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THE RESPONSE OF UNGULATES TO RAINFALL ALONG THE RIVERBEDS OF THE SOUTHERN KALAHARI 1972 – 1982

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Abstract – The responses of springbok *Antidorcas marsupialis*, gemsbok *Oryx gazella*, blue wildebeest *Connochaetes taurinus* and red hartebeest *Alcelaphus buselaphus* to rainfall along the riverbeds of the southern Kalahari are analysed. Springbok reacted most rapidly to rainfall along the riverbeds and, by browsing in dry times, maintained a fairly stable presence throughout the year, although the actual number present in any one year was dependent on annual rainfall. Gemsbok responded more slowly to rainfall and reached their highest numbers in years of high rainfall when the grasses were tall and mature, after which they rapidly departed from the riverbeds. Red hartebeest also reached their highest numbers during the rainy season, but departed slightly more slowly than gemsbok. In dry years, they too, failed to come into the riverbeds. Blue wildebeest in the vicinity of the riverbeds tended to be more sedentary than the other species. The presence of potable artificial water appeared to be more important for wildebeest than for the other species and, although rainfall was undoubtedly an important factor in regulating their numbers along the riverbeds, they depended to a greater extent on breeding success and mortality factors, than on emigration and immigration. The overall seasonal pattern of ungulate abundance along the riverbeds in the southern Kalahari was one of wet season concentrations and dry season dispersion.

Introduction

The southern Kalahari, with the Kalahari Gemsbok (Republic of South Africa) and neighbouring Gemsbok (Republic of Botswana) National Parks, is one of the largest conservation areas in the world, encompassing an area of 36 200 km^2. The most heavily utilised habitats of this region are the riverbeds of the Auob and Nossob (Fig. 1), which support widely fluctuating numbers of springbok *Antidorcas marsupialis*, gemsbok *Oryx gazella*, blue wildebeest *Connochaetes taurinus* and red hartebeest *Alcelaphus buselaphus* (Table 1). In this paper we describe the fluctuations in ungulate numbers along the riverbeds over an 11-year period and analyse the factors responsible for them, as part of a long-term investigation aimed at gaining a better understanding of the workings of this huge ecosystem. Previous observations of ungulate movements and numbers along these riverbeds have been reported on by Eloff (1959a, 1959b, 1961, 1962, 1966), Bothma (1971, 1972), Bothma & Mills (1977) and Mills (1977).

Table 1

Maximum and minimum counts of four species of ungulates along the Auob and Nossob riverbeds between 1972 and 1982

Species	Auob		Nossob	
	Maximum	Minimum	Maximum	Minimum
Springbok	6 028 (Apr. 75)	113 (Nov. 82)	7 350 (Feb. 74)	816 (Dec. 72)
Gemsbok	343 (Apr. 79)	3 (Nov. 75)	1 690 (Mar. 77)	7 (Nov. 82)
Wildebeest	539 (Mar. 79)	27 (Dec. 82)	994 (Aug. 79)	28 (Apr. 72)
Hartebeest	25 (Apr. 81)	0 (Numerous occasions)	992 (Feb. 76)	23 (Jun. 82)

Of the four ungulate species under discussion, the blue wildebeest and red hartebeest are almost exclusively grazers, the gemsbok is a mixed feeder, although predominantly a grazer, and the springbok is a true mixed feeder, mainly grazing during the rains and mainly browsing during the dry times (Eloff 1959a, 1959b, 1961, 1962; Leistner 1959, 1967; personal observations).

The study area

The Auob and Nossob riverbeds (Fig. 1) are relicts of a wetter epoch of some 1 000 years ago and seldom flow today. The Auob flowed twice during the study, in 1973 and 1974, the Nossob has not flowed since 1963 (E. le Riche *pers. comm.*).

The Auob riverbed is a narrow channel of 100 m–500 m wide with generally steep banks of limestone to a depth of 30 m–50 m. In the north banks are more gentle-sloping and in some areas dunes form the bank of the river. The riverbed runs for approximately 117 km through the Kalahari Gemsbok National Park (KGNP), before flowing into the Nossob just north of Twee Rivieren (Fig. 1). There are 17 windmills, more or less evenly spaced along the course of the riverbed, most of which deliver potable water (Child, Parris & Le Riche 1971; E. le Riche *pers. comm.*).

