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(With 3 figures in the text)

Size and age/sex composition were recorded for social groups of seven ungulate species over two years. Most species showed seasonal changes which were correlated with rainfall or with their breeding cycle. Group sizes tended to increase during the rainy seasons, although some species, particularly wildebeeste, also aggregated strongly on fresh burns. For all seasonally breeding species, the average male had little contact with females during the conception peak, although female herds almost invariably had about one attendant male.

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Introduction

Despite recent interest in comparative studies of the social behaviour of African ungulates (Geist, 1974; Jarman, 1974; Estes, 1974; Leuthold, 1977; Jarman & Jarman, 1979), most of the available data on social groupings are essentially descriptive. Leuthold & Leuthold (1975) and Rodgers (1977) present basic quantitative data for several species, but to test the syntheses summarized in Jarman (1974) and Geist (1974) requires much more detailed information on group size and structure, and on how these vary within and between populations, than are currently available.

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Jarman (1974) sought to explain the social organization of African antelope in terms of their ecology. Emphasizing the limitations imposed on species by their body size, he grouped them into five classes (*A–E* below), identifying several behavioural and ecological gradients across these classes. These classes are presented below. Estes (1974) and Leuthold (1977) present alternative classifications.

Class *A* usually seen singly or in pairs; little seasonal change in habitat choice or home range; territorial, the territories coinciding with home ranges; cryptic anti-predator behaviour; mainly browsers, selecting highly nutritious food items; weight 1–20 kg. *B*: group size 1–12 (this may vary seasonally); usually several female/offspring units within the home range of a single (territorial) male; cryptic; browse or graze off selected plant parts; 15–200 kg. *C*: group size six to several hundred, varying with season and region; usually females are highly gregarious and males are either solitary and territorial or else in “bachelor” herds; these species may either hide or flee from predators; feeding is typically flexible, both feeding habitat and plant species choice varying with season; 20–200 kg. *D*: groups may be of similar size and type to those of class “*C*”, but these species may also form large, cohesive “super-herds” of thousands of animals near localized food resources or when migrating; such “facultative aggregations” may distort the basic territorial organization either flee from predators or show communal defence; “bulk roughage” feeders, accepting variety of grasses but selecting for growth stage and plant part; habitat choice may reflect seasonal changes in grass growth within the home range; 100–250 kg. *E*: may live permanently in herds of several hundred, with males and females together, although bachelor herds may also occur; greater herd stability than in class “*D*”, but herds may move large distances to follow food resources; in terms of food quality, the least selective of the antelope; communal defence against predators, flight; 200–700 kg.

Variations in group size and structure are clearly basic features of these classes and should be quantified wherever possible if the concepts summarized by Geist (1974) and Jarman (1974) are to be tested and developed. During a two year study of ungulate ecology at Kyle Recreational Park, the present author was able to obtain comparative grouping data for several ungulate species. These include: from class “*B*”, the Common reedbuck, (*Redunca arundinum*); from class “*C*”, Impala (*Aepyceros melampus*) and Greater kudu (*Tragelaphus strepsiceros*), and from class “*D*”, Tsessebe (*Damaliscus lunatus*) and Blue wildebeest (*Connochaetes taurinus*). Data for Plains zebra (*Equus burchelli*) and White rhinoceros (*Ceratotherium simum*) are also presented.

Methods

The study area

The study was carried out at Kyle Recreational Park, Zimbabwe (31°00'E, 20°10'S) from July 1976 to July 1978. The area available to most large ungulates is about 3700 ha, bounded by a lake shore and a game fence. The Park is on the southern edge of the central Zimbabwean plateau at 1050 m altitude. The mean annual precipitation of 820 mm falls mainly as summer rains from November to March inclusive; other precipitation is usually “guti”: light mist from low-lying clouds. During the study, rainfall at Kyle was markedly higher than the long-term average (1135 mm in 1976–77 and 1200 mm in 1977–78; Zimbabwean Meteorological Office records from Lake Kyle Fisheries Research Centre). About one fifth of the reserve was burnt for management purposes each year: in the study area (Ferrari & Walker, 1974). This study was mainly restricted to a central open grassland and savanna in November in 1977.

The vegetation of the region is "deciduous miombo savanna woodland" (Wild & Fernandes, 1967), characterized by *Brachystegia spiciformis* and *Julbernardia globiflora*; burning and woodcutting before the park was established has left a patchwork of vegetation types within the park, ranging from sub-climax grassland to true *Brachystegia* woodland. Thirteen vegetation types have been described in the area (Ferrar & Walker, 1974). This study was mainly restricted to a central open grassland and savanna area, most of the grassland being characterized by either *Hyperthelia dissoluta*, *Loudetia simplex* or *Brachiaria brizantha*, the savanna by *Acacia* species.

