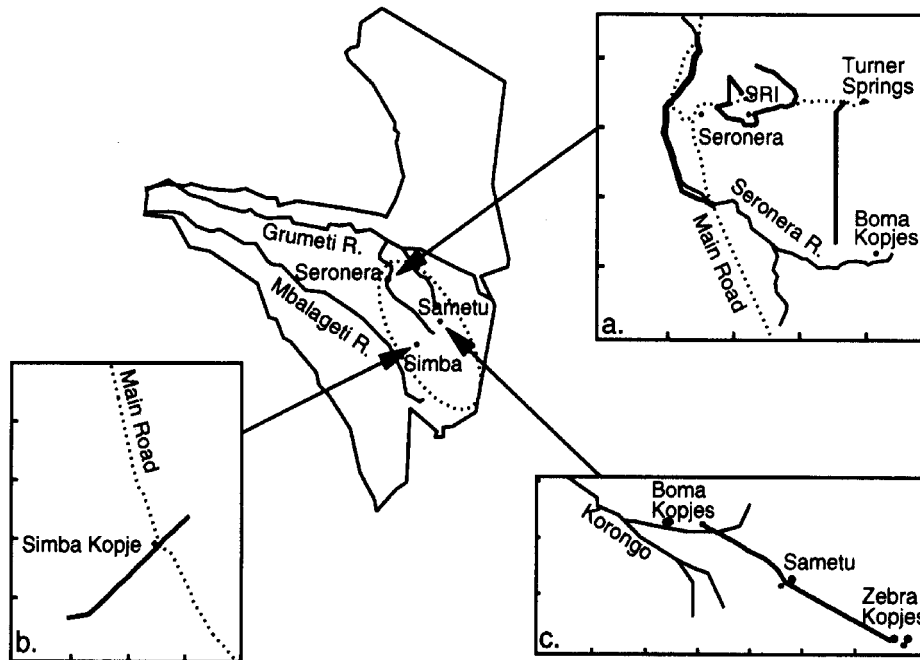


Figure 14.1 Location of transects in: (a) the Seronera woodlands and (b and c) the central plains. Ticks along the axes mark 5 km intervals. Dotted oval in the central map indicates the approximate limits of the long-term records.

past 25 years, and the study population currently comprises about 200 individuals in twenty prides. “Woodlands” prides live in habitat dominated by *Acacia*, *Commiphora*, and *Balanites* trees in the area located between Nyaraswiga Hill and Turner’s Springs. “Plains” prides range in the open grasslands of the central plains south of the Seronera and Ngare Nanyuki Rivers. “Edge” prides live along the woodlands/plains boundary.

#### Short-Term Data

**Hunting Observations.** Data in this chapter are restricted to female lions, since they are the principal hunters (Schaller 1972; Scheel and Packer 1991). Hunting activities of radio-collared females and their companions were recorded during 96-hour watches just before or after each full moon. Lions were located by radiotelemetry and followed continuously for 96 hours. Night observations were made with light-intensifying goggles and  $8 \times 35$  binoculars. Between September 1984 and December 1987, 198 hunts were recorded in 3,500 hours of observation of prides from all three habitats (Scheel and Packer 1991; Scheel 1993). Lion hunting frequency is measured as the number of hunts per day, whether or not the hunt was successful. Hunts are defined as movement toward potential prey by at least one lion exhibiting a typical stalking stance (see Scheel and Packer 1991).

**Prey Density.** Each month between July 1986 and December 1987, herbivores were censused along five fixed transects (fig. 14.1) varying from 11 to 21 km in length. All animals within 500 m of the transect were recorded, except when visibility was limited by brush or terrain, in which case the sampling area was reduced accordingly. Three transects were located in woodland habitat, two in the plains. One woodlands transect followed the course of the Seronera River.

In addition, all herbivores within 1,000 m of lions were censused hourly during the 96-hour follows. Prey censuses could be performed during moonlit nights, but no counts were attempted on dark nights. Prey density is the number of individuals recorded each day within 1,000 m of the lions. Analyses of lion hunting frequency on each prey species are restricted to only those observation periods when at least one animal of that species was present.

### Long-Term Data

**Lion Sightings and Carcass Records.** Most data have been collected from opportunistic "sightings" between June 1966 and September 1991. More systematic observations date from 1984, when females in a dozen prides were fitted with radio collars. All sightings include the location of each lion group and details of each prey item (species, age/sex class, and, where known, whether the carcass was obtained by predation or scavenging). Only one sighting is included from each pride each day, and we exclude all sightings in which prides had moved outside their typical habitat ( $N = 51$  of 9,436 sightings and 22 of 1,481 carcasses). Scavenged carcasses are excluded from all analyses. Quantity of meat available from each carcass is estimated as in Packer, Scheel, and Pusey (1990).

