POPULATIONS IN A TRANSVAAL LOWVELD NATURE RESERVE

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INTRODUCTION

Predation constitutes an important feature of the biotic environment of wild ungulates and has probably exerted considerable influence on ungulate populations throughout their evolutionary history. Agricultural and industrial advancement has led to the extermination of large mammalian predators from major portions of their original range in southern Africa, but they are still afforded sanctuary in national parks, game reserves and other natural and wilderness areas. As such areas are often small and are required to maintain a more or less complete biota, a thorough understanding of large mammalian predator-prey relationships is a prerequisite to scientific management and perpetuation. Of particular importance is the regulating effect large predators have on wild ungulate populations.

From the variety of ecological terms applicable to predation, the one favoured in this paper is "regulating factor" which is described by Solomon (1964) as a natural density-dependent process which actively curtails increases in population density when this is high but contributes to a population build-up in cases of low density in a passive fashion by relaxing any such curtailing effect. The term seems appropriate in view of the fact that predation on the larger ungulates, as described in numerous scientific and lay texts, appears to vary in intensity in proportion to ungulate density.

Although a regulating effect on ungulate populations in various parts of the world has been noted by field researchers, the extent of such regulation varies considerably. In some cases predation has been found to be a limiting factor of certain ungulate populations. The best known example is that of the Kaibab Plateau in Arizona, North America, where extensive control of potential deer predators led to a tremendous irruption of the resident mule deer *Odocoileus hemionus* population (Rasmussen 1941). In Alaska, Murie (1944) credited wolves *Canis lupus* with effectively limiting Dall sheep *Ovis dalli* populations by killing large numbers of lambs. Leopold et al (1947), in a survey of deer irruptions in North America found that in practically all cases such irruptions followed on predator control. Conversely, however, it was found that predation was not an important regulating factor in the case of the bison *Bison bison* (Soper 1941, Fuller 1962), the barren-ground caribou *Rangifer arcticus* (Banfield 1954, Kelsall 1960) or white-tailed deer *Odocoileus virginianus* in some areas (Stenlund 1955). In selected national parks and game sanctuaries in India, Schaller (1967) found tiger *Panthera tigris* predation to be a considerable population depressant on several ungulate species and a population limiting factor in at least one species, the barasingha *Cervus duvauceli*. On the African continent the only quantitative appraisal of predation as an ungulate regulating factor thus far recorded appears to be that of Talbot

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and Talbot (1963) on the white-bearded wildebeest *Connochaetes taurinus* on the extensive open savanna of Kenya, where predation was found to be considerably overshadowed by other mortality factors such as accidents and disease.

Although carried out on widely varying types of communities, these findings have all pointed to the close relationship between predation on large ungulates and local environmental conditions. Factors of special importance appear to be size of the ungulate home range, type of terrain, degree of vegetative cover and protection, and the efficacy of other population regulating factors.

In the lowveld region of the eastern Transvaal there are several large nature reserves maintained as wilderness areas under private ownership. These provide sanctuary for most indigenous ungulate and large predator species occurring in the south-eastern sub-tropical savanna region. Some of these reserves are completely enclosed by foot-and-mouth disease control fences which preclude dispersal to surrounding areas. This paper describes a study undertaken to evaluate the regulating effect of predation on the ungulate populations in one of the areas, the Timbavati Private Nature Reserve, and particularly to determine to what extent predation may act as a population limiting factor.

THE STUDY AREA

The Timbavati Private Nature Reserve is a privately owned 210 square mile area, entirely fenced with a six foot high game fence. It borders the Kruger National Park along its 20 mile long eastern boundary, European owned ranching areas on the northern and western sides and Bantu Trust territory along the southern boundary. The boundary fence was erected in 1960-1961 as a foot-and-mouth disease control measure; prior to this the larger ungulates were known to move seasonally in and out of the reserve.

The topography is gently undulating and the reserve lies within the area designated phytogeographically as "lowveld savanna" at an altitude of 1,000-1,500 feet above sea-level. Rainfall is seasonal, falling mainly between November and March and averages 15 to 25 inches per year, although this fluctuates considerably. Numerous small water courses feed three main rivers, the Timbavati, Hlalarumi and Sohebele, which flow intermittently during the wet season and provide scattered drinking pools for game in the dry winter. Water supplies have been supplemented by several perennial dams.

The vegetation is heterogeneous, varying from open savanna with tall or short grass through moderately dense woodland to dense riparian woodland. Ungulates show marked preferences for certain vegetation types and current studies indicate that predation may be an important factor in inducing such selectivity.

Of the ungulates present, impala *Aepyceros melampus*, blue wildebeest *Connochaetes taurinus*, zebra *Equus burchelli*, giraffe *Giraffa camelopardalis*, kudu *Tragelaphus strepsiceros*, waterbuck *Kobus ellipsiprymnus* and warthog *Phacochoerus aethiopicus* are the most common. Tsessebe *Damaliscus lunatus*, reedbuck *Redunca arundinum*, bushbuck *Tragelaphus scriptus*, buffalo *Syncerus caffer* and bushpig *Potamochoerus porcus* were too scarce to be included in the study. Grey duiker *Sylvicapra grimmia* and steenbok *Raphicerus campestris* are widespread

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but were not included in this study because their small size precluded any form of reliable census over such a large area and kill data were rarely available.

Lion *Panthera leo*, leopard *Panthera pardus*, spotted hyaena *Crocuta crocuta* and black-backed jackal *Canis mesomelas* are the most important and most numerous large ungulate predators, while cheetah *Acinonyx jubatus*, wild dog *Lycaon pictus*, and side-striped jackal *Canis adustus* are not as wide-spread. The brown hyaena *Hyaena brunnea* is extremely rare and only one crocodile *Crocodilus niloticus* has been recorded in the reserve.

The Timbavati Private Nature Reserve is maintained purely as a wilderness area for private recreational purposes. No form of agricultural pursuit is permitted and all domestic stock are banned from the area. The common wild ungulates are sport-hunted by owners, but hunting removes no more than an estimated 1-2% of each population annually. Impala are the exception and were cropped in 1965 to reduce excessive numbers in some depleted areas; in that year population depletion due to hunting and cropping is estimated to have been about 15-20%. Lions are occasionally hunted, and hyaenas and jackals are sometimes shot when proving a nuisance around camps, but no form of general predator control is practised.

TABLE 1

NUMBERS OF UNGULATES HUNTED AND CROPPED IN TIMBAVATI PRIVATE NATURE RESERVE FROM MAY, 1964, TO APRIL, 1967, AS DETERMINED FROM COMPLETED HUNTING PERMITS

	May, 1964- *April*, 1965	*May*, 1965- *April*, 1966	*May*, 1966- *April*, 1967
Impala	171	741	459
Wildebeest	37	71	78
Zebra	10	17	12
Giraffe*	7	—	2
Kudu	11	6	13
Warthog	—	3	—
Waterbuck	—	—	—

Reports on general seasonal movements of game prior to the erection of boundary fences tend to be contradictory, but there is agreement that the farms adjoining the present north-western boundary of the Timbavati reserve were the traditional summer grazing areas of wildebeest and zebra. This pattern has been maintained and wildebeest and zebra tend to concentrate in the north-western corner of the reserve during the rainy season, and to move southwards for the duration of the dry season. Movements of other game are more sporadic; they disperse during the rains and concentrate around perennial water supplies in the dry winter. As a result of heavy prolonged use in the growing season by impala, wildebeest and zebra, the north-western areas have deteriorated considerably and have a low carrying capacity in the winter months. Large-scale mortalities as a result of starvation in the winter

* Giraffe were shot because of maiming by snares or disease (papillomatosis).

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and early spring occurred twice during the study period in this area, affecting chiefly impala, giraffe and kudu. Wildebeest and zebra were not affected as the majority spent the winter on excellent range in the south. Starvation mortalities, as discussed below, had a marked effect on ungulate numbers and population structure.

The boundary fence acts as a deterrent to animals, but is not game-proof. It is frequently broken by elephants, buffalo and giraffe. Kudu and occasionally impala clear it with ease, while warthogs burrow beneath it. However, with the exception of kudu and possibly warthogs, large-scale movements of ungulates in and out of the Timbavati Private Nature Reserve were not detected during the study period. Lions, hyaenas and jackals were observed to move freely in and out of the reserve.

CENSUSING PREY POPULATIONS

The large size of the study area combined with generally dense vegetative cover and limitations on available manpower necessitated some form of sample count to obtain periodic estimations of ungulate numbers. The method used was the road-strip count as modified by Hirst (in press), using a selected network of roads and tracks as the cruise-line and a two-man observer crew mounted in a four-wheel drive vehicle. Width of strip covered by the observers was determined for each ungulate species and strip area varied from approximately 14% of the total area for species such as kudu to about 20% for giraffe. Counting was carried out over ten consecutive days and two censuses per year were made—one in November or December before the lambing and calving season of the seasonally breeding impala and wildebeest and before the advent of the heavy summer rains, and the other in April or May before the commencement of the dry season. As shown by Hirst (op. cit) road-strip censuses give a correct estimate of ungulate populations but within wide confidence limits, and a population estimate for a savanna woodland area such as the Timbavati reserve based on sufficient replicates is approximately the mean $\pm$ 30% at the 95% level. Replicate counts of the whole Timbavati reserve could not be made because of the size of the area but as each count was in fact made up of ten separate counts of separate blocks it was considered likely that the correct population estimate in fact fell within the range of the estimate $\pm$ 30%.

The age- and sex-structures of the ungulate populations were determined by direct observation with the use of binoculars in the field during road-strip censuses and by observation at drinking points and known preferred localities. Only three age classes could be distinguished with certainty in the various species and these were termed "fully-grown", "partly-grown" and "juvenile". In the seasonal breeders such as impala and wildebeest, the term "juvenile" was applied to the young of the year and "partly-grown" to young of the previous year. In the case of impala, partly-grown ewes could not be distinguished with certainty from fully-grown ewes during pre-winter counts as impala rarely stood long enough to permit prolonged observation and comparison of relative body sizes; these two age-classes were thus grouped for this sample period. In the other species the term "juvenile" referred generally to animals less than six months old as judged by mental comparison with known-age specimens in captivity, and partly-grown animals were approximately from six months to two years of age.

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Further division of the partly-grown category was attempted initially but was found to be so subjective as to render classification unreliable. Sexes were distinguishable in fully-grown animals by the presence or absence of horns in impala, waterbuck and kudu, and by the external genitalia and general bodily appearance in giraffe, wildebeest, zebra and warthog.

