Abnormal levels of disease and predation as limiting factors for wildebeest in the Etosha National Park

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ABSTRACT

Investigations between 1975–78 established that a combination of disease, namely anthrax, and excessive numbers of predators, especially lion, were responsible for the sharp decline in wildebeest numbers. On average, 62 % of all wildebeest carcases tested positive for anthrax, while predators were not susceptible to anthrax. The levels of other disease and parasites were low. Predator–prey ratios were estimated to be between 1:72–105 which are higher than average. Primary factors for raised anthrax and predator levels were the fencing of Etosha which precludes migration, the development of alkaline gravel pits for road building, and the construction of artificial water points.

CONTENTS

1 INTRODUCTION

An aim of the investigation into the ecology of the blue wildebeest *Connochaetes taurinus* in the Etosha National Park (Berry, 1980) was to establish whether disease and parasites had contributed to the sharp decline in wildebeest numbers in Etosha. Veterinary aspects of wildlife management have sometimes been regarded as a specialist field by ecologists and are consequently viewed in isolation when identifying the factors which may limit or reduce populations. Thus, whilst some investigations of wildebeest reproduction and population ecology have excluded the disease/parasite factor (Attwell, 1977), others have drawn attention to the significant role it can play (Talbot and Talbot, 1963; Watson, 1967). For example, the disappearance of rinderpest virus from the Serengeti wildebeest at about the end of 1961 (Watson, 1967) resulted in a 263 % increase in the population over a 10-year period (Sinclair, 1973). I therefore enlisted the aid of veterinary specialists to make a study of the pathology and parasite loads existing seasonally in Etosha's wildebeest. In addition, I referred to the extensive veterinary investigation carried out by Ebedes (1976a, b) which reviewed the epizoötiology of anthrax *Bacillus anthracis* in large herbivores in Ethosha.

I also considered the role of predators and scavengers. Predation of herbivores and the presence of scavengers are natural phenomena and are desirable in any large area set aside for the conservation of wild animals (Estes, 1967; Hirst, 1969; Pienaar, 1969; Kruuk, 1972; Schaller, 1972). However, because all terrestrial systems have been influenced by man, it is possible that this natural equilibrium can become unstable, resulting in an abnormal predator–prey ratio (Smuts, 1975, 1976, 1978a, b, c). I consequently examined the numbers, age–sex ratios, group size, prey preferences and estimated the food intake of large predators and scavengers in Etosha. These data were used to establish whether the predator–prey ratio was within acceptable limits when compared to other African conservation areas. In Etosha, information on large predators and scavengers is limited to the lion and cheetah, with a few records of observed kills by spotted hyaena, leopard, wild dog and black-backed jackal. No other relevant data exist for these species, apart from casual sightings. I have therefore been obliged to refer to subjective observations made by staff and tourists when dealing with the lesser known species. In addition, since virtually nothing is known about the predator–prey relationship in the bush and woodlands of Etosha, I have dealt only with the situation relating to the plains, which are the major habitat of wildebeest.

2 METHODS

2.1 Carcases

During a three-year period (1976–78), field diagnosis of anthrax was based on the procedure established by Ebedes (1976a). Because the presence of lions at a carcase did not necessarily indicate death by predation, all such cases where the "kill" had not been witnessed, were examined microscopically for anthrax by taking bloodsmears. Only undecomposed carcases were suitable for field diagnosis of anthrax.

2.2 Immobilisation

A total of 60 wildebeest were immobilised on a seasonal basis during the period 1976–78. From these, ectoparasites were collected and where dermal lesions or apparent mange were present, skin scrapings were taken and preserved in 70 % ethanol for laboratory investigation.

2.3 Sampling by shooting

In 1978 eight wildebeest were selectively shot at the height of the wet season (February) and similarly, eight were shot at the height of the dry season (November). Subsequent to these samplings, a further nine wildebeest were shot in February 1979 to provide additional veterinary material. These 25 animals were individually selected by veterinarians as being representative of the population and likely carriers of disease and parasites. The carcases were autopsied by a team of three veterinarians, and organs, tissues, blood, urine and faeces were taken for detailed laboratory analyses.

2.4 Number of predators, age–sex ratios and group size

To estimate the predator and scavenger populations in the areas inhabited by wildebeest and other large herbivores sharing the grasslands, I relied on counts made by nature conservators, research workers and my ground and aerial observations during the period 1974–78. Data on age-sex ratios and group size were recorded on punch cards and subsequently coded on to Fortran sheets for sorting by a Univac 1106 computer. Additional information was obtained from questionnaires which were handed out to tourists.

2.5 Preferred prey species

Prey preference could be obtained for lion, cheetah and spotted hyaena and were calculated from the formula used by Pienaar (1969), Rudnai (1974) and Smuts (1975):

$$PR = \frac{F}{A}$$

where PR = preference rating
F = relative frequency with which a particular prey species is killed (%)
A = relative abundance of the prey species (%)

As pointed out by Schaller (1972), the term "preference" is misleading in that a kill also signifies the prey's availability and vulnerability. I have accordingly considered the preference rating to be an expression of these two factors as well.

2.6 Estimated food intake per predator species

With no data available from Etosha, I referred to the comprehensive investigations of Wright (1960), Kruuk (1972), Schaller (1972), Eloff (1973) and Bryden (1976). From their data it was possible to extrapolate the estimated amount of food required annually by lion, cheetah and spotted hyaena on the plains of Etosha. Although the preferred prey species of large predators differs greatly between various areas in Africa (Bourliere, 1963), the amount of food required by large carnivores is probably consistent at 4–6 % of their body mass per day (Kruuk, 1972; Schaller, 1972; Smuts, 1975). Consequently, by applying a mean daily food intake of 5 % of body mass I was able to estimate the amount of food required by the major predators and scavengers at Etosha with a reasonable degree of confidence and then balance this requirement against the live mass of available prey.