**Rainfall.** Monthly rainfall totals are available from gauges maintained by the Serengeti Ecological Monitoring Programme. Representative gauges from the woodlands ( $n = 6$ ) and plains ( $n = 10$ ) provide data for at least 200 months between June 1966 and September 1991. Rainfall is averaged across all gauges within each habitat each month, and "seasonal rainfall" is the total of these averages for the entire season. The wet season runs from November to the following May, the dry season from June to October (Hilborn et al., chap. 29; Sinclair 1979b). Note that seasonal rainfall is correlated between plains and woodlands (fig. 14.2).

**Prey Population Sizes.** Ungulate population sizes are estimated from published censuses (wildebeest and zebra: see Campbell 1989; Thomson's gazelle: Borner et al. 1987; Dublin et al. 1990; buffalo: Sinclair 1977; Campbell 1989). We estimate population size between censuses by linear interpolation and assume that populations have remained constant in the

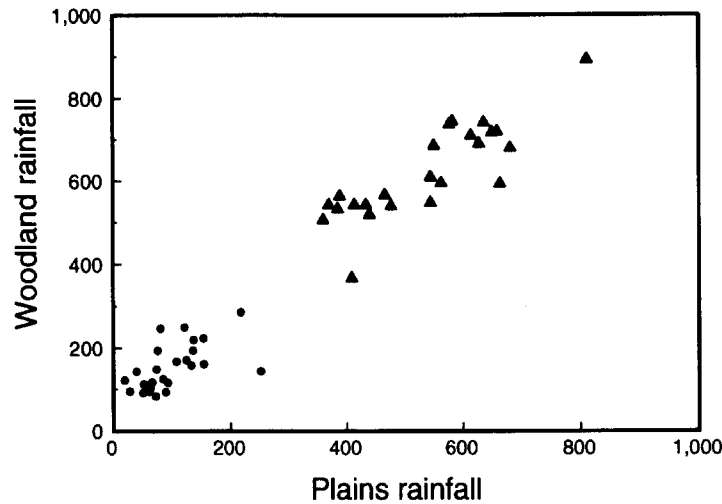


Figure 14.2 Correlations of seasonal rainfall between plains and woodlands habitats, 1966–1991. Dry season, circles (Spearman rank correlation = .65,  $n = 25$  years); wet season, triangles (Spearman = .81).

years following the most recent census. Because of conflicting estimates for the population size of Thomson's gazelle in the early 1980s, we estimate the population from 1983 to 1988 to have been the average of figures presented by Borner et al. (1987) and Dublin et al. (1990).

The Serengeti buffalo population decreased significantly between 1975 and 1986, but the decrease was limited to the far northern and western sectors of the Serengeti (Dublin et al. 1990). Because these regions are well outside the lion study area, and the buffalo population in the southeastern Serengeti has not been affected by high levels of poaching (Campbell 1989), we have excluded this decrease from our population estimates. Note that the wildebeest and buffalo population sizes have been closely correlated over the past 25 years (fig. 14.3).

### Statistical Analysis

To analyze hunting frequency in relation to local prey density, we use stepwise linear regression at a significance level of .01. All data collected during the same 96-hour watch are treated as a single independent point ( $n = 36$ ).

Seasonal differences across habitats in both transect prey density and carcass frequency are analyzed by ANOVAs at a significance level of .05 (SYSTAT: Wilkinson 1988). Each census of the same transect is treated as an independent sample ( $n = 103$ ). For seasonal variation in carcass frequency, each pride is treated as a single sample, data from the appropriate season are lumped across years, and the dependent variable is the proportion of sightings with carcasses of each species. Each species is considered separately, and the proportions are transformed by an arc-

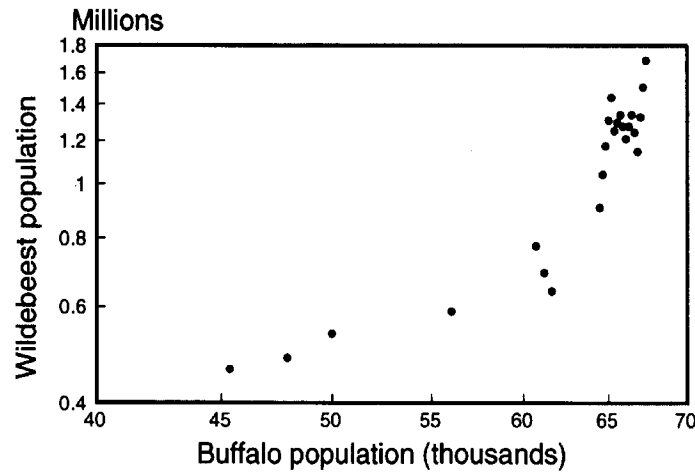


Figure 14.3 Correlation between wildebeest and buffalo populations in the Serengeti (Spearman = .86).

sine—square root transformation. The categorical variables are season (wet or dry) and habitat (woodland, edge, or plains).

