Afr. J. Ecol. 1999, Volume 37, pages 12–26

The abundance of large wild herbivores in a semi-arid savanna in relation to seasons, pans and livestock

ROGER BERGSTRÖM[1] and CHRISTINA SKARPE[2]

[1]*Department of Animal Ecology, Swedish University of Agricultural Sciences, Bäcklösavägen 8, S-756 51 Uppsala, Sweden,* [2]*Norwegian Institute for Nature Research (NINA), Tungasletta 2, N-7005 Trondheim, Norway*

Summary

Large herbivores, including livestock and ostrich, were counted along a 200-km long track in south-western Kalahari, Botswana. Altogether, 37 counts were made during different seasons. The number of animals seen and group size were recorded. These variables were compared with monthly and accumulated rainfall (number of animals and group size) and distance to pans (number of animals). Observations of game and livestock were also related to distance to villages. In four of the seven studied species, most animals were seen during the wet season. Group size also varied between seasons apart from the non-gregarious steenbok and duiker. Number of animals and group size were in some cases correlated with rainfall during the month of observation or with accumulated rainfall during the preceding months. The various species were more often observed close to pans than further away from the pans. Compared to livestock, game was on average observed >10 km further away from the villages. Few observations of game were made between village centres and the livestock observations most distant from the village.

Key words: Botswana, group size, Kalahari, ostrich, rainfall

Résumé

On a dénombré les grands herbivores, y compris le bétail et les autruches, le long d'une piste de 200 km dans le sud-ouest du Kalahari, au Botswana. En tout, on a fait 37 comptages en différentes saisons. On a noté le nombre des animaux aperçus et la taille des groupes. On a comparé ces variables avec les chutes de pluies mensuelles et totales (nombre d'animaux et taille des groupes) et avec l'éloignement des cuvettes (nombre d'animaux). Les observations de gibier et de bétail ont aussi été liées à la distance par rapport aux villages. Pour quatre des sept espèces étudiées, la plupart des animaux étaient aperçus pendant la saison des pluies. La taille des groupes variait aussi selon les saisons sauf pour les deux espèces non grégaires, le steenbok et la céphalophe. Le nombre des animaux et la taille du groupe étaient dans certains cas liés aux chutes de pluie du mois de l'observation ou au total des pluies durant les mois qui avaient précédé. Les différentes espèces ont été observées plus souvent près des cuvettes que loin d'elles. Par rapport au bétail, les animaux sauvages étaient

Correspondence: Roger Bergström, fax: +46 18 30 02 46, e-mail: roger.bergstrom@sjf.slu.se

observés en moyenne >10 km plus loin des villages. On a observé peu de gibier entre le centre des villages et le bétail qui se trouvait le plus loin des villages.

Introduction

Variation in topography, soil conditions, fire regimes, intra- and inter-annual variations in rainfall, as well as spatial and temporal distribution of surface water, is important in determining the heterogeneity of savanna structure and function on different scales (Frost *et al*., 1986). This heterogeneity, expressed as, e.g. the diversity of plant communities and habitat types, is of utmost importance for density, distribution and habitat utilization by large herbivores (McNaughton & Georgiadis, 1986; Dunham, 1994; Ben-Shahar, 1995).

Irregular water availability in semi-arid savannas affects both the possibilities of drinking and the distribution, quantity and quality of food for large herbivores (McNaughton & Georgiadis, 1986; Skarpe & Bergström, 1986). In the semi-arid savannas of southern Africa and especially in the Kalahari, many, but not all, species of herbivores undertake long-distance movements in response to water and food availability (Crowe, 1995). Migrations in the savannas of southern Africa are more opportunistic and facultative than those in the eastern part of the continent (DHV, 1979; Walker, 1979).

In the sand-covered, slightly undulating landscape of the Kalahari, two features add conspicuously to the heterogeneity of the area: pans and villages or cattle posts with surrounding cattle ranges. The pans in western Kalahari are shallow, often rounded depressions, commonly with a diameter of between 200 and 2000 m. They have soils with relatively high silt and clay content, they hold water after rain and they have, compared to the surrounding savannas, a vegetation that differs in species and life form composition (Leistner, 1967; Parris & Child, 1973). These characters may attract large herbivores and their associated predators (Parris & Child, 1973; Milton, Dean & Siegfried, 1994).

In the Kalahari, as in most of Africa, human settlements and activities have affected wildlife populations negatively (Crowe, 1995; Happold, 1995). Villages and cattle posts with surrounding livestock ranges have changed wildlife habitats (Parris & Child, 1973), mainly due to intensive grazing, that often results in considerable vegetational changes (Skarpe, 1986). Direct disturbance, including hunting by humans, may also have an impact on wildlife habitat around villages (Parris & Child, 1973).

In the present study it was predicted that: (1) the abundance of large herbivores in a specific area will correlate with rainfall, (2) pans will attract herbivores, and (3) villages with surrounding livestock ranges will deter wild large herbivores.