During the study period which lasted from June, 1964, to May, 1967, three pre-summer and three pre-winter censuses were made. The few juvenile impala and wildebeest which were present when the pre-summer counts were made were not recorded. The study period was short when the complexities and ecological interrelationships of predation are considered, but the data obtained from repeated censuses plus data obtained on predator kills and other forms of mortality were sufficient to point to some noteworthy trends in the general pattern of large ungulate predation.

COLLECTION OF KILL DATA

The warden, bantu rangers and bantu caretakers undertook the collection of kill data. Predator kills were located during routine patrols and in most cases were revealed by the presence of vultures in the vicinity; in some cases predators were found in possession. When the responsible predator was absent, the surrounding area was searched for spoor and other evidence to reveal the predator's identity. This could not always be determined as in some cases vultures and the principal scavengers—hyaenas and jackals—obliterated all other spoor in the vicinity. Leopard kills were frequently found hanging in trees.

Death due to starvation was difficult to determine at times, particularly in the case of impala. Hyaenas and jackals normally scavenged on such carcasses, but in addition were observed to assume the role of predators and attack individuals in poor and weakened condition. The decision as to whether the cause of mortality was hyaenas, jackals or starvation was thus arbitrary in many cases, although this had little effect on the final analysis. The decision as to whether an animal had died from starvation was based on a combination of findings, viz., the poor or even emaciated condition of the carcass and of live animals of the same species in the immediate vicinity; the condition of the range where the carcass was located; the time of year when the carcass was found; the absence of any signs of predators other than hyaenas or jackals in the vicinity and the absence of any signs of a chase or struggle with predators. The great majority of starvation deaths occurred in late autumn, winter and early spring in the northern and north-western areas of the reserve where range conditions were poor. Large numbers of carcasses of impala and giraffe were retrieved within circumscribed areas within the space of a few weeks during late winter and early spring.

Collection of kill data was biased in several respects. Sampling was not uniform over the whole area as deployment of bantu staff depended on the size of each owner's portion of the reserve. To ensure unbiased reporting, spot checks were carried out on reported kills and the skulls of killed animals were recovered. Skull or jawbone recovery was not possible in all cases as hyaenas frequently dragged or carried the head of a kill off, and as the area was under private ownership the retrieval of skulls could not be insisted upon. Recovery of kills was more efficient in the case of the larger ungulates than with smaller ones as the latter were frequently completely consumed by the predator, leaving nothing to attract vultures.

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A large hyaena was observed to consume an entire impala lamb within three minutes, and a pride of lions are capable of similar treatment of a full-grown impala or a juvenile or partly-grown wildebeest.

A degree of seasonal bias was present in kill recovery due to better visibility in the dry season and the fact that predators, principally lions, tended to attack game which were concentrating around dry-season waterholes and which in turn were frequently visited by patrolling rangers. However, in a large number of cases a dry-season peak of kill recoveries was coupled with reports of increased sightings of large predators in the dry season, indicating that predator numbers were in fact appreciably higher in the dry season. During periods of heavy starvation mortality in the depleted portions of the reserve, special patrols were made to locate carcasses, and the carcass recovery rate was thus considerably higher than during other times of the year.

Other causes of mortality besides those mentioned were poaching and accidents. Poaching was infrequent and a negligible mortality factor. Accidents included fatal collisions with the boundary fence, deaths due to intraspecific fighting and bogging down in waterholes. No other forms of mortality, e.g., from fatal diseases, were observed during the study period and as the fence precluded general movements in or out of the area with possible exceptions in the cases of kudu and warthog, all population losses could be ascribed to the mortality factors described above, chiefly predation and winter starvation.

During the study period of thirty-six months a total of 1,618 predator kills, starvation mortalities and accident mortalities was accumulated, comprising 747 records for impala, wildebeest 322, zebra 52, giraffe 317, kudu 110, waterbuck 45 and warthog 25. In the case of the seasonal breeders such as impala and wildebeest, a rough estimate of sampling intensity could be obtained by comparing the number of recovered carcasses to the number of animals actually removed, the latter figure being obtained from the census data (Tables 4 and 8). Field determination of mature female: new-born young ratios plus inspection of numerous shot mature females for pregnancy indicated that at least 90% of all full-grown impala and wildebeest females gave birth each year, and thus the annual recruitment to each population could be estimated from the numbers of full-grown females. These computations suggested an actual loss of some 8,300 impala and 2,900 wildebeest during the three-year period which in turn indicates a sampling intensity of some 10%. As discussed below, a large percentage of killed animals were lambs or calves, the carcasses of which were normally almost totally consumed, leaving little to attract attention in the field. Sampling intensity in the case of giraffe was probably a great deal higher due to their large size and the fact that a large number died within a relatively short period in a small area, thus facilitating the location of carcasses.

Recovered skulls and/or jawbones of killed ungulates were placed into 5 age classes on the basis of tooth eruption and wear as shown in Table 2. Teeth ageing criteria for impala were based on Child (1964), for wildebeest on Talbot & Talbot (op. cit.) and for zebra on Klingel (1965). Standard criteria for the other species were lacking and the criteria as used for impala and wildebeest were applied. Age class I corresponds to the "juvenile" category, class II to the "partly-grown" class and classes III, IV and V to "young prime", "prime" and "old" respectively.

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TABLE 2

AGE CLASSES OF WILD UNGULATES IN THE TIMBAVATI PRIVATE NATURE RESERVE, BASED ON ERUPTION AND WEAR OF TEETH

Age class	*Characteristics.*
I Juvenile	Artiodactyla—milk premolars erupting to fully erupted, first molar starting to erupt. Zebra—milk incisors erupted but third incisor not in wear, milk premolars erupted and in wear, first molar not erupted.
II Partly-grown	Artiodactyla—first molar fully erupted, second molar erupting or fully-erupted, third molar may be visible. Zebra—milk incisors well worn, first molar erupting or fully erupted, second molar not erupted.
III Young prime	Artiodactyla—milk premolars being replaced by permanent premolars, first and second molars erupted, third premolar erupting, first and possibly second milk incisors being replaced by permanent incisors. Zebra—milk incisors present and well worn, first molar well worn, second molar present and possibly slightly worn, third molar not erupted.
IV Prime	Artiodactyla—all permanent teeth present. Wear variable from slight to heavy but only moderate on third molar, incisors and canines worn but high. Zebra—all permanent teeth present, infundibula of incisors oval or elongated.
V Old	Artiodactyla—heavy wear on all teeth possibly to gum-line on buccal aspect, infundibula worn away on molars except possible remnant on third molar. Zebra—heavy wear on incisors, infundibula round-oval to round to absent.

To obtain a composite picture of predation in relation to population size and structure and general environmental conditions, the causes of mortality expressed on a percentage basis were compared to total population estimates, population structure expressed on a percentage basis and rainfall. These are shown graphically in Figures 1 to 7.

PREDATION ON IMPALA

Impala were subject to mortality from all six predator species plus accidental deaths as well as starvation deaths in late winter and early spring in certain depleted areas. The number of starvation death recoveries was considerably higher than those due to other mortality causes (Table 3). Of the predators, leopards took by far the greatest number, followed by jackals hyaenas, cheetahs, lions and wild dogs in that order.

Comparison of these records must be made in the light of prevailing ecological conditions. Recoveries for lions probably underestimated the true position, as lions usually associated in prides or pairs and could consume an impala almost completely, leaving little to attract attention. Similarly, leopards tended to hide their prey in dense bush or in high trees. Records for starvation deaths over-estimate the actual position, as many of these cases occurred within a relatively circumscribed area and carcass recovery was more efficient. This was

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TABLE 3

NUMBERS OF IMPALA CARCASSES OF ALL AGE AND SEX CLASSES RETRIEVED PER SEASON FROM JUNE, 1964, TO MAY, 1967: TIMBAVATI PRIVATE NATURE RESERVE

Mortality factor	*June - Aug., 64*	*Sept.- Nov., 64*	*Dec.- Feb., 65*	*March - May, 65*	*June- Aug., 65*	*Sept.- Nov., 65*	*Dec.- Feb., 66*	*March - May, 66*	*June - Aug., 66*	*Sept.- Nov., 66*	*Dec.- Feb., 67*	*March - May 67*	*Total*
Lions	2	1	—	1	6	1	4	4	4	5	1	3	32
Leopards	6	13	5	22	29	25	10	13	13	6	2	11	155
Cheetahs	—	5	4	4	12	2	2	2	—	5	3	1	40
Wild dogs	—	5	1	1	—	—	—	—	—	—	—	4	11
Hyaenas	4	27	—	4	9	3	1	—	4	—	1	2	55
Jackals	3	40	7	—	7	9	5	1	1	2	4	—	79
Starvation	—	231	—	2	15	37	—	—	1	—	—	—	286
Accidents	—	—	1	—	9	1	2	2	3	—	4	2	24
Unknown	6	24	7	2	4	10	2	3	1	3	2	1	65
	21	346	25	36	91	88	26	25	27	21	17	24	747

TABLE 3

AGE CLASSES OF IMPALA KILLED BY PREDATORS AND OTHER MORTALITY FACTORS AS DETERMINED FROM SKULLS AND/OR JAWBONES OF RETREIVED SPECIMENS

Age class										
I	Males	—	1	—	—	—	3	—	—	4
Juvenile	Females	1	2	—	1	—	—	—	—	4
	Total	1	3	—	1	—	3	—	—	8
II	Males	—	8	2	—	—	—	4	—	14
Partly-	Females	1	4	1	—	—	1	4	1	12
grown	Total	1	12	3	—	—	1	8	1	26
III	Males	—	3	1	—	—	—	3	—	7
Young	Females	—	5	1	—	—	—	4	—	10
prime	Total	—	8	2	—	—	—	7	—	17
IV	Males	—	17	1	2	3	5	23	1	52
Prime	Females	1	19	1	—	—	8	35	—	64
	Total	1	36	2	2	3	13	58	1	116
V	Males	—	—	1	—	—	1	2	—	4
Old	Females	2	1	3	—	—	1	1	—	8
	Total	2	1	4	—	—	2	3	—	12
	Total	5	60	11	3	3	19	76	2	179

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also the case with the large number of kills recorded for hyaenas and jackals during the late winter of 1964 as all the impala killed during this period were in very poor condition and were killed within the same depleted area. Field observations indicated that hyaenas and jackals killed large numbers of impala lambs during the lambing season, but these were usually totally consumed. Although kill recovery was more efficient over the whole reserve during the dry season, there was a definite indication of increased predator activity at this time correlated with a decrease in the physical condition of the impala and therefore increased vulnerability. The general picture presented by kill records is probably accurate, i.e., sustained predation by leopards, cheetahs and lions throughout the year with peaks in the dry seasons; heavy predation on individuals in poor condition by hyaenas and jackals during stress periods and on lambs during the lambing period, and an overshadowing of predation mortality by starvation deaths at times of critical food shortage in some areas.