Changes in carcass frequency across years (1966–1991) are analyzed with logistic regression models, and each lion sighting is treated as an independent point. The dependent variable is the presence or absence of a carcass at each lion sighting, and carcasses that persisted longer than one day are counted only once. Analyses are separated by species, season, and habitat, and regressions include sightings from all prides in a given habitat. We test six independent variables: the population size of the prey species (when available), size of the wildebeest population (for all species), size of the buffalo population, the preceding season's rainfall, the current season's rainfall, and the proportion of sightings at which a wildebeest carcass was found (this variable is not included in the wildebeest analysis). Population data are entered into all analyses as  $\log(\text{population size})$ , and independent variables are removed from the logistic models in a reverse stepwise fashion. Because six regressions (two seasons by three habitats) are performed on each species, the significance level is set at .01 to reduce the incidence of spurious correlations.

## RESULTS AND DISCUSSION

Between 1966 and 1991, female lions were observed feeding from 1,459 carcasses. Seven species accounted for over 90% of the total (both in numbers of carcasses and in kilograms of meat): wildebeest, zebra, Thomson's gazelle, buffalo, warthog, kongoni (hartebeest), and topi (fig. 14.4). Because of their adjacent rank in the lions' diet, relatively small sample size, and similar body size, we have combined topi and kongoni into a single prey "type" for the following analyses. Note that by including op-

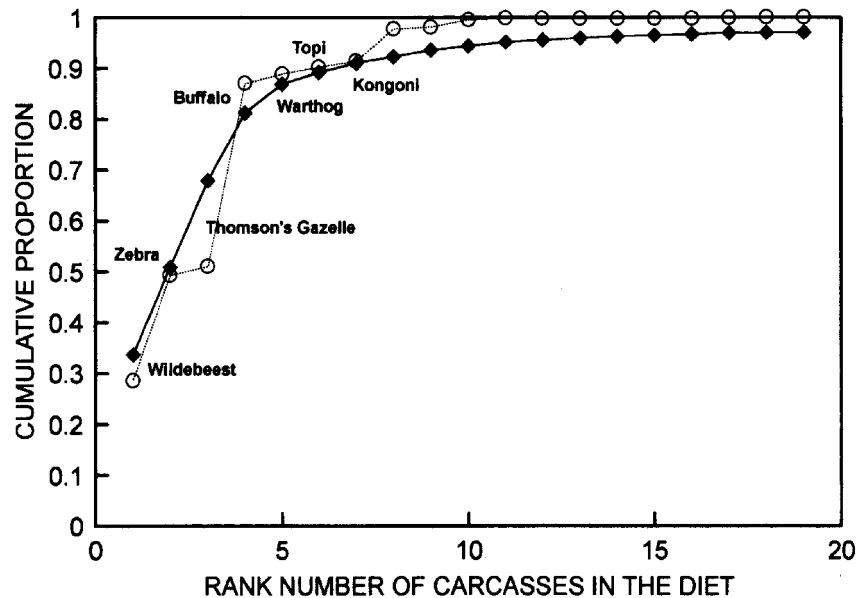


Figure 14.4 Proportion of each prey species in the lions' diet during 1966–1991, ranked by number of carcasses (triangles) and by kilograms of meat (circles). Note that although buffalo ranked only third in the number of carcasses, buffalo make the greatest contribution to the lions' diet in terms of kilograms of meat.

portunistic observations we underestimate the contribution of small prey species because small prey items are often consumed as soon as they are captured (see Bertram 1979). However, direct observations suggest that such small prey are rare and, in terms of biomass, make an insignificant contribution to the lions' total food intake (Schaller 1972; Packer, Scheel, and Pusey 1990; Hanby, Bygott, and Packer, chap. 15).

### Hunting Frequencies

Local densities of the six major prey types varied dramatically from one 96-hour watch to the next, and the lions hunted wildebeest, warthog, and Thomson's gazelle significantly more often when those species were most abundant (fig. 14.5). Hunting rates for zebra and topi/kongoni show similar trends, but these are not statistically significant. In contrast, lions showed no tendency to vary their hunting frequency according to the local density of buffalo. Only large prides attempt to capture buffalo, and lions prefer to attack solitary bulls rather than herds (Packer, Scheel, and Pusey 1990; Scheel 1993), presumably because buffalo herds actively defend themselves and can even kill a lion (Packer 1986).