3 RESULTS

3.1 Anthrax diagnosis

The diagnosis level of anthrax is given for wildebeest and the other large herbivore species occurring on the grasslands of Etosha (Table 1). From the data collected it is clearly evident that wildebeest were severely decimated by anthrax, followed by zebra, springbok and gemsbok. No anthrax was diagnosed in red hartebeest and ostrich during this period but this may have been due to the small sample. As can be expected the number of carcases found where the cause of death was unknown was high (48 % in wildebeest, 46 % in zebra, 31 % in springbok, 54 % in gemsbok, 50 % in red hartebeest and 52 % in ostrich; $\overline{x}$=47 %). This was due to the rapidity with which carcases decomposed or were scavenged in Etosha.

3.2 Other infections and general pathology

The findings of Basson (1979) indicate that the pathologically poor condition of seven of the 25 wildebeest examined could be related to increased parasitism and/or diseases such as infectious pustula vulva-vaginitis (IPV) (=infectious bovine rhinotracheitus) and brain lesions. This was regarded as being significant.

3.3 Endoparasites

The reports of Thomas (1978) and Biggs and Anthonissen (1978, 1979) show that all parasite burdens were very low if judged against standard criteria for herbivores.

3.4 Ectoparasites

The reports of Biggs and Anthonissen (1978, 1979) indicate that tick and lice burdens were exceptionally low. In spite of regular *Gedoelstia* pathology, the loads of this dipteran larva were regarded as low to typical and the parasite–host relationship appeared stable. Nevertheless, the possibility of mortality in calves as a result of gedoelstiasis does exist.

TABLE 1: Incidence of anthrax in relation to total recorded mortality in wildebeest and other large herbivores in Etosha (1976–78)

Season	Species	Mortality					
		Anthrax positive	Anthrax negative	Other causes including predation	Cause unknown	Total positive and negative and other causes	Anthrax positive as percentage of total
Wet, hot season (Jan. to April)	Wildebeest	22	3	4	14	29	76
	Zebra	60	21	36	82	117	51
	Springbok	16	3	21	13	40	40
	Gemsbok	0	0	8	7	8	0
	Hartebeest	0	0	1	0	1	0
	Ostrich	0	0	4	4	4	0
Dry, cold season (March to Aug.)	Wildebeest	8	1	4	24	13	62
	Zebra	10	3	29	32	42	24
	Springbok	2	2	41	17	45	4
	Gemsbok	0	0	5	6	5	0
	Hartebeest	0	0	1	0	1	0
	Ostrich	0	0	10	3	10	0
Dry, hot season (Sept. to Dec.)	Wildebeest	11	2	11	23	24	46
	Zebra	11	0	17	45	28	39
	Springbok	6	1	24	23	31	19
	Gemsbok	2	0	6	12	8	25
	Hartebeest	0	0	1	3	1	0
	Ostrich	0	0	7	16	7	0
Total for three years	Wildebeest	41	6	19	61	66	62
	Zebra	81	24	82	159	187	43
	Springbok	24	6	86	53	116	21
	Gemsbok	2	0	19	25	21	10
	Hartebeest	0	0	3	3	3	0
	Ostrich	0	0	21	23	21	0