The species studied comprise most of the ungulate biomass; other species present in quantity include: giraffe (*Giraffa camelopardis*), buffalo (*Syncerus caffer*), Grey duiker (*Sylvicapra grimmia*), and steenbok (*Raphicerus campestris*). Predation is light, the only large predator being Leopard, (*Panthera pardus*), at low densities.

Transects

Standard road transects were driven through the open grassland and savanna areas of the reserve at intervals of from two to three weeks throughout the study period, except for October 1976 and March and April 1977, when no vehicle was available. Two routes were used, totalling 64 km; each alternated between afternoon and morning on successive surveys. Transects were driven in the early morning (within three hours of sunrise) or late afternoon (within three hours of sunset) at 10–15 kph, always with the same observer (the author). Whenever ungulates were sighted, the car was stopped and the group's size and age/sex composition was recorded. 7 × 50 binoculars were used to check the group size and composition, but groups were located initially by naked eye.

To facilitate interspecific comparisons, only three age sex classes are used in the following analysis. While some species could be classified in great detail, classes of one species were not necessarily compatible with those of another. Animals were therefore classified either as males or females considered to be at least potentially capable of reproducing (i.e. adults or subadults of each sex) or else as "young".

Describing groups

A group was taken as any collection of animals showing co-ordinated activity, e.g. heading in the same direction and stopping and starting at about the same time. If, as in a diffuse grazing group, this definition was uncertain, a maximum inclusion distance of 50 m separation from the nearest neighbour was used to define the group boundaries. This criterion was based partly on observation of co-ordinated groups and was partly imposed by practical considerations: the visibility in many parts of Kyle was such that an animal more than 50 m away from its companions and on the far side of the group from the observer might easily be missed. Ideally, the inclusion distance for such species as tsessebe should have been larger. Solitary animals were treated as groups of size one.

Although mean group size is the basic statistic given by transect (or any other "cross sectional") studies, it need not be very useful in describing social organizations, since the species may be found in more than one type of herd. Also, mean group size has little to do with the size of the group containing the average individual. This is more accurately described by the typical group size (Jarman, 1974; Underwood, 1978) which, together with the derived age/sex class companionship indices (Underwood, in press) gives, for example, the total number of social partners immediately available to the average animal, information clearly of interest to the student of social behaviour.

These indices concentrate on the individual animals sighted, taking, for example, the number of companions of a given age/sex class found with each male and averaging this over all males sighted. Since there might be more than one male in a given group, these observations are not independent; the statistical properties of the indices are complex (compare Lloyd's, 1967 treatment of a related, but simpler, index) and it is not yet possible to compare two indices and show that they differ significantly.

However, significance tests of differences in mean group size almost certainly give a conservative estimate of the significance of the corresponding typical group size comparison (Underwood, 1978). Mean group size is therefore given alongside the more descriptive indices presented below. In examining the data for correlation with rainfall, each monthly companionship index is treated as a single observation, rather than the result of up to 200 group sightings.

Grouping behaviour changes through the day for most species studied, particularly Impala, herds seen at dawn sometimes splitting into smaller foraging groups during the day and reassembling at or after dusk. The data presented necessarily describe the daytime foraging groups. Variation due to diurnal changes was minimized since records were taken at fixed times of day.

Seasonal changes

It is clearly important to discriminate as far as possible between those seasonal changes in behaviour resulting directly from changes in the environment, and those which are part of a long term adaptation. For example, if neonate survival depends on herd protection, an increase in female herd size during or before the birth season may be due less to an improved food supply reducing competition (a short term response), than to females accepting more competition to keep their young in the herd: in the latter case, births would ideally be timed so that food is abundant and competition low (a long term response). Short term responses, by definition, "track" the environment closely and are sensitive to departures from the average seasonal cycle. Grouping behaviour which is a long term adaptation would be relatively insensitive to such departures, any behavioural changes tending to follow the average seasonal cycle rather than the current one.

In the latter case, birth or mating aggregations might reasonably be expected to be timed so that the available food supply can support them. To distinguish as far as possible between observed variations which may be due to long term adaptation and those which cannot be explained in this way, a correlation analysis was performed on grouping statistics (mean total group size and number of females in the group containing the average female) and rainfall both in the current month and in the same month averaged over the previous fifteen years. Partial correlations of grouping statistics with rainfall, correcting for "expected" rainfall, were then calculated.