The numbers of the various age and sex classes of the population at the selected sample periods were determined from road-strip census data (Table 5, Figure 1) but due to the wide confidence limits, some changes could not be noted with certainty. The first census was made immediately after the heavy mortalities of late winter, 1964, and numbers declined significantly until the end of winter, 1965, when they commenced to rise; the trend at the end of the study period in May, 1967, was still up. The number of males, both fully- and partly-grown, declined from the end of 1964 to the end of 1965 and the number of fully-grown males appears to have remained constant at that level while indications are that partly-grown males declined still further in number. The number of impala males hunted and cropped during these periods could only have contributed to the decline in a very small measure and predation, mainly by leopards, appears to be the responsible factor. Examination of the age classes killed by predators (Table 4) and comparison to population age and sex classes show that relatively more fully-grown and partly-grown males were taken than were females of the same categories respectively. Males consort in small herds of up to about a dozen animals and are probably more vulnerable to a stalking predator than are females which associate in large female herds numbering usually fifty to several hundred animals and which can maintain surveillance over their immediate surroundings more efficiently than can smaller male herds. It was noted, however, that hyaenas and jackals frequently loitered near large female-juvenile herds and the impala merely kept a reasonable distance between the predator and themselves and did not scatter as occurred when lions were near. On three separate occasions hyaenas or jackals were seen to run down impala lambs without any form of preparatory stalking. Impala lambs were heavily preyed upon by hyaenas and jackals during the summer months from birth until approximately six months of age, although as explained above, this age class is poorly represented in collected skull data. Mature ewe: lamb ratios varied considerably from herd to herd depending on how much depredation had been suffered from prowling hyaenas and jackals. Field counts indicated that in unmolested herds at least 90% of fully-grown ewes lambed annually, whereas the proportion of full-grown ewes with lambs in the three late autumn censuses was 40-45%, indicating a considerable loss of lambs from these two predator-scavengers. Decline in numbers of females paralleled the decline of males from 1964 to 1965, but thereafter female survival rate appeared to improve and female numbers increased significantly, with a corresponding widening in male : female ratios.

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TABLE 5

IMPALA POPULATION STRUCTURE DETERMINED FROM ROAD-STRIP CENSUS DATA FOR SIX SAMPLE PERIODS: TIMBAVATI PRIVATE NATURE RESERVE

		Males		*Females*		*Juveniles**	*Total*
		Fully-grown	*Partly-grown*	*Fully-grown*	*Partly-grown*		
November, 1964	Estimate	2,548	601	4,135	1,061	—	8,345
	Probable confidence limits†	1,784-3,312	421-781	2,894-5,376	743-1,379	—	5,842-10,848
	% of total population ..	30·5	7·2	49·5	12·7	—	99·9
April, 1965	Estimate	2,213		4,709		1,647	8,569
	Probable confidence limits†	1,549-2,877		3,296-6,122		1,153-2,141	5,998-11,140
	% of total population ..	25·8		54·9		19·2	99·9
December, 1965	Estimate	1,482	309	2,152	409	—	4,352
	Probable confidence limits†	1,037-1,927	216-402	1,506-2,798	286-532	—	3,045-5,659
	% of total population ..	34·1	7·1	49·5	·9·4	—	100·1
May, 1966	Estimate	1,060		3,328		1,365	5,753
	Probable confidence limits†	742-1,378		2,330-4,327		955-1,774	4,027-7,479
	% of total population ..	21·6		55·6		22·8	100·0
December, 1966	Estimate	1,007	155	2,995	856	—	5,013
	Probable confidence limits†	705-1,309	108-202	2,096-3,894	599-1,113	—	3,508-6,518
	% of total population ..	20·1	3·1	59·8	17·1	—	100·0
April, 1967	Estimate	1,093		4,076		1,842	7,011
	Probable confidence limits†	765-1,421		2,853-5,299		1,289-2,395	4,907-9,115
	% of total population ..	15·6		58·2		26·3	100·1

†Confidence limits computed as estimate ± 30%. See text.

*Juveniles ignored in pre-summer counts. See text.

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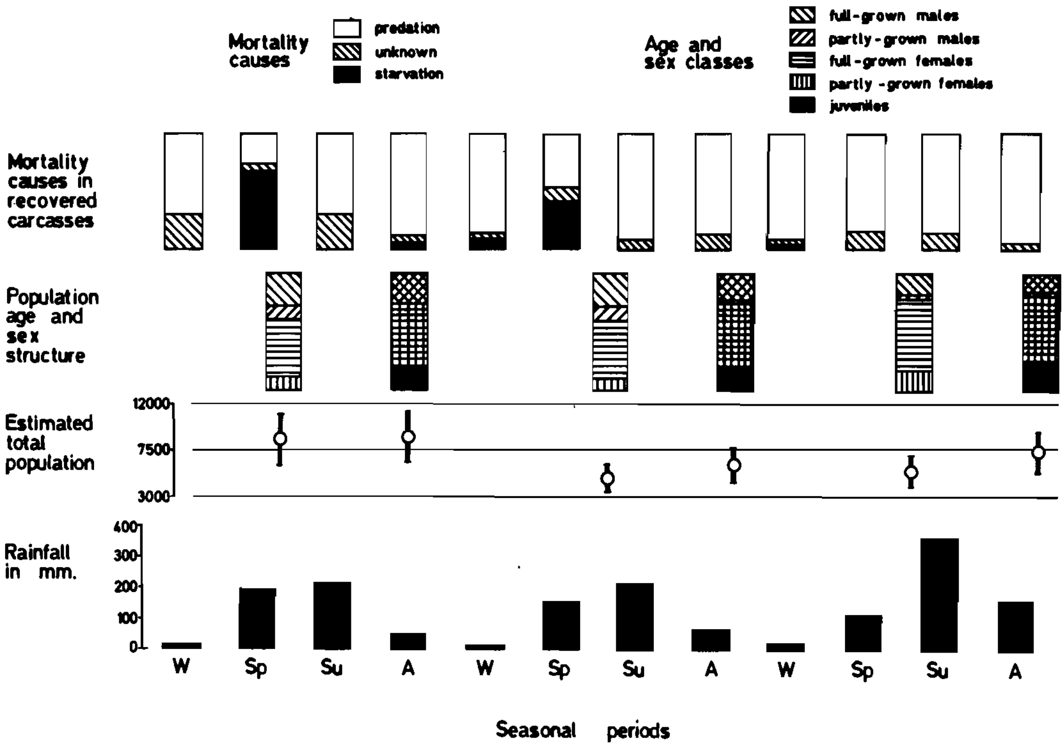

FIGURE 1

Impala — comparing total populations, population structure as percentages, mortality causes as percentages and seasonal rainfall during a three-year study period; Timbavati Private Nature Reserve.

The somewhat wide age classes used to categorise the mortalities plus the lack of data on juvenile kills precludes the construction of a proper life table for impala. However, the data in Table 4 suggest that if impala can survive the heavy losses prevalent amongst lambs, they are thereafter killed or die at a reasonably constant rate.

Despite heavy losses amongst the juveniles and subsequent losses from all six predators, impala populations are definitely not limited by predation but increase fairly rapidly until checked drastically by critical food shortage. Predation is a considerable population depressant, however, as population growth would be considerably accelerated in its absence. The available data suggest that sex structure of the population is materially affected by predation.

PREDATION ON WILDEBEEST

In contrast to impala, wildebeest were preyed upon by only four predators, lions being by far the most important (Table 6). Only two records were collected for leopard kills and three for cheetah kills and all were calves or partly-grown animals. Hyaenas took a relatively

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TABLE 6

NUMBERS OF WILDEBEEST CARCASSES OF ALL AGE AND SEX CLASSES RETRIEVED PER SEASON FROM JUNE, 1964, TO MAY, 1967; TIMBAVATI PRIVATE NATURE RESERVE

Mortality factor	*June - Aug., 64*	*Sept.- Nov., 64*	*Dec.- Feb., 65*	*March - May, 65*	*June - Aug., 65*	*Sept.- Nov., 65*	*Dec.- Feb., 66*	*March - May, 66*	*June - Aug., 66*	*Sept.- Nov., 66*	*Dec.- Feb., 67*	*March - May, 67*	
Lions	3	15	8	13	12	33	29	47	27	38	34	32	291
Leopards	—	—	—	—	—	1	—	—	—	—	1	—	2
Cheetahs	—	—	—	—	—	—	2	1	—	—	—	—	3
Hyaenas	—	—	—	1	—	4	1	—	—	—	1	—	7
Starvation	—	—	—	—	—	—	—	—	—	1	1	—	2
Accidents	—	—	—	—	—	1	—	1	—	—	—	—	2
Unknown	—	—	4	—	—	3	—	—	3	1	2	2	15
	3	15	12	14	12	42	32	49	30	40	39	34	322

TABLE 7

WILDEBEEST POPULATION STRUCTURE DETERMINED FROM ROAD-STRIP CENSUS DATA FOR SIX SAMPLE PERIODS: TIMBAVATI PRIVATE NATURE RESERVE

		Fully-grown		*Partly-grown*	*Juveniles**	*Total*
		Males	*Females*			
November, 1964	Estimate	405	1,296	376	—	2,077
	Probable confidence limits	283-527	907-1,685	263-489	—	1,453-2701
	% of total population	19·5	62·4	18·1	—	100·0
April, 1965	Estimate	569	1,479	363	633	3,044
	Probable confidence limits	398-740	1,035-1,923	254-472	443-823	2,130-3,958
	% of total population	18·7	48·6	11·9	20·8	100·0
December, 1965	Estimate	436	1,244	407	—	2,087
	Probable confidence limits	305-567	871-1,617	285-529	—	1,461-2,713
	% of total population	20·9	59·6	19·5	—	100·0
May, 1966	Estimate	444	1,439	277	500	2,660
	Probable confidence limits	311-577	1,007-1,871	194-360	350-650	1,862-3,458
	% of total population	16·7	54·1	10·4	18·8	100·0
December, 1966	Estimate	897	1,303	349	—	2,549
	Probable confidence limits	628-1,166	912-1,694	241-457	—	1,781-3,317
	% of total population	35·2	51·1	13·7	—	100·0
April, 1967	Estimate	414	1,091	354	726	2,585
	Probable confidence limits	290-538	764-1,418	248-460	508-944	1,810-3,360
	% of total population	16·0	42·2	13·7	28·1	100·0