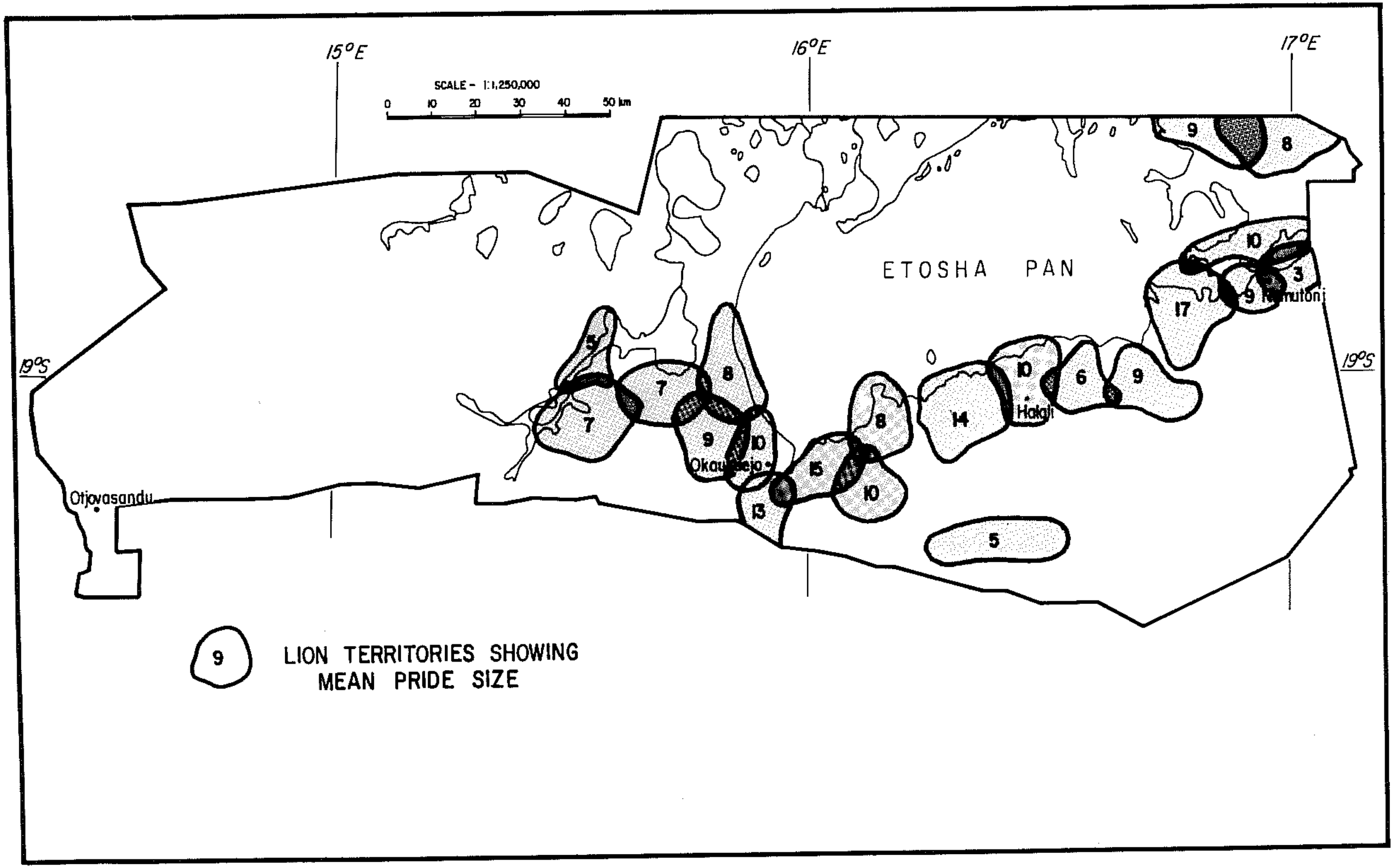

FIGURE 1: Dry season pride areas and ranges of 21 known lion groups on Etosha's grasslands (1974–78).

3.5 Estimated predator–scavenger populations and their composition

3.5.1 Lion

The dry season pride areas of resident lion and ranging nomadic groups (as defined by Schaller, 1972) which inhabited the Etosha plains during the period 1974–78 are shown in Fig. 1. Pride areas were fairly distinct during the dry season when availability of drinking water restricted the movements of predators and most prey species. In all, there were 21 known areas on the Etosha plains which were inhabited by resident prides or nomadic groups. Pride areas became obscure during the wet season when distribution of prey changed and wet conditions prevented vehicles from leaving the roads. The mean pride or group size in each area or range was calculated from observations during the five-year period (n=356 observations on 2 562 lions). The overall mean pride/group size was 7,2 (range 2–30, SD ± 4,53), with a yearly mean of 285 individuals present. I was able to age and sex 565 lion. Adult sex ratio was 1 male : 1,03 female (n=354) which was not disparate at P>0,70. Immature lion (0–3 years) made up 37 % of my sightings.

By comparison, Schaller (1972) found that Serengeti lion pride sizes was 15 (range 4–37) and nomadic group size was 2,8 (range 2–13) giving an overall average of four lion in prides and groups. Their sex ratio was 1 male : 0,92 female (P>0,50), whilst 43 % of the lion on the Serengeti plains were sub-adult (0–4 years). Thus the mean pride/group size in Etosha was larger than in Serengeti, although the age–sex ratios were similar. Etosha's pride/group size of 7,2 is also greater than the figure of 4–5 given for Zambia by Mitchell *et al.* (1965), but is more in keeping with the group size of 6 reported in East Africa by Wright (1960). In contrast, Smuts (1975) reported an average of 11,8 lion per pride/group in the central Kruger Park.

My figure of 285 lion inhabiting the Etosha plains is likely to be an underestimate since only limited observations were available from some of the areas and lion are usually undercounted from the ground or by aircraft (Schaller, 1972; Smuts, 1975). Because no correction factor for undercounting bias is known for free-ranging lion, I assumed that approximately 70 % of the total population were seen by ground counts. Consequently I applied an arbitrary correction factor of 1,4 to the average count of 285 lion, which provided a theoretical total of 400 lion that may have been present on the plains of Etosha during this study. I subsequently used a range of 285–400 lion when calculating predator density and food intake, since it is likely that the actual number of lion present fell within these minimum and maximum figures.

The plains of Etosha cover 8,1 % of the total area, namely 1 793 km^2 (Le Roux, 1977). Applying my estimates of between 285 and 400 lion, the density is one lion/4,5–6,3 km^2. These first approximations are well within the range of lion densities found elsewhere in Africa. For example, one lion/2,6 km^2 in Manyara Park, one lion/3,7 km^2 in Ngorongoro Crater, one lion/4,6 km^2 in Nairobi Park (Schaller, 1972) and one lion/7,9 km^2 in Kruger Park (Smuts, 1975). My estimates of the lion population on Etosha's plains therefore appear to be of the right order of magnitude.

3.5.2 Cheetah

The records show that, on average, there were 70–80 cheetah inhabiting Etosha's plains between 1974–78. Allowing for double-counting as well as for undercounting, I consider that a population figure of 50–100 cheetah is realistic. These estimates give a density of one cheetah/18–36 km^2. In comparison, Nairobi Park supported one cheetah/4,42 km^2 (McLaughlin, 1970), while Kruger Park had one cheetah/72 km^2 (Pienaar, 1969) and Serengeti's density was one cheetah/102–107 km^2 (Schaller, 1972). Group size at Etosha varied from 2–5. The most adults reported together were three, whilst groups of 4–5 animals were females with up to four cubs.

