CHAPTER 7.

THE EFFECT OF PREDATION ON HERBIVORE POPULATIONS IN SMALL RESERVES.

The effect of predation by large carnivores on populations of their prey species is a complex and controversial subject. Predation is widely assumed to regulate or even diminish herbivore populations and as a result, predators are widely persecuted by interest groups such as hunters, game farmers and managers of some reserves (Keith, 1974; Bergerud, 1985; Skogland, 1991) . However, studies which unequivocally demonstrate the impact of predation in large mammal communities are sparse. Quantification of this impact requires very precise data which are often difficult to gather, particularly in studies of large mammals. This includes accurate estimates of the numbers of predators and prey species in an area, the pattern of predation with respect to herbivore demographic characteristics, the contribution of predation to overall prey mortality and other sources of mortality in prey populations (Mills, 1990).

Previous work on large mammal predator-prey systems in Africa suggests that predation generally has little regulating effect on prey populations. Herbivore populations appear to periodically escape high predation pressure either by migratory movements such as wildebeest in the Serengeti (Sinclair *et al,* 1985), white-eared kob in Sudan (Fryxell & Sinclair, 1998) and zebra in the Kruger National Park (Mills & Shenk, 1992), or by being nomadic or semi-nomadic such as the large ungulate assemblage of the southern Kalahari (Mills, 1990). However, while regulation for migratory herds appears rare, resident populations of prey species may be more heavily impacted by predation. Fryxell, Greever & Sinclair (1988) suggested that the low population densities of resident herbivore prey species increased the potential for a regulatory effect by predation. Their models predicted that as few as 1000 predators (lions and hyaenas) could regulate a resident wildebeest population below 85,000 in the Serengeti. In contrast, this number of predators could not regulate a migratory herd. Lending support to their models, Sinclair (1995) presented evidence that resident topi, impala, Thompson's gazelle and warthog were limited by predation in the Serengeti-Mara ecosystem and Mills & Shenk (1992) demonstrated that resident wildebeest in the south-eastern region of the Kruger National Park were more heavily impacted by lion predation than seasonally migratory zebras.

In small reserves such as Phinda, the opportunity for herds to temporally or spatially escape predation may be limited. Reintroduced lions and cheetahs established small to medium-sized home ranges (Chapter 4) which they could easily traverse in a day or night. Furthermore, although the intensity of use of different areas of home ranges

varied periodically, lions and cheetahs were present in all areas of the reserve in more-or-less uniform densities which increased during the course of this study. Accordingly, while rates of predation were not strictly constant in all areas of Phinda at all times, populations of prey animals were unable to move to areas where predation by lions and cheetahs was reduced for substantial periods, as occurs in migratory herds such as in the Serengeti.

Such a situation may give rise to a population decline if predation mortality outweighs annual recruitment. For example, in south-eastern British Columbia, wolves prey on two adjacent populations of caribou. In the Wells Gray Park area, caribou migrate beyond wolf range in the summer and seasonally avoid predation (Seip, 1992). This population experiences high recruitment rates averaging 37 calves per 100 females. Caribou from the Quesnel Lake area nearby experience year-round predation and recruitment is only 2.5 calves per 100 females. Adult mortality is 29%, far higher than the recruitment rate and the population is declining, possibly towards extinction (Seip, 1992).

In this Chapter, I attempt to examine the impact of predation on resident herbivore populations in small reserves. I reasoned that conditions at Phinda were ideal for considerable impact on herbivore populations, particularly as lion and cheetah numbers increased following introduction. In order to investigate the possible role of predation on ungulates at Phinda, in conjunction with daily monitoring of reintroduced lions and cheetahs, I made seasonal estimates of the numbers and population characteristics of prey species available to them for the duration of the study. My aim was to document any impact on prey populations over time in a small enclosed area where ungulates had no refuge from predation.

METHODS.

As Phinda is traversed by an extensive network of roads and has considerable areas of dense vegetation which do not permit accurate aerial counts, I sampled herbivores based on a road strip sampling technique similar to that used by Hirst (1969, 1975). I drove two separate transect routes totalling 64km which passed through all vegetation types present on Phinda. The same two routes were used for the entire study. I counted herbivores on a seasonal basis. For each season, I drove each route three times over a 6-8 day period (i.e: six counts), alternating the direction driven on consecutive counts. All counts were made in the early morning usually between 06:00-10:00 on clear, still days. Vehicle speed was maintained at 10-15km/h by running the vehicle in low-range 4 wheel drive in which it essentially 'drives itself' at a constant speed in first gear.

I counted eight species of ungulates which I anticipated would be likely prey for reintroduced felids and which were visible enough to census. These species were giraffe, impala, kudu, nyala, reedbuck, warthog, wildebeest and zebra. As it transpired, these species constituted eight of the 10 most important prey species (as percentage of kills and biomass consumed) for lions and cheetahs (Chapter 6). I initially attempted to also count red duiker and common duiker (the other two species of the 10 most frequently preyed upon species) as well as suni and steenbok. However, due to their secretive habits and difficulty of viewing, I saw them rarely during counts and did not gather enough data to give reliable population estimates.

I calculated the mean visible distance of each species in each habitat type by use of range-finder binoculars to determine the width of the effective strip. Within each habitat type I recorded the distance from the road ungulates disappeared from view and averaged them to give the mean visibility limit for each species, yielding a specific strip width for each habitat type. I only counted ungulates on the driver's side of the road as visibility was not consistent for both sides of the vehicle and furthermore, vegetation types frequently differed markedly on opposite sides of the road due largely to human activity such as bush clearing and former cultivated land. Density of each species in each habitat was calculated according to the following formula:

$$Density = \frac{number\ animals\ counted}{distance\ driven\ in\ each\ habitat\ type \times effective\ strip\ width}.$$

As used here, where mean visibility limit determines strip width, this methodology is considered to yield reasonably accurate estimates for African ungulate populations in variable woodland habitat (Eberhardt, 1968; Hirst, 1969; Caughley, 1977). The eight ungulate species observed from the road were counted and classified by age (juvenile, sub-adult and adult) and sex. Juveniles were not sexed and it was generally not possible to accurately sex subadult zebras and warthogs, though I recorded it where it was obvious. To estimate the total population of each prey species at Phinda, I multiplied the calculated mean density (i.e. from the six counts) of each species in each habitat type by the total area covered by each habitat. I calculated the coverage of each habitat type using ArcView GIS software on the digitised vegetation map I derived in Chapter 2 (Figure 5). Total numbers of animals for each habitat type were tallied to give total population estimates for Phinda.

I have excluded from the analyses counts from Winter 1992 when I first arrived at Phinda. I was inexperienced in the counting method and spotting game. Furthermore, having accustomed myself to the entire reserve, I modified the route by Spring 1992 to

ensure the census included all habitat types. Using data from Spring 1992 to Winter 1995, I compared seasonal fluctuations in ungulate numbers using a one-way ANOVA for each species to assess if differences were significant across seasons.

To compare the impact of predation, one would ideally compare rates of predation with ungulate population fluctuations. However, as I mostly relied on opportunistic recovery of kill data (Chapter 6), my estimations of predation rates are biased towards large species, adult animals rather than juveniles, and animals which were more likely to be victims of predation in open habitats where I could travel. Accordingly, I used the growth in lion and cheetah numbers as an index of predation pressure on herbivore populations. To examine the relationship between lion and cheetah numbers, and ungulate numbers, I used the seasonal mean number of lions and cheetahs in terms of Female Equivalent Units as described in Chapter 6 (see Figure 52). I then analysed the ungulate population data using single and multiple regression analyses where the independent variables were lion and cheetah numbers and the dependent variables were population estimates of each of the eight ungulate species. To avoid spurious correlations, I excluded giraffes, warthogs, wildebeests and zebras from the regression with cheetah numbers: these species each comprised less than 5% of cheetah kills and were too numerous for cheetah predation to have any impact on their numbers. I also included seasonal rainfall data as an independent variable in the regression analysis, testing for both current and previous season's rainfall.