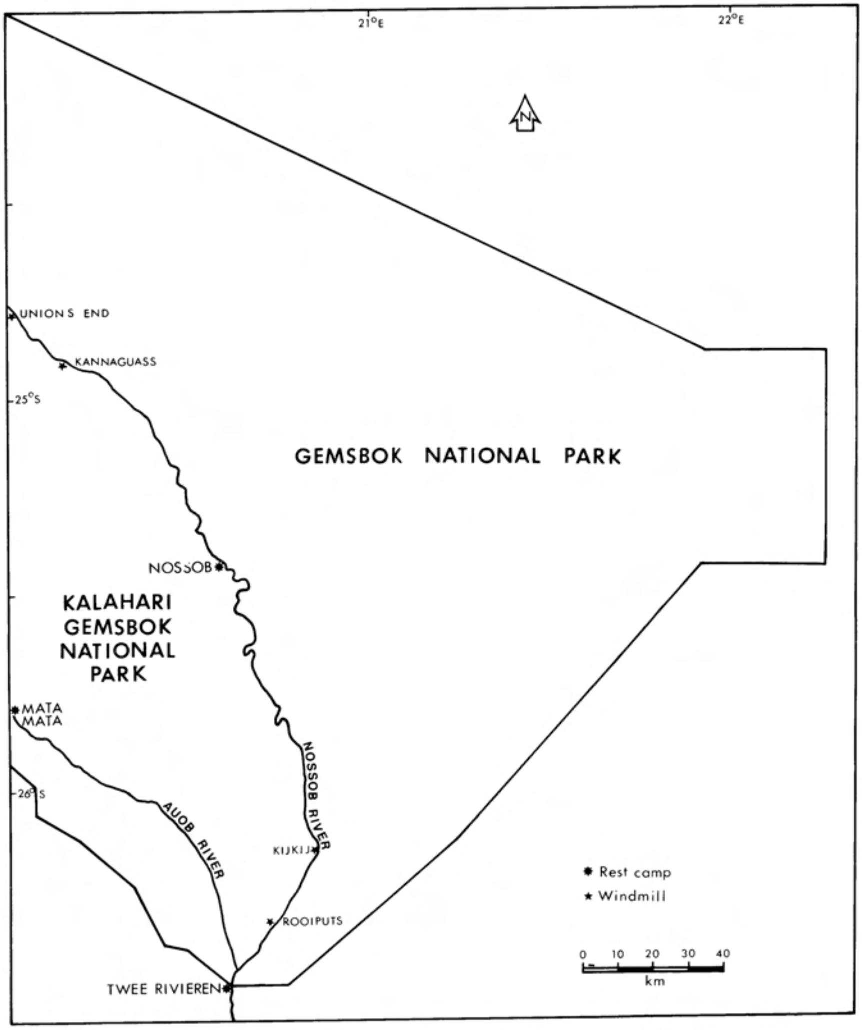

Fig. 1. The southern Kalahari conservation areas showing the Auob and Nossob riverbeds and other places mentioned in the text.

The vegetation along the Auob riverbed comprises large *Acacia haematoxylon* and *Acacia erioloba* trees, the bush *Acacia mellifera* subsp. *detinens*, the dwarf shrubs *Rhigozum trichotomum* and *Monechma australe*, the perennial grasses *Panicum coloratum, Stipagrostis obtusa* and *Stipagrostis uniplumis* and the annual grasses *Schmidtia kalahariensis* and *Eragrostis* sp. (Leistner 1967; Leistner & Werger 1973).

The Nossob riverbed is generally wider than the Auob, in places being over 1 000 m wide. The banks are generally more gentle-sloping and, particularly in the north, form large sandy limestone flats. The Nossob riverbed runs for approximately 300 km through the KGNP and at mid-stream forms the boundary with the

Gemsbok National Park in Botswana (Fig. 1). There are 24 windmills along the Nossob, most of which deliver highly mineralized water, except for some close to Twee Rivieren and Nossob camps, and at Kannagauss and Union's End (Fig. 1) (Child *et al.* 1971; E. le Riche *pers. comm.*).

The vegetation along the Nossob riverbed is similar to that along the Auob, except that *A. haematoxylon* trees are rarely found north of Kijkij (Fig. 1) and dwarf shrubs are less common. The sandy limestone flats support large stands of the perennial grass *Stipagrostis obtusa.*

Surrounding these two riverbeds is a vast area of red, windblown sand piled into dunes which supports a rather different vegetation. The most common tree is *Boscia albitrunca,* and *A. erioloba* and *A. haematoxylon* occur mainly in a far more stunted form. The perennial grasses are taller, comprising mainly *Eragrostis lehmanniana, Asthenatherum glaucum, Eragrostis meridionalis, Stipagrostis amabilis* and *Stipagrostis ciliata* (Leistner 1967; Leistner & Werger 1973).