3.5.3 Spotted hyaena

The number of spotted hyaena, hereafter referred to as hyaena, inhabiting the plains of Etosha is unknown and I have used the ratio of hyaena : lion from other areas to estimate a figure. Nonetheless, my casual observations and those of other observers at Etosha indicate that the hyaena population is substantial and my initial estimates can therefore be regarded as realistic. The ratio of hyaena : lion in Ngorongoro Crater is 6,1:1 and in Serengeti it is 1,25–1,50:1 (Kruuk, 1972; Schaller, 1972). In the Kruger Park it is 2,73:1 (Smuts, 1975), while in the adjoining Timbavati Nature Reserve it approximates 1:1 (Bearder, 1975). Thus it appears that in large, relatively natural conservation areas there are at least as many hyaena as lion and often more. Consequently, I estimated the hyaena population on Etosha's plains to be the same as for lion, namely 285–400. These figures are probably conservative.

Hyaena packs of more than three adults were frequently seen in Etosha. The largest pack encountered in daytime was 12 and at night a pack of 23 was observed. By comparison, up to 25 hyaena in a pack were recorded at Serengeti – Ngorongoro (Kruuk, 1972). Since pack formation indicates either active hunting or patrolling of territory boundaries (the latter in itself indicates a fairly dense hyaena population according to Kruuk, 1972), it appears that Etosha's hyaena hunt frequently. The records at Etosha show that healthy, adult zebra, wildebeest, kudu and springbok have been successfully hunted and killed by hyaena packs. This in turn indicates that at certain times of the year scavenging from lion kills is insufficient to meet the food demand of hyaena.

3.5.4 Other predators and scavengers

No information exists on the numbers of leopard and brown hyaena in Etosha, while in the case of wild dog it is virtually certain that they did not inhabit the plains during 1974–78. I estimate that there may be 1 000 – 2 000 black-backed jackal on the plains, giving a density of 1 jackal/0,9 – 1,8 km^2. Up to 52 jackal have been recorded at a zebra carcass and groups approximating 30 are frequently encountered at anthrax carcases. There is no doubt that the jackal population is high and my estimates may well be conservative.

I have not considered vultures and other avian carrion eaters in my estimates of predator–scavenger biomass, since they are not necessarily resident on the plains. The omittance of these other mammalian and avian species lends conservative bias to the estimated predator-scavenger biomass and consequently to the predator : prey ratios. This bias may, however, be offset to an extent by the fact that the major carnivores I have considered also predate and scavenge species other than the large herbivores included in my estimates.

3.6 Preferred prey species

The prey preferences of lion, cheetah and hyaena are given in Table 2. Lion showed the greatest preference for gemsbok, followed by wildebeest, zebra, ostrich and springbok. In other areas where gemsbok are common, for example the Kalahari Park, they are frequently taken by lion (Eloff, 1964). However, prey preference is largely dictated by availability of species. For instance buffalo made up 9 % of the lion's diet in Kruger Park (Pienaar, 1969), 15 % in Serengeti (Schaller, 1972; Sinclair, 1977), but constituted 62 % of the prey species at Manyara Park, an area where buffalo outnumbered all other prey species (Makacha and Schaller, 1969). Likewise at Kruger Park, where impala were the most plentiful prey species, they constituted the highest frequency (31,3 %) of food for lion (Smuts, 1978b).

I suspect that the preference shown for gemsbok in Etosha may be due to the establishment of artificial drinking places where gemsbok, a species which is relatively independent of drinking water, are found in the dry season. Consequently, these boreholes support large groups of lion. Under natural (waterless) conditions, no lion could be resident in such areas of Etosha during the eight months of dry season. A similar situation was found to exist in Wankie Park, where gemsbok and eland suffered disease and predation stresses beyond their adaptive capabilities (Davison and Davison, 1968). Furthermore, eland in Etosha have also been greatly reduced in numbers and increased predation may well be a major contributory factor.

Wildebeest are marginally preferred to zebra by hunting lion in Etosha (preference rating = 2,98 compared to 2,53). In Kruger Park the PR for wildebeest ranged from 2,21 – 4,35, while that for zebra was 1,43 – 2,37, making wildebeest preferred above zebra, on a yearly basis, for a period of 20 years (Smuts, 1975). The PR values were of a similar magnitude in Nairobi Park, where wildebeest PR = 1,83–4,20 and zebra PR = 0,81–1,98 (Rudnai, 1974). Wildebeest were also preferred above zebra by lion in the Timbavati Reserve, Eastern Transvaal (Hirst, 1969).

TABLE 2: Preferred prey species of lion, cheetah and spotted hyaena on the grasslands of Etosha (1974–78)

Predator	Prey species	No. of kills recorded	Relative kill frequency (%)	Relative abundance of prey (%)	Prey preference rating*
Lion	Wildebeest	21	19,1	6,4	2,98
	Zebra	67	60,9	24,1	2,53
	Springbok	12	10,9	65,0	0,17
	Gemsbok	9	8,2	2,3	3,57
	Red hartebeest	0	0,0	0,2	0,00
	Ostrich	1	0,9	2,0	0,45
Cheetah	Wildebeest	2	3,2	6,4	0,50
	Zebra	0	0,0	24,1	0,00
	Springbok	61	96,8	65,0	1,49
	Gemsbok	0	0,0	2,3	0,00
	Red hartebeest	0	0,0	0,2	0,00
	Ostrich	0	0,0	2,0	0,00
Spotted hyaena	Wildebeest	2	22,2	6,4	3,47
	Zebra	5	55,6	24,1	2,31
	Springbok	2	22,2	65,0	0,34
	Gemsbok	0	0,0	2,3	0,00
	Red hartebeest	0	0,0	0,2	0,00
	Ostrich	0	0,0	2,0	0,00

$$*\text{Preference rating} = \frac{\text{Relative kill frequency}}{\text{Relative abundance of prey}}$$