RESULTS

Table 32 and Figures 44 to 51 show the results of herbivore counts for each species. The road strip method using mean visibility limits for counting ungulates generally appeared to provide reasonable population estimates of each species, though as Hirst (1969) has indicated, results tend to be subject to high variation. Replicate counts diminish this problem to some extent and confidence intervals for the mean population estimate of each species for the entire study period were generally between 6-15% (Table 32). For southern reedbuck, this figure was 27%, probably due to this species' shyness and low numbers in Phinda meaning they were frequently not sighted during counts. A greater number of replicate counts would reduce this variation but the method is highly labour intensive and time-consuming.

Mean density estimates of ungulate species at Phinda were generally similar to those from the neighbouring Mkuzi Game Reserve (Table 32). The estimated density of impalas was considerably lower whereas densities of warthogs, wildebeest and zebras were

all approximately double that of Mkuzi. The estimated densities of ungulates in different habitat types is presented in Table 33.

Species	Mean Density (km^{-2}), Mkuzi GR	Mean Density (km^{-2}), Phinda	Mean population estimate ($\pm$ SD), Phinda	Mean biomass (kg/km^2), Phinda
Giraffe	0.49	0.41	67 $\pm$ 11	307.5
Impala	20.60	11.71	1932 $\pm$ 223	468.4
Kudu	1.78	1.52	252 $\pm$ 33	206.7
Nyala	11.10	12.84	2124 $\pm$ 212	770.4
Reedbuck	0.87	0.48	79 $\pm$ 22	24.0
Warthog	2.20	5.15	852 $\pm$ 119	231.8
Wildebeest	1.43	3.80	628 $\pm$ 73	627.0
Zebra	1.85	3.10	512 $\pm$ 34	620.0
Total			6446	1996.3

Table 32. Overall density, population and biomass estimates of 8 common ungulates in Phinda, Spring 1992-Winter 1995 with mean density estimates from Mkuzi Game Reserve for comparison (source: Goodman, 1990). Biomass estimate calculated using mean mass figures in Goodman (1990:p97.).

Three ungulate species appeared to show a consistent pattern of decline from Spring 1992 to Winter 1995: reedbuck, warthog and wildebeest (Figs 48-50). One-way ANOVA analysis comparing population trends for each species between seasons showed the difference was significant for wildebeest (F = 2.30, p = 0.019, df = 11). All other species did not have significant differences. For wildebeest, post-hoc comparisons (Tukey's HSD test) confirmed that seasons towards the end of the study generally had significantly lower population estimates than during the rest of the study period .

Prey species	DMB	Grass	MBC	MBO	Palm	RSC	RSO	RF	SF
giraffe	0.52	0.43	0.33	1.05	0.69	0.07	0.81	0.43	0
impala	6.29	32.10	4.29	26.63	19.19	4.09	21.19	8.32	3.77
kudu	2.51	1.38	2.62	2.75	1.31	0.61	1.93	0	0
nyala	2.30	10.12	9.37	23.0	0.33	11.29	32.95	3.60	21.47
reedbuck	0	3.03	0.05	0.25	1.81	0	0.19	0.67	0
warthog	0	11.41	5.53	15.41	7.18	1.65	5.89	0	0
wildebeest	3.78	11.27	2.77	10.08	5.79	0.67	4.39	0.67	0
zebra	1.36	9.73	1.66	6.99	4.70	0.87	3.97	2.20	0.95