### Prey Density and Carcass Records

Precise records of local prey density do not exist for each of the past 25 years. However, vegetation growth and hence migratory movements depend on rainfall (McNaughton 1979; Maddock 1979; Sinclair 1979a);

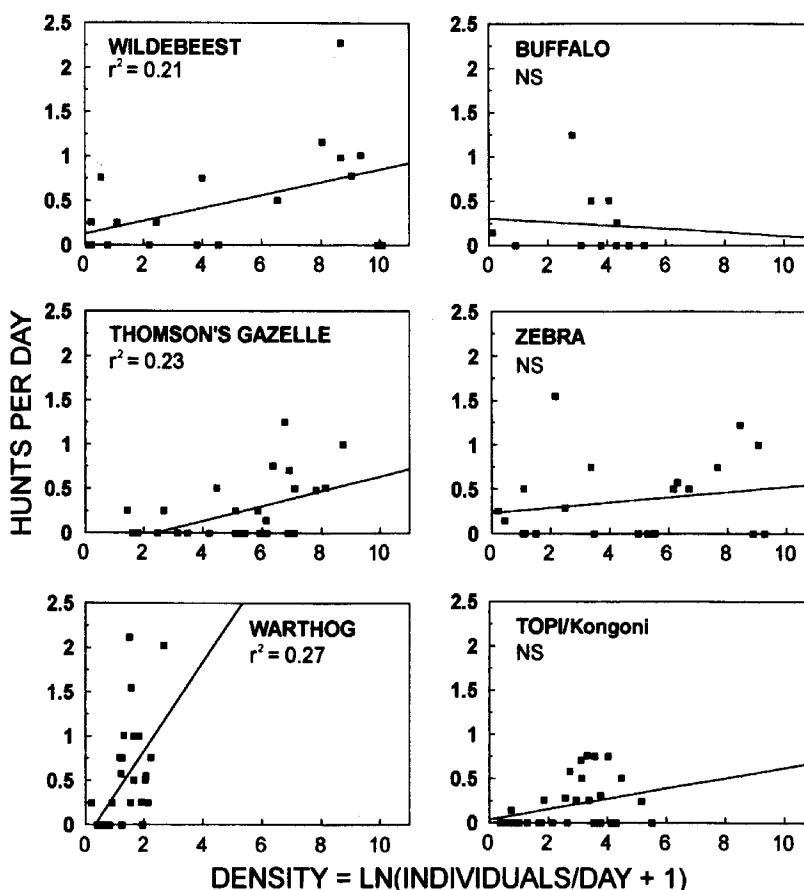


Figure 14.5 Frequency of lion hunts on each prey species plotted against the density of that species over a 4-day period. The regressions for wildebeest ( $T = 2.8$ ), Thomson's gazelle ( $T = 2.8$ ), and warthog ( $T = 3.0$ ) are all significant ( $P < .01$ ).

thus wildebeest and zebra are abundant in the southeastern Serengeti only during the wet season (Maddock 1979). In the following sections, we confirm the overall association between rainfall and local prey density (both between and within seasons), then use variation in rainfall and in the population size of each prey species as correlates of local prey abundance. These analyses assume that different conditions (e.g., rainfall, season, etc.) do not alter the probability of sighting lions with a carcass of each species, and thus that the proportion of sightings with carcasses reflects the underlying predation rate. Note, however, that this measure is too coarse to distinguish whether variation in predation rates results exclusively from changes in local prey density or from changes in lion preference.

**Seasonal Variation.** Across seasons, the transect data from 1986–1987 and the diet data from 1966–1991 show a similar pattern (table 14.1). Wildebeest were more locally abundant and more commonly found as



Table 14.1 Variation in local prey density across seasons.

Prey species	Prey density along transects (1986–1987)	Carcasses at lion sightings (1966–1991)
Wildebeest	Wet > Dry*	Wet > Dry***
Zebra	NS	Wet > Dry*
Thomson's gazelle	Dry > Wet**	Dry > Wet**
Buffalo	NS	NS
Topi/Kongoni	NS	NS
Warthog	Dry > Wet***	Dry > Wet***

\* $P \leq .05$ , \*\* $P \leq .01$ , \*\*\* $P \leq .001$ .

carcasses in the wet season, whereas Thomson's gazelle and warthog were more common in the dry season. While zebra densities did not vary significantly across seasons, zebra carcasses were more common in the wet season. There were no significant seasonal differences in the transect density or carcass frequency of buffalo or topi/hartebeest.

The prey censuses from the 96-hour watches indicate that prey abundance on the plains varies with rainfall within the same season. During the dry season, prey density correlates with average monthly rainfall from the preceding month. Wildebeest density was significantly higher following wet months (linear regression,  $T = 23.4$ ,  $r^2 = .99$ ,  $n = 5$ ,  $p < .01$ ), whereas the density of Thomson's gazelle declined following wet months ( $T = -5.0$ ,  $r^2 = .85$ ,  $n = 5$ ,  $p < .05$ ). Trends in the other prey species are not significant, but rainfall data are available for only a subset of the 96-hour watches. Too few data are available to perform a similar analysis in the woodlands.

**Variation across Habitats.** Only topi/kongoni density varied significantly across transects in 1986–1987 (table 14.2), and only these species were more common in the woodlands than on the plains (fig. 14.6). Over the past 25 years, the predation rate on several species has varied significantly across habitats. Compared with edge and plains lions, the woodlands lions were found more frequently with buffalo and warthog carcasses during the wet season and with buffalo carcasses during the dry season (table 14.2, fig. 14.6). In the dry season, edge lions were found more frequently with warthog carcasses.