Study system

The study area between the villages of Hukuntsi (24°04′ S 21°40′ E) and Ncojane (23°09 S 20°17 E) in the Kalahari, western Botswana (Fig. 1) is a savanna on fairly homogeneous nutrient-poor sand and with no permanent surface water (Bergström & Skarpe, 1985). Average annual precipitation, mainly falling during summer (November–April), is $\approx$300 mm (coefficient of variation: 45%; Pike, 1971). Most of the study period 1975–80, was within a period with good rains ending in 1979 (Spinage,

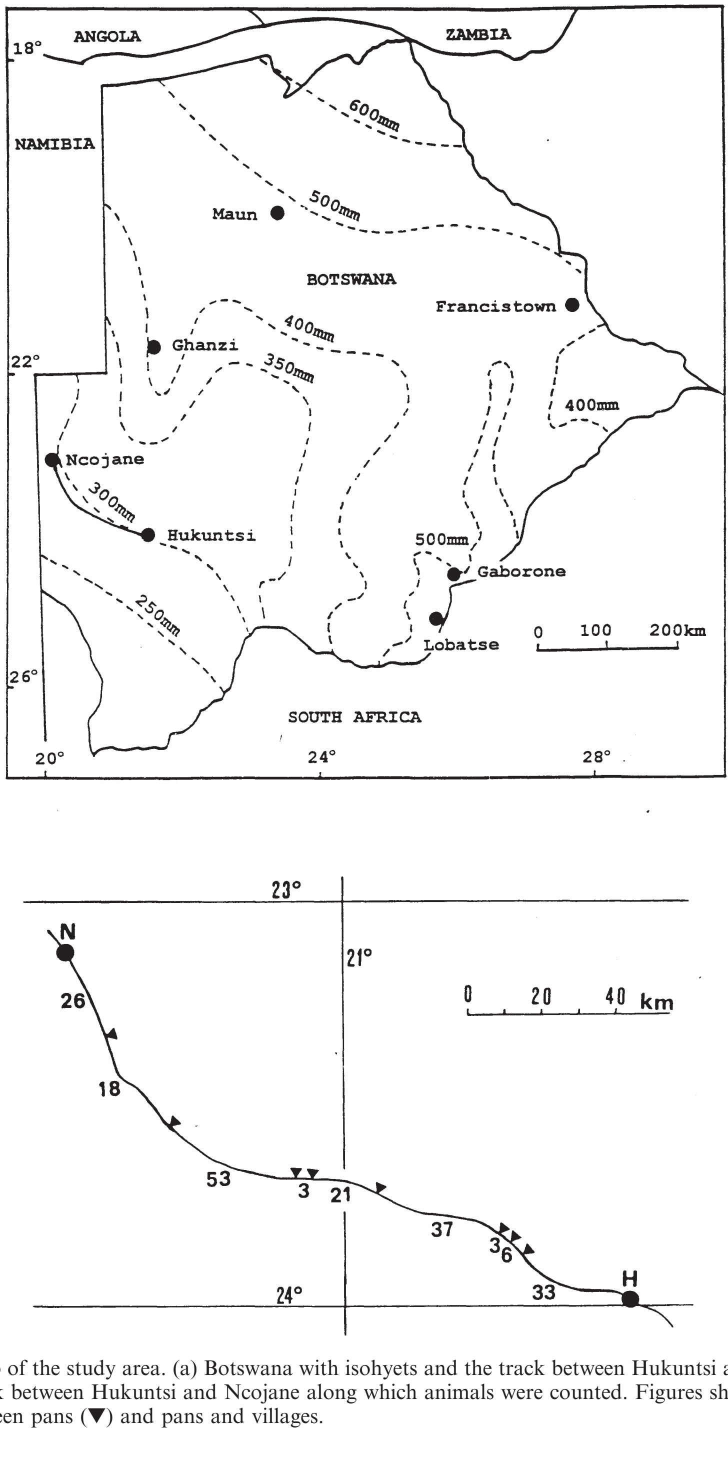

Fig. 1. Map of the study area. (a) Botswana with isohyets and the track between Hukuntsi and Ncojane, (b) the track between Hukuntsi and Ncojane along which animals were counted. Figures show distances in km between pans (▼) and pans and villages.

Table 1. Species, type of feeder and live body weight (kg) of large herbivores in the study area. G = preferential grazer, B = preferential browser, M = mixed feeder

Common name	Species name	Type of feeder	Live weight (kg)
Springbok	*Antidorcas marsupialis* (Zimmermann)	M	40–45
Red hartebeest	*Alcelaphus buselaphus* (Pallas)	G	130–170
Blue wildebeest	*Connochaetes taurinus* (Burchell)	G	190–210
Gemsbok	*Oryx gazella* (L.)	G	230–260
Grey duiker	*Sylvicapra grimmia* (L.)	B	15–16
Steenbok	*Raphicerus camelus* (Thunberg)	B (M)	11–13
Greater kudu	*Tragelaphus strepsicerus* (Pallas)	B	220–325
Eland	*Taurotragus oryx* (Pallas)	B	680–720
Ostrich	*Struthio camelus* (L.)	—	70–90

1992). The vegetation is a shrub savanna with the tree and shrub layer dominated by deciduous, microphyllous *Acacia* species and the field layer by perennial, tufted grasses (Skarpe, 1986).

Altogether, nine species of large wild herbivores (body weight>10 kg) roam the south-western part of Botswana (Table 1), but the populations of some of these species have declined during the last decades (Spinage, 1992; Crowe, 1995).

The track along which the monitoring was undertaken (Fig. 1), runs through a slightly raised region, known as the 'Schwelle', which extends in a NW–SE direction through the Kalahari, This region is rich in pans, and the track originates from the time of ox wagons (about 100 years ago), and runs from pan to pan to provide water for people and beasts. Therefore, pan areas were over-represented along the track in comparison with a random line of the same length between Hukuntsi and Ncojane (Department of Surveys and Lands, 1989, Botswana map 1:500 000 sheet 6).