Table 33. Estimated mean density (km^{-2}) of 8 common ungulates in Phinda, Spring 1992-Winter 1995 in each habitat type. Habitat types are described in Chapter 2: DMB = dry mountain bushveld; Grass = grasslands; MBC = closed mixed bushveld; MBO = open mixed bushveld; Palm = palmveld; RSC = closed red sand bushveld; RSO = open red sand bushveld; RF = riparian forest; SF = sandforest.
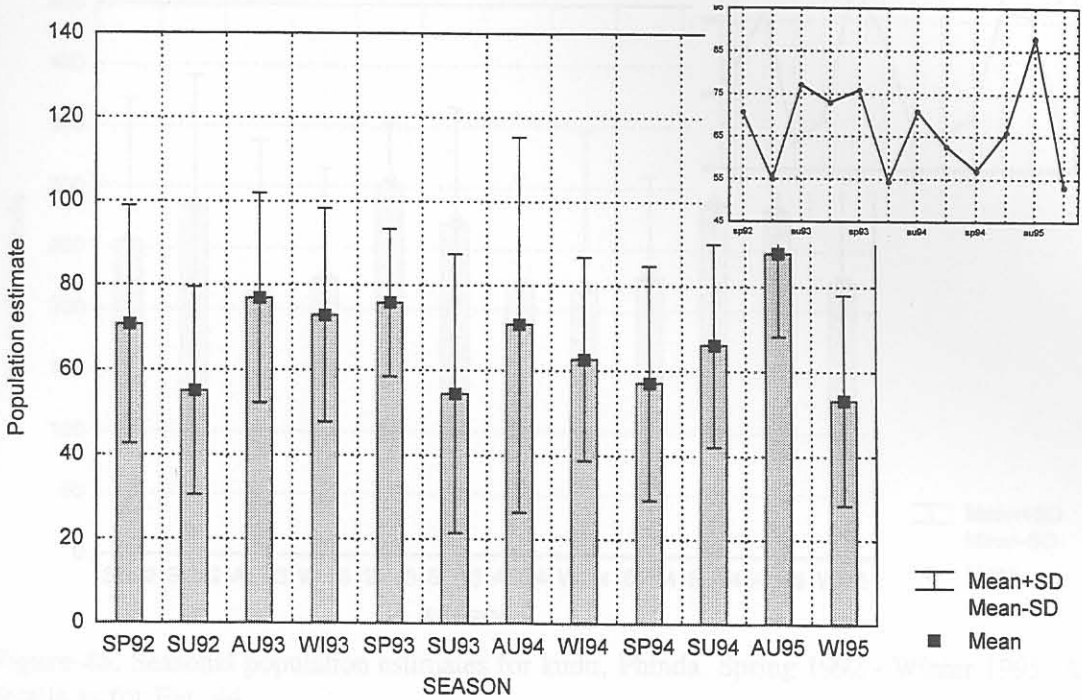
Figure 44. Seasonal population estimates for giraffe, Phinda, Spring 1992 - Winter 1995. Error bars depict standard deviation. Inset graph depicts population fluctuation for mean values only.