The southern Kalahari experiences large temperature fluctuations both on a daily and a seasonal basis. The maximum temperature in summer is usually between 30 ° and 40 °C and the minimum temperature in winter 5 ° to –5 °C. The study area falls between the 200 mm and 250 mm rainfall isohyets, rainfall being erratic and mainly falling in late summer. The year can be divided into three seasons: the hot wet season, January to April; the cold dry season, May to August; and the hot dry season, September to December (Mills & Retief 1984).

Methods

From 1972 to 1982 regular counts of springbok, gemsbok, blue wildebeest and red hartebeest were made along the Auob and Nossob riverbeds from a slow moving vehicle. Counts were carried out in all months of the year although a count was not made each month. The mean number of counts per year along the Auob was 8,7 ± S.D. 2,5 and the mean number along the Nossob was 9,1 ± S.D. 1,8. All ungulates visible from the roads running along the riverbeds were counted and the same route was driven on each count.

Rainfall was monitored at three weather stations along the riverbeds: at Twee Rivieren, Mata Mata and Nossob (Fig. 1). The rainfall figures used in the analyses are the relevant means for the three stations.

The data were analysed by combining the counts for the two riverbeds. For each species an overall fluctuation ratio was calculated by dividing the lowest mean monthly count into the highest and an annual fluctuation ratio by dividing the lowest average annual abundance into the highest.

Correlation co-efficients were calculated for the numbers of each of the four species counted in a month versus the rainfall for that month, the rainfall in the previous month, the rainfall two months before and the rainfall three months before the count, in order to measure the length of time that rainfall had an effect on the presence of the four species along the riverbeds. In addition, correlation co-efficients were calculated for the numbers of each species counted in a month and the rainfall of that month, the rainfall over the previous two months, three months etc., up to 10 months, in order to measure the effect that accumulated rainfall had on the ungulate numbers along the riverbeds.

Results

The annual cycle

Figure 2 shows the average numbers of each species of ungulate counted along the riverbeds for each month of the year, as well as the average rainfall for each month during the study period. It is stressed that this is the overall pattern and that there is a large measure of annual variation. The following results, therefore, must be seen in this light.

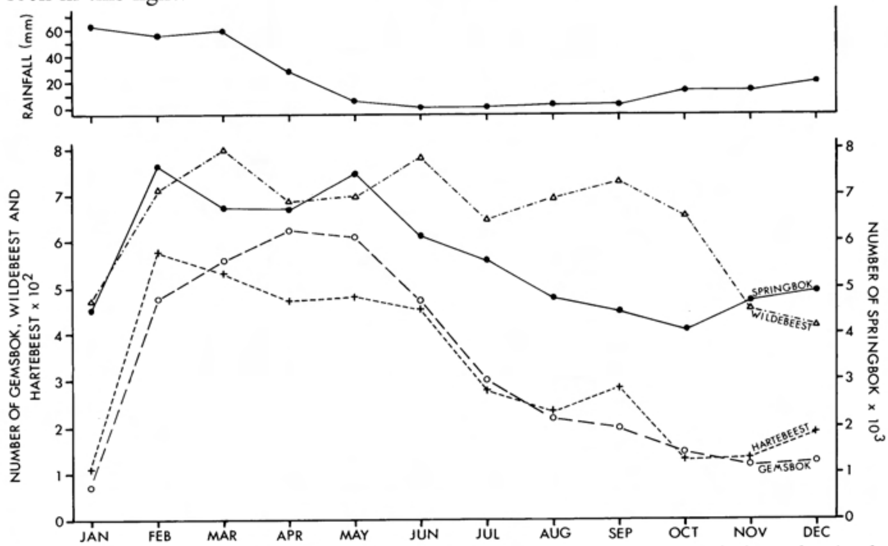

Fig. 2. The average number of each of four species of ungulate counted along the Auob and Nossob riverbeds and the average rainfall for each month for the period 1972–1982.

Rainfall is highly seasonal; on average 77,8% fell between January and April, 3,5% between May and August and 18,6% between September and December. There is a clear relationship between rainfall and the numbers of all species found along the riverbeds, although the specific responses of each species do differ.

Springbok show a rapid response to rain, reaching their highest numbers along the riverbeds between February and May. Through the rest of the year springbok numbers gradually decrease reaching a trough in October. The overall fluctuation ratio for springbok was 1,9, showing a rather stable presence along the riverbeds at all times of the year. Observations on marked springbok have shown that they move extensively along the riverbeds, frequently moving from one riverbed to the other, often concentrating in areas where vegetation conditions are best, particularly after local rain showers (Mills *in prep.*).