The technique of providing drinking water for humans and livestock from deep drilled boreholes has led to an increase in both number and distribution of the human population and of livestock in the Kalahari (DHV, 1979). In 1972, Hukuntsi and Ncojane had, respectively, a minimum of *c.* 5000 and 3800 head of cattle (Botswana Ministry of Agriculture, unpublished vaccination figures). In 1967, 1500–2000 people inhabited each village (Kuper, 1970). The human population density in the whole region, Ghanzi and Kgalagadi districts, was below 0.2 people/km^2.

Methods

Animal counts

Large wild herbivores (Table 1) including livestock and ostriches were counted on 37 occasions at irregular intervals from December 1975 to June 1980 along a 200-km long track between the two villages, Hukuntsi and Ncojane (Fig. 1). Twenty-two of the censuses were undertaken during the wet season, November to April, and 15 during the dry season, May to October. Except for August (no trip), two to six trips (mean = 3.4, SD = 1.1) were made per month. The track had an extremely low traffic intensity the whole year around. The counts were usually made by two people in a four wheel drive vehicle driven at an average speed of 20 km/h. All game and livestock sighted from the vehicle were recorded together with distance in km (odometer readings) from either the centre of Hukuntsi or Ncojane. For wild animals, the species and number of individuals, irrespective of animal category, were recorded. The position of each pan along the track was also identified through odometer readings (Fig. 1).

Nine wild large herbivore species (Table 1) and livestock (cattle and goats) were counted in the present study. Two of the species, eland and greater kudu, were seen only seven times each during the whole study period and were therefore excluded from the analyses.

Due to plant growth, the visibility along the track changed with season, although the fairly open vegetation minimized this problem. The average visibility was estimated to be about 300 m on each side of the track. The low or non-existing vegetation on pans resulted in higher visibility but, due to the relatively small size of most pans, this increased visibility did not affect the results significantly. Possible bias due to increased visibility was expected to be strongest for the smallest antelopes, but they were rarely seen on pans.

The spatial resolution was the 1-km sections along the track. Thus, animals of the same species observed within one km section were regarded as one observation, and average group size was calculated as total number of animals observed divided by number of observations. For the correlation analyses, monthly rainfall data for Tshane (10 km from Hukuntsi) were obtained from Botswana Weather Bureau (unpublished). The graphical presentation of the long-term average monthly rainfall is based on the database by Leemans & Cramer (1991).

Data treatment

Correlations between animal numbers and rainfall data, distances from pans and from villages were tested with the Spearman rank correlation. The observed number of animals at different distances from pans was tested against regular distribution with the chi-square test for goodness of fit. In these analyses, distances were calculated from each pan up to half-way to the next pan. Further, the km sections between the villages and the nearest pans, 32 km from Hukuntsi and 25 km from Ncojane, were excluded to avoid interference from disturbances close to the villages. Differences between wet and dry season distances for closest observation to villages were tested with Mann–Whitney *U*-test and so were differences between km readings for livestock and each game species.

Results

Animal numbers and group size

During the 37 trips over the 200-km route, 2400 observations were made of 33,000 animals. There was a considerable variation in number of animals observed between different months (Fig. 2a). More wildebeest were seen per trip in the wet season than in the dry, and springbok, hartebeest and steenbok showed the same trend. Numbers of gemsbok, duiker and ostrich varied between months, but showed no clear seasonal trend. Numbers of springbok and wildebeest varied most between months (Fig. 2a). On four trips in the dry season wildebeest were not seen at all.

(a)