For species known to breed seasonally at Kyle, the conception peak was estimated by counting back from the observed birth peak, using gestation period records taken from Child *et al.* (1972, Tsessebe); Braack (1973, wildbeeste), Skinner (1973, Impala, kudu); Dittrich (1970, kudu); Cowley (1975, Impala); Mentis (1972, all species).

Results

General

Group size varied between months over the whole study period for most species. Table I and Fig. 1 summarize the data for all groups: similar variations occurred in particular types of groups and in the ratio of group types seen. For several species, notably Impala, subclasses of groups containing males could be recognized: males with female herds, solitary individuals and all-male groups. The proportion of these herds varied through the year for several species, solitaries and male/female herds usually increasing relative to all-male herds during the conception peak (Fig. 2). Concentrating on the conception peak, together with one month either side of this, the companionship indices of the "average" male differed sharply from those of males with at least one female companion. (Table II). Although reed-buck and rhinoceros had no known conception peak, data for the whole year for these species are included in Table II for comparison.

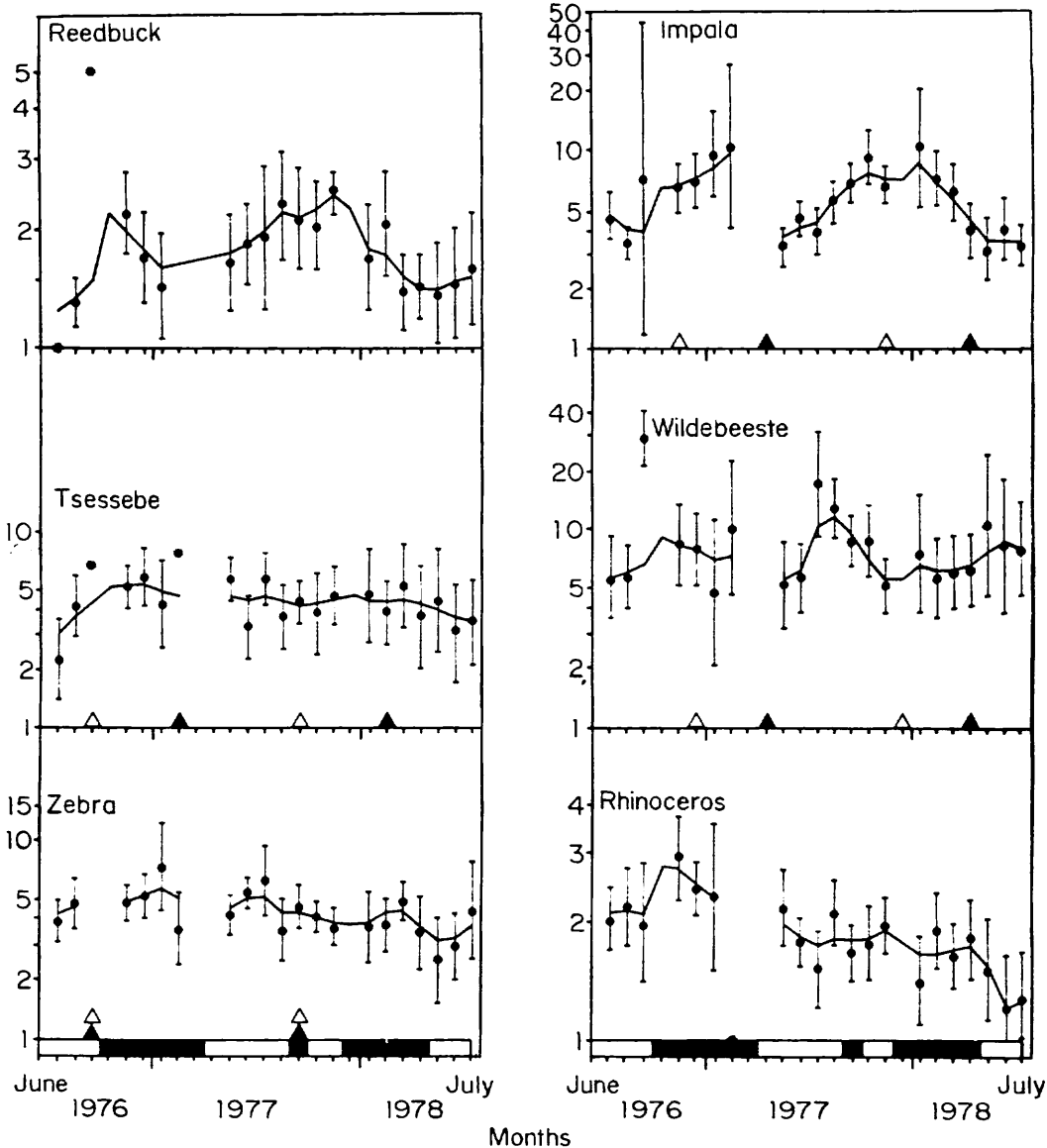


FIG. 1. Variation in monthly records of group size in six ungulate species at Kyle Recreational park. Vertical bars indicate 95% confidence limits for the mean, circles show the mean for a particular month. The lines connecting month to month connect the smoothed means. Points were smoothed by:

$$(x_{(i-1)}n_{(i-1)} + 2x_i n_i + x_{(i+1)}n_{(i+1)}) / (n_{(i-1)} + 2n_i + n_{(i+1)}),$$

where x is the mean for the i th month and n is the number of groups sighted during that month. Hollow triangles, observed birth peak; filled triangles, estimated conception peak. Filled horizontal bars indicate the growing season, estimated from the rainfall data. Means and confidence limits were calculated using log-transformed data.

TABLE I

Results of Kruskal-Wallis one way analysis of group sizes of seven species of ungulates at Kyle Recreational Park; sightings broken down by month

Species	Each month separately			Same month for each year		
	Chi-square	P	d.f.	Chi-square	P	d.f.
Reedbuck	37.9	0.006	17	25.7	0.007	11
Impala	93.1	0.000	20	83.5	0.000	11
Tsessebe	23.0	0.287	20	13.9	0.237	11
Wildebeeste	36.2	0.014	20	8.8	0.645	11
Kudu	47.2	0.000	19	40.2	0.000	11
Zebra	32.4	0.028	19	11.9	0.368	11
Rhinoceros	48.9	0.000	20	25.8	0.007	11

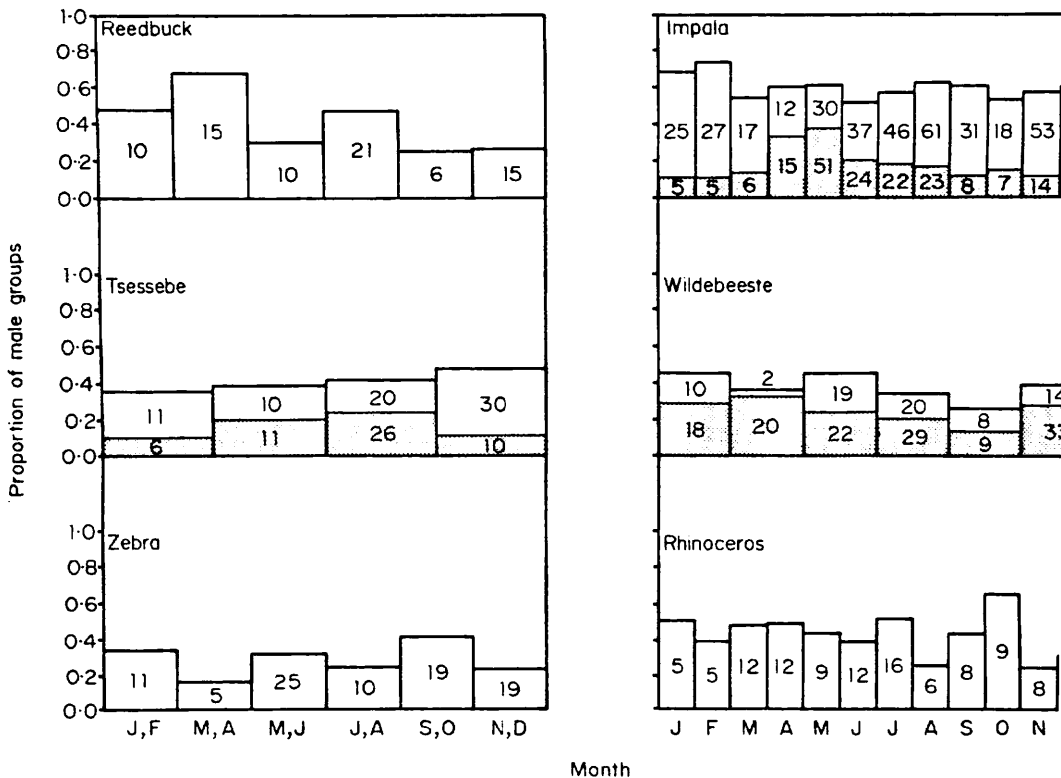


FIG. 2. Variations in the proportions of groups containing males of six ungulate species at Kyle Recreational Park through the year. Data from different months pooled to give reasonable chi-square expectations. Histograms indicate the proportion of groups containing males which did not contain females. Where possible, the cells are subdivided into solitary male sightings (shaded) and bachelor herds (clear). Kudu are not included, since sighting rates were too low to allow a meaningful pooling of months. Chi-values for the significance of changes in proportions were: reedbuck, 21.5 (5 d.f.); Impala, 71.7 (22 d.f.); Tsessebe, 12.5 (6 d.f.); wildebeeste, 19.2 (10 d.f.); zebra, 8.54 (5 d.f.); rhinoceros, 13.7 (11 d.f.).