Red hartebeest hardly ever come into the Auob riverbed (Table 2), the most ever counted along this riverbed being 25 (Table 1). Along the Nossob they respond rapidly to rainfall, reaching a peak in February – March, but from June onwards their numbers drop steadily reaching their lowest point in October – November (Fig. 2). The overall fluctuation ratio for hartebeest was 5,2, showing a comparatively large amount of movement in and out of the riverbeds. Observations on

Table 2

Average number of four species of ungulates counted along the Auob and Nossob riverbeds between 1972 and 1982

Species	Auob		Nossob	
	No. counted	No./km	No. counted	No./km
Springbok	2 177	18,6	3 667	12,4
Gemsbok	76	0,6	283	1,0
Wildebeest	241	2,1	427	1,4
Hartebeest	4	0,03	342	1,2

marked hartebeest showed a strong tendency for these antelope to return to the same areas of the riverbed each year (Mills *in prep.*).

Gemsbok also respond rapidly to rainfall along the riverbeds, but they reach their peak somewhat later than the previous mentioned two species (April – May). Then they rapidly move out of the riverbeds (Fig. 2). The overall fluctuation ratio for gemsbok was 8,4, showing the largest amount of movement in and out of the riverbed of all four species.

Blue wildebeest show the most deviant annual cyclic pattern. Although they do respond to rainfall by moving into the riverbeds in February, their numbers fluctuate little until November when, for three months their numbers remain low (Fig. 2). The overall annual fluctuation ratio for wildebeest was 1,9, the same as for springbok, and indicative of a rather stable population along the riverbeds. Observations of marked wildebeest show that they generally move less extensively along the riverbeds than springbok do (Mills *in prep.*). In addition, even during the months November to January, they do not appear to move far from the riverbeds. Aerial surveys have also tended to confirm this. For example, in December 1978 during a ground count along the Auob riverbed 79 wildebeest were counted, whereas six days previously, during an aerial count along the riverbed and adjoining dune areas, 371 wildebeest were counted, most of them just out of the riverbed.

Along the Nossob riverbed wildebeest were rather patchily distributed. This distribution was related to the presence of windmills with potable water, there being two main areas: one in the lower Nossob around Rooiputs windmill, the other around Nossob camp just over half way up the riverbed. Smaller concentrations of wildebeest occurred around Kannagauss and Union's End windmills in the upper Nossob (Fig. 1) (Mills & Retief *in prep.*).

Figures 3 and 4 show the specific responses of the ungulates to rainfall. Figure 3 shows how the correlations between total counts and rainfall in a month vary with increasing number of months lag. Springbok show the quickest reaction to rainfall, with the only significant correlation between rainfall in a month and the number counted that month. With lags of one and two months between rainfall and counts

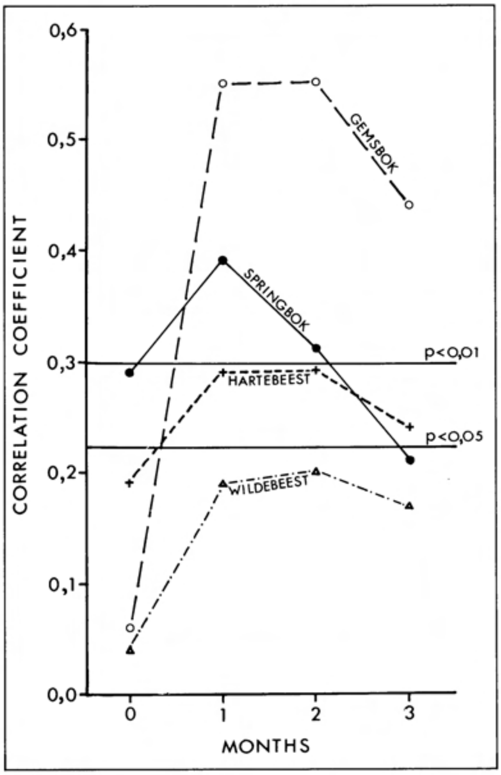

Fig. 3. Correlation co-efficients for each of four species of ungulate counted along the Auob and Nossob riverbeds in a month against lagged rainfall. 0 = the number counted in a month against the rainfall for that month. 1 = the number counted in a month against rainfall the previous month. 2 = the number counted in a month against rainfall the month before last etc.