TABLE 3: Estimated amount of prey killed and carcases scavenged annually by lion, cheetah and spotted hyaena on the grasslands of Etosha (1974—78)

Predator/scavenger species	Population		Mean live mass (kg)		Total live mass (kg)		Total annual food requirement (kg)
	Adult	Immature	Adult	Immature	Adult	Immature	
Lion	180—252	105—148	145	73	26 100 —37 296	7 665— 10 804	819 561—1 167 507
Cheetah	33—68	15—32	60	30	1 980 — 4 020	510— 990	61 348—123 435
Spotted hyaena	215—300	70—100	52	26	11 180 —15 600	1 820— 2 600	189 800—265 720
Totals	—	—	—	—	39 260 —56 916	9 995— 14 394	1 070 709—1 556 662

Predictably, cheetah prey mainly on springbok in Etosha, although wildebeest, especially calves, may be taken. Wildebeest appear to head the list of prey preferences of hyaena in Etosha, ranking above zebra and springbok. The small sample size (n=9 kills) may, however, have biased the findings.

3.7 Live mass of food required annually

Applying a mean daily food intake of 5 % of body mass, I estimated the food requirement in Etosha's large, plains-dwelling carnivores (Table 3). As mentioned previously, leopard, wild dog, brown hyaena, jackal and vultures were omitted from these estimates. Furthermore, I presumed that 37 % of the lion population was immature, basing this on field observations in Etosha. For cheetah, 32 % of the population was taken to be immature (Schaller, 1972) and in the case of hyaena this figure was 25 % (Kruuk, 1972). Live mass of the three carnivore species was based on the means recorded by Kruuk (1972) and Schaller (1972).

Because lion and cheetah, on average, leave 33 % and 35 % of a carcass uneaten respectively (Schaller, 1972), I have estimated the total food actually killed to be accordingly higher. In the case of hyaena, my assumption was that almost 100 % of a carcass was consumed (Kruuk, 1972; personal observation).

The estimates result in a total food requirement plus uneaten residues of approximately 1—1,5 million kilogram prey annually. I wish to reiterate that these figures should be considered initial approximations, since my calculations are based on several unproven assumptions.

3.8 Predator—prey live mass ratios

Estimates of the ratios of predator to prey on the Etosha plains are given in Table 4. To calculate these ratios I used the estimated maximum and minimum total live mass of the three major predators, namely lion, cheetah and hyaena as derived in Table 3. This range of predator live mass was related to the live mass of wildebeest and the other five major herbivore species which inhabit the plains. In estimating the live mass of prey, I took into account the contribution made to each species' population by the different age and sex classes, using the appropriate body mass of each age—sex class (Berry, 1980). Furthermore, I used the mean population of each prey species during the period 1974—78 to correspond with the mean predator populations for the same period.

Thereby, the total predator—scavenger live mass was estimated to lie between 49 255 and 71 310 kg and the total live mass of prey was estimated at 5 151 013 kg, as shown in Table 4. This gives a minimum predator : prey ratio of 1:72 and a maximum of 1:105. A comparison of these ratios to those found elsewhere in Africa is made in Table 5. Etosha appears to have a greater proportion of lion to prey than most other conservation areas for which data are available. It must, however, be remembered that Schaller's (1972) ratios for Serengeti include all major predators, whereas the other sources refer specifically to lion : prey ratios. For this reason I have presented Etosha's ratios in both ways.

In central Kruger Park, which has similar ratios to Etosha, a total of 335 lions and 297 hyaena, representing 63 % and 80 % of the numbers in one area, were cropped between 1974—77 (Smuts, 1975, 1978c). Despite this high rate of predator control, lion regained 90 % of their former level within 17 months while hyaena were slow to recolonise (Smuts, 1978a). Therefore it seems that the question of direct predator control at Etosha would have to be approached with caution in view of the limited success achieved elsewhere.

The 1—1,5 million kilogram prey removed annually (Table 3) is 21—30 % of the estimated herbivore live mass of 5 million kilogram (Table 4). This rate of removal by predators is two to three times that in the Serengeti where 9—10 % of the prey biomass is taken by predators (Schaller, 1972), whose findings indicated a dearth of large carnivores. The relative paucity of prey at Etosha can be illustrated by the prey biomass which is estimated at 2 873 kg/km^2 compared to 20 712 kg

TABLE 4: Estimated mean predator—prey live mass ratios on the grasslands of Etosha (1974—78)

Predator species	Predator live mass (kg)	Prey species	Prey live mass (kg)	Predator—prey ratios
Lion	33 765—48 100	Burchell's zebra	3 564 112	
Cheetah	2 490— 5 010	Wildebeest	521 250	
Spotted hyaena	13 000—18 200	Springbok	700 681	
		Gemsbok	261 295	1:72
		Red hartebeest	18 160	to
		Ostrich	85 515	1:105
Total predator live mass	49 255—71 310	Total prey live mass	5 151 013	

TABLE 5: Comparison of predator—prey ratios on the grasslands of Etosha with other areas of Africa

Area	Lion: Prey ratio and Predator : Prey ratio	Source
Albert Park	1 : 360*	Bourliere (1965)
Kagera Park	1 : 300*	Bourliere (1965)
Tarangire Game Reserve	1 : 292*	Lamprey (1964)
Ngorongoro Crater	1 : 260*	Lamprey (1964)
	1 : 100**	Schaller (1972)
Serengeti Park	1 : 250—300**	Schaller (1972)
Manyara Park	1 : 174**	Schaller (1972)
Nairobi Park	1 : 100**	Schaller (1972)
Kruger Park	1 : 100**	Pienaar (1969)
	1 : 100—116*	Smuts (1976)
	1 : 57—149*	Smuts (1978c)
Etosha Park	1 : 107—153*	Present study
	1 : 72—105**	Present study

* Lion : prey ratio
** Predator : prey ratio

prey/km^2 in Serengeti (Schaller, 1972). Moreover, the lion biomass in Etosha is estimated between 18,8—26,8 kg/km^2 which is higher than the range of 13,6—20,5 kg/km^2 found in four areas of the Kruger Park (Smuts, 1978c) despite the fact that he applied a mean adult body mass of 158 kg for lion which is 9 % higher than the figure of 145 kg which I used.