Note that the transects were censused only over a 2-year period and were located primarily in the southern woodlands and northern plains, while the lion sightings extended over a far longer time period and a broader area of woodland and plains habitat (see fig. 14.1). Thus differences in predation rates (carcasses) that were not mirrored in the transect prey densities may still reflect substantial differences in local prey abundance: all other surveys have shown that buffalo and warthog are more common in the woodlands than on the plains (Jarman and Sinclair 1979; Hanby and Bygott 1979; Campbell 1989).

Table 14.2 Variation in local prey density across habitats.

Prey species	Prey density along transects (1986–1987)	Carcasses at lion sightings (1966–1991)	
		Wet season	Dry season
Wildebeest	NS	NS	NS
Zebra	NS	NS	NS
Thomson's gazelle	NS	NS	NS
Buffalo	NS	W > E > P***	W > E > P***
Topi/Kongoni	W > P***	NS	NS
Warthog	NS	W > E and P**	E > W and P**

Note: W, woodlands; E, edge; P, plains. See table 14.1 for significance levels.

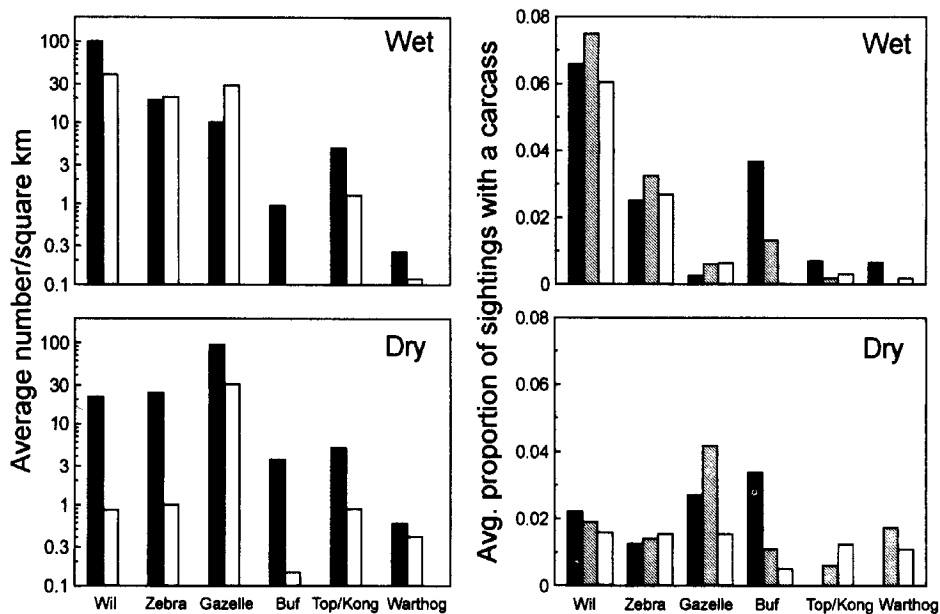


Figure 14.6 Seasonal variation in herbivore density along transects (left) and in proportion of sightings with carcasses (right) in the wet season (top) and dry season (bottom). Woodlands, solid bars; edge, hatched bars; plains, open bars. See tables 14.1 and 14.2 for statistics.

**Rainfall Variation across Years.** Because of the extreme variation in rainfall from one year to the next (Norton-Griffiths, Herlocker, and Pennycook 1975; Hilborn et al., chap. 29), local prey density during a given season can vary strikingly across years (see above; Maddock 1979; Packer et al. 1988).

Rainfall during the dry season attracts wildebeest into our study area (see above; Maddock 1979; McNaughton 1979), and thus dry season rainfall is positively correlated with the incidence of wildebeest carcasses in each habitat (table 14.3, fig. 14.7). High wet season rainfall on the plains delays the wildebeest migration through the Seronera region until the beginning of the dry season (Maddock 1979), thus increasing dry season predation rates (fig. 14.7). Finally, higher wet season rainfall in the

Table 14.3 Correlations of four rainfall variables (woodland/plains wet/dry season totals) with the presence of carcasses at lion sightings during the dry season.

Prey species	Habitat		
	Woodland	Edge	Plains
Wildebeest	Woodland dry +***	Woodland dry +*** Plains wet +**	Plains dry +**
Zebra	NS	NS	Woodland wet -***
Thomson's gazelle	NS	NS	NS
Buffalo	NS	NS	n.d.
Topi/Kongoni	NS	n.d.	NS
Warthog	NS	NS	NS

Note: Columns indicate habitat in which lions were found with carcasses of each prey species. Text in cells indicates habitat and season for which rainfall was significantly correlated with the frequency of carcasses. Sign indicates direction of correlation. See table 14.1 for significance levels. n.d., insufficient data.