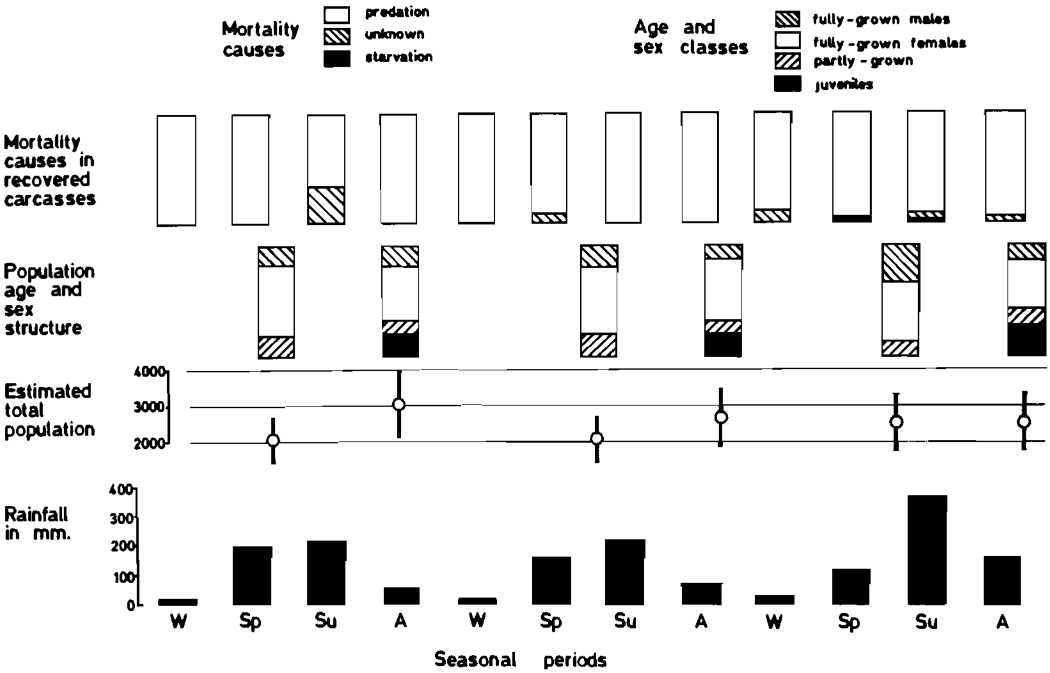

FIGURE 2

Wildebeest — comparing total populations, population structure as percentages, mortality causes as percentages and seasonal rainfall during a three-year study period; Timbavati Private Nature Reserve.

small number of wildebeest, and skull ageing analysis (Table 8) indicates that fully-grown animals were taken as well as young ones. Freshly killed wildebeest were recovered and found to be in excellent condition; indications were that hyaenas teamed up into packs to hunt down adult wildebeest. Whitfield (personal communication) reported seeing some twenty hyaenas in a group, although they were not hunting at the time. It is noted that pack-hunting by hyaenas is regarded as a normal occurrence in the Kalahari National Park (Eloff 1964) and on the Serengeti plains of East Africa (Kruuk 1966).

The population trend during the three year study appeared to be either stable or slightly up (Figure 2). With few exceptions population structure remained relatively stable during the study period (Table 7); partly-grown wildebeest suffered increased losses between March, 1966, and May, 1966, and full-grown males showed an unaccountable rise from May, 1966, to December, 1966, with a subsequent drop back to the previous level by April, 1967.

As in the case of impala, kill recoveries were biased inasmuch as the remains of juvenile and partly grown animals were not easily found. Field observation indicated that calving rates were very high and in excess of 90%. From Table 7 it appears that the number of breeding females in the reserve totalled approximately 900-1,100 during the study period and that the number of cows with calves at foot in the fall of 1965, 1966 and 1967 was about 60%, 50%

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TABLE 8

AGE CLASSES OF WILDEBEEST KILLED BY LIONS, HYAENAS AND UNKNOWN PREDATORS AS DETERMINED FROM SKULLS AND/OR JAWBONES OF RETRIEVED SPECIMENS.

Age class		*Lions*	*Hyaenas*	*Unknown Predator*	*Total*
I	Males	—	—	—	—
Juvenile	Females	—	—	—	—
	Unknown sex	3	—	—	3
	Total	3	—	—	3
II	Males	2	1	—	3
Partly-grown	Females	4	—	—	4
	Unknown sex	4	—	2	6
	Total	10	1	2	13
III	Males	4	—	—	4
Young prime	Females	3	1	—	4
	Total	7	1	—	8
IV	Males	28	2	1	31
Prime	Females	24	2	4	30
	Total	52	4	5	61
V	Males	4	—	—	4
Old	Females	—	—	—	—
	Total	4	—	—	4
	Total	76	6	7	89

and 70% respectively. By spring, 1965, the yearling : adult cow ratio was down from 60 : 100 to 40 : 100, and by spring, 1966 from 50 : 100 to 35 : 100. Skull age class data (Table 8) do not reflect this latter loss amongst yearlings as relatively few immature skulls were recoverable, but these data do suggest that subsequent losses were not uniformly distributed over the whole population, but were heaviest in the prime age and lightest in young prime animals and old animals. Fully-grown male wildebeest were noticeably more affected by lion predation than were fully-grown females and these were mainly single bulls. Many single bulls were found in the company of other species, notably impala, zebra and giraffe, and this behavioural adaptation probably served to reduce a lone bull's high vulnerability to lions.

Wildebeest are not sedentary in Timbavati as are impala, but in company with zebra undertake well-defined seasonal movements to the northern areas during the rainy season and return to their dry-season grazing areas near the Timbavati River in the south of the

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reserve when temperatures drop. This is in effect a form of natural rotational use of grazing and during the study period all wildebeest remained in excellent condition. Two cases of death due to starvation are reported in the tables, both in very young calves which had probably lost their mothers; no cases of starvation in the other age classes are known to have occurred. Despite their seasonal trekking, wildebeest in woodland savanna are remarkably stenoecious (Hirst unpublished data) and their present selected ranges are fully utilised with some deterioration in the north-western areas. Preferred habitats are generally various forms of open tree savanna or clearings in woodland.

Of all the ungulates present in Timbavati, wildebeest are most affected by predation as their numbers appear either to remain stable or to increase at a very slow rate (Figure 2), and starvation mortalities play no role in population regulation. Two possible causes for this effective limitation by lion predation are suggested, viz., a preference for wildebeest as prey by lions or a higher incidence of contact between wildebeest and hunting lions, brought about by similar habitat preferences.

The determination of prey preferences requires an unbiased sample of kills for any one predator species and the comparison of this to the composition of the prey available in the area effectively covered by the predator within a given period during which environmental conditions remain relatively stable. The data collected in this work do not permit of such a critical analysis, but the kill recovery figures do suggest that wildebeest are killed by lions in far greater numbers than could be explained on the basis of random contact, which in turn suggests a predilection for wildebeest by lions. Lions are found in varied habitats in Timbavati, from open plains to dense thickets but their hunting habits suggest that they prefer an open area in which to hunt so that they can rush towards their selected prey unimpeded by numerous trees or dense shrubs. Chosen wildebeest habitat in Timbavati would suit such requirements very well, and this fact may expose wildebeest to a high incidence of lion predation. Cause and effect may be reversible in this theory however, as wildebeest may in fact select such open habitats so that they can detect approaching lions at a distance. It is significant that zebra and impala also make use of the same habitats as do wildebeest yet are not taken by lions to nearly the same extent. It is suggested then that a predilection for wildebeest, and especially immature wildebeest by lions is the primary reason for population depression, and that habitat selection may assist lions in preying more effectively on this species.

PREDATION ON ZEBRA

Predation on zebra followed the same general pattern as in wildebeest which is possibly to be expected in view of the numerous ecological similarities between these species. Two records were obtained of hyaenas and jackals pulling down young foals; all other predation records were for lions (Table 9). Only a small number of skulls from zebra kills were retrieved (Table 11). An interesting feature was the age of two specimens, which according to the age criteria suggested by Klingel (1965) were 11-13 years old.

Juveniles and partly-grown animals constituted small proportions of the total population at all six census periods (Table 10) which is indicative of the high rate of predation loss

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TABLE 9

NUMBERS OF ZEBRA CARCASSES OF ALL AGE AND SEX CLASSES RETRIEVED PER SEASON FROM JUNE, 1964 TO MAY, 1967; TIMBAVATI PRIVATE RESERVE

Mortality factor	*June - Aug., 64*	*Sept.- Nov., 64*	*Dec.- Feb., 65*	*March - May, 65*	*June - Aug., 65*	*Sept.- Nov., 65*	*Dec.- Feb., 66*	*March - May, 66*	*June - Aug., 66*	*Sept.- Nov., 66*	*Dec.- Feb., 67*	*March - May, 67*	
Lions	1	2	—	2	2	5	8	5	7	4	4	4	44
Hyaenas	—	—	—	—	—	—	1	—	—	—	—	—	1
Jackals	—	1	—	—	—	—	—	—	—	—	—	—	1
Accidents	—	—	3	—	—	—	—	—	1	—	1	—	5
Unknown	—	—	—	—	—	—	1	—	—	—	—	—	1
	1	3	3	2	2	5	10	5	8	4	5	4	52

TABLE 10

ZEBRA POPULATION STRUCTURE DETERMINED FROM ROAD-STRIP CENSUS DATA FOR SIX SAMPLE PERIODS: TIMBAVATI PRIVATE NATURE RESERVE