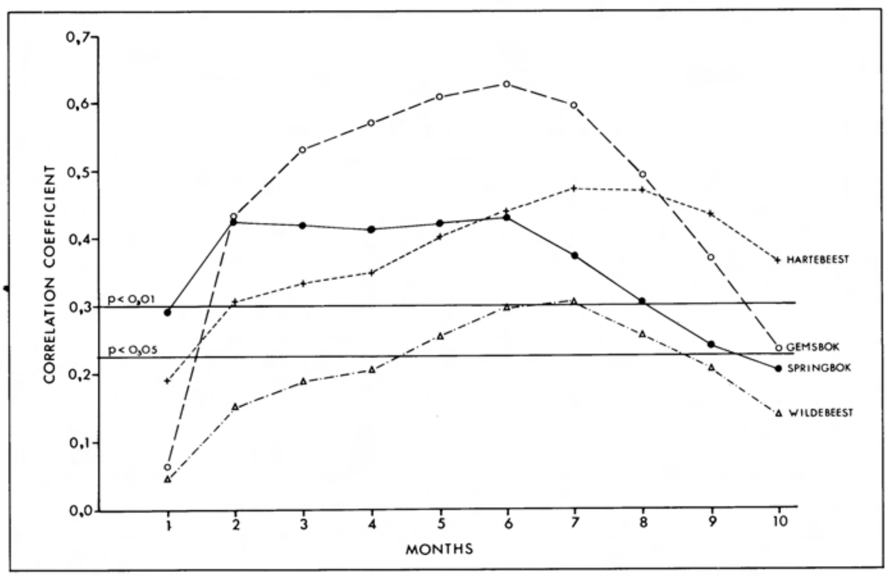

Fig. 4. Correlation co-efficients for each of four species of ungulate counted along the Auob and Nossob riverbeds against accumulated rainfall. 1 = the number counted in a month against that month's rainfall. 2 = the number counted in a month against rainfall over the previous two months etc.

gemsbok show the highest correlations and even after a lag of three months rainfall they show a highly significant correlation. Springbok and to a lesser extent hartebeest, also show significant correlations with a one and two month lag, although for both species the correlations decrease markedly by the third month. Wildebeest numbers were not found to be significantly correlated with a single month's rainfall, irrespective of lag.

Figure 4 shows how the correlations between total counts and accumulated rainfall vary. Springbok rapidly reach a plateau, with no appreciable increase in correlations with more than two months of accumulated rainfall. Gemsbok correlations increase steadily, reaching their highest level with six months of accumulated rainfall. Hartebeest correlations increase more gradually than gemsbok, reaching the peak at seven months of accumulated rainfall, thereafter maintaining a highly significant correlation through to the tenth month. Wildebeest correlations do not reach significant levels until five months of accumulated rainfall, thereafter maintaining significant but relatively lower correlations up to eight months of accumulated rainfall.

The 11-year pattern

Figure 5 shows the average annual abundance of each of the four species along the riverbeds each year from 1972 to 1982, as well as the rainfall for each year. A significant correlation between average annual abundance and annual rainfall for the 11-year period occurred for springbok ($r = 0{,}620$; $P < 0{,}05$), gemsbok ($r = 0{,}619$; $P < 0{,}05$) and red hartebeest ($r = 0{,}754$; $P < 0{,}01$), but not for blue wildebeest ($r = 0{,}120$; $P > 0{,}05$). Springbok numbers fluctuated the least with an annual fluctuation ratio of 2,1, followed by wildebeest 4,2, gemsbok 5,2 and hartebeest 16,8. Hartebeest numbers in particular dropped drastically along the Nossob riverbed as the dry years of the early 1980's progressed (Fig. 5).

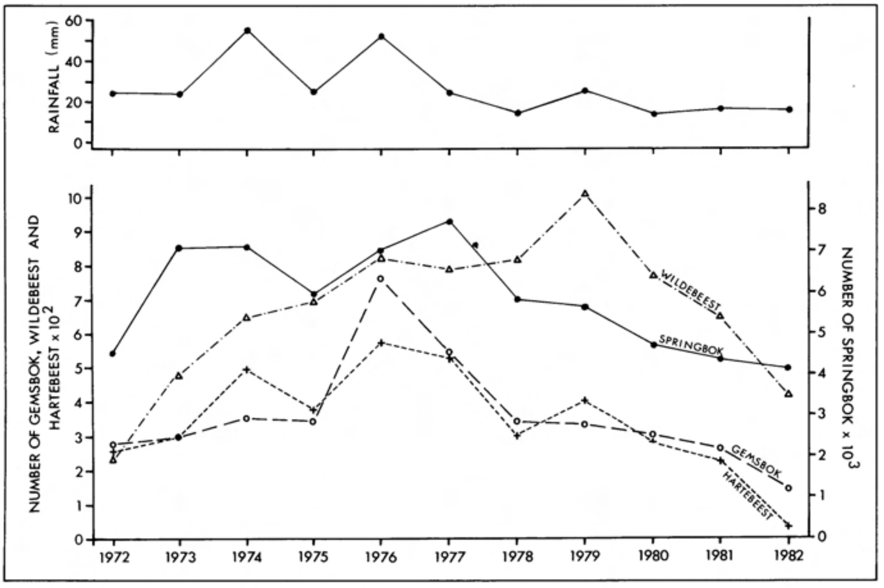

Fig. 5. The average number of each of four species of ungulate counted along the Auob and Nossob riverbeds each year and the rainfall for that year.