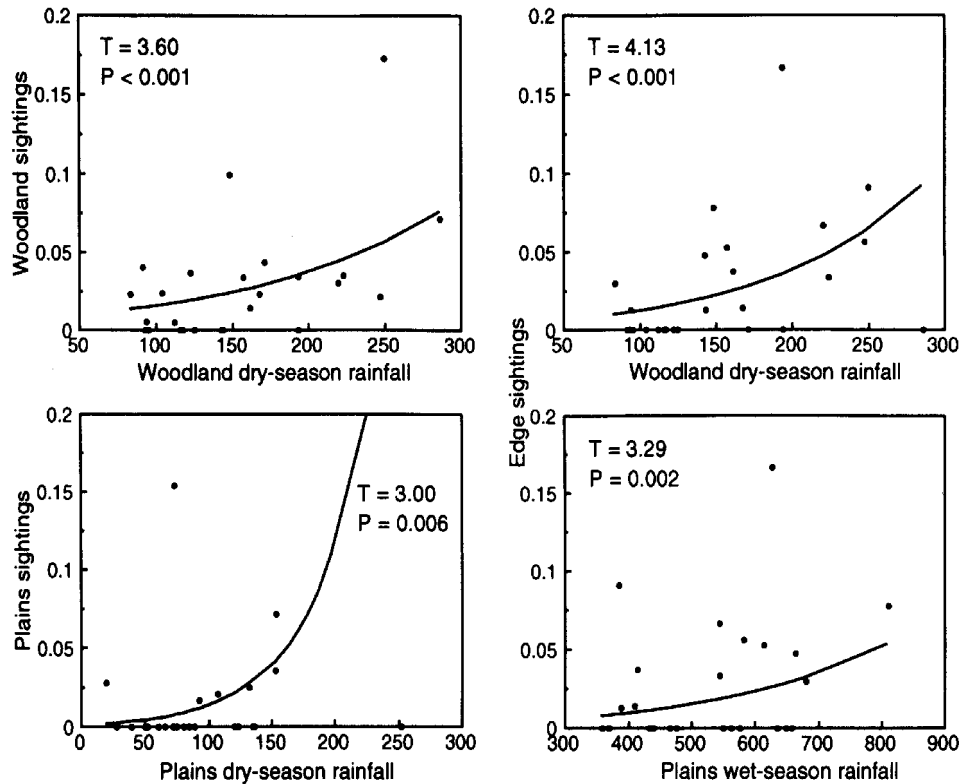


Figure 14.7 Significant correlations between rainfall and dry season sightings of lions with wildebeest carcasses (see table 14.3). Each point represents the proportion of lion sightings at which a carcass was found in a given season in that habitat. Sample size per point varies from 5 to 300. Statistics are from logistic regressions containing all significant predictors indicated in tables 14.3–14.6. Solid lines indicate values predicted by the logistic models.

woodlands decreases dry season predation on zebra on the plains (table 14.3). This pattern may result from the tendency of zebra to leave the plains sooner in years of heavy wet season rainfall (Maddock 1979).

Correlations between rainfall and wet season predation rates (table 14.4) are also consistent with patterns of prey movement. Following dry seasons with above-average rainfall, wet season predation rates decline for wildebeest, topi/kongoni, zebra, and Thomson's gazelle (fig. 14.8). Migrants that have been attracted to the southeastern Serengeti by high dry season rainfall move out to the eastern plains at the onset of the wet season (also see Maddock 1979; McNaughton 1979), thus reducing predation rates in our study area for the remainder of the wet season.

Wildebeest predation is significantly affected by rainfall within the wet season (table 14.4). The wildebeest rarely return to the woodlands during heavy wet seasons, thus remaining out of reach of the woodlands lions.

**Ungulate Population Sizes and Changes in Vegetation.** Testing for correlations between predation rates and prey population sizes is complicated by the similar recoveries in the wildebeest and buffalo population sizes following the rinderpest epizootic (Sinclair 1979a; Campbell 1989; see fig. 14.2). Further, the Serengeti landscape has changed markedly over the past 25 years. The region surrounding the Seronera River was kept clear of brush by park policy until 1969 (G. Schaller, B. C. R. Bertram, pers. comm.). Subsequently, reduced levels of burning led to a continuous increase in brushy vegetation in the woodlands and edge habitats (Sinclair, chap. 5). Because of covariation between these variables, the following analyses must be interpreted with caution.

Lion predation rates are correlated with the population sizes of several Serengeti ungulates (tables 14.5 and 14.6; note that insufficient data are available to include warthog or topi/kongoni population sizes in this analysis). Woodland predation on buffalo increased with the buffalo population (fig. 14.9), and predation rates on Thomson's gazelle varied with the gazelle population in two habitats. However, predation rates on wildebeest, zebra, and gazelle all declined with increasing populations of either wildebeest or buffalo (fig. 14.9). Because of colinearity between the wildebeest and buffalo population sizes, we cannot reliably distinguish which species has the greater effect in these last three cases. However, because lions have *reduced* their predation rates on wildebeest as the wildebeest/buffalo populations *increased*, the simplest explanation would be that lions have replaced wildebeest, zebra, and gazelle with greater numbers of buffalo. Alternatively, these three species may have spent less time in the southeastern Serengeti as the buffalo population, wildebeest population, or woody vegetation increased.