		Fully-grown		*Partly-grown*	*Juveniles*	*Total*
		Males	*Females*			
	Estimate	114	446	51	23	634
November, 1964	Probable confidence limits	80-148	312-580	36-66	16-30	444-824
	% of total population	18·0	70·2	8·1	3·7	100·0
	Estimate	163	424	53	149	789
April, 1965	Probable confidence limits	114-212	297-551	37-69	104-194	552-1,026
	% of total population	20·7	53·7	6·7	18·9	100·0
	Estimate	128	551	78	75	832
December, 1965	Probable confidence limits	90-166	386-716	55-101	52-98	583-1,081
	% of total population	15·4	66·2	9·4	9·0	100·0
	Estimate	121	554	50	91	816
May, 1966	Probable confidence limits	85-157	388-720	35-65	64-118	572-1,060
	% of total population	14·8	67·9	6·2	11·1	100·0
	Estimate	156	618	142	64	980
December 1966	Probable confidence limits	109-203	433-803	99-185	45-83	686-1,274
	% of total population	15·8	63·1	14·5	6·5	99·9
	Estimate	215	459	97	120	891
April, 1967	Probable confidence limits	151-280	321-597	68-126	84-156	624-1,159
	% of total population	24·1	51·5	10·9	13·4	99·9

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TABLE 11

AGE CLASSES OF ZEBRA KILLED BY LIONS AND UNKNOWN PREDATORS AS DETERMINED FROM SKULLS AND/OR JAWBONES OF RETRIEVED SPECIMENS; TIMBAVATI PRIVATE NATURE RESERVE

Age class		*Lions*	*Unknown*	*Total*
I	Males	—	—	—
Juvenile	Females	—	—	—
	Unknown sex	3	—	3
	Total	3	—	3
II	Males	—	—	—
Partly-	Females	1	—	1
grown	Total	1	—	1
III	Males	—	—	—
Young	Females	—	—	—
prime	Total	—	—	—
IV	Males	1	—	1
Prime	Females	2	2	4
	Total	3	2	5
V	Males	2	—	2
Old	Females	1	—	1
	Total	3	—	3
	Total	10	2	12

amongst these age classes. Skull age class data suggest that once this period was passed individuals were highly resistant to lion predation during the young prime stage and then were killed at an approximate steady rate until a relatively old age. As with the other ungulates the proportion of juvenile kills recovered was very low.

In the Timbavati reserve, zebra foaled at any time of the year but with a marked peak from December to February. Population age and sex structure fluctuated mainly because of the periodic appearance and loss of juveniles. The partly grown age class fluctuated in number for the same reason. Within broad limits, fully grown females remained at a steady number while fully grown males did the same except towards the end of the study period when they showed a sharp rise.

No pronounced rise or fall in numbers could be detected during the study period (Figure 3), but the general population trend appeared to be slightly up. As in the case of wildebeest, lion predation was a marked population depressant, but is probably not the ultimate limiting factor. It is worthy of note that the main difference between the patterns of

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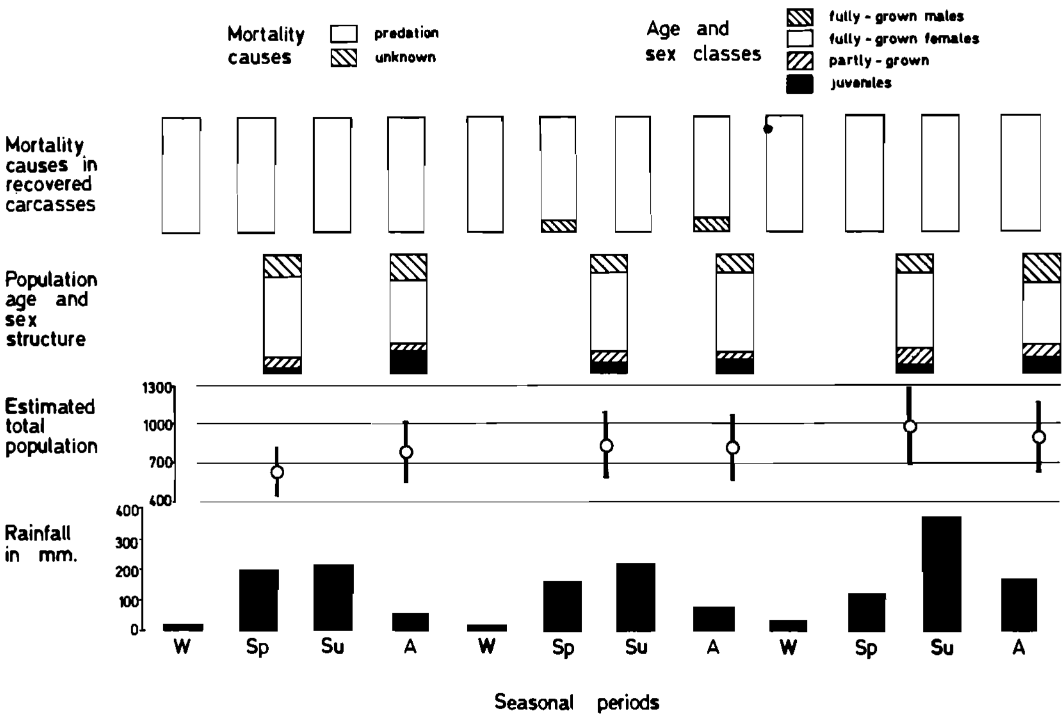

FIGURE 3

Zebra — comparing total populations, population structure as percentages, mortality causes as percentages and seasonal rainfall during a three-year study period; Timbavati Private Nature Reserve.

predation in wildebeest and zebra was the fact that zebra were not preyed upon by lions to nearly the same extent as were wildebeest.

PREDATION ON GIRAFFE

Predation on giraffe deviated from the pattern discussed so far as it tended to be markedly seasonal in nature. Giraffe are formidable prey animals and apart from one record for a leopard killing a calf and a record for hyaenas doing likewise, the only predators capable of attacking a giraffe successfully were lions operating in a pride.

Giraffe were noticeably affected by starvation during a critical period at the end of winter in 1965 in the north-western areas and to a lesser extent in the winters of 1964 and 1966. During these stress periods the incidence of lion predation rose considerably (Table 12) in the depleted areas. Skulls of giraffe succumbing during this period were not collected but were field-checked by the warden; virtually all fell into the prime and old age classes. This correlates with census data collected before and after the mortalities (Table 13, Figure 4), the latter figures also indicate a loss of calves during this period which in the absence of the

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TABLE 12

NUMBERS OF GIRAFFE CARCASSES OF ALL AGE AND SEX CLASSES RETRIEVED PER SEASON FROM JUNE, 1964 TO MAY, 1967; TIMBAVATI PRIVATE RESERVE

Mortality factor	*June-Aug., 64*	*Sept.-Nov., 64*	*Dec.-Feb., 65*	*March-May, 65*	*June-Aug., 65*	*Sept.-Nov., 65*	*Dec.-Feb., 66*	*March-May, 66*	*June-Aug., 66*	*Sept.-Nov., 66*	*Dec.-Feb., 67*	*March-May, 67*	
Lions	—	14	5	4	41	19	1	1	2	4	9	3	103
Leopards	—	—	—	—	—	—	—	—	—	—	—	1	1
Hyaenas	—	—	—	—	1	—	—	—	—	—	—	—	1
Starvation	—	5	4	1	23	146	—	—	2	1	—	—	182
Accident	—	3	—	1	8	6	—	1	1	1	—	2	23
U known	—	—	1	—	1	—	—	1	1	—	—	3	7
	—	22	10	6	74	171	1	3	6	6	9	9	317

TABLE 13

GIRAFFE POPULATION STRUCTURE DETERMINED FROM ROAD-STRIP CENSUS DATA FOR SIX SAMPLE PERIODS: TIMBAVATI PRIVATE NATURE RESERVE

		Fully-grown		*Partly-grown*		*Juveniles*	*Total*
		Males	*Females*	*Males*	*Females*		
	Estimate	365	703	17	62	87	1,234
November,	Probable confidence limits	255-475	492-914	12-22	43-81	60-114	862-1,606
1964	% of total population ..	29·6	57·0	1·4	5·0	7·0	100·0
	Estimate	468	579	18	51	56	1,172
April,	Probable confidence limits ..	328-608	405-753	13-23	36-66	39-73	821-1,523
1965	% of total population ..	39·9	49·4	1·5	4·4	4·8	100·0
	Estimate	334	415	25	111	13	898
December,	Probable confidence limits ..	234-434	290-540	17-33	78-144	9-17	628-1,168
1965	% of total population ..	37·2	46·2	2·8	12·4	1·4	100·0
	Estimate	580	423	118	29	108	1,258
May,	Probable confidence limits ..	406-754	269-550	83-153	20-38	75-141	853-1,636
1966	% of total population ..	46·1	33·6	9·4	2·3	8·6	100·0
	Estimate	506	555	43	24	73	1,201
December,	Probable confidence limits ..	354-658	388-722	30-56	17-31	51-95	840-1,562
1966	% of total population ..	42·1	46·2	3·6	2·0	6·1	100·0
	Estimate	417	547	13	65	143	1,185
April,	Probable confidence limits ..	292-542	383-711	9-17	45-85	100-186	829-1,541
1967	% of total population ..	35·2	46·2	1·1	5·5	12·1	100·1

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TABLE 14

AGE CLASSES OF GIRAFFE KILLED BY LIONS AS DETERMINED FROM SKULLS AND/OR JAWBONES OF RETRIEVED SPECIMENS: TIMBAVATI PRIVATE NATURE RESERVE

Age class			*Age class*		
I	Males	—	IV	Males	12
II	Females	—	Prime	Females	6
Juvenile	Unknown sex	6		Unknown sex	2
	Total	6		Total	20
II	Males	—	V	Males	4
Partly-	Females	2	Old	Females	2
grown	Unknown sex	7		Unknown sex	—
	Total	9		Total	6
III	Males	2		Total males	18
Young	Females	—		Total females	10
prime	Unknown sex	—		Total unknown sex	15
	Total	2		Total	43