Blue wildebeest numbers along the riverbeds increased steadily from 1972 to 1976, when they levelled out. They then increased sharply in 1979, after which they dropped sharply. The 1972 to 1976 increase is believed to be mainly a result of an increase in the resident population, and has been ascribed to a combination of high rainfall and the erection of boreholes with potable water along parts of the Nossob riverbed (Bothma & Mills 1977). The 1979 peak was undoubtedly a result of a large influx of many thousands of wildebeest into the southern Kalahari from the north-east between June and October. Between 1978 and 1982 non-violent mortality imposed heavy losses on the wildebeest population (Mills *in prep.*). Although there was no significant correlation between average annual abundance and rainfall for wildebeest, there was a significant correlation between average annual abundance and the accumulated rainfall over the previous three years, if the abnormal year 1979 was omitted (r = 0,630; $P < 0{,}05$).

Differences between the Auob and Nossob riverbeds

Table 2 shows the average number of each species of ungulate counted over the study period along each of the riverbeds. Bearing in mind that the Nossob is for the most part at least twice as wide as the Auob is, it is clear from this Table that the Auob supports a far higher density of springbok and wildebeest than does the Nossob. Gemsbok are present in more or less the same densities along the two riverbeds and hartebeest are almost exclusively confined to the Nossob riverbed.

The differences in density of springbok along the two riverbeds tends to be most marked during the dry seasons. Because of its far larger surface area the Nossob always has more springbok along it than the Auob, but the differences between the two rivers, expressed as the ratio of the mean Nossob count for that month to the mean Auob count, is less for counts made during the six driest months of the year ($\bar{x}$ = 1,4) than for those made during the six wettest months ($\bar{x}$ = 2,0).

Comparison with previous studies

In most cases the numbers of ungulates counted along the riverbeds during the present study far exceeded those counted by Eloff (1959a, 1959b, 1961, 1962) between 1957 and 1960 and, to a lesser extent those counted by Bothma (1971) in 1970 and 1971. The mean densities of springbok along the Auob and Nossob riverbeds during Eloff's study were 0,7/km and 1,9/km respectively, the densities of gemsbok for the two rivers were 1,7/km and 0,8/km, the densities of wildebeest 0,5/km and 0,07/km and the densities of hartebeest 0,009/km and 0,5/km. Comparison of these densities with those in Table 2 show very much lower densities in Eloff's data for all species except for gemsbok, which along the Auob were at a higher density. Densities are not given in Bothma's (1971) data, but evidence for low ungulate numbers along the riverbeds can be gleaned from the fact that the highest count of all species combined along the Nossob riverbed was 2 338 animals, which is below the mean for the present study period (Table 2). Rainfall was also apparently far lower during these two study periods. The mean rainfall for Twee Rivieren for the years 1941–1960 was 148,1 mm (official weather bureau records), and Eloff describes conditions along the riverbeds during most of his visits as very dry. The mean for the three weather stations mentioned earlier in 1970 and 1971 was 120,8 mm and 172,0 mm respectively. The overall mean of these three weather stations during the present study was 265,4 mm.

Discussion

A close relationship between rainfall and net primary production above ground in arid and semi-arid areas has been shown in a number of studies: see, for example, Rosenzweig (1968), Phillipson (1975) and Seely & Louw (1980). The vegetation along riverbeds of the southern Kalahari is richer in minerals than the vegetation in the dunes and some of the dominant grasses, particularly *Panicum coloratum* and *Stipagrostis obtusa*, are of the highest quality grasses in the area (Leistner 1967). These factors are most likely responsible for the positive reaction to rainfall of the ungulates along the riverbeds in both the short and long term, as has also been shown in previous studies (Bothma 1971, 1972; Bothma & Mills 1977). During dry times many of the grasses along the riverbeds die back to pieces of stubble and the lower quality grasses in the dunes are all that is available to the grazers.

Of the four species, springbok reacted most rapidly to the new growth generated by rainfaill (Fig. 3), their small mouths enabling them to crop the sprouting vegetation at ground level. One month after rainfall there was an even more marked response, presumably as more food became available. The accumulation of more than two months rainfall, however, did not increase the response of springbok (Fig. 4). During dry times springbok are able to switch their diet from predominantly grazing to browsing the dwarf shrubs and *Acacia*'s along the riverbeds (Leistner 1967; personal observations). This, coupled with a probable preference for short grass areas, enables a substantial number of springbok to remain in the riverbeds throughout the year (Fig. 2), although the actual number present in any one year was dependent on annual rainfall (Fig. 5).