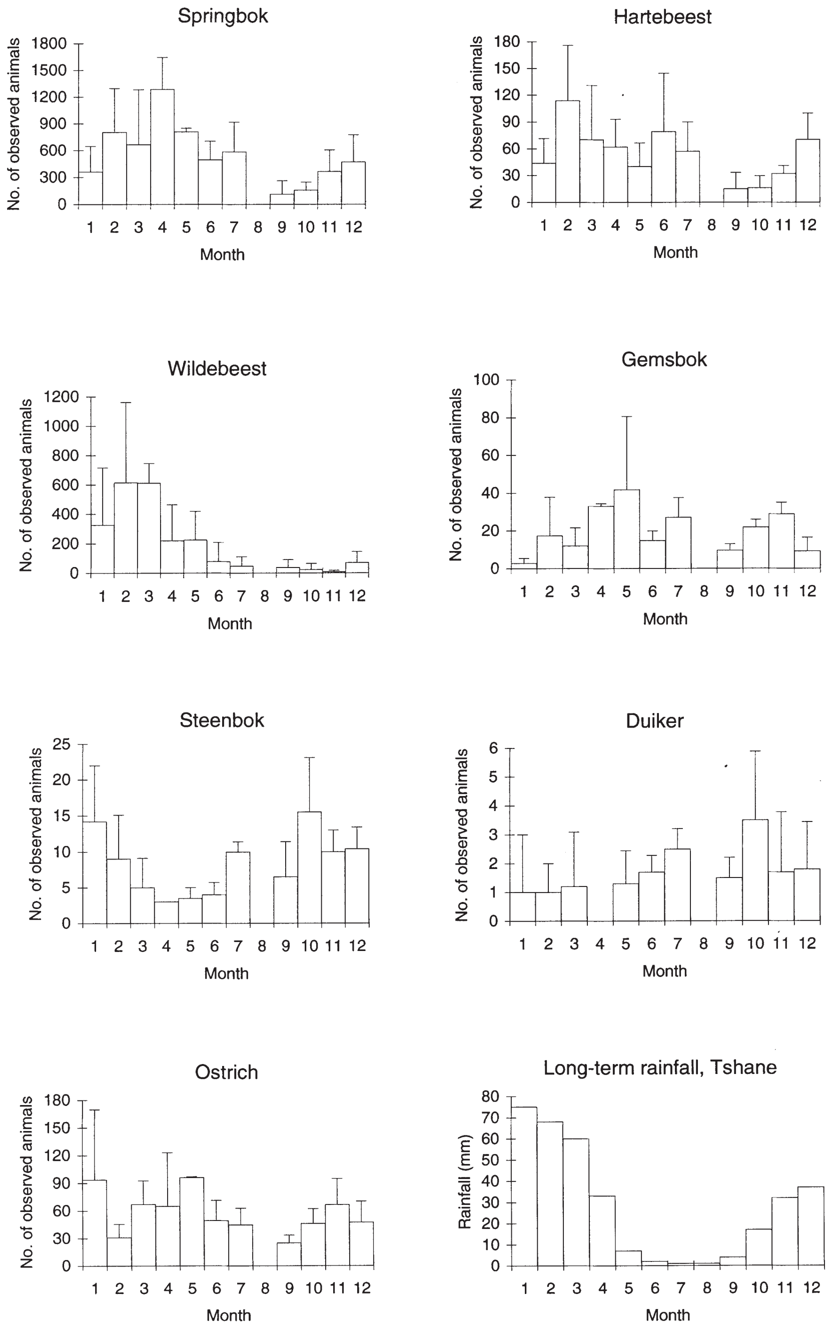

Fig. 2. (a) Average number (±SE) of animals observed per trip and (b) average group size (±SE) of animals per trip for all months (except August when no observations were made) and average monthly rainfall.

(b)

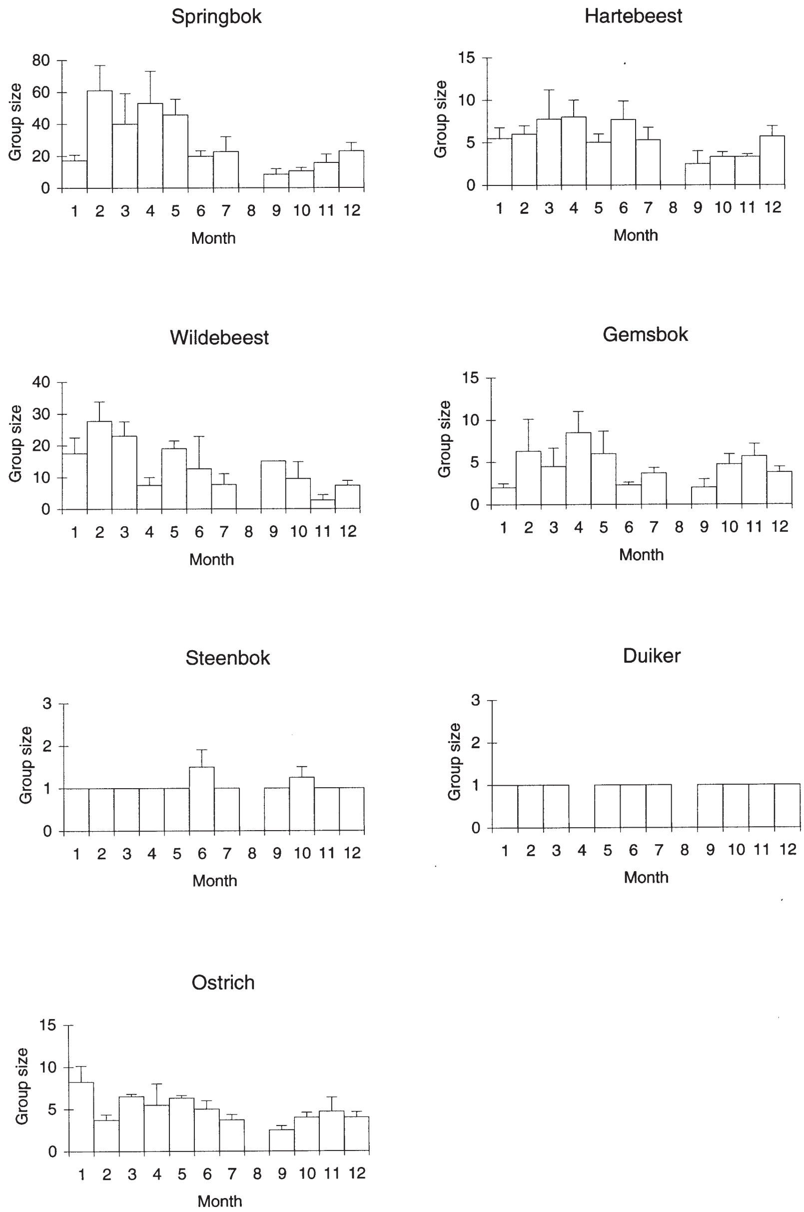
Springbok
Hartebeest
Wildebeest
Gemsbok
Steenbok
Duiker
Ostrich
Group size
Month
1 2 3 4 5 6 7 8 9 10 11 12

Fig. 2, cont.