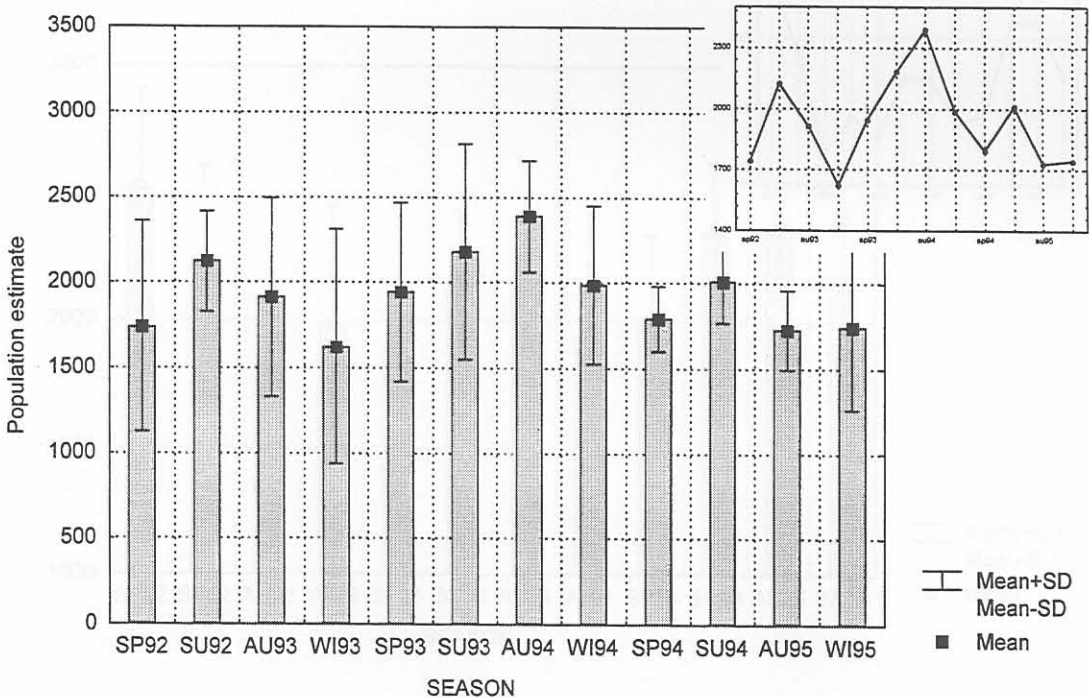
Figure 45. Seasonal population estimates for impala, Phinda, Spring 1992 - Winter 1995. All details as for Fig. 44.
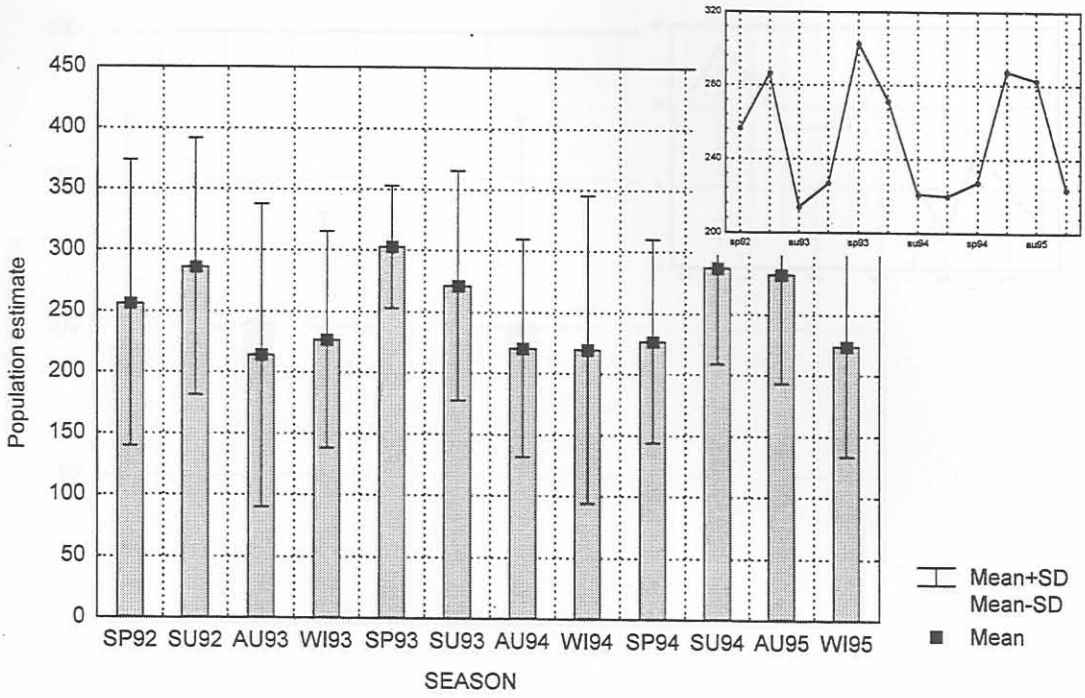
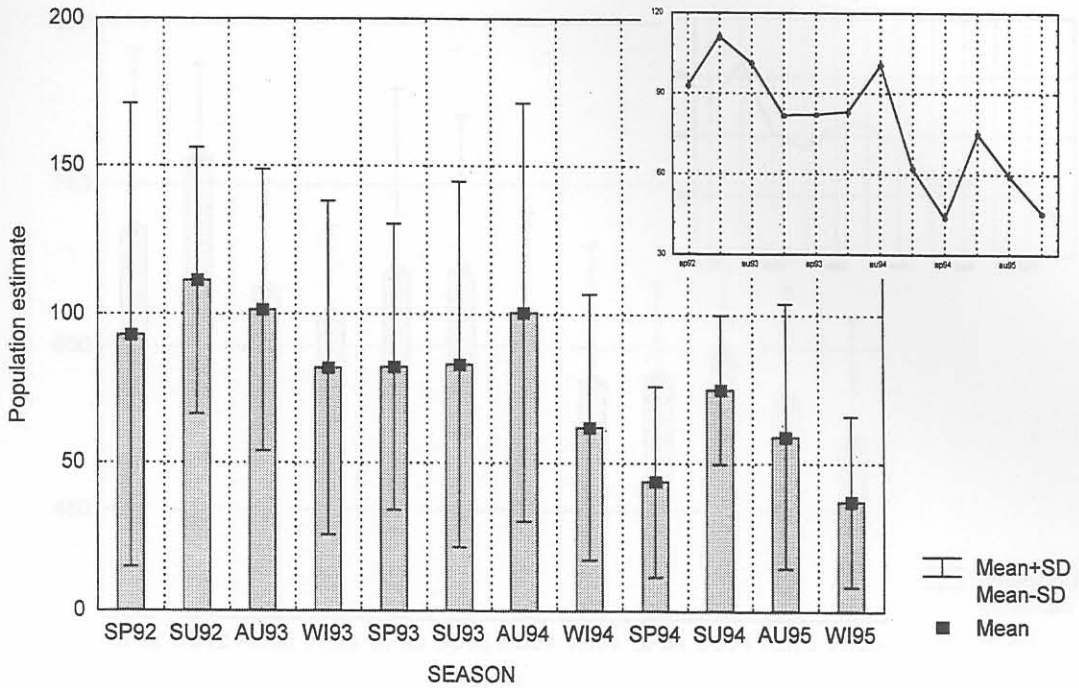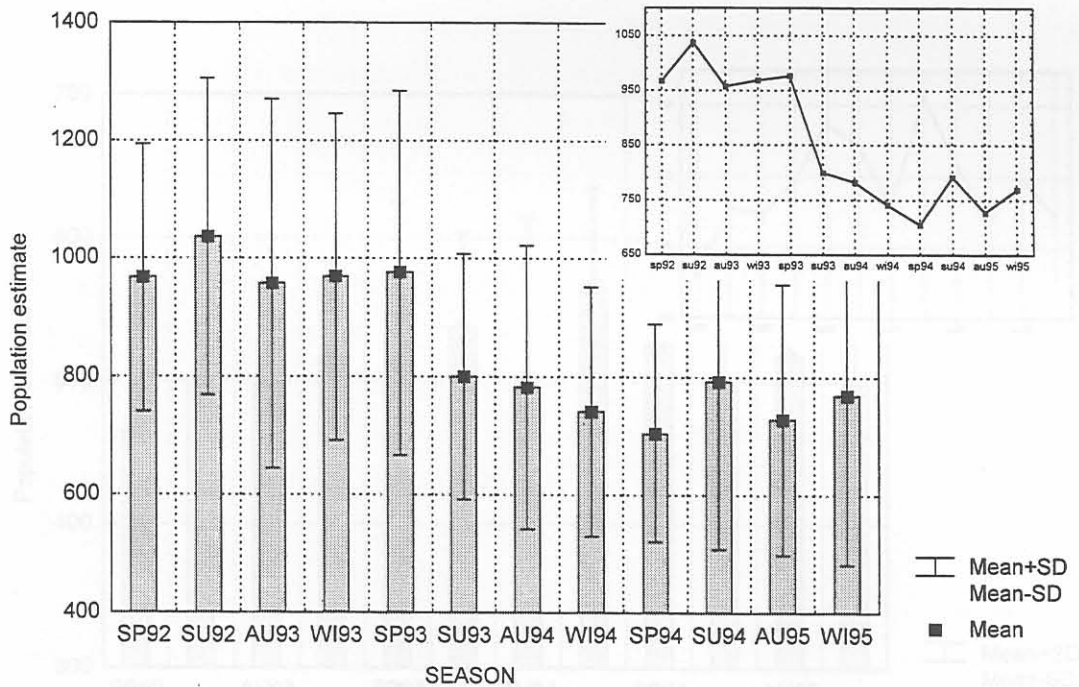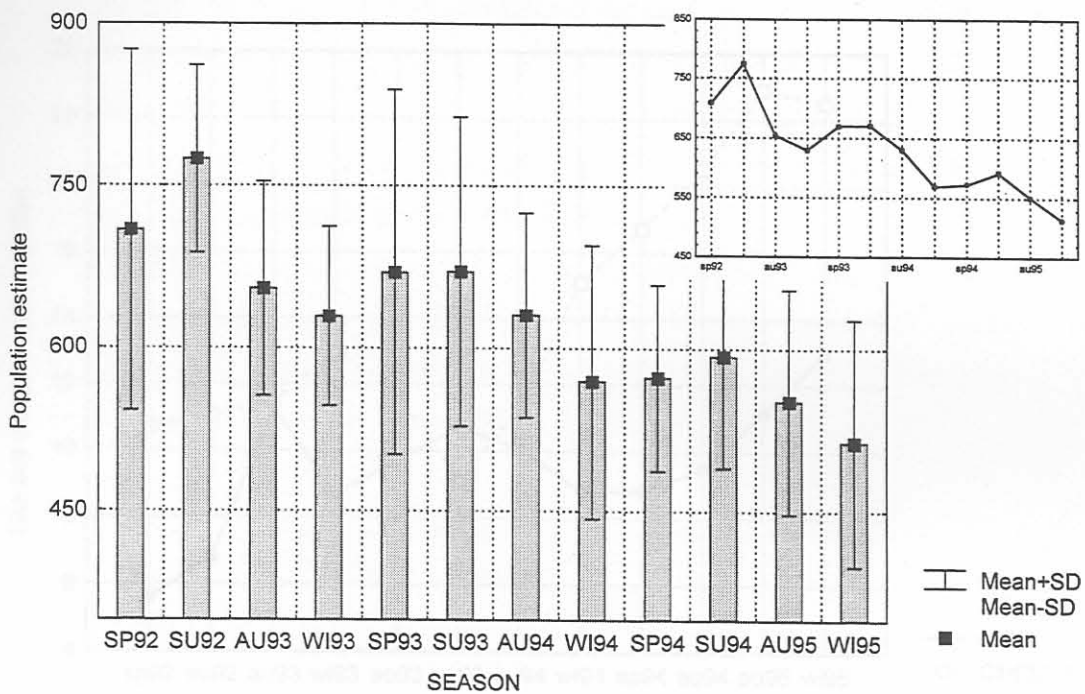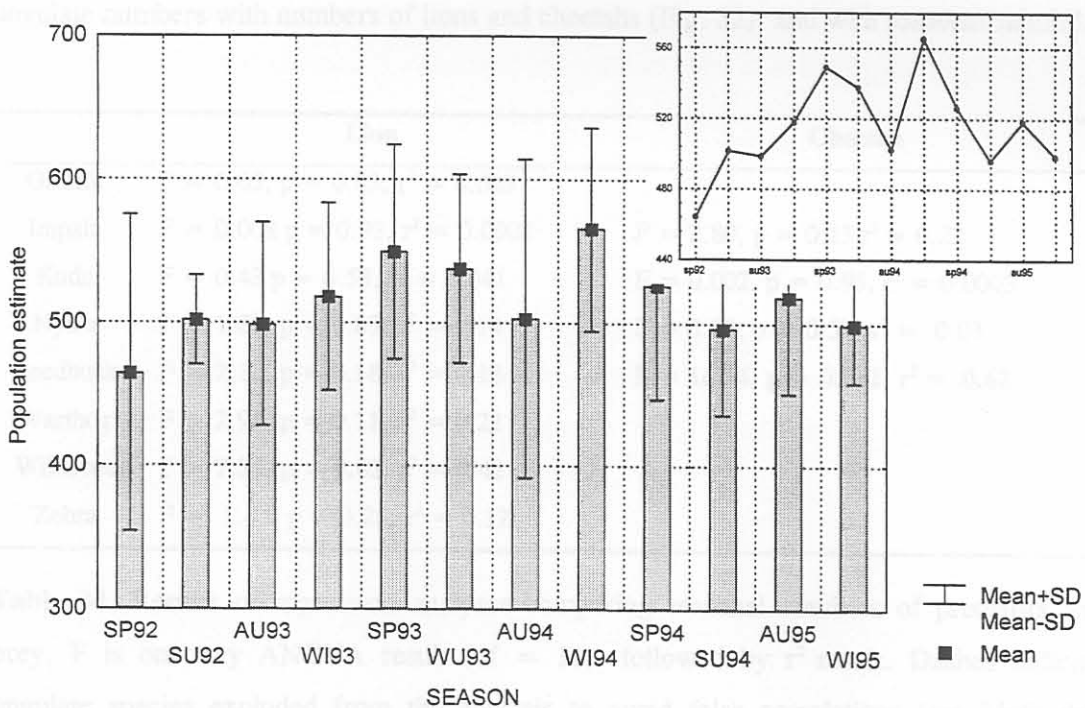**Figure 46.** Seasonal population estimates for kudu, Phinda, Spring 1992 - Winter 1995. All details as for Fig. 44.
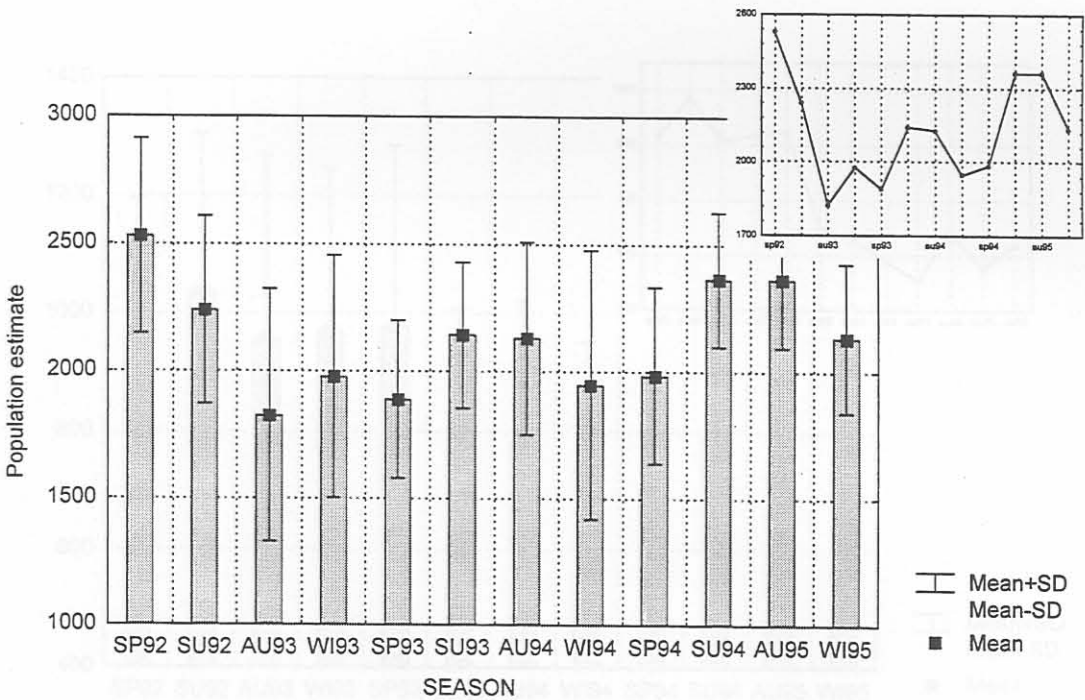