Gemsbok reacted most strongly to rainfall after a time lag of one to two months (Fig. 3) and also reacted markedly to sustained rainfall (Fig. 4). Their highest numbers along the riverbeds occurred during high rainfall years when the grasses were tall and had matured, suggesting that when in this condition the grasses were most attractive to gemsbok. They rapidly left the riverbeds as conditions became dry (Fig. 2) and in years of low rainfall hardly came into the riverbeds at all. This was particularly so towards the end of the study when a series of dry years ensued (Fig. 5) and the trend is continuing into 1983 as conditions remain dry (personal observations).

Hartebeest, which were almost exclusively confined to the Nossob riverbed (Table 2), also reacted most strongly to rainfall after a time lag of one to two months, although not to the same extent as gemsbok did (Fig. 3). They also responded to the effects of the accumulation of rainfall in a generally less sensitive but longer acting manner than gemsbok (Fig. 4), and did not move out of the riverbed as quickly as gemsbok did (Fig. 2). In years of high rainfall, therefore, the Nossob riverbed and environs provided food for hartebeest for a longer period than for gemsbok. Like the gemsbok, very few hartebeest came into the riverbed during dry years.

Wildebeest did not respond as rapidly, nor as intensively, to rainfall as did the other species (Figs. 2, 3 and 4). It was, in fact, only after five months accumulated rainfall that significant correlations between rainfall and the number of wildebeest were found. The fact that wildebeest maintained a constant presence along the riverbeds for most of the year irrespective of rainfall (Fig. 2), suggests that these significant correlation values reached by wildebeest versus accumulated rainfall (Fig. 4), were due more to their temporary evacuation of the riverbeds following a series of dry months than to a direct positive reaction to rainfall.

Wildebeest comprise two distinct populations in the southern Kalahari: a highly nomadic population, which is apparently independent of surface water, and a smaller, sedentary population inhabiting the riverbeds. The provision of potable water along the riverbeds has led to the establishment of the sedentary population (Eloff 1966; Bothma & Mills 1977), and these wildebeest seem to be dependent on this water (Mills & Retief 1984). The nomadic population is independent of surface water, but possibly dependent on water storing plants such as the tsama *Citrullus lanatus* and gemsbok cucumber *Acanthosicyos naudinianus*. This population is apparently unique as elsewhere in Africa blue wildebeest are regarded as obligate drinkers (Talbot & Talbot 1963; Taylor 1968; Young 1970; Western 1975; Berry & Louw 1982).

During the high rainfall years in the early and middle 1970's the sedentary wildebeest population underwent a sharp increase (Bothma & Mills 1977; this study), but eventually, as conditions became progressively drier, the population declined (Fig. 5), due mainly to poor reproductive success and high non-violent mortality (Mills *in prep.*). This process is also continuing into 1983 (personal observations). Thus, unlike the other three species which were able to move rapidly in and out of the riverbeds depending on conditions, the numbers of resident wildebeest along the riverbeds depended to a greater extent on breeding success and mortality factors than on emigration and immigration.

The difference in density of the ungulates along the two riverbeds during this study (Table 2) is noteworthy. The Auob supported a substantially higher density of springbok and wildebeest, but hardly any hartebeest, the majority of which were to be found along the Nossob riverbed. Only gemsbok occurred at more or less equal densities along the two riverbeds. The Auob has a greater density and variety of dwarf shrubs along its banks than the Nossob does and also the *Acacia* trees along the Auob have more branches close to the ground. During the dry season, therefore, there was a higher density of browse material available for springbok along the Auob than the Nossob. The Auob was, therefore, a more important dry season habitat for this species than the Nossob was, and the differences in density of springbok along the two riverbeds is thought to be mainly due to this fact. The reason for the higher density of wildebeest along the Auob may be due to the higher incidence of potable water along its course. Finally, hartebeest were closely associated with the large, sandy, limestone flats along the Nossob, a habitat which is not found along the Auob. This may explain the almost total absence of hartebeest along the Auob.

The 1970's were a decade of extremely high rainfall for the southern Kalahari. During the 11-year study the annual rainfall fell below 240 mm in only four years and the years 1974 and 1976 were the two wettest years on record. This resulted in generally higher ungulate densities along the riverbeds relative to more normal times (Eloff 1959a, 1959b, 1961, 1962; Bothma 1971, 1972), with the exception of gemsbok along the Auob riverbed. The apparent drop in gemsbok numbers along the Auob riverbed in recent years, despite the increase in rainfall, is difficult to understand. It may be that the Auob riverbed provides ideal dry season habitat for this species, or it may be that competition from increasing numbers of either wildebeest or springbok has had a detrimental effect on the gemsbok population.