4 DISCUSSION

4.1 Anthrax

The viable nature and ecology of anthrax have been adequately dealt with by Van Ness (1971) and Ebedes (1976b). In Etosha, soils in the areas inhabited by wildebeest are highly alkaline, thereby providing conditions under which anthrax bacilli flourish. Furthermore, the creation of numerous gravel pits for road building in Etosha boosted the disease's incidence by creating favourable incubator areas for sporulation. Ebedes (1976b) confirmed that the manner in which anthrax could be transmitted, namely, by infected carcases, faeces, predators, scavengers, birds and insects, as well as by water and wind, made it practically impossible to eliminate the disease in an area the size of Etosha. He also related the greatly increased incidence of anthrax in Etosha since 1966 to the emergence of over-utilised grazing areas. These "slum areas" (Ebedes, 1976a) were created by the construction of drinking troughs in the areas previously occupied by migrant herds in the rainy season only.

The findings of Ebedes (1976a, b) were supported by my observations during this five-year investigation. In addition, I am of the opinion that anthrax has resulted in an ideal situation in which predators and scavengers can increase to an unnatural level. My supposition is partly derived from the high incidence of anthrax in relation to recorded mortality (Table 1), where it is apparent that a surplus of meat from carcases would be available. When it is considered that anthrax-infected carcases were especially abundant during the wet season, a period in which predators would normally experience greater difficulty in obtaining food (Schaller, 1972; Smuts, 1975, 1978c), the advantage to lions and hyaenas is obvious. The combination of anthrax and increased predation pressure has in turn been reflected in declining herbivore populations, notably wildebeest and zebra. The impact of anthrax on the reproductive component of the wildebeest population should also be considered. For example, the majority of wildebeest cows died of anthrax during the wet season when they were nearing full-term pregnancy or had recently calved. This resulted in "double deaths" and may have contributed to a high antenatal and neo-natal mortality since milk-dependent calves are suckled only by their mother and are not fostered by other cows. There was no significant difference in mortality of the sexes in the sample collected by Ebedes (1976b): 308 bulls : 303 cows ($P>0,80$). In the present study the sample reflected a more distorted sex ratio of 24 bulls : 15 cows which was not significant at $P>0,02$. This may have been due to the much smaller sample size.

It appeared that wildebeest were more susceptible than zebra to anthrax (Table 1) because the total number of anthrax-positive carcases located in relation to the total population was 1,93 times higher in the case of wildebeest. Ebedes (1976b) mentioned that possibly 50 % of all anthrax-infected carcases were located, but I am of the opinion that in wildebeest a much lower percentage was located. I base this on the fact that 48 % of my sample was made up of dehydrated or decomposed carcases from which no positive field diagnosis was possible.

Furthermore, a predated carcass was seldom found in a relatively intact, mummified state which characterised an anthrax epidemic, when more meat was made available to scavengers than could be utilised. None of these frequently occurring dried-out carcases or remains could be positively diagnosed in the field. Moreover, while herbivores were fatally affected by anthrax, no records of predators or scavengers dying of the disease were obtained during a seven-year investigation by Ebedes (1976b) or during the present study. Consequently, carnivores fed freely from anthrax-infected carcases, or drank from infected water, thereby gaining advantageously over the susceptible herbivore populations.

Thus I consider anthrax to be a primary and major factor in the decline of wildebeest in Etosha. The data in support of this are quantifiably demonstrable from both Ebedes' (1976a, b) findings and my results, namely, that in our respective samples 74 % and 62 % of all diagnosed deaths in wildebeest were positive for anthrax. Other herbivores, especially zebra, appeared to be similarly affected and this was reflected in their declining numbers (Berry, 1980).

4.2 Other pathological conditions and parasites

The autopsy findings indicated that two age classes especially showed levels of viral infection and/or parasitism which could be considered potentially fatal (Basson, 1979, pers. comm.). These were the very young calves (<2 months) in which disease, notably IPV, resulted in prominent brain lesions and the 1—2 year old immatures which exhibited widespread lesions from migrating *Gedoelstia* larvae. In comparison, the older, weaning calves (2—9 months) and wildebeest older than two years were noticeably less prone to these conditions. These findings dovetail well with my surmise that there was a high mortality of neo-natal calves, which, because it could not be quantitatively determined, has been included in a theoretical population model as a reduced birth-rate in adult cows, namely 0,35 (Berry, 1981). Similarly, the pathology of 1—2 year old wildebeest was well correlated to my field counts where there was a greater decline in the number of calves achieving immaturity (8 % decrease) than in the number of immatures achieving sub-adulthood (4 % decrease).

The autopsy findings also confirmed a high incidence of *Gedoelstia* larvae, and the burden carried by young calves pointed to the possibility of occasional deaths in young animals as a result of gedoelstiasis. However, this ectoparasite was not present in abnormally high levels in Etosha's wildebeest. The remaining parasite loads, especially ectoparasites, were exceptionally low in all specimens examined and were regarded as having no significant effect on the population's mortality (Biggs, 1979, pers comm.).