Figure 47. Seasonal population estimates for nyala, Phinda, Spring 1992 - Winter 1995. All details as for Fig. 44.

Figure 48. Seasonal population estimates for reedbuck, Phinda, Spring 1992 - Winter 1995. All details as for Fig. 44.

Figure 49. Seasonal population estimates for warthog, Phinda, Spring 1992 - Winter 1995. All details as for Fig. 44.

Figure 50 Seasonal population estimates for wildebeest, Phinda, Spring 1992 - Winter 1995. All details as for Fig. 44.

Figure 51. Seasonal population estimates for zebra, Phinda, Spring 1992 - Winter 1995. All details as for Fig. 44.
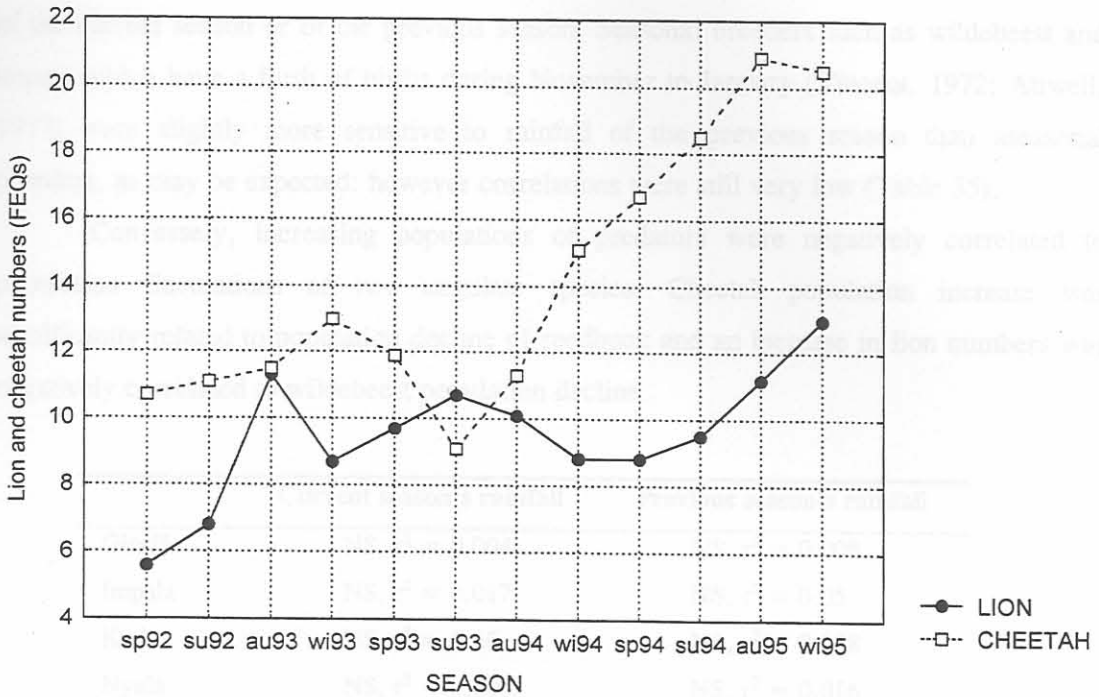
Figure 52. Seasonal lion and cheetah numbers at Phinda, expressed as FEQs.

Tables 34 and 35 show the results of regression analyses comparing seasonal ungulate numbers with numbers of lions and cheetahs (Fig. 52), and with seasonal rainfall.

	Lion	Cheetah
Giraffe	$F = 0.05$, $p = 0.83$, $r^2 = 0.005$	-
Impala	$F = 0.008$ $p = 0.93$, $r^2 = 0.0008$	$F = 2.80$, $p = 0.13$ $r^2 = 0.22$
Kudu	$F = 0.43$ $p = 0.53$, $r^2 = 0.041$	$F = 0.002$, $p = 0.95$, $r^2 = 0.0003$
Nyala	$F = 1.58$, $p = 0.83$, $r^2 = 0.14$	$F = 0.30$, $p = 0.59$, $r^2 = 0.03$
Reedbuck	$F = 2.12$, $p = 0.18$, $r^2 = 0.18$	**$F = 16.54$, $p = 0.002$, $r^2 = 0.62$**
Warthog	$F = 2.95$, $p = 0.11$, $r^2 = 0.22$	
Wildebeest	**$F = 7.36$, $p = 0.02$ $r^2 = 0.42$**	-
Zebra	$F = 1.47$, $p = 0.25$, $r^2 = 0.12$	-

Table 34. Results of regression analyses comparing seasonal numbers of predators and prey. F is one-way ANOVA result (df = 11), followed by r^2 result. Dashes indicate ungulate species excluded from the analysis to avoid false correlations (see Methods). Significant results (at $p < 0.05$) indicated in boldtype.

Fluctuations in ungulate numbers did not appear to be related to rainfall, either that of the current season or of the previous season. Seasonal breeders such as wildebeest and impala which have a flush of births during November to January (Vincent, 1972; Attwell, 1977) were slightly more sensitive to rainfall of the previous season than aseasonal breeders, as may be expected: however correlations were still very low (Table 35).

Conversely, increasing populations of predators were negatively correlated to population fluctuations of two ungulate species. Cheetah population increase was significantly related to population decline of reedbuck and an increase in lion numbers was negatively correlated to wildebeest population decline.

	Current season's rainfall	Previous season's rainfall
Giraffe	NS, $r^2 = 0.004$	NS, $r^2 = 0.008$
Impala	NS, $r^2 = 0.017$	NS, $r^2 = 0.05$
Kudu	NS, $r^2 = 0.26$	NS, $r^2 = 0.088$
Nyala	NS, $r^2 = 0.0002$	NS, $r^2 = 0.016$
Reedbuck	NS, $r^2 = 0.003$	NS, $r^2 = 0.001$
Warthog	NS, $r^2 = 0.0001$	NS, $r^2 = 0.025$
Wildebeest	NS, $r^2 = 0.064$	NS, $r^2 = 0.14$
Zebra	NS, $r^2 = 0.032$	NS, $r^2 = 0.001$

Table 35: Results of regression analysis comparing seasonal numbers of ungulate species and current and previous season's rainfall. NS indicates non-significant at $p = 0.05$, df = 11.

Figures 53-58 show seasonal changes in the ratio of common prey species killed by lions and cheetahs. The strongest evidence of a pattern of prey switching was for lions which reduced predation on wildebeest and nyalas and increased predation on warthogs following Spring 1993 (Fig. 56). Cheetahs maintained high levels of predation on nyalas and impalas but drops in predation on impalas were associated with peaks in nyala predation, and vice-versa. (Fig. 53).
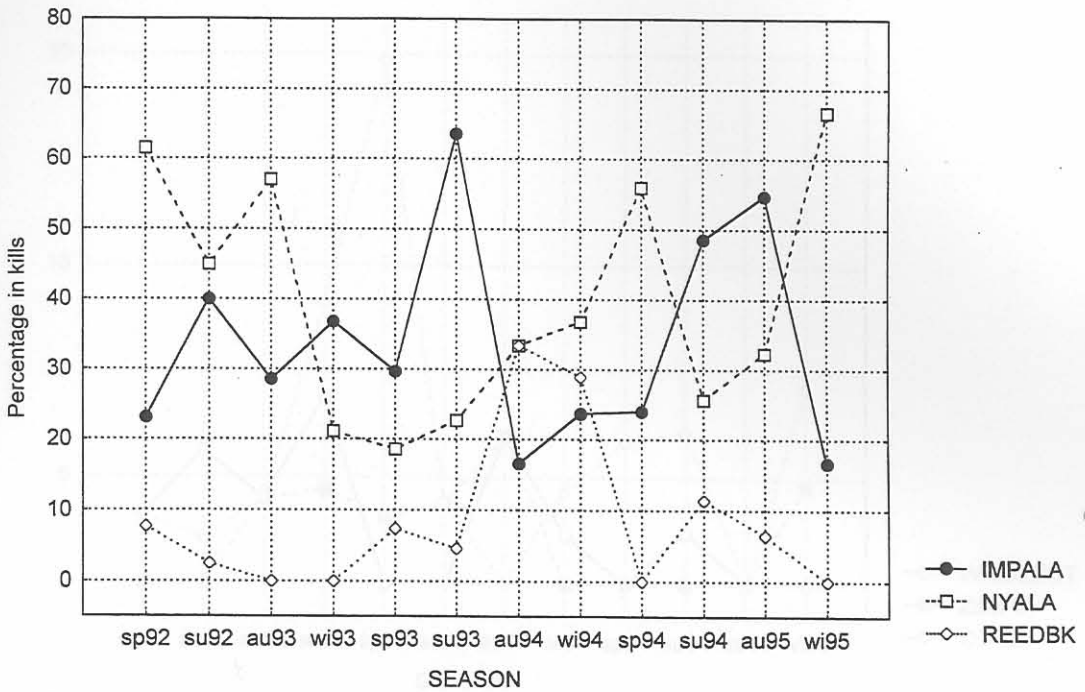
Figure 53. Seasonal predation rates by cheetahs on impala, nyala and reedbuck.
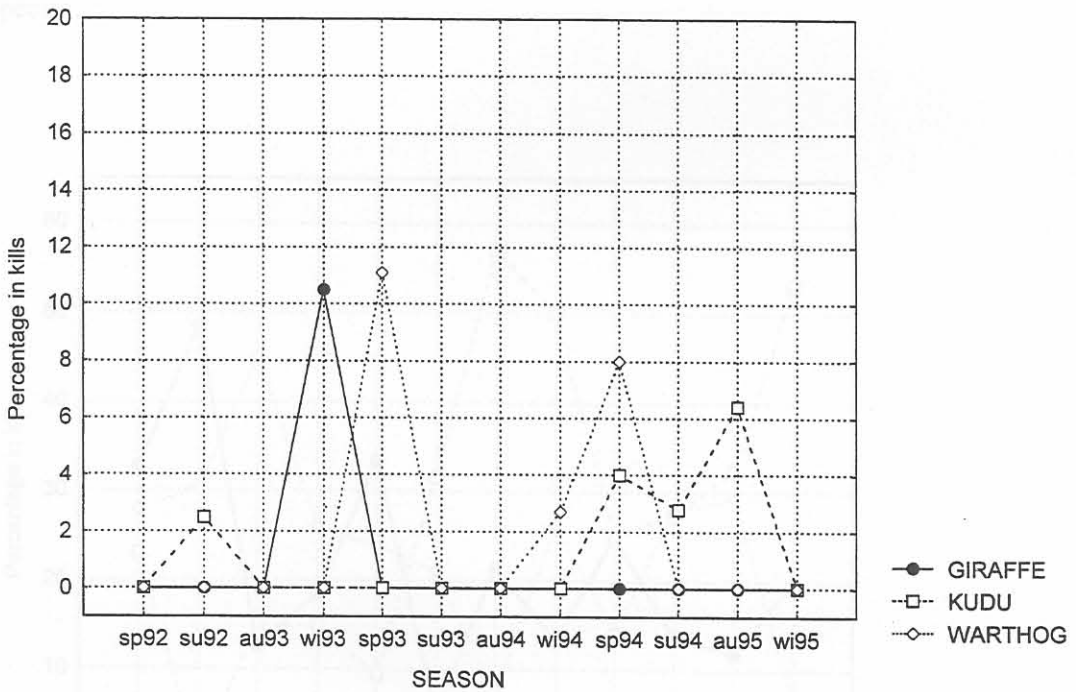