The overall seasonal pattern of ungulate abundance along the riverbeds in the southern Kalahari is one of wet-season concentrations and dry-season dispersion; the exact opposite to the patterns occurring in the better watered areas of Africa. This system has evolved under conditions in which free-standing water is available erratically and for short periods only. The provision of artificial water along the riverbeds and in the dune areas has done little to change this pattern, except to an extent in the case of wildebeest. The ungulates mainly concentrate in the areas where water provision is highest during the rains and disperse into areas where little or no surface water is available when conditions are driest.

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REFERENCES

BERRY, H. H. and G. N. LOUW. 1982. Nutritional measurements in a population of free-ranging wildebeest in the Etosha National Park. *Madoqua* 13: 101-125.

BOTHMA, J. DU P. 1971. Notes on river habitat used by the larger ungulates in the Kalahari Gemsbok National Park. *Koedoe* 14: 33-48.

BOTHMA, J. DU P. 1972. Short term response in ungulate numbers to rainfall in the Nossob River of the Kalahari Gemsbok National Park. *Koedoe* 15: 127-134.

BOTHMA, J. DU P. and M. G. L. MILLS. 1977. Ungulate abundance in the Nossob River Valley, Kalahari Desert. *Proc. XIII Int. Cong. Game Biol.*, Atlanta, Georgia, U.S.A.: 90-102.

CHILD, G., R. PARRIS and E. LE RICHE. 1971. Use of mineralised water by Kalahari wildlife and its effects on habitats. *E. Afr. Wildl. J.* 9: 125-142.

ELOFF, F. C. 1959a. Observations on the migrations and habits of the antelopes of the Kalahari Gemsbok Park. Part 1. *Koedoe* 2: 1-29.

ELOFF, F. C. 1959b. Observations on the migrations and habits of the antelopes of the Kalahari Gemsbok Park. Part 2. *Koedoe* 2: 30-51.

ELOFF, F. C. 1961. Observations on the migrations and habits of the antelopes of the Kalahari Gemsbok Park. Part 3. *Koedoe* 4: 18-30.

ELOFF, F. C. 1962. Observations on the migrations and habits of the antelopes of the Kalahari Gemsbok Park. Part 4. *Koedoe* 5: 128-136.

ELOFF, F. C. 1966. Range extension of the blue wildebeest. *Koedoe* 9: 34-36.

LEISTNER, O. A. 1959. Notes on the vegetation of the Kalahari Gemsbok National Park with special reference to its influence on the distribution of antelopes. *Koedoe* 2: 128-151.

LEISTNER, O. A. 1967. The plant ecology of the southern Kalahari. *Mem. bot. Surv. S.Afr.* 38: 1-172.

LEISTNER, O. A. and M. J. A WERGER. 1973. Southern Kalahari phytosociology. *Vegetatio* 28: 353-397.

MILLS, M. G. L. 1977. The distribution and abundance of ungulates in the Auob river valley, Kalahari Gemsbok National Park, 1972–1976. Internal Report of National Parks Board of Trustees (unpublished).

MILLS, M. G. L. and P. F. RETIEF. 1984. The effect of windmill closure on the movement patterns of ungulates along the Auob riverbed. *Koedoe* 27 (Supplement): 107-118.

PHILLIPSON, J. 1975. Rainfall, primary production and carrying capacity of Tsavo National Park (East), Kenya. *E. Afr. Wildl. J.* 13: 171-201.

ROSENZWEIG, M. L. 1968. Net primary productivity of terrestrial communities: prediction from climatological data. *Am. Nat.* 102: 74-76.

SEELY, M. K. and G. N. LOUW. 1980. First approximation of the effects of rainfall on the ecology and energetics of a Namib desert dune ecosystem. *J. Arid Environ.* 3: 25-54.

TALBOT, L. M. and M. H. TALBOT. 1963. The wildebeest in western Masailand. *Wildl. Monogr.* No. 12.

TAYLOR, C. R. 1968. The minimum water requirements of some east African bovids. *Symp. zool. Soc. Lond.* 21: 195-206.

WESTERN, D. 1975. Water availability and its influence on the structure and dynamics of a savannah large mammal community. *E. Afr. Wildl. J.* 13: 265-286.

YOUNG, E. 1970. *Water as faktor in die ekologie van wild in die Nasionale Krugerwildtuin.* D.Sc. dissertation. University of Pretoria, Pretoria.