TABLE II

The association between males and females during the conception peak for ungulates at Kyle Recreational Park, July 1976–July 1978

Species	Number of companions during the conception peak					
	Of all males		Of males with at least one female		Of all females	
	Males	Females	Males	Females	Males	Females
Reedbuck (B, 1)	0.541	1.177	0.590	1.807	0.974	0.922
Impala (C, 5a)	4.355	1.741	1.145	7.234	1.181	9.510
Tsessebe (D, 5a)	2.296	1.185	0.235	3.765	1.000	4.344
Wildebeeste (D, 5a)	4.716	1.084	0.750	6.438	1.020	10.337
Kudu (C, ?)	0.818	1.046	0.286	3.286	0.489	2.170
Zebra (-, 1c)	2.328	1.023	0.293	3.195	1.202	2.900
Rhinoceros (-, 6)	0.324	1.088	0.464	1.760	0.785	0.932

Values in brackets after species' names give Jarman's (1974) and Leuthold's (1977) classification of the species' feeding style and social organization respectively.

There was a significant correlation between female/female companionship (the number of females in the group containing the average female) and rainfall in the same month (Table II), but once the effects of a possible long term adaptation to the "expected" rainfall were removed, all partial correlations were weak. If grouping data for the same month in each of the two years are pooled for correlation with average rainfall, as was done by Rodgers (1977), similar but slightly stronger correlations to those in Table III are found. Female/female companionship is used in the correlation analysis because female grouping is often considered to be basically governed by ecological factors, male groupings being adaptations to female distribution and mating opportunities (Jarman, 1974; Geist, 1974). Most indices were lower during the dry season than during the rains (Fig. 3).

Burns

All species studied, particularly wildebeeste, tended to aggregate on fresh burns. Such aggregations often gave a first impression of being a single amorphous herd but when the criteria for defining group limits were applied, aggregations were usually found to consist of several groups which were close to one another but discrete, moving independently and showing different activities. Social grouping indices, therefore, were not necessarily affected by the dry season burns, despite these aggregations (Fig. 3).

For wildebeeste, burns were the main cause of seasonal variation in grouping behaviour. After about a week of confusion when they first moved onto a burn, they tended to forage in subgroups, each subgroup retiring to a separate area for resting or rumination bouts: subgroups left the burn in the early evening, each in a different direction, to graze in longer grass. The subgroups had the same size range (15–40 individuals) as foraging groups at other times of the year and were so independent of each other a month after the burn that they were classified as separate herds. Groups of other species were more clearly separate when on the burns, although there was rarely any overt sign of mutual avoidance.

TABLE III

Results of Kendall correlation analyses on group size and rainfall statistics for ungulates at Kyle Recreational Park, Zimbabwe

Species (n)	Female/female companionship				Correlation with rainfall		Mean monthly group size	
	Current rainfall	Average rainfall	Current, controlling for average	Average, controlling for current	Current rainfall	Average rainfall	Current, controlling for average	Average, controlling for current
Reedbuck (20)	0.132	0.273	-0.042	0.245	0.021	0.082	-0.035	0.087
Impala (20)	0.495**	0.660**	0.165	0.522	0.448**	0.493**	0.218	0.314
Tsessebe (20)	-0.095	0.092	-0.189	0.187	0.238	0.365*	0.026	0.286
Wildebceeste (21)	-0.019	-0.118	0.065	-0.133	-0.095	-0.197	0.030	-0.179
Kudu (16)	0.185	0.505**	-0.171	0.501	0.422*	0.484**	0.189	0.319
Zebra (20)	-0.026	0.066	-0.089	0.102	-0.021	0.016	-0.039	0.036
Rhinoceros (20)	-0.021	0.150	-0.140	0.203	-0.081	0.143	-0.211	0.240