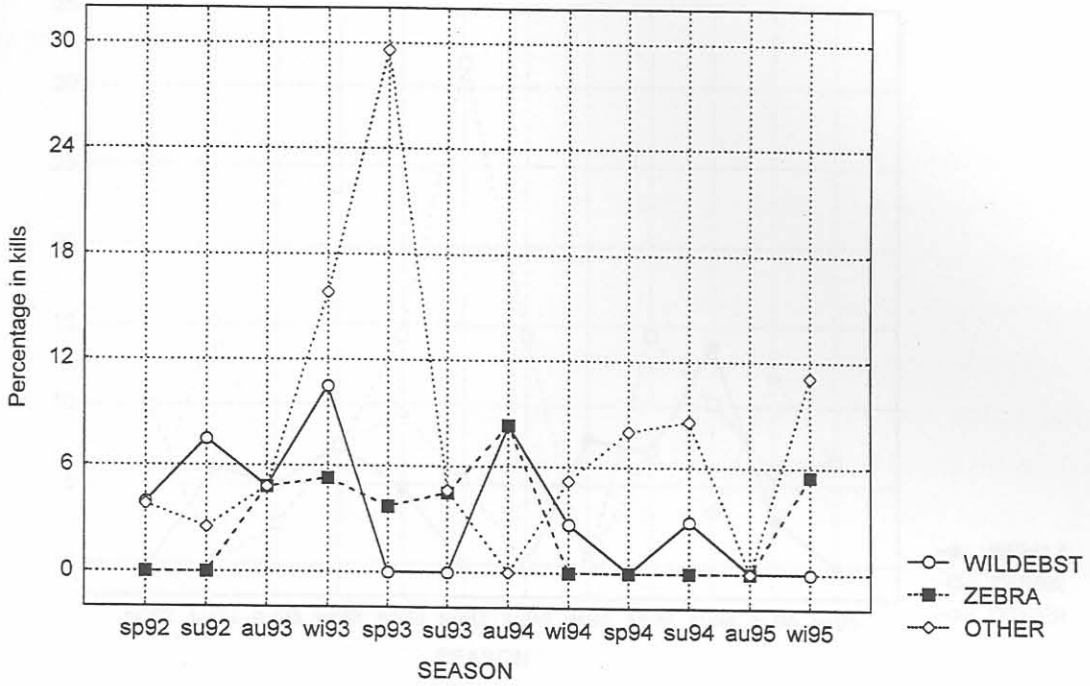**Figure 54.** Seasonal predation rates by cheetahs on giraffe, kudu and warthog.

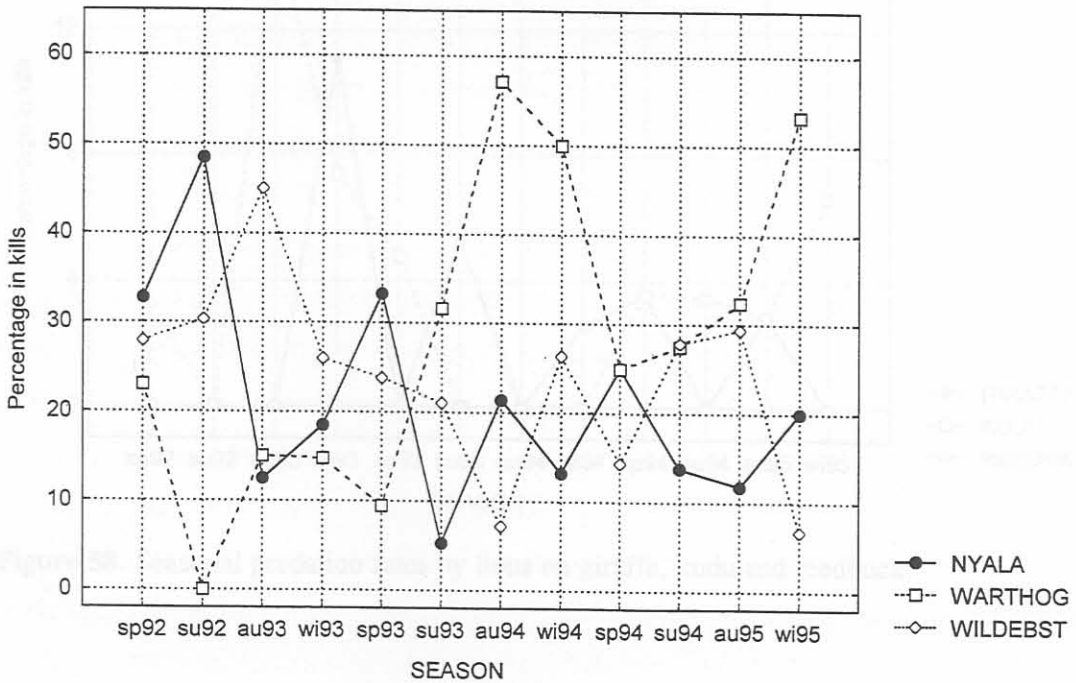**Figure 55.** Seasonal predation rates by cheetahs on wildebeest, zebra and other prey species.