Table 14.4 Correlations of four rainfall variables (woodland/plains wet/dry season totals) with the presence of carcasses at lion sightings during the wet season.

Prey species	Habitat		
	Woodland	Edge	Plains
Wildebeest	Woodland wet -*** Plains dry -***	NS	NS
Zebra	NS	Plains dry -***	NS
Thomson's gazelle	NS	NS	Woodland dry -**
Buffalo	NS	NS	n.d.
Topi/Kongoni	Plains dry -**	n.d.	n.d.
Warthog	NS	n.d.	n.d.

Note: Columns indicate habitat in which lions were found with carcasses of each prey species. Text in cells indicates habitat and season for which rainfall was significantly correlated with the frequency of carcasses. Sign indicates direction of correlation. See table 14.1 for significance levels. n.d., insufficient data.

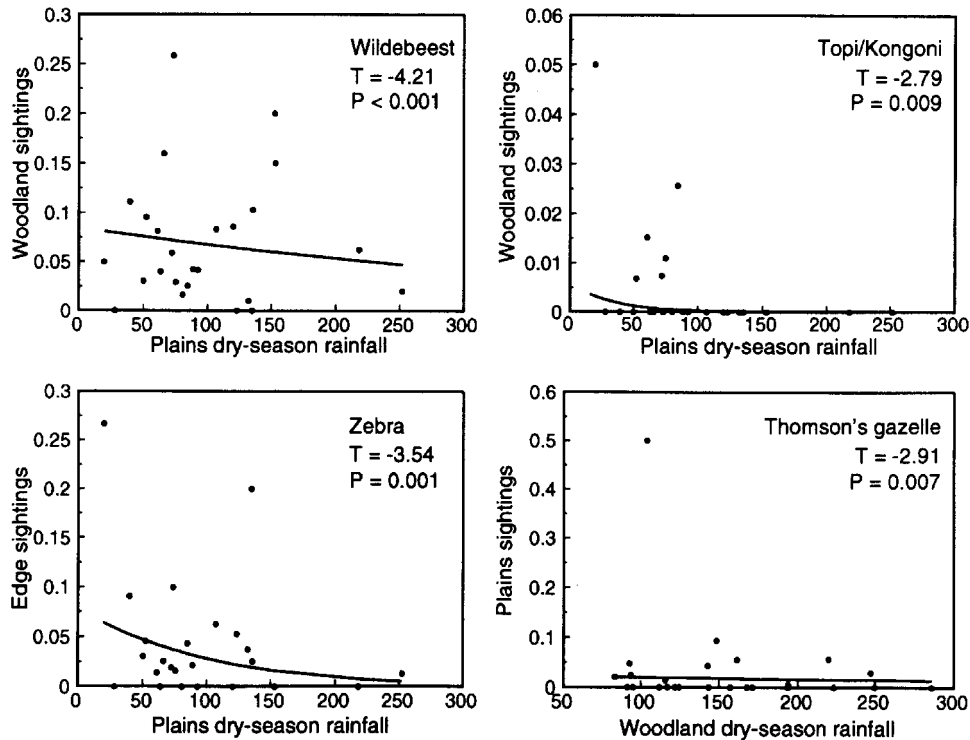


Figure 14.8 Significant correlations between dry season rainfall and sightings in the following wet season of lions with carcasses of each species (see table 14.4 for predictors). Details as in figure 14.7.

## CONCLUSIONS

Lion predation on each prey species changes between seasons, across habitats, and from year to year. Most of this variation can be attributed to the annual migration of wildebeest, zebra, and gazelle. Prey movements throughout the year are driven by rainfall, and rainfall varies from one year to the next. Lions hunt several prey species in proportion to their

Table 14.5 Correlations of prey population sizes with the presence of carcasses at lion sightings during the dry season.

Prey species	Habitat		
	Woodland	Edge	Plains
Wildebeest	NS	NS	Buffalo or wildebeest - **
Zebra	NS	Buffalo or wildebeest - ***	NS
Thomson's gazelle	Buffalo or wildebeest - ***	Thomson's gazelle + ***	NS
Buffalo	Buffalo only + **	NS	n.d.
Topi/Kongoni	NS	n.d.	NS
Warthog	NS	NS	NS

Note: Columns indicate habitat in which lions were found with carcasses of each prey species. Cells indicate Serengeti-wide population sizes (prey species were considered only when sufficient data were available) that were significantly correlated with the presence of carcasses. Sign indicates direction of correlation. See table 14.1 for significance levels. n.d., insufficient data.

Table 14.6 Correlations of prey population sizes with the presence of carcasses at lion sightings during the wet season.