¹ * $P < 0.05$

¹ ** $P < 0.01$

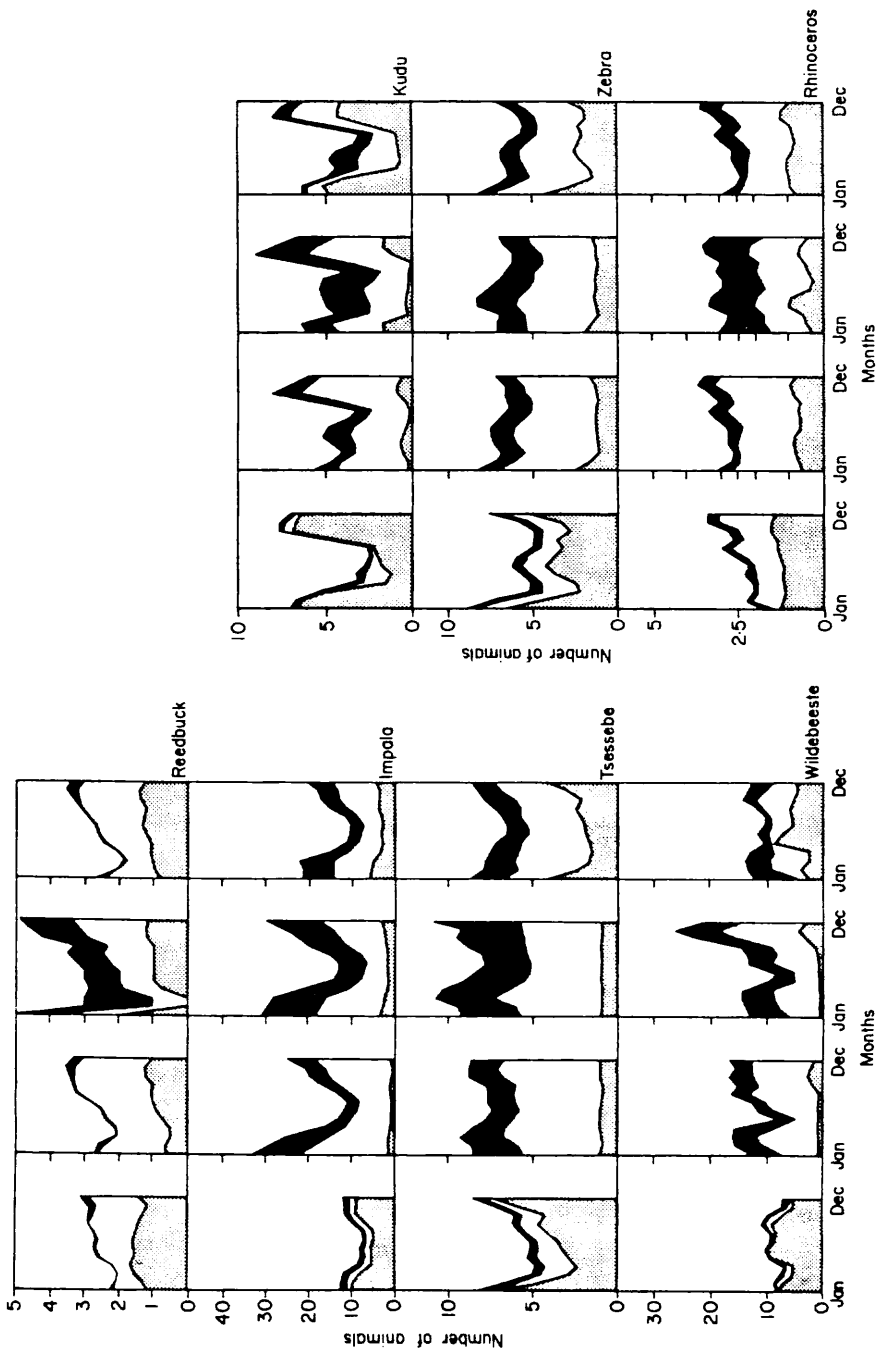


FIG. 3. Seasonal variations in the composition of the group containing the average individual of seven ungulate species at Kyle Recreational Park. Grey: females; black: young. From left to right, the focal animals are the average male, the average female, the average young, and the average animal, regardless of age/sex class.

Reproduction and grouping

Incidental behavioural observations suggest that the males of all three territorial species with known calving peaks had seasonal territories. Impala male territorial behaviour (calling, herding females, fighting) was obvious and was seen mainly at or near the conception peak. Wildebeeste and Tsessebe territorial behaviour was seen much less often and was not so strongly limited to the conception peak (author's unpublished records).