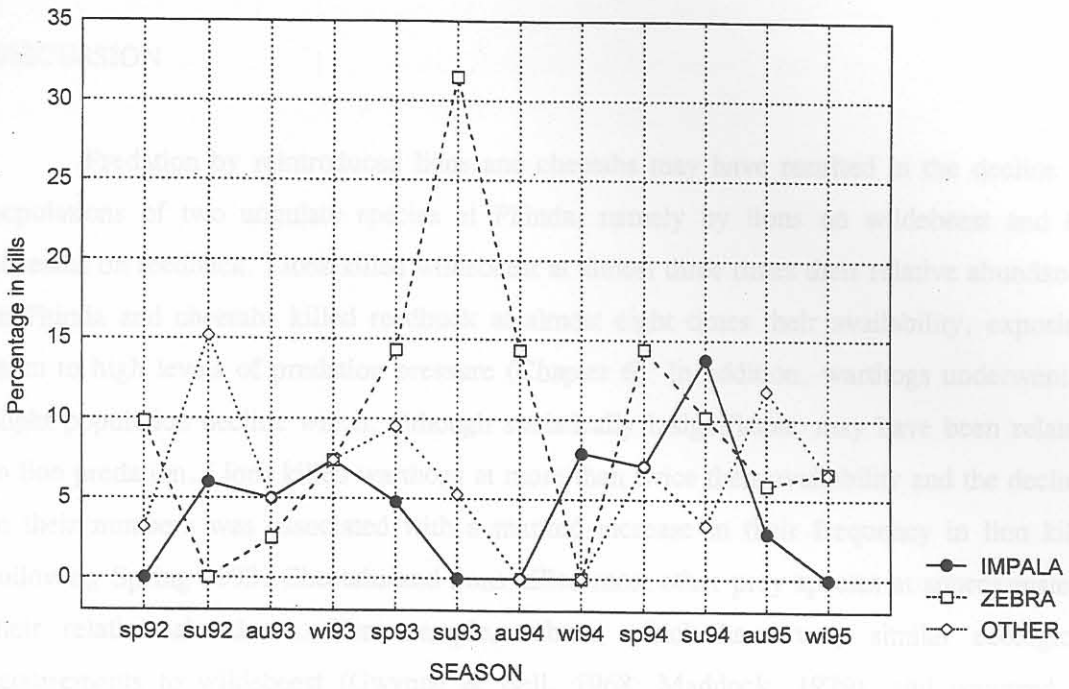**Figure 56.** Seasonal predation rates by lions on nyala, warthog and wildebeest.

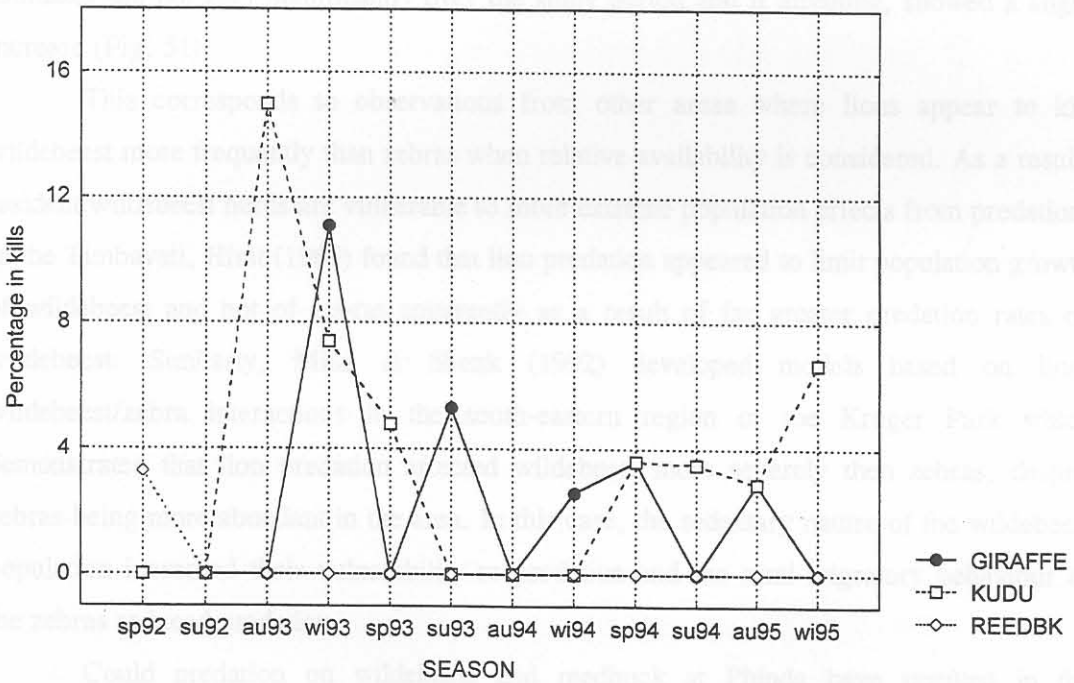**Figure 57.** Seasonal predation rates by lions on impala, zebra and other prey species.

Figure 58. Seasonal predation rates by lions on giraffe, kudu and reedbuck.

DISCUSSION

Predation by reintroduced lions and cheetahs may have resulted in the decline of populations of two ungulate species at Phinda, namely by lions on wildebeest and by cheetahs on reedbuck. Lions killed wildebeest at almost three times their relative abundance in Phinda and cheetahs killed reedbuck at almost eight times their availability, exposing them to high levels of predation pressure (Chapter 6). In addition, warthogs underwent a slight population decline which, although statistically insignificant, may have been related to lion predation. Lions killed warthogs at more than twice their availability and the decline in their numbers was associated with a marked increase in their frequency in lion kills following Spring 1993. Cheetahs and lions killed most other prey species at approximately their relative abundance. For example, zebras, which have very similar ecological requirements to wildebeest (Gwynne & Bell, 1968; Maddock, 1979), and occurred in similar numbers to wildebeest (Table 32), constituted 8.0% of available herbivores and 8.9% of lion kills at Phinda (Chapter 6). In contrast to wildebeest, zebra population estimates did not alter significantly over the study period and if anything, showed a slight increase (Fig. 51).

This corresponds to observations from other areas where lions appear to kill wildebeest more frequently than zebras when relative availability is considered. As a result, resident wildebeest herds are vulnerable to more extreme population effects from predation. In the Timbavati, Hirst (1969) found that lion predation appeared to limit population growth of wildebeest and not of zebras apparently as a result of far greater predation rates on wildebeest. Similarly, Mills & Shenk (1992) developed models based on lion-wildebeest/zebra interactions in the south-eastern region of the Kruger Park which demonstrated that lion predation affected wildebeest more severely then zebras, despite zebras being more abundant in the area. In this case, the sedentary nature of the wildebeest population increased their vulnerability to predation and the semi-migratory behaviour of the zebras reduced predation.

Could predation on wildebeest and reedbuck at Phinda have resulted in the observed declines in their populations? For this to occur, a number of factors need to be operating. Mortality in the prey population must be greater than the net recruitment. This can occur when there is no refuge from predation for prey, predators have an alternative source of prey to maintain numbers when the primary prey reach low numbers and

predators do not exhibit prey switching (Caughley & Sinclair, 1992). At Phinda, the first two conditions were clearly operating. Herbivores experienced year-round predation where they were unable to migrate to predation free (or reduced) refuges. Secondly, wildebeest and reedbuck were preferred prey by lions and cheetahs respectively, but alternative species such as nyalas and impalas were very numerous (and killed at approximately their availability), so lions and cheetahs had an alternative food resource on which they could easily maintain their populations. In the case of cheetahs, impalas and nyalas were more important than reedbuck as prey species, and predation levels on these two species showed some evidence of being negatively associated. Reedbuck were not the primary prey in terms of numbers killed and hence the role of prey switching in reducing the impact of predation was not strictly relevant here. On the other hand, lions appeared to reduce predation levels on wildebeest and 'compensate' with increased predation on warthogs during the course of the study. That wildebeest numbers continued to decline despite slightly reduced predation levels may reflect the presence of more lions as their population grew: although wildebeest decreased in terms of their frequency in lions' diet, the numbers killed remained relatively consistent (Chapter 6).