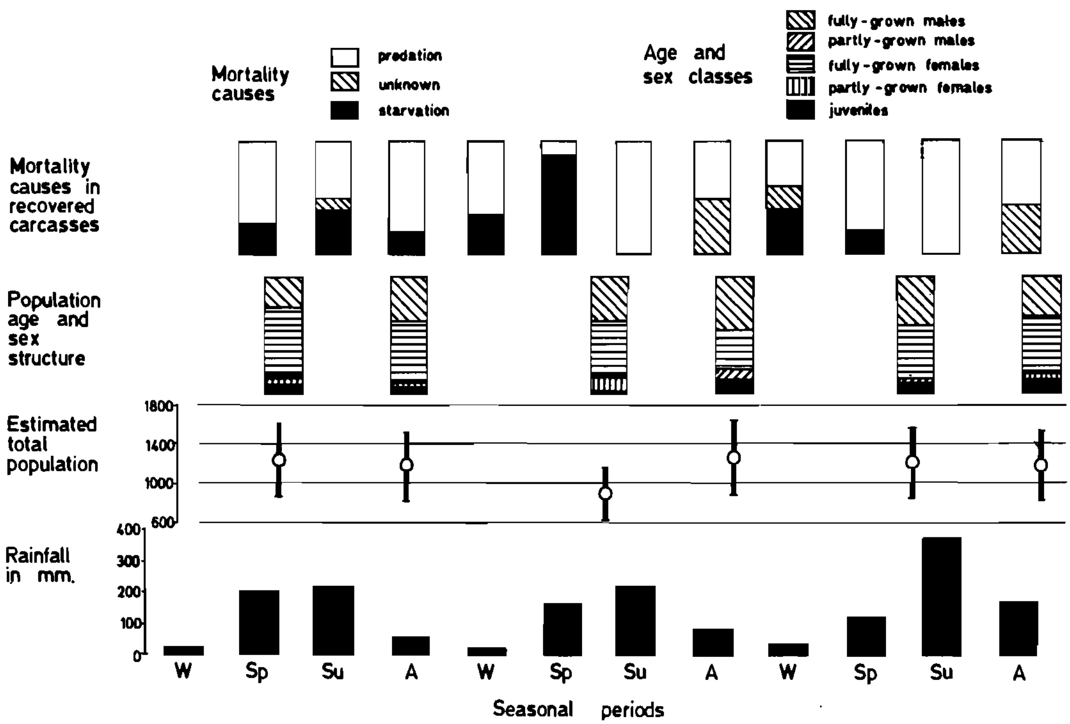

FIGURE 4

Giraffe — comparing total populations, population structure as percentages, mortality causes as percentages and seasonal rainfall during a three-year study period; Timbavati Private Nature Reserve.

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TABLE 15

AGE CLASSES OF KUDU KILLED BY LIONS AND OTHER MORTALITY FACTORS AS DETERMINED FROM SKULLS AND/OR JAWBONES OF RETRIEVED SPECIMENS; TIMBAVATI PRIVATE NATURE RESERVE

Age class		*Lions*	*Starvation*	*Unknown*	*Total*
I	Males	—	—	—	—
Juvenile	Females	—	—	—	—
	Total	—	—	—	—
II	Males	—	2	1	3
Partly-	Females	—	3	—	3
grown	Total	—	5	1	6
III	Males	—	—	—	—
prime	Females	—	—	—	—
Young	Total	—	—	—	—
IV	Males	1	2	4	7
Prime	Females	1	3	3	7
	Total	2	5	7	14
V	Males	—	1	—	1
Old	Females	—	—	1	1
	Total	—	1	1	2
	Total	2	11	9	22

dams were probably pulled down by predators. Skulls and jawbones collected from lion kills during other periods were examined (Table 14) and even though material from age class I was grossly under-represented, it still formed a significant part of the collected material.

The population trend determined from the available data (Figure 4) seemed to be stable with a drop after the 1965 mortalities followed by a rapid return to the previous level largely through the appearance of large numbers of calves in the southern and eastern parts of the reserve. The study period was too short to detect any possible upward trend, but if such a trend is present it will necessarily be slow due to removal of calves and young animals by lions. Population age and sex ratios remained reasonably stable except for the decrease in fully grown animals lost from starvation.

PREDATION ON KUDU

In common with impala, kudu were preyed upon by all six predators and in addition suffered losses through starvation and various accidents. Most records were obtained for lion predation (Table 17) and the population structure during the study period (Table 16) suggests a very

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TABLE 16

KUDU POPULATION STRUCTURE DETERMINED FROM ROAD-STRIP CENSUS DATA FOR SIX SAMPLE PERIODS: TIMBAVATI PRIVATE NATURE RESERVE

		Fully-grown		*Partly-grown*		*Juveniles*	*Total*
		Males	*Females*	*Males*	*Females*		
November, 1964	Estimate	43	453	27	70	59	652
	Probable confidence limits	30-56	317-589	19-35	49-91	41-77	456-848
	% of total population	6·6	69·7	4·1	10·7	9·0	100·1
April, 1965	Estimate	124	465	32	94	106	821
	Probable confidence limits	87-161	325-605	22-42	66-122	74-138	574-1,068
	% of total population	15·1	56·6	3·9	11·4	12·9	99·9
December, 1965	Estimates	66	397	9	—	—	472
	Probable confidence limits	48-86	278-516	6-12	—	—	332-614
	% of total population	14·0	84·0	2·0	—	—	100·0
May, 1966	Estimate	72	272	—	—	57	401
	Probable confidence limits	50-94	190-354	—	—	40-74	280-522
	% of total population	17·9	67·9	—	—	14·3	100·1
December, 1966	Estimate	118	321	—	34	25	498
	Probable confidence limits	83-153	225-417	—	24-44	17-33	349-647
	% of total population	23·7	64·4	—	6·8	5·1	100·0
April, 1967	Estimate	115	335	9	57	105	621
	Probable confidence limits	80-150	234-436	6-12	40-74	73-137	433-809
	% of total population	18·5	53·8	1·5	9·2	16·9	99·9

TABLE 17

NUMBERS OF KUDU CARCASSES OF ALL AGE AND SEX CLASSES RETRIEVED PER SEASON FROM JUNE, 1964, TO MAY, 1967; TIMBAVATI PRIVATE RESERVE

Mortality factor	*June-Aug., 64*	*Sept.-Nov., 64*	*Dec.-Feb., 65*	*March-May, 65*	*June-Aug., 65*	*Sept.-Nov., 65*	*Dec.-Feb., 66*	*March-May, 66*	*June-Aug., 66*	*Sept.-Nov., 66*	*Dec.-Feb., 67*	*March-May, 67*	
Lions	1	5	—	4	8	8	2	1	7	—	1	3	40
Leopards	—	—	—	1	—	3	3	—	—	—	—	1	8
Cheetahs	—	—	1	—	—	2	—	—	1	—	—	—	4
Wild dogs	—	1	—	—	—	—	—	2	1	—	—	4	8
Hyaenas	1	2	—	—	—	2	—	—	—	—	1	—	6
Jackals	—	—	1	—	—	—	—	—	—	—	—	—	1
Starvation	—	10	—	—	6	21	—	—	—	—	—	—	37
Accidents	—	—	1	—	1	—	—	—	—	—	—	—	2
Unknown	—	—	—	—	2	1	—	—	—	1	—	—	4
		18	3	5	17	37	5	3	9	1	2	8	110

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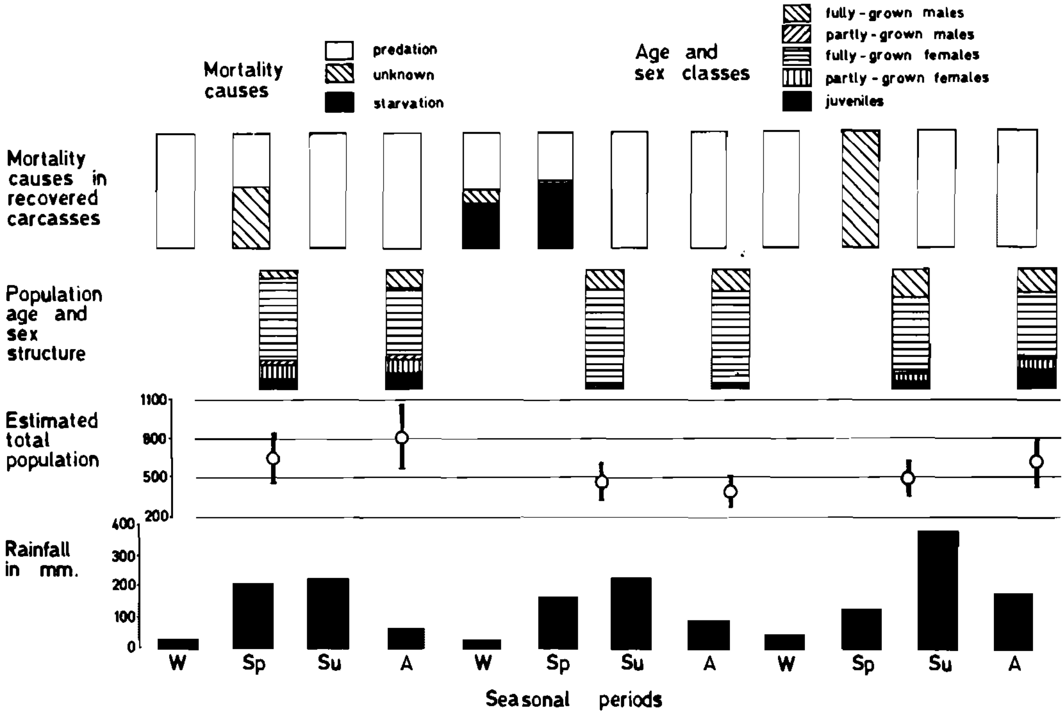

FIGURE 5
Kudu — comparing total populations, population structure as percentages, mortality causes as percentages and seasonal rainfall during a three-year study period; Timbavati Private Nature Reserve.

heavy mortality amongst calves and young animals, which during some censuses were not even seen, although no skulls of juvenile animals were found. The figures obtained for recovered kills may thus considerably underestimate the importance of leopards, cheetahs, wild dogs and hyaenas as population depressant factors in the case of kudu. Data from recovered skulls indicated a heavy loss amongst partly-grown kudu from starvation.

Apart from the fluctuations induced in the population structure by the appearance and loss of juveniles the number of fully grown males fluctuated considerably, and more than could be explained in terms of recruitment and loss. Taking into account this age-group's far-ranging habits and disregard for fences it seems likely that the kudu population was materially affected by irregular influxes and effluxes from and to adjacent areas. During the study period the population trend appeared to be up until the mortalities in late winter 1965 when numbers dropped significantly (Figure 5). From this point the trend has again been sharply up. The proportion of fully grown females has paralleled the general trend and the prime age class was most affected by lion predation and by starvation. Fully grown male kudu were considerably more affected by both lion predation and by starvation than were fully grown females.