Group size varied between months and seasons (Fig. 2b). There was a trend for springbok, hartebeest, wildebeest, gemsbok and ostrich to form larger groups in the mid and late rainy season than in the dry season. Springbok and wildebeest showed the largest relative variation in average group size, whereas steenbok and duiker were mostly observed singly. In 10% of the observations of steenbok more than one animal was seen and only in three cases were more than two steenbok observed together.

Correlations with rainfall

Total number of animals and average group size of springbok, wildebeest and ostrich were in many cases positively correlated with rainfall for the preceding months (Table 2). An accumulation of rainfall for several preceding months gave stronger correlations. Wildebeest seemed to track the rainfall most closely, as the rainfall during the month of observation was correlated significantly with the number of observed animals. Number of steenbok was negatively correlated with rainfall during the last 2 and 3 months. Numbers and group size of gemsbok and duiker showed no correlation with rainfall (Table 2a). For gemsbok, number of observations, but not number of animals or group size, was negatively correlated with rainfall during the current and previous month. Herd size of hartebeest, but not number of observed animals, correlated with rainfall 3 months before the observations.

Distance to pans

All species showed a strong deviation from an even distribution (χ^2-test, $P < 0.0001$) in relation to pans. The most clear pattern was shown by springbok and ostrich which occurred more often than expected within 4 km of the pans and further away less often than expected (Fig. 3). For wildebeest, hartebeest and gemsbok, observed numbers exceeded expected numbers close to pans and furthest away from pans, whereas observed numbers were below expected for all other km sections. The pattern of animal occurrence was similar at the different pans, but gemsbok concentrated particularly on the two largest pans, which also were those furthest away from villages. Steenbok and duiker (not shown in Fig. 3) showed no pattern ($P > 0.05$) in differences between observed and expected numbers. There was a tendency for springbok, gemsbok and ostrich to be more concentrated in the vicinity of pans during the wet season than the dry season.

Distance to villages

Livestock was observed on average up to 10–20 km from the villages (Table 3). Distances for all wild herbivores were significantly different from these distances (Mann–Whitney *U*-test; $P < 0.05$ in all cases). Ostrich, steenbok, springbok and hartebeest were the species observed closest to the villages, followed by wildebeest and duiker. Gemsbok were generally not observed less than 66–76 km from villages, i.e. on a very short section of the track. The distances for the different species were ranked in about the same way in relation to the two villages and seasons, i.e. all columns in Table 3 were significantly and positively correlated with each other (Spearman rank correlation, $r_s = 0.82–0.88$; $P < 0.05$), except for Hukuntsi wet season

Table 2. Spearman rank correlation between rainfall and number of animals and group size. Rainfall variables are: month of observation (m0), last month (m–1), 2 months ago (m–2), 3 months ago (m–3), sum of last 2 (m0–1), 3 (m0–2) and 4 (m0–3) months, sum of rainfall 1 and 2 months (m1–2) and 1, 2 and 3 months (m1–3) ago. NS = not significant (P>0.05), *P<0.01, **P<0.001

		Rainfall								
Species		m0	m–1	m–2	m–3	m0–1	m0–2	m0–3	m1–2	m1–3
Springbok	Number	NS	NS	**	**	NS	NS	**	**	**
	Group	NS	NS	**	**	NS	*	**	**	**
Hartebeest	Number	NS	NS	NS	NS	NS	NS	NS	NS	NS
	Group	NS	NS	NS	*	NS	NS	NS	NS	NS
Wildebeest	Number	*	**	*	NS	**	**	**	**	**
	Group	NS	**	*	NS	**	**	**	**	*
Gemsbok	Number	NS	NS	NS	NS	NS	NS	NS	NS	NS
	Group	NS	NS	NS	NS	NS	NS	NS	NS	NS
Steenbok	Number	NS	NS	–	–	NS	NS	NS	NS	–
	Group	NS	NS	NS	NS	NS	NS	NS	NS	NS
Duiker	Number	NS	NS	NS	NS	NS	NS	NS	NS	NS
	Group	NS	NS	NS	NS	NS	NS	NS	NS	NS
Ostrich	Number	NS	NS	NS	NS	NS	NS	*	*	*
	Group	NS	*	NS	NS	NS	*	**	**	**