Accordingly, conditions at Phinda existed for considerable impact by predation on herbivore populations. However, establishing actual recruitment from the juvenile component of the population may be confounded by my observations on neonate survival, particularly for reedbuck. I do not have good data on survival of reedbuck lambs which were difficult to census. Although reedbuck in the region display a weak birth peak in the summer, lambs may be born at any time of the year (Jungius, 1970) so there is no conspicuous flush of young which would enable a reasonable estimation of annual lamb survival from the seasonal censuses I conducted. In addition, lambs are hidden by the females in long grass away from the herd for up to four months (Jungius, 1970; Howard, 1986) and as a result, were difficult to see and assign an age during counts. Conversely, wildebeest have a flush of births from November to March and calves accompany their mothers from birth (Attwell, 1977), which allowed me to make accurate estimates of the percentage of the juvenile cohort surviving from the previous season. Juvenile wildebeest constituted a mean of 23.2% of the population in summer but only 4.5% by the following spring. Finding kills or remains of juvenile ungulates is rare, so I am unable to say with certainty that predation on juvenile wildebeest accounted entirely for the decline. Other factors such as accidents, weakness at birth and abandonment (Page, 1985; Adams *et al,* 1988; Linnell, *et al* 1995) probably accounted for some losses. However, Linnell and co-

workers (1995) demonstrated that predation was the single greatest cause of death for juvenile ungulates in a review of 98 studies of ungulate mortality, and was also probably the major cause of death for ungulates at Phinda (see below). Furthermore, all juvenile wildebeest on which I observed lions and cheetahs feeding ($n = 26$: Chapter 6), they had killed rather than scavenged or obtained by other means, though two of those were lone calves which appeared to have lost their herd. Although mean adult wildebeest mortality by predation was only 4.8% of the population per year (Chapter 6), this alone exceeds recruitment from the juvenile component. Moreover, predation during the sub-adult period removes additional individuals before they reproduce. Accordingly, all the evidence suggests predation was a compelling factor in the decline of wildebeest at Phinda.

Having said this, other factors may have contributed to herbivore population fluctuations and need to be considered. I do not have good data on other sources of mortality in ungulates during the study period. However, the low numbers of dead ungulates which lions scavenged ($n = 24$ excluding carcasses appropriated from other carnivores: 7.5% of all carcasses of known origin, Chapter 6) is illustrative that large scale mortality from other causes did not seem to be occurring. In addition to the 24 animals which lions found dead, I found dead ungulates only on a further 21 occasions, 10 of which were deaths by snaring. Deaths by snaring other than those I recorded were not noted during the study period so I have no estimate how important this was as a source of mortality to ungulates. However, for 1996 and 1997, when such records were kept, a total of only four and five ungulates were killed in snares respectively: two of these mortalities were wildebeest, none were reedbucks[1]. Although I believe snaring was more severe in 1992-1993 (see Chapter 5), it appears not to have been a major source of mortality to wildebeest and reedbucks at Phinda.

Of the other 11 dead ungulates I found, three animals died from being caught in the boundary fence and two were trapped in deep mud at the edge of pans. The other deaths were for reasons I could not identify, though they may have been from starvation. Large scale mortality due to food shortages during dry seasons has been shown to regulate numerous ungulate populations by decreasing survival of both calves and adults (Sinclair, 1979; Maddock, 1979). Rainfall is the single most important variable affecting availability of food and, therefore, starvation-related mortality of ungulates in the dry season (Sinclair, 1979). Dry season rainfall (April to September) for 1992 was only 29.5mm compared to a mean of 131.8 $\pm$ 99.8mm for a 10 year period 1988-1997, and annual rainfall in 1992 was

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[1] Lewis, A. Phinda Resource Reserve, Private Bag 6001, Hluhluwe, 3960, RSA. Tel. 035 562 0271

the lowest for any year of this period (South African Weather Bureau, Pretoria). However, all other dry seasons of the same period experienced rainfall within one standard deviation or greater than the mean so if drought contributed to ungulate mortality, it was probably only during 1992. Furthermore, Phinda management employs a rotational fire regime to stimulate new growth of grasses and artificially maintains water points so that seasonal shortages of food and water which lead to mortality of resident ungulates elsewhere (Maddock, 1979) are less extreme. All these factors suggest that food shortage was not a major cause of mortality for ungulates during the study and that most ungulates at Phinda died by predation.

Quality of food resources may have been a factor in ungulate population declines. In Tanzania's Ngorongoro Crater, resident wildebeest and other ruminant grazers declined in numbers over a 30 year period in response to diminished quality of food resources (Runyoro et al, 1994). Two wildebeest and one zebra carcase (all adults) I examined during the dry season of 1992 had full stomachs, though only of mature grasses which may not supply enough nutrients to maintain digestion (McNaughton, 1985). I did not attempt to assess the quality of available forage for herbivores during my study so I cannot eliminate this as a possible factor. However, given that there was little evidence of large-scale starvation, if forage quality was contributing to wildebeest mortality, it was probably as a secondary factor to the role played by predation. Unlike non-ruminants such as zebras which are able to tolerate large quantities of mature fibrous grasses, wildebeest require high quality grasses to satisfy their nutritional requirements (Demment & van Soest 1985). It is possible that wildebeest were struggling to meet their nutritional requirements and were in poor condition. This may also apply to warthogs which, like wildebeest, prefer short, young grass, though they are able to supplement their diet during the dry season by digging for grass rhizomes (Mason, 1982). If wildebeest and warthogs were in poor condition as a result of low forage quality, large scale starvation need not have been occurring for this to have effects at the population level. For example, poor nutrition can diminish lactation in ungulate females and lower the condition of juveniles, making them more vulnerable to predation (McNaughton, 1985; Linnell et al, 1995). The combination of high predation pressure on animals in poor condition might have been responsible for the population declines observed here. However, as I made no estimation of the condition of prey animals during my study, this remains speculative. The interaction between predation and the availability of resources for herbivores would be a fruitful area to examine in small, enclosed reserves. This is particularly pertinent in a 'reclaimed' conservation area such as Phinda where historical disturbance by cultivation and high livestock density may have

considerable impact in altering the structure of grass communities (Moll, 1982; Goodman, 1990, Runyoro *et al*, 1994).

It is possible that wildebeest, warthog and reedbuck numbers were declining in response to adjusted carrying capacity. Ben-Shahar (1993) demonstrated that wildebeest and zebra populations in the 540km^2 Sabi-Sand Wildtuin underwent a gradual decline over 25 years following fencing, possibly as populations adjusted to confinement in an area of lower carrying capacity. At Phinda, densities of three species (warthog, wildebeest and zebra) were high compared to neighbouring Mkuzi Reserve (Table 32) and for the latter two species, had recently been supplemented by translocations between 1990-1991 (Chapter 2). The decline of wildebeest at Phinda may have been an adjustment following supplementation if carrying capacity was reduced. However, wildebeest were historically far more abundant in the region, estimated at a density of 10.3 km^{-2} in Mkuzi in 1963 (Goodman 1990:108) and up until 1984, had been subject to a culling program which aimed to stabilise their population at a density of 3.5 km^{-2} which the region could evidently support with ease (Goodman 1990:108). Furthermore, Phinda's translocated wildebeest originated from much smaller fenced areas (<50km^2) lacking large predators, where their estimated density was higher than at Phinda, yet these populations were apparently growing and had sustained annual harvesting by humans (live sales and hunting) of between 5 and 15% since at least the mid-1980s (Carlisle, *pers comm*[2]). Accordingly, it seems unlikely that the decline in wildebeest numbers was a result of the supplementary translocations and fencing. Interestingly, wildebeest numbers are apparently still declining at Phinda and at the end of 1997 numbered an estimated 350 (Lewis, *pers comm*[3]).

This has important implications for small reserves with resident populations of herbivores. As many reserves in South Africa and indeed all areas reintroducing large predators, Phinda is entirely fenced. As a result, herbivores are limited in their ability to migrate away from areas of high predation pressure. Where such reserves are small as at Phinda, predators can conceivably follow preferred prey throughout the entire reserve and high rates of predation such as occurred here with wildebeest and reedbuck can be maintained. Where conditions exist that predators can sustain their numbers on alternative, abundant prey species, species at low densities which experience high predation pressure may undergo a population decline. It remains to be seen whether such a scenario will lead to the extinction of a species in a small reserve, but presumably at the rate of decrease observed during the present study, wildebeest and reedbuck will decline to a population level from which they are unable to recover. An attempt to restore eland at Phinda in 1996

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[3] Lewis, A. Phinda Resource Reserve, Private Bag 6001, Hluhluwe, 3960, RSA. Tel. 035 562 0271.

failed because only 20 animals were released. Lion pressure quickly fragmented the herd and the released animals were killed within six months. In response to such a possibility occurring with wildebeest and reedbuck populations, Phinda management has taken some radical and financially costly action. Since 1996, 30 lions have been captured at Phinda and translocated to other reserves, and supplemental translocations of wildebeest were resumed in 1998. It will be interesting to assess the response of ungulate populations following these activities.