4.3 Combined effect of predation and disease

In Etosha, a portion of the carnivores' food is provided by diseased animals which die of anthrax (Table 1). Thus, during an anthrax epidemic, lion and hyaena are not required to hunt but can live off the abundant supply of diseased meat without suffering any apparent clinical ill-effects. Nevertheless, lion may continue to hunt in the presence of diseased carcases and there are records of Etosha lion ignoring several zebra which had died of anthrax, to commence a successful hunt on healthy zebra in the vicinity. Under these circumstances the live mass of herbivores removed by the combined effect of predation and disease would be higher than the estimates of 1—1,5 million kilogram obtained in Table 3. Even if this were not the case, my estimates can still be considered conservative because, during an anthrax epidemic, more herbivores die than can be eaten by the large carnivores (Section 4.1).

I therefore consider my estimate that 21—30 % of the large herbivore live mass was removed annually from the Etosha plains to be realistic. Taking the minimum estimate of 21 % removal, it is clear that neither wildebeest nor zebra which together comprise 80 % of the lion's recorded diet (Table 2) and 77 % of the recorded cases of anthrax (Table 1) can withstand these mortality pressures. Consequently, it is not surprising that wildebeest and zebra, with recruitment rates to the breeding stock of 11—18 % and about 8 % respectively (Berry, 1980) are decreasing in numbers at Etosha. The wildebeest population decreased by 24 % and the zebra population by 43 % during the period of study (1974—78). These declines were inversely proportional to the different recruitment rates of wildebeest and zebra. For example, the mean recruitment rate of wildebeest was

14,5 % which was 1,8 times higher than that of 8 % for zebra and the decline in zebra numbers was 1,8 times greater than wildebeest.

If the wildebeest and zebra populations decline further, which seems likely at this stage because of the endemic nature of anthrax, then they could become relatively unavailable to hunting lion which would be forced to turn to alternative prey species (Smuts, 1978b). This may in turn result in increased predation on bush and woodland dwellers such as giraffe, kudu, gemsbok and eland.

Finally, the status of springbok in Etosha supports my findings that the combined effect of predation and disease is the major cause of declining wildebeest and zebra numbers. Springbok have increased more than threefold in numbers (9 800 to 32 000) between 1974—78. They also died of anthrax (15 % of all anthrax-infested carcases found were springbok; Table 1) but apparently not to the extent that wildebeest and zebra died. Also, the relative predation rate of springbok was far lower than either wildebeest or zebra. Springbok constituted 17,8 % of the live mass removal by predators, compared to 65,4 % by wildebeest and zebra combined (Tables 2 and 3). It can be argued that recording of anthrax and predation in springbok were biased in favour of the larger herbivores because of the rapidity with which springbok carcases are obliterated. This may partly be the case, but it is nullified to a large extent by the fact that Etosha's springbok population increased by a factor of 3,3 in five years. It appears that the differential disease and predation pressures which exist between the springbok population and the wildebeest and zebra populations are justifiable reasons for their respective increase and decreases in numbers.

5 CONCLUSIONS

Before the introduction of artificial drinking places in Etosha from 1951 onwards, the cyclical nature of herbivore movements to and from preferred grazing areas was evident (Bigalke, 1961). Refer also in this regard to Berry (1980) in which I review the development of Etosha for tourism. Consequently, in pristine times, the short rainy season provided an abundance of temporary drinking places for grazers such as wildebeest as well as attracting them to the apparently preferred annual grasses in the Okaukuejo area, which are high in nutrients (Berry, 1980). However, before the advent of permanent drinking troughs, the migratory herds vacated these "wet season dispersal areas" (Bigalke, 1961) when the ephemeral rainwater pools dried. Thereby a natural, rotational grazing system operated which precluded predators and scavengers from establishing permanent populations in large parts of the Okaukuejo area. Also, in the absence of roads and accompanying gravel pits, the disease factor was not yet epidemic in any part of Etosha (Section 4.1).

The provision of artificial watering points in the form of drinking troughs and gravel pits modified the earlier migratory tendencies of herbivores and, at the same time, stabilised the environment for predators and scavengers. Following on this, the reduced need to migrate has resulted in smaller group sizes of wildebeest (Berry, 1981). This in turn makes them more vulnerable to predation and especially increases neo-natal mortality by rendering calves more easily available to hyaena (Smuts, 1978b). In the present study in Etosha, hyaena scats were found to contain foetal and newborn wildebeest calf hooves as well as amounts of wildebeest calf tail hairs (Report No. 1768/77, S.A. Police Forensic Laboratories, 1977). Thus wildebeest and other large herbivores in Etosha have to contend not only with an increased lion population which has expanded spatially, but also with a substantial hyaena population which can alternate efficiently between scavenging and predating. Cheetah may also exert predation pressure on wildebeest calves.

In addition, wildebeest form a major prey item of lion and hyaena. If the combined effects of this predation are coupled to my findings that 62 % of all deaths in wildebeest were caused by disease, namely anthrax (Table 1), then it follows that the pressure exerted by predators and disease is the major reason for the decline of wildebeest in Etosha during the period of study. Moreover, this assertion is supported by the fact that the quantity and quality of nutrients and water were not limiting during my investigation (Berry, 1980). This was also evident in the good nutritional status of the wildebeest.