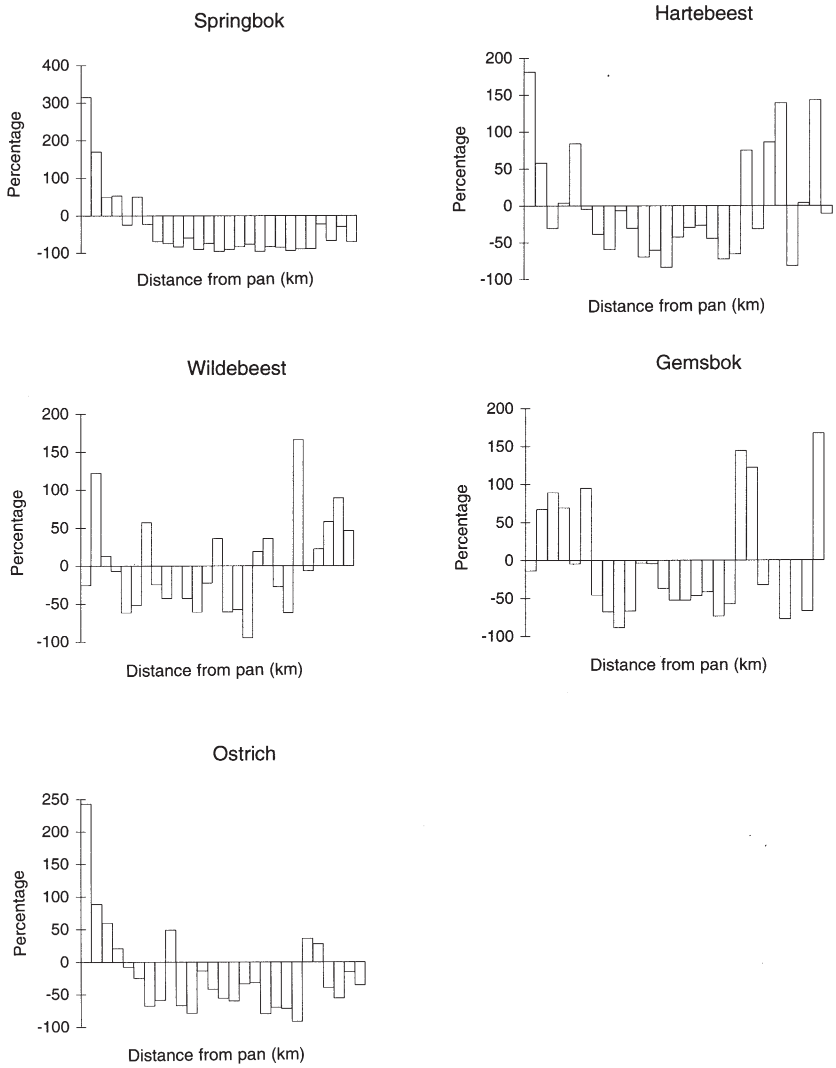

Fig. 3. Deviation in percentage of observed numbers of animals from expected at different distances from pans.

and Ncojane dry season ($r_s = 0.73$; $P < 0.06$). The differences in mean distances between wet and dry season within villages and species were non-significant for all species except for springbok (Table 3). Springbok were found further away from Ncojane in the wet season, and there was a trend for hartebeest to be further away from both villages during dry season.

Discussion

Seasonal variation

The road-side counts revealed considerable seasonal variation in numbers of several herbivore species. Changes in population size as well as small and large scale

Table 3. Mean maximum (livestock) and minimum (wild herbivores) distances between village centre and observation of each species. Mean (±SE) distances are separated for wet and dry season and for the two villages. The distances for all herbivores are compared with distances for livestock. *P<0.05, **P<0.01, ***P<0.001

	Distance from Hukuntsi (km)			Distance from Ncojane (km)		
Species	Wet season	Dry season	*P*<	Wet season	Dry season	*P*<
Livestock	19.6 (2.1)	22.0 (4.6)	0.940	15.6 (2.1)	9.8 (1.6)	0.113
Springbok	32.6 (1.0)***	36.2 (1.9)**	0.146	34.4 (2.5)***	22.9 (3.0)**	0.015*
Hartebeest	37.0 (3.2)***	44.3 (4.2)**	0.078	38.7 (3.0)***	56.7 (7.0)***	0.060
Wildebeest	46.8 (4.3)***	51.5 (7.8)**	0.617	34.3 (3.0)***	44.1 (5.9)***	0.201
Gemsbok	65.8 (5.2)***	68.5 (5.0)***	0.785	76.2 (5.2)***	71.2 (3.7)***	0.218
Duiker	63.5 (11.2)**	44.7 (8.9)*	0.208	46.0 (7.6)***	37.1 (7.4)**	0.405
Steenbok	35.3 (4.2)**	46.4 (6.5)**	0.269	27.7 (4.4)*	26.9 (6.3)*	0.725

redistributions may have contributed to the changes in animal abundance. The general group size, as well as the tendency for larger groups to be formed during the rainy season and to split up during the dry season, supports results from other studies (Bigalke, 1972; Jarman, 1973; Nagy & Knight, 1994). For most species, the variation in numbers observed between seasons was considered too big to be explained merely through calving and mortality.

Springbok, hartebeest and wildebeest are reported to be highly mobile with wet season concentrations in the 'Schwelle' region, where they also calve (Spinage & Matlhare, 1992; Crowe, 1995). Wildebeest are most water-dependent (Mills, Biggs & Whyte, 1995) and move both towards north-east, south and south-west (Crowe, 1995) or undertake more or less nomadic movements within the Kalahari (DHV, 1979). Hartebeest have been reported to move extensively and to spend the dry season in the Central Kalahari Game Reserve (Crowe, 1995), whereas springbok show localized movements (DHV, 1979). The territory-holding steenbok and duiker are sedentary and the formation of pairs as well as lambing may explain the observed patterns.

The large-scale spatial and temporal heterogeneity in abundance and quality of food and mineral supplies can, together with predation, be driving forces in various types of migration. (Fryxell & Sinclair, 1988; Bonifica, 1992).