Prey species	Habitat		
	Woodland	Edge	Plains
Wildebeest	Buffalo only - **	Buffalo or wildebeest - **	NS
Zebra	NS	Buffalo or wildebeest - **	NS
Thomson's gazelle	NS	NS	Thomson's gazelle + ***
Buffalo	NS	NS	n.d.
Topi/Kongoni	NS	n.d.	n.d.
Warthog	NS	n.d.	n.d.

Note: Columns indicate habitat in which lions were found with carcasses of each prey species. Cells indicate Serengeti-wide population sizes (prey species were considered only when sufficient data were available) that were significantly correlated with the presence of carcasses. Sign indicates direction of correlation. See table 14.1 for significance levels. n.d., insufficient data.

local density (fig. 14.5), and that density is constantly changing (fig. 14.6, tables 14.1 and 14.2).

Predation on buffalo is consistently greater in the woodlands than on the plains (fig. 14.6). Thus, the woodlands lions may be buffered against seasonal changes in prey density by greater access to prey during those seasons when migrant species are locally scarce (see also Hanby, Bygott, and Packer, chap. 15).

Predation on wildebeest is highest when dry season rainfall attracts the herds to the study area (table 14.3) and lowest when wet season rainfall is high (table 14.4). However, wet season predation on migratory or semimigratory species declines following a rainy dry season (table 14.4), and wet season predation on resident species does not increase in compensation. Lion reproductive rates are highest in years with rainy dry sea-

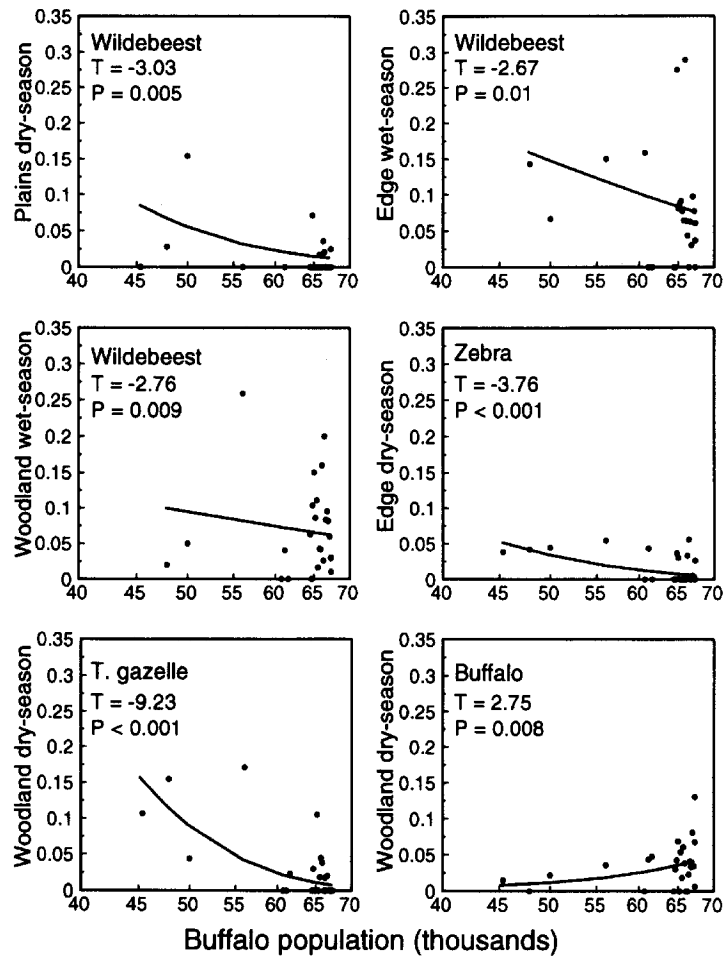


Figure 14.9 Significant correlations between the overall population size of Serengeti buffalo and lion predation rates on different prey species (see tables 14.5 and 14.6). Details as in figure 14.7.

sons or dry wet seasons (Packer et al. 1988), years when the wildebeest remain in the study area for more months of the year.

Predation on Thomson's gazelle varies with the size of the gazelle population. Predation rates on wildebeest, zebra and gazelle were higher in the 1960s (Schaller 1972) than in either the 1970s (see Hanby, Bygott, and Packer, chap. 15) or the 1980s (Packer, Scheel, and Pusey 1990). These declines have coincided with the recovery of the wildebeest and buffalo populations from the rinderpest epizootic. Predation on buffalo has increased over the same time, suggesting that the size of the buffalo population has had the most significant long-term effect (tables 14.5 and 14.6).

Our findings not only confirm the importance of the migratory prey to the lions, but also highlight the extent to which lions rely on buffalo in the absence of the migratory species. While buffalo in our part of the

Serengeti have been well protected over the past 25 years, buffalo numbers have declined drastically in the northern part of the park. This decline could well have altered the diet or population size of the northern lions.

#### ACKNOWLEDGMENTS

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