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Table 18

WATERBUCK POPULATION STRUCTURE DETERMINED FROM ROAD-STRIP CENSUS DATA FOR SIX SAMPLE PERIODS: TIMBAVATI PRIVATE NATURE RESERVE

		Fully-grown		*Partly-grown*		*Juveniles*	*Total*
		Males	*Females*	*Males*	*Females*		
November, 1964	Estimate	38	46	—	—	—	84
	Probable confidence limits ..	27-49	32-60	—	—	—	59-109
	% of total population ..	45·5	54·5	—	—	—	100·0
April, 1965	Estimate	11	48	10	5	7	81
	Probable confidence limits ..	8-14	34-62	7-13	3-7	5-9	57-105
	% of total population ..	13·8	59·2	12·3	6·2	8·5	100·0
December, 1965	Estimate	14	32	16	9	—	71
	Probable confidence limits ..	10-18	22-42	11-21	6-12	—	49-93
	% of total population ..	20·0	45·0	23·0	12·0	—	100·0
May, 1966	Estimate	22	77	74	19	77	269
	Probable confidence limits ..	15-29	54-100	52-96	13-25	54-100	188-350
	% of total population ..	8·2	28·5	27·5	7·2	28·5	99·9
December, 1966	Estimate	20	76	10	20	—	126
	Probable confidence limits ..	14-26	53-99	7-13	16-26	—	90-164
	% of total population ..	16·0	60·0	8·0	16·0	—	100·0
April, 1967	Estimate	19	144	10	10	20	203
	Probable confidence limits ..	13-25	101-187	7-13	7-13	14-26	142-264
	% of total population ..	9·5	71·4	4·8	4·8	9·6	100·1

Table 19

NUMBERS OF WATERBUCK CARCASSES OF ALL AGE AND SEX CLASSES RETRIEVED PER SEASON FROM JUNE, 1964, TO MAY, 1967; TIMBAVATI PRIVATE NATURE RESERVE

Mortality factor	*June - Aug., 64*	*Sept.- Nov., 64*	*Dec.- Feb., 65*	*March - May, 65*	*June - Aug., 65*	*Sept.- Nov., 65*	*Dec.- Feb., 66*	*March - May, 66*	*June - Aug., 66*	*Sept.- Nov., 66*	*Dec.- Feb., 67*	*March - May, 67*	
Lions	—	—	—	3	1	5	2	6	5	6	2	1	31
Leopards	—	—	—	—	—	—	1	—	—	—	—	—	1
Hyaenas	1	—	—	—	—	—	1	—	—	—	—	1	3
Jackals	—	—	—	1	—	—	—	—	—	—	—	—	1
Starvation	—	6	—	1	—	1	—	—	—	—	—	—	8
Unknown	—	—	—	—	—	—	—	—	—	1	—	—	1
	1	6	—	5	1	6	4	6	5	7	2	2	45

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TABLE 20

AGE CLASSES OF WATERBUCK KILLED BY LIONS AND ACCIDENTS AS DETERMINED FROM SKULLS AND/OR JAWBONES OF RETRIEVED SPECIMENS; TIMBAVATI PRIVATE NATURE RESERVE

Age class		*Lions*	*Accidents*	*Total*
IV	Males	4	2	6
Prime	Females	9	—	9
	Total	13	2	15
V	Males	2	—	2
Old	Females	—	—	—
	Total	2	—	2
	Total	15	2	17

PREDATION ON WATERBUCK

Because of their relatively low numbers and a preference for dense riparian vegetation, waterbuck are difficult to census adequately and results of road-strip censuses for this species must be regarded with caution. The data collected (Table 18) indicate the heaviest losses to have occurred amongst adult males and partly grown and juvenile animals.

Apart from three animals killed by hyaenas and one calf killed by jacka's lion predation and starvation were responsible for all recorded mortalities. It is significant that about 75% of recorded lion kills were from the northern area along the Hlalarumi River and were, as far as is known from field observations, killed by the same pride of lions which were permanently resident in the area. Skulls collected from several of these kills revealed a notable bias towards full-grown males. Although no skulls from juvenile or partly grown carcasses were recovered, it is evident that these age classes were heavily preyed upon, probably chiefly by lions, but with leopards and hyaenas possibly taking a considerable number.

Waterbuck population trends during the study period were erratic but there was a correlation between population increases and rainfall, i.e., between an upward trend and the condition and density of selected waterbuck habitat (Figure 6). This factor, together with the noted losses due to starvation during a critical winter (Table 19) suggest that despite heavy lion predation, waterbuck populations are mainly a function of the habitat and that habitat condition will be the key factor in determining the degree of regulating effect predation will have on waterbuck populations.

PREDATION ON WARTHOG

Warthog are the least numerous of the ungulates in the Timbavati reserve and are unique in being the only multiparous species. They are also the only ungulate species capable of

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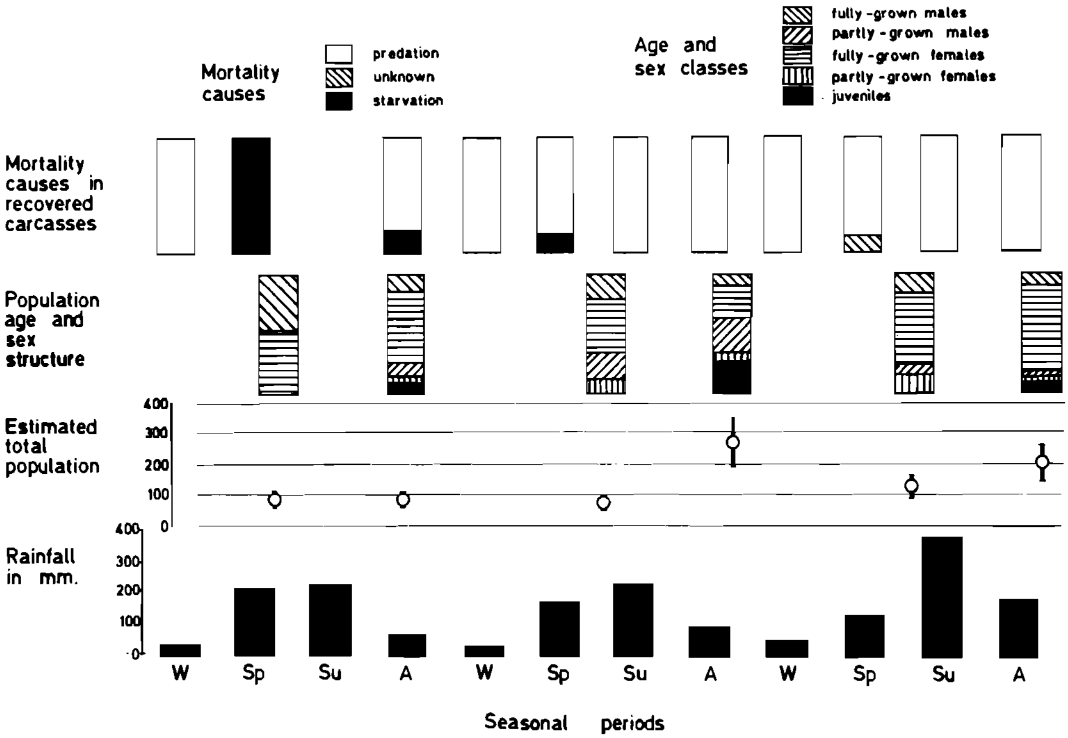

FIGURE 6
Waterbuck — comparing total populations, population structure as percentages, mortality causes as percentages and seasonal rainfall during a three-year study period; Timbavati Private Nature Reserve.

burrowing under fences and from the number of such burrows which are found all along the boundary fence it appears as if populations are subject to a marked degree of change. During the study period the numbers of fully-grown males showed a slight downward trend with females an upward trend. The numbers of partly-grown animals and juveniles fluctuated markedly, indicating that recruitment was to a large extent counteracted by heavy losses in these age classes. The general population trend was up, with large numbers of young animals being observed during the latter part of the study when habitat conditions were very good.

Kill records (Table 22) indicated that lions were the chief predators of the mature age-classes, but that starvation mortalities considerably outstripped predation losses. The few skulls obtained were of old animals. No juvenile or partly grown kills were recovered, but it is evident from the rapid disappearance of these age-classes from the population (Figure 7) that they were heavily preyed upon, probably by a wide variety of predators.

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WARTHOG POPULATION STRUCTURE DETERMINED FROM ROAD-STRIP CENSUS DATA FOR SIX SAMPLE PERIODS: TIMBAVATI PRIVATE NATURE RESERVE

		Fully-grown		*Partly-grown*	*Juveniles*	*Total*
		Male	*Female*			
November, 1964	Estimate	38	40	14	—	92
	Probable confidence limits	27-49	28-52	10-18	—	65-119
	% of total population	41·3	43·5	15·3	—	100·1
April, 1965	Estimate	30	32	6	10	78
	Probable confidence limits	21-39	22-42	4-8	7-13	54-102
	% of total population	38·4	41·0	7·7	12·8	99·9
December, 1965	Estimate	47	55	24	—	126
	Probable confidence limits	33-61	38-72	17-31	—	88-164
	% of total population	37·5	43·6	18·8	—	99·9
May, 1966	Estimate	26	26	—	78	130
	Probable confidence limits	18-34	18-34	—	55-101	91-169
	% of total population	20·0	20·0	—	60·0	100·0
December, 1966	Estimate	14	55	14	—	83
	Probable confidence limits	10-18	38-72	10-18	—	58-108
	% of total population	16·7	66·7	16·8	—	100·0
April, 1967	Estimate	9	77	124	77	287
	Probable confidence limits	6-12	54-100	87-161	54-100	201-373
	% of total population	3·3	26·7	43·3	26·7	100·0

TABLE 22

NUMBERS OF WARTHOG CARCASSES OF ALL AGE AND SEX CLASSES RETRIEVED PER SEASON FROM JUNE, 1964, TO MAY, 1967; TIMBAVATI PRIVATE NATURE RESERVE.