The present data indicated a wet season concentration in the 'Schwelle' region, a concentration that also has been noted by several other authors (e.g. Bonifica, 1992; Crowe, 1995). There is an increasing rainfall towards north and north-east of the study area. South and south-west of the area, the Kalahari contains a couple of irregularly flowing rivers along the border of Botswana. In that direction, the mean annual rainfall decreases (Pike, 1971). Ringrose *et al.* (1997) noted through interpretation of satellite imageries that the 'Schwelle' has a lower plant biomass than the surrounding areas. Generalized vegetation indexes presented for different months (Potsdam Institute of Climate Impact Research, W. Cramer, pers. comm.) identify the 'Schwelle' to have relatively high biomass values in late wet season (February–April). The biomass of both grass and woody species is expected to increase towards the north-east, with an increasing rainfall (see review by Rutherford, 1980) and a close relationship between production of C_4 grasses and rainfall (Epstein *et al.*, 1997). On the other hand, a lower biomass may indicate a better food quality, as an inverse relationship has been observed between nitrogen and biomass in dry savannas (Penning de Vries & Djitèye, 1982).

The observed patterns in animal abundance indicate that the migratory species during early wet season move towards areas with lower food biomass, a pattern that has been observed for other migrating ungulates (Maddock, 1979; Fryxell & Sinclair, 1988).

During the dry season, drinking water is generally not available within the present range of the studied herbivores. During the wet season, water occurs mostly in discrete small patches (pans) or temporarily flowing rivers. Considering the high density of pans in the study area, this could enhance further the value of the 'Schwelle' as a wet season concentration area, although the present data show that some species concentrate around the pans even if they did not contain water (see below).

In summary, the concentration of large herbivores in the 'Schwelle' region may have evolved as a response to several favourable conditions: a relatively good food abundance during some periods, a comparatively good food quality (cf Fryxell & Sinclair, 1988) and an availability of water and mineral licks at pans.

It can not be ruled out that migration from the 'Schwelle' reduces the risk of predation (cf. Fryxell & Sinclair, 1988). The data available for a discussion of such a hypothesis are too scanty.

Abundance in relation to pans and villages

Pans are important for wildlife in southern Africa and especially in the Kalahari (Parris & Child, 1973) as they provide mineral licks (Parris, 1971), a relatively nutrient-rich vegetation (DHV, 1979) and, temporarily, drinking water. According to the present data, the herbivores concentrate around the pans, up to a few km. The increase in animal abundance some kilometres from the pan may be a response to depleting food resources close to pans. The relatively weak relation found between numbers of wildebeest and distance to pans (Fig. 3) might be due to these large-bodied grazers in big groups not being able to find enough grazing in vicinity of the pans or to an underestimation of wildebeest numbers due to a lack of night observations (DHV, 1979). Springbok, gemsbok, hartebeest and wildebeest were seen licking the bottom material in pans. Some springboks shot at one of the pans had more than 0.1 l of clay in their guts (pers. obs.).

Springbok, gemsbok and ostrich utilized the pans more in the rainy season than in the dry, independent of whether pans held water or not. For the first two species, similar behaviour has been reported by Bothma (1972), and Owens & Owens (1978), although Bigalke (1972) claims that grazing at pans is particularly important for springbok in the dry season.

Springbok generally prefer the short vegetation at pans and in fossil river valleys, and were found by DHV (1979) mainly on the 'Schwelle' and in the pan-rich areas around Mabua Sehube, south of the present study area. This species preferentially feeds on short grass in the wet season and browses, primarily from the dwarf shrubs surrounding the pans, in the dry season (Bigalke, 1972). In addition, gemsbok and hartebeest graze the closely cropped grass around the pans as well as feeding in the surrounding savanna (DHV, 1979). The utilization of browse on some shrub species has been recorded as being much higher at the pans than in the surrounding savanna (pers. obs.). The grazeable biomass around the pans during most of the year is very low, but quality is high, and as water and salt licks act as attractants, animal presence and grazing intensity in the vicinity is little affected by declining forage availability (Knight, 1995).

In most cases, wild herbivores were counted 10 km further (compared to cattle) away from the villages. There is likely to be a high incidence of direct disturbance, including hunting by people, and heavy grazing by livestock around the villages causing a shortage of preferred food. Parris & Child (1973) recorded similar exclusion of indigenous ungulates by livestock grazing around old/large villages in the Kalahari, whereas domestic and wild animals mixed around small villages with little livestock. DHV (1979) found gemsbok, particularly, to be strikingly absent from all areas with human influence, a pattern which is supported by this study. The disappearance of the palatable grasses, and an often subsequent increase of annual grasses and/or woody species, due to heavy grazing by livestock (Skarpe, 1986) reduces the quality of the habitat for wild grazers like hartebeest and wildebeest, and also for mixed feeders like springbok. Cattle are preferential grazers, but in the Kalahari often depend on browse for much of the dry season (APRU, 1980), and goats browse all the year, and together they may well cause a decline in the availability of high quality browse.

References

APRU (1980) *Ten Years of Animal Production and Range Research in Botswana.* Animal Production Research Unit, Ministry of Agriculture, Botswana.

Ben-Shahar, R. (1995) Habitat classification in relation to movements and densities of ungulates in a semi-arid savanna. *Afr. J. Ecol.* **33,** 50–63.

Bergström, R. & Skarpe, C. (1985) Characteristics of the Kalahari sand in western Botswana. *Meddelanden fran Växtbiologiska Institutionen, Uppsala 1985,* 3.

Bigalke, R.C. (1972) Observations on the behaviour and feeding habits of the springbok, *Antidorcas marsupialis*. *Zool. Afric.* **7,** 333–359.

Bonifica, (1992) *Initial Measures for the Conservation of the Kalahari Ecosystem*. Final Report to Department of Wildlife and National Parks, Government of Botswana.

Bothma, J. du P. (1972) Short term response in ungulate numbers to rainfall in the Nossop river of the Kalahari Gemsbok National Park. *Koedoe* **15,** 127–134.

