

AN EVALUATION OF SEASONAL MOVEMENT IN GREATER KUDU POPULATIONS – *TRAGELAPHUS STREPSICEROS* PALLAS – IN THREE LOCALITIES IN SOUTHERN AFRICA.

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With the emergence of more intensive studies of southern African wildlife in the last decade, greater emphasis has been placed on species-specific parameters useful to management. Among other aspects requiring attention, the distribution of populations must be examined to establish basic requirements for the species' continued survival, and once these have been determined, the minimum ecological unit for an animal is better understood. All too frequently population behavioural characteristics are ignored as a gauge to environmental needs, and physical measurements of the habitat are viewed only from an anthropomorphic standpoint. In this evaluation of population movements, various environmental factors are assessed in terms of the annual cycle, for which the species has evolved a behaviour best suited to its continued survival in present conditions.

Unlike some other bovids, greater kudu (*Tragelaphus strepsiceros*) do not migrate, but confine themselves to a restricted area throughout the year (Stevenson-Hamilton 1947). The limits of this restricted range obviously vary considerably between different parts of its wide distribution in Africa, but presumably the limits of the range of any one population are governed by the availability of required environmental factors. Seasonal changes in range have been noted casually by several early authors on wildlife in Africa (Selous 1881; Lydekker 1908; Shortridge 1934), and most rural residents know that the kudu in any particular district are to be found in different localities at various seasons.

Kudu populations studied in three separate areas of southern Africa have all shown a marked seasonal change in range within relatively narrow distance limits, making collection of data on these movements a feasible undertaking. Details of seasonal changes in the distribution of kudu in two areas have been described by Simpson & Cowie (1967) and Simpson (1968), and since then a considerable amount of additional data have been obtained in a third locality, substantiating earlier observations. The essence of the data from all three areas can be briefly summarised as follows: Animals are widely dispersed over most of their range during the summer rains; at the onset of the cold season in April/May, there is a movement on to higher ground, followed by the gradual filtering back of the animals to low-lying areas as the dry season progresses. With the advent of the rains again, general dispersal over the whole range occurs. There is no need to elaborate further on actual seasonal movement here, but rather my purpose is to examine environmental factors associated with this behavioural characteristic.

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## THE STUDY AREAS

The Guluene/Chefu area lies in the south east corner of Rhodesia, approximately 21°45'S, 31°45'E, and is on the edge of the lowveld peneplain between 328 and 525 m above sea level. The country is rugged, the climate dry and hot, and the rainfall averages less than 305mm per annum. The major vegetation type in the area is classified by Rattray (1961) as being *Colophospermum* tree/bush savanna, with scattered thickets of *Androstachys* sp. found along the tops of the escarpments, and some riparian fringe developed along the major rivers (Simpson 1968).

Doddieburn Game Ranch in south west Rhodesia, at approximately 21°25'S, 29°28'E, has been reported on in some detail (Dasmann & Mossman 1962a, b, c; Simpson & Cowie 1967). While still a part of the lowveld peneplain, the altitude averages 721m, and the rainfall is somewhat higher at about 381mm a year. Temperatures show a wider range between seasons than found in the Guluene/Chefu, and the topography is less broken and severe. The vegetation of the area shows a high degree of interspersed (Simpson & Cowie 1967), with the dominant vegetation being *Colophospermum* in either an open woodland or a denser, low growing scrub.

The Chobe area in Botswana, approximately 17°45'S, 25°00'E, is on the edge of the central Kalahari Sands plateau, and shows a relatively uniform catena dropping from the sand ridge at about 984m, down to the Chobe river in the north, some 100m lower. Temperatures range from about 38°C in October to an average of around 17°C during the coldest months. Rainfall is confined to the summer and averages about 685mm per annum. The vegetation has been analysed by Child (1968); this consists broadly of Kalahari woodland, xeric thickets of *Baphia obovata* and *Combretum zeyheri*, more mesic thickets of *Bauhinia macrantha*, *Dichrostachys cinerea*, and *Combretum eleagnoides* under Riverine Acacia woodland, and a well developed Riparian fringe along the permanent Chobe river.

All three areas had a healthy and viable kudu population as well as several other big game species. The Guluene/Chefu area was intensively hunted as part of a Tsetse Control game elimination programme, and all kudu were shot on sight. Doddieburn game ranch was a private game utilisation organisation where a limited number of animals were cropped each year on a sustained yield basis. The Chobe area had a high kudu population, and being part of the Chobe National Park, animals were undisturbed and ideal for observation and the collection of data on behaviour. Despite the variations in the degree of stress on the reviewed populations, there was a remarkable consistency in the seasonal movement patterns recorded from each locality.

## RESULTS AND DISCUSSION

When discussing the significance of any behaviour in an animal population, data are of necessity a compendium of observations and indirect measurements which frequently defy quantitative assessment. In dealing with an extremely wary species such as kudu, the interpretation of behaviour is further hindered by the relatively few opportunities for prolonged observation, and by limited visibility in the field. The following evaluation of environmental factors in relation to behaviour is based on extensive observation on the species over several years, and the resultant familiarity with the animal's ways. Indirect measurements were made where these were possible, and they have been used to assess the veracity of value judgements.

### Topography

While kudu occur in completely flat country, most authors agree that this species prefers broken or disturbed areas (Shortridge 1934; Stevenson-Hamilton 1947; Smithers 1966). All three localities assessed showed a greater concentration of animals in the more hilly parts of their range. The importance of topography in kudu distribution is not immediately apparent, but observation and field data offered some possible explanations as to its significance.

The population movement on to higher ground during the cold season (April to July) indicated that these areas offered some species requirement at this time of year, or alternatively, that the lower lying parts of the range became inhospitable to kudu. During the winter months the phenomenon of cold air drainage has a marked local effect on temperature over much of inland Africa. This effect was clearly seen at two weather stations in the Chobe area: these were within one mile of one another, but there was a 100 m difference in altitude. While the average maximum temperatures for June and July were about the same for each station, average minimum temperatures at the lower station were about 7°C less than those recorded at the higher point (Table 1). More detailed evaluation of the situation revealed that there may be as much as a 10°C difference between a point along the cold air drainage line and another point about 5m higher up the slope.

TABLE 1  
WINTER TEMPERATURES AT TWO STATIONS IN THE CHOBE NATIONAL PARK  
WITH AN ALTITUDINAL DIFFERENCE OF APPROXIMATELY 100 m

	Upper Station (Sand Ridge)		Lower Station (Chobe Camp)	
	June	July	June	July
Days sampled .. ..	16	16	16	16
Mean maximum (°C) ..	24,0	25,5	24,4	25,9
Mean minimum (°C) ..	9,5	12,0	3,1	4,6
Average temperature ..	16,7	18,7	13,7	15,2
Daily range .. ..	14,5	13,5	21,3	21,3

Examination of the cold season distribution of kudu on Doddieburn ranch (Simpson & Cowie 1967) showed a tendency for animals to concentrate