Mortality factor	*June-Aug., 64*	*Sept.-Nov., 64*	*Dec.-Feb., 65*	*March-May, 65*	*June-Aug., 65*	*Sept.-Nov., 65*	*Dec.-Feb., 66*	*March-May, 66*	*June-Aug., 66*	*Sept.-Nov., 66*	*Dec.-Feb., 67*	*March-May, 67*	
Lions	—	1	1	—	—	—	—	1	2	1	—	—	6
Leopards	—	1	—	—	—	—	—	—	—	—	—	—	1
Starvation	—	15	—	—	—	2	—	—	—	—	—	—	17
Unknown	—	1	—	—	—	—	—	—	—	—	—	—	1
	—	18	1	—	—	2	—	1	2	1	—	—	25

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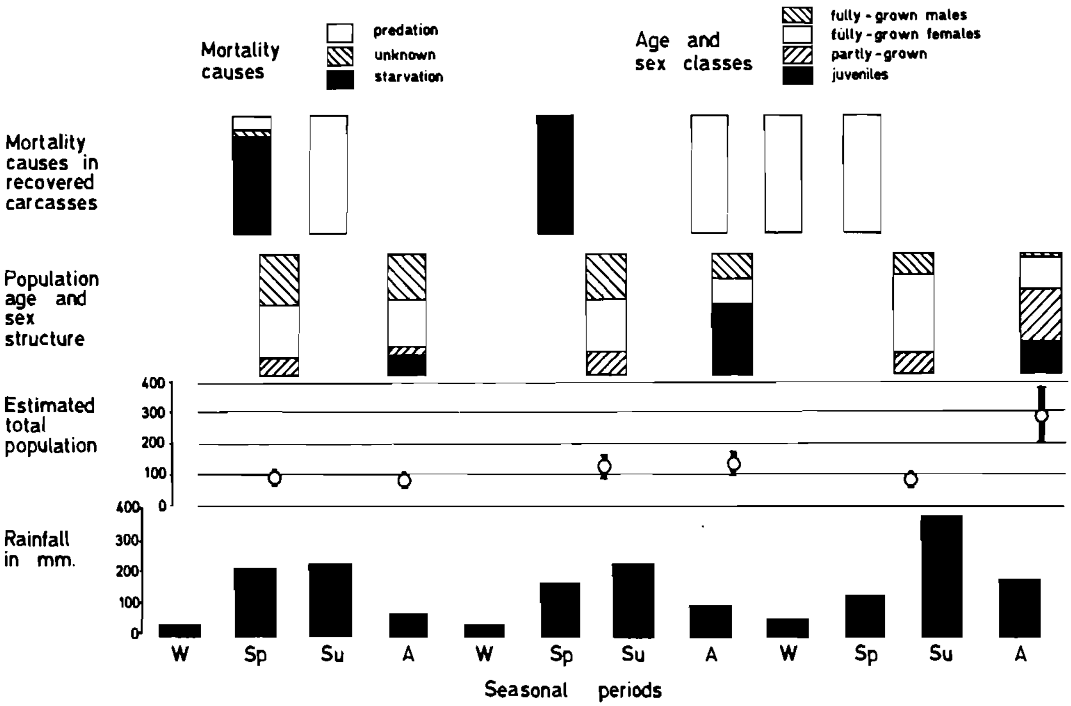

FIGURE 7
Warthog — comparing total populations, population structure as percentages, mortality causes as percentages and seasonal rainfall during a three-year study period; Timbavati Private Nature Reserve.

PREDATOR AND PREY POPULATION INTERRELATIONSHIPS

An important point arising from the consideration of a natural area such as Timbavati where six predator species prey on a collective population of seven ungulate species is the degree of population interrelationship which exists and especially to what extent one prey species may act as a buffer for another prey species. In considering these aspects hyaenas and jackals are considered as predators, despite their scavenging habits.

In Timbavati, impala and kudu were preyed upon by all six predator species; all six contributed substantially to losses amongst impala, but jackal were probably not important as far as kudu were concerned. Wildebeest were killed by lions chiefly, with leopards, cheetahs and hyaenas filling a minor role. No wild dog kills for wildebeest were recorded but this was due to the scarcity of wild dogs in the area as they are known to prey on wildebeest in other savanna regions (Mitchell *et al* 1965) and must be regarded as potential predators in Timbavati. Zebra were killed by lion mainly with a few records for hyaenas and jackals killing juveniles. Leopards, cheetahs and wild dogs may be regarded as potential predators on young zebra. Waterbuck are taken by lions mainly, with leopards, hyaenas and jackals

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filling a minor role. As with wildebeest, the scarcity of wild dogs is probably the reason why this species failed to prey on waterbuck in Timbavati. Although cheetah are not very common, it is postulated that differences in selected habitat probably separate this predator from waterbuck. Lions are the most important predators on giraffe with leopards and hyaenas of minor importance while lions again play the most important role in the case of warthog, although the records collected for warthog are probably misleading because of their small numbers and wide distribution over the whole reserve.

Lions thus fill a commanding position as predators with the widest possible range of prey species. The fact that kills of young animals are not recovered to the same extent as are those of adult animals makes direct comparison between prey species invalid as a means of determining prey preferences, which in any case are probably flexible and determined by prevailing ungulate densities, hunting conditions, habitat condition, size of pride, etc. An increase in the number of recovered kills of giraffe during the June-August, 1965, period was found to be correlated with a drop in the number of wildebeest recoveries, indicating that lions would readily change their prey preferences if presented with a highly susceptible prey population. A key factor in deciding prey preferences is susceptibility, which would adequately explain the predilection of lions for immature wildebeest and zebra during good seasons, and for giraffe in poor condition during critical periods. Waterbuck appear to be highly preferred as a prey species as relatively far more kills were recorded in proportion to population size than for any other species. This may be due to the waterbuck's sedentary habits and its restricted range of habitat along watercourses, rivers and near waterholes where the degree of contact with lions is probably high. The role of impala and warthog as prey species for lions are probably underestimated by the figures available as these kills are not as easily detected as are kills of the larger species.

Leopards utilise impala as the bulk of their diet but have a fairly wide range of prey species to which they can turn when impala are temporarily out of reach. They appear quite capable of attacking the young of the larger ungulates, and impala are probably a valuable buffer for these other species as their superior numbers ensures a higher degree of contact with leopards. A similar situation exists in the case of cheetah, which however, may not be quite as flexible in their selection of prey because of physical limitations.

Hyaenas and jackals represent predators which show the highest degree of flexibility in their dietary requirements and in their behavioural adaptations to prevailing conditions. While making use of carrion when it is available, hyaenas act as a major depressant on impala populations by taking a substantial part of the yearly lamb crop, and by pulling down individuals in poor condition at the end of the dry season. They are also capable of working as a team to pull down larger ungulates including giraffe when the opportunity is present. Jackals exhibited a similar degree of adaptability. Their ability to exist on vegetable matter and invertebrates is known (Grafton 1965) and in Timbavati they were known to take a variety of game, from birds and rodents to impala lambs and adults and even young zebra, waterbuck and kudu. They constituted as important a regulating factor of impala populations as did hyaenas. The ability of hyaenas and jackals to change their habits according to existing conditions is a valuable one in a natural area where conditions are constantly changing and

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where natural controls such as predation play an important role in maintaining community stability.

The fact that impala constituted numerically at least half of the total large ungulate population at any one time, and that they were preyed upon by all the large predators, indicates that this species was important as a buffer, which is here taken to mean an alternate prey species which serves to decrease predation on another species (Dasmann 1964). This is mainly true for lion predation, as impala normally constitutes the staple diet for all the other predators. Impala are more euryoecious than most other ungulates in woodland savanna (Hirst unpublished data), and contact between them and predators is likely to be high. The importance of vulnerability in the buffering phenomenon is demonstrated by the correlation between a drop in lion predation on wildebeest and a rise in lion predation on temporarily susceptible giraffe in poor condition.

PREDATION AS A POPULATION REGULATING FACTOR

On the basis of collected data, the ungulates in Timbavati can be divided into two main groups, viz., those where the populations are either stable or only slightly increasing and where the populations keep within their food supply by seasonal movements within the reserve, and those species where the general population trend in the presence of predation is up and where starvation mortalities operate at critical periods to reduce numbers drastically. Wildebeest and zebra constitute the first group, the other ungulates falling into the second group.

The general pattern of predation appears to be similar for all ungulate species, i.e., juveniles and partly grown animals bear the brunt of predation, young prime animals have a higher resistance and the remaining age classes show approximately a uniform degree of susceptibility.

Except in the case of impala, lions are the most important predators concerned with population regulation. Bias in the collection of kill information makes direct species comparison invalid, but the data do indicate that lions tend to concentrate on immature wildebeest, immature zebra and waterbuck of all age classes. Differences in lion predation between the species appears to be mainly one of degree.

Although the study period was relatively short, the general trends in population growth and limitation were clear. The implications for management of an area such as Timbavati are equally clear. Predation cannot be expected to remove population surpluses in all ungulate species, and in most cases it cannot prevent losses from critical food shortage. Artificial population control in the form of hunting, controlled cropping or large-scale translocation is required on a sustained basis.

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SUMMARY

A three-year study was made of impala, blue wildebeest, zebra, giraffe, kudu, waterbuck and warthog populations on the 210 square mile Timbavati Private Nature Reserve in the subtropical woodland savanna of the eastern Transvaal lowveld. Data were collected on the size and age and sex structure of each population and on the age and sex classes killed by lions, leopards, cheetahs, wild dogs, spotted hyaenas, black-backed jackals, by starvation and other causes.

Impala were utilised as prey by all large predators, including hyaenas and jackals which preyed heavily on lambs and on individuals in poor physical condition. Impala were the staple prey of leopards, cheetahs and wild dogs. Predation did not prevent heavy losses from starvation at the end of the dry season. Fully- and partly-grown males which consorted in small herds were more susceptible to predation than were females which gathered in large herds. Giraffe were formidable prey animals and were taken by lions mainly during the dry season. Starvation mortalities exceeded losses from predation. Kudu were taken by all predators, but mainly by lions, and here too starvation was more important than predation in population regulation. Fully-grown males were significantly more susceptible to lion predation and to starvation than were fully-grown females, and partly-grown kudu were highly susceptible to starvation. Lions took a large toll of waterbuck, especially waterbuck bulls but starvation deaths occurred which suggested that habitat conditions were important in population regulation. Predation and starvation kept warthog populations at a low level despite this species being multiparous.

Juvenile and partly-grown wildebeest and zebra were subject to heavy predation by lions, as a result of which wildebeest and zebra populations remained either stable or increased only slightly during the study period. No starvation deaths are known to have occurred in these two species, which trekked seasonally from one part of the reserve to another. Solitary wildebeest bulls were highly susceptible to lion predation.

Generally the young and immature age classes of all ungulate species showed the highest susceptibility to predation, young prime animals were more resistant, and the remaining age classes were approximately uniformly susceptible.

By virtue of their numbers, wide choice of habitats and acceptance as prey by all predators impala constituted an important buffer species for other ungulate populations. Lions readily switched their preferences from wildebeest and zebra to giraffe when the latter were temporarily highly susceptible during critical periods of browse shortage in late winter.

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