Whereas predation may have a negligible effect in a system such as Serengeti (Schaller, 1972), where herbivore mortality was attributable mostly to malnutrition and disease (Watson, 1967; Bell, 1969; Sinclair, 1977), predation can, under certain circumstances, such as were encountered in Ngorongoro Crater and Kruger Park, have a considerable effect on the herbivore population (Kruuk, 1972; Smuts, 1975, 1976, 1978b, c). It appears that the special conditions in Etosha, which have resulted from man's impact on the environment in the form of fences, roads and artificial drinking places, have created abnormal disease and predation levels, causing wildebeest numbers to decline drastically.

6 SUMMARY

An investigation was undertaken to establish whether the declining wildebeest numbers in Etosha could be related to veterinary causes. This was achieved by monitoring a total of 127 wildebeest carcases and 337 carcases of Burchell's zebra, gemsbok, springbok, red hartebeest and ostrich over a period of three years. In the same period a total of 60 immobilised wildebeest were visually examined for external parasites and peripheral blood smears were made for blood parasites. In addition, 25 wildebeest were selectively sampled for detailed pathological and parasitological investigation.

Fresh carcass diagnosis yielded blood smears which were positive for anthrax *Bacillus anthracis* in 62 % of

wildebeest, 43 % of zebra, 21 % of springbok, 10 % of gemsbok and were anthrax-negative in hartebeest and ostrich. Anthrax mortality reached a predictable peak in wildebeest, zebra and springbok during the rainy season when 76 %, 51 % and 40 % of anthrax deaths occurred in these species respectively.

The low endoparasite profile in wildebeest was regarded as an insignificant factor for limiting the population. Similarly, the ectoparasite burden was exceptionally low, except for *Gedoelstia* larval counts which approached typical herbivore levels.

The special conditions existing in wildebeest habitat in Etosha favoured anthrax viability and the disease was regarded as having become endemic with epidemics occurring during the wet season. An abundance of anthrax-infected carcases during the wet season probably resulted in increased predator—scavenger populations. Carnivores were apparently not fatally affected by anthrax. There was no significant sex link in wildebeest mortality from anthrax but the deaths of reproductive cows naturally also resulted in the loss of foetuses and neo-natal calves.

Reviewing the disease and parasite pressure on wildebeest in Etosha, it is evident that anthrax was a primary and major factor in the reduction of the population up to the present time and that it will not be possible to eliminate it in the foreseeable future. Other diseases and parasites were found to be insignificant in comparison to anthrax, but gedoelstiasis and IPV are potentially fatal conditions which, if they were to become severe, could result in increased mortality.

The role of predators and scavengers on the Etosha plains was examined in relation to the declining wildebeest population during the period 1974—78. The estimated 285—400 lion, which included resident prides and ranging nomads, had a group size of 7,2 and an adult ratio of 1 male : 1,03 females. Immatures comprised 37 % of the sightings. A total of 21 known pride areas or nomadic ranges were located on the plains during the dry season, but the situation in the wet season was unknown. Density was 1 lion/4,5—6,3 km^2, which was comparable to other areas in Africa.

Between 50—100 cheetah inhabited the plains, with a density of 1 cheetah/18—36 km^2. Spotted hyaena numbers were estimated from data of other areas, assuming a ratio of 1 hyaena : 1 lion. This gave an estimated population of 285—400 hyaena. Packs of up to 23 hyaena in Etosha indicated frequent hunting and records of kills on zebra, wildebeest, kudu and springbok were obtained. An initial estimate of black-backed jackal numbers (1 000—2 000) gave a density of 1 jackal/0,9—1,8 km^2, the large population being indicative of a substantial predator population. Up to 52 jackal were seen at one zebra carcass.

Preferred prey species of lion in Etosha were gemsbok, wildebeest, zebra, ostrich and springbok in declining order of magnitude. Cheetah preferred springbok above all else but sometimes killed wildebeest calves. Hyaena showed a preference for wildebeest, followed by zebra and springbok.

Based on a mean daily food intake of 5 % of body mass, the lion, cheetah and hyaena populations on the plains were estimated to require 1—1,5 million kilogram of food annually, including uneaten residues. This demand represented a yearly removal of 21—30 % from the total live mass of the six major herbivore species, namely wildebeest, zebra, springbok, gemsbok, hartebeest and ostrich.

In Etosha, lion : prey ratios were 1 : 107—153 and the ratios of lion / cheetah / hyaena : prey were 72—105. These ratios were higher than in most other areas and of the same order as those in the Kruger Park where the predator density was considered high enough to warrant control. Lion biomass in Etosha was also estimated to be higher than in the Kruger National Park, namely 18,8—26,8 kg/km^2 compared to 13,6—20,5 kg/km^2.

Predators and scavengers in Etosha benefitted from the surplus of meat which was provided by anthrax-infected carcases. Thereby their numbers may have increased and the combined effects of disease and predation were considered to be the main reason for the decline in wildebeest and zebra numbers. Together, wildebeest and zebra formed 80 % of the lion's recorded diet and 77 % of the recorded cases of anthrax. In contrast the springbok population, being relatively much less affected by both disease and predation, increased by a factor of 3,3 during the five-year period.

The overall conclusion reached in this investigation was that the earlier, natural movements of the migratory herbivores in Etosha have been modified by fences, roadbuilding and artificial, permanent drinking places. Disease, especially anthrax, has become endemic in areas where gravel pits occur, while the predator—scavenger populations have stabilised and increased where artificial water has been provided. Furthermore, disease is complementary to predation by providing an abundance of carcases during anthrax epidemics. Taking into account the findings that neither food nor water were limiting to the wildebeest population and the fact that their nutritional status was good, it was evident that disease and predation had combined under the special conditions existing in Etosha and together were the major cause of the decline in wildebeest and also in zebra numbers.

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