Crowe, D. (1995) Status of selected wildlife resources in Botswana and recommendations for conservation actions. In: *Proceedings of a Symposium on the Present Status of Wildlife and its Future in Botswana* (Ed. K. Leggett). The Kalahari Conservation Society and The Chobe Wildlife Trust, Gaborone.

DHV (1979) *Countrywide Animal and Range Assessment Project*. Final report DHV Consulting Engineers to the Republic of Botswana, Ministry of Commerce and Industry, Department of Wildlife, National Parks and Tourism.

Dunham, K.M. (1994) The effect of drought on the large mammal populations of Zambesi riverine woodlands. *J. Zool.* **234,** 489–526.

Epstein, H.E., Lauenroth, W.K., Burke, I.C. & Coffin, D.P. (1997) Productivity patterns of C_3 and C_4 functional types in the U.S. great plains. *Ecology* **78,** 722–731.

Frost, P.G.H., Meneaut, J.-C., Walker, B.H., Medina, E., Solbrig, O.T. & Swift, M. (1986) *Responses of Savannas to Stress and Disturbance. Biology International Special Issue 10.*

Fryxell, J.M. & Sinclair, A.R.E. (1988) Causes and consequenses of migration by large herbivores. *Trends Ecol. Evol.* **3,** 237–241.

Happold, D.C.D. (1995) The interactions between humans and mammals in Africa in relation to conservation: a review. *Biodiv. Cons.* **4,** 395–414.

Jarman, P.J. (1973) The social organisation of antelope in relation to their ecology. *Behaviour* **48,** 215–267.

Knight, M.H. (1995) Drought-related mortality of wildlife in the southern Kalahari and the role of man. *Afr. J. Ecol.* **33,** 373–394.

Kuper, A. (1970) *Kalahari Village Politics*. Cambridge Studies in Social Anthropology. Cambridge University Press, Cambridge.

Leemans, R. & Cramer, W. (1991) *The IIASA Climate Database for Mean Monthly Values of Temperature, Precipitation and Cloudiness on a Terrestrial Grid*. IIASA, Laxenburg.

Leistner, O.A. (1967) *The Plant Ecology of the Southern Kalahari*. Botanical Survey Memoir no. 38. Government Printer, Pretoria.

Maddock, L. (1979) The 'migration' and grazing succession. In: *Serengeti: Dynamics of an Ecosystem* (Eds A.R.E. Sinclair and M. Norton-Griffiths). University of Chicago Press.

McNaughton, S.J. & Georgiadis, N.G. (1986) Ecology of African grazing and browsing animals. *Ann. Rev. Ecol. Syst.* **17,** 39–65.

Mills, M.G.L., Biggs, H.C. & Whyte, I.J. (1995) The relationships between rainfall, lion predation and population trends in African herbivores. *Wildl. Res.* **22,** 75– 88.

Milton, S.J., Dean, W.R.J. & Siegfried, W.R. (1994) Food selection by ostrich in Southern Africa. *J. Wildl. Manage.* **58,** 234–248.

Nagy, K.A. & Knight, M.H. (1994) Energy, water and food use by springbok antelope (*Antidorcas marsupialis*) in the Kalahari desert. *J. Mamm.* **75,** 860–872.

Owens, M.J. & Owens, D.D. (1978) *Central Kalahari Range Study*. Project Report. Department of Wildlife, Gaborone.

PARRIS, R. (1971) The ecology and behaviour of wildlife in the Kalahari. *Botswana Notes and Records, Spec. Ed.* **1,** 96–107.

PARRIS, R. & CHILD, G. (1973) The importance of pans to wildlife in the Kalahari and the effect of human settlements on these areas. *J. S. Afr. Wildl. Mgmt Ass.* **3,** 1–8.

PENNING DE VRIES, F.W.T. & DJITÈYE, M.A. (1982) *La Productivité des Paturages Sahéliens*. Centre for Agricultural Publishing and Documentation, Wageningen.

PIKE, J.G. (1971) Rainfall over Botswana. *Botswana Notes and Records* **1,** 69–75.

RINGROSE, S., VANDERPOST, C., KWEREPE, R. & MULALU, M. (1997) *Comparison of Range Degradation in Botswana using Satellite Imagery*. Final Report of an ODA Commissioned Joint Project, University of Botswana.

RUTHERFORD, M.C. (1980) Annual plant production-precipitation relations in arid and semi-arid regions. *S. Afr. J. Sci.* **76,** 53–56.

SKARPE, C. (1986) Plant community structure in relation to grazing and environmental changes along a north–south transect in the western Kalahari. *Vegetatio* **68,** 3–18.

SKARPE, C. & BERGSTRÖM, R. (1986) Nutrient content and digestibility of forage plants in relation to plant phenology and rainfall in the Kalahari, Botswana. *J. arid Environ.* **11,** 147–164.

SPINAGE, C.A. (1992) The decline of the Kalahari wildebeest. *Oryx* **26,** 147–150.

SPINAGE, C.A. & MATLHARE, J.M. (1992) Is the Kalahari cornucopia fact or fiction? A predictive model. *J. appl. Ecol.* **29,** 605–610.

WALKER, B.H. (1979) Game ranching in Africa. In: *Management of Semi-Arid Ecosystems* (Ed. B.H. Walker). Elsevier, Amsterdam.

(Manuscript accepted 27 October 1997)