For several species, behaviour linked to reproduction had an obvious effect on grouping. Rutting Impala males often tried to control the movements of females, possibly contributing to the general decline in measures of female companionship during the estimated conception peak. While most herds of female Impala had only one male with them during the conception peak, occasionally large, predominantly male, herds were seen with one or two males and several females. This was not seen in other species. Solitary Impala females were often seen during the birth peak, apparently being about to lamb or having recently lambed (neonate lambs were rarely seen until the females formed nursery herds). Tsessebe territories were almost completely contiguous with the home range of a particular female herd (judging by herd size and age structure), although the male might not be seen in the immediate neighbourhood of the female herd. The only obvious changes in Tsessebe female herds were during the birth season, from September onward, when yearlings were produced and driven out by the males and individual females might be seen at some distance from the group with a creche of up to six calves. Zebra were usually seen either in bachelor groups or harems: harems varied very little in size through the year and, while they concentrated on the burns, they were rarely close together. Zebra bachelor herd sizes were more changeable, peaking during the early rains, rather than following the burns (Fig. 3). Indices of grouping behaviour therefore varied through the year, female experience (essentially, herd size) being more constant. During the conception peak, these bachelor male herds were sometimes seen trailing several hundred metres behind a harem herd for several hours.

Trend

Only one species, rhinoceros, showed a strong trend through the study period (Table IV). The significance tests are based on pairwise comparisons, so the marginally significant trend for zebra is probably not meaningful). At the start of the study, up to nine rhinoceros

TABLE IV

Trends in monthly mean group size of seven species of ungulate at Kyle Recreational Park (means obtained from transformed data) through the study period. Spearman rank correlation, two tailed test of significance

Species	Correlation	<i>n</i>	Probability
Reedbuck	-0.093	20	0.696
Impala	-0.208	21	0.336
Tsessebe	-0.321	21	0.156
Wildebeeste	0.118	21	0.610
Kudu	0.233	19	0.336
Zebra	-0.495	20	0.027
Rhinoceros	-0.557	21	0.009

seen together near wallows but these were probably very temporary aggregations. Possibly because the high rainfall and high water table from 1976–78 increased the number of suitable wallowing sites, such large groups became scarce.

Discussion

Scale effects

Grouping data and incidental behavioural observations were not obviously incompatible with the qualitative descriptions of the social organization of the various species as summarised by Leuthold (1977) and given in more detail by Estes (1966), Jungius (1971), Joubert (1972), Klingel (1972), Owen-Smith (1975) and Jarman (1979). Reedbuck, Impala, Tsessebe, wildebeeste and White rhinoceros are usually thought of as showing classical territoriality, although Tsessebe might be classified with Plains zebra as having a "harem" based mating system. Kudu social organization is still unclear (Leuthold, 1977).

At Kyle, zebra and wildebeeste were among the species with the most stable group size through the year. Although both may form large, amorphous aggregations elsewhere, Plains zebra always retain the harem as the basic social unit (review, Leuthold, 1977: 202–204) while some wildebeeste may be in comparatively small "semi-exclusive" herds, even when most of the population is migratory (Estes, 1966). The normal sighting of these species at Kyle was, apparently, a fairly stable social unit (bachelor herd, breeding herd, or breeding male with or without females). Impala and kudu groups, on the other hand, varied much more with the seasons, suggesting that these "sedentary" species were the most affected by seasonal changes, responding by varying the size of subgroups of the social unit.

This is consistent with Jarman's (1974) classifications. The small size of Kyle and the favourable conditions during the study, coupled with the permanent water supply, would rarely present a resource distribution likely to concentrate or disperse the coarser feeders, while the more selective species, Jarman's class "C" feeders, would be sensitive to changes in particular plant species (Owen-Smith, 1979; Dunham, 1980), rather than in vegetation types, and are therefore be more likely to be affected by seasonal changes in food resources at Kyle. The effect of burning, the only factor acting on a scale likely to affect the coarser feeders, was probably minimized by the exceptional rains and high water table during the study. While herbivores at Kyle favour burns, (Ferrar & Walker, 1974) a space-time system (Hediger, 1950) seems to operate such that a seemingly amorphous mass of Impala or wildebeeste on a burn in fact consisted of several discrete social groups, as defined by the criteria used. These criteria were chosen to describe the social partners immediately available to an observed animal.

Rainfall and grouping

If rainfall is used as an index of productivity, Table III suggests that most species at Kyle are fairly insensitive to departures from the "expected" seasonal food distribution. With a high correlation between average and current rainfall at Kyle during the study, there may have been too few observations to distinguish between the two possibilities. However, re-examination of Rodgers' (1977) records for Impala and wildebeeste, using a similar partial correlation analysis to that presented above, also shows only a weak correlation between group size and actual rainfall, once the expected rainfall is controlled for (Table V). The question thus arises as to how relevant, as opposed to other seasonal factors, rainfall is.

TABLE V

The relationship between rainfall in the previous two months and mean group size for impala and wildebeeste. Kendall correlation partial correlation, controlling for the mean rainfall for those two months over the study period. Data from Rodgers (1977) for Selous Game Park, Tanzania

Species	Period	Correlation			Group size and current rainfall controlling for mean rainfall
		Group size and current rainfall	Group size and mean rainfall	Current rainfall and mean rainfall	
Impala	Nov.-Jan. only	0.495	0.495	0.509	0.325
	All records	0.382	0.449	0.667	0.124
Wildebeeste	Nov.-Jan. only	0.175	0.234	0.509	0.133
	All records	0.414	0.419	0.666	0.195

Rainfall alone has often been used to estimate the food resources of African ungulates, notably by Phillipson (1975) and Coe, Cumming & Phillipson (1976), but the relationship underlying such studies (Rosensweig, 1968), has recently been challenged (Rutherford, 1977). However, while the regression equation for productivity against rainfall may vary between habitat types, net annual above ground production within a given habitat type increases with increasing rainfall (Rutherford, 1977) and, within a particular habitat, more production is closely related to the rainfall in the preceding months. One assumption using rainfall as an index of productivity may have been seriously violated: several seasons of heavy rains left Kyle with a high water table, so that for some months the actual evapotranspiration could probably not be equated with the rain received. It is not clear whether this also applies to Rodgers' (1977) data.

Rainfall has been used as an indicator for factors likely to affect aggregations by several authors (Leuthold, 1976; Rodgers, 1977; Dunham, 1979; Jarman & Jarman, 1979; Underwood, in press). Its best documented effect is on the migratory ungulates in the Serengeti ecosystem (review in Maddock, 1979). For resident populations, however, the causal relationships involved are unclear. Jarman & Jarman (1979) emphasize the quantity and distribution of the food supply as the link between seasonal conditions (particularly rainfall) and Impala group size and structure. They note that primary production changes through the rains from shoot and flowers to leaves and storage organs: since moribund material also increases towards the end of the rains, the effect of rainfall on foraging behaviour may change qualitatively through the season. Restricting the analysis of Rodgers' data to the first three months of the expected rainy season does suggest that the actual rainfall is more influential than during the rest of the year, at least for Impala (Table V). Wildebeeste records vary so much between years that any relationship is masked. While wildebeeste records were too few to be analysed in this way, a similar relationship seems to hold.

The difficulty is not that rainfall has little effect on productivity, and so on group size and behaviour, but rather that in a short term study the effect is both complex and easily masked by, or confused with, other seasonal factors. Rainfall may help to define the growing season

but more climatic and environmental data are needed to clarify the fine scale effects likely to affect grouping behaviour in such areas as Kyle.

Group size and the breeding cycle

In all species with known birth seasons at Kyle, the social experience of the average male during the conception peak (as measured by companionship indices) differed greatly from that of males who were in groups with at least one female (Table II). While more information is needed about the behaviour of females in oestrus (as opposed to the average female), about the incidence of oestrus, and about the turnover of males in female herds, Table II suggests that the social organization of these species does effectively ensure some males of at least short term exclusive access to females, at the expense of most males in the population. A partial exception is the kudu, which may differ from the other antelope considered here in lacking a territorial mating system (Leuthold, 1977; Owen-Smith, 1977). It is unclear, however, whether many kudu females being unaccompanied by males during the conception peak (other species having an average of about one male per female group) is a cause or a result of this difference.

Non-seasonal factors

Seasonal variation is described and discussed above, but herding behaviour also varied greatly within months, even for groups of a particular type. Obvious influences were: local variations in the terrain, affecting visibility and therefore group cohesion; the recent history of individual group members; and, diurnal variations in response to light or temperature. These factors were not within the scope of the study, and are mentioned only to illustrate that a given group's size and structure is not purely due to the time of year.

Summary

The size and age/sex composition of social groups of reedbuck, Impala, Tsessebe, Blue wildebeeste, Greater kudu, Plains zebra and White rhinoceros were recorded at Kyle Recreational Park, Zimbabwe, from July 1976 to July 1978. Both mean group size and group structure varied seasonally for most species. Some of these variations were correlated with rainfall, although it was not clear how far such correlations were due to direct responses to changes in primary productivity, as indicated by rainfall, and how far to long term adaptations to seasonal productivity.

While groups were usually largest in the rainy season, pre-rains burns also caused aggregations, particularly of wildebeeste. These latter aggregations rarely acted as cohesive social units. The resource distribution at Kyle apparently affected grouping behaviour of Impala and kudu most strongly, coarser feeders having less variable groups.

During the conception peak of the seasonally breeding species, most males had little contact with females, while most female herds had a single attendant male, the social organization of most species apparently ensuring some males of at least short term exclusive access to females. An exception here, kudu, is the one species having many female herds unaccompanied by males during the conception peak: this may be linked to a more general difference between its mating system and those of the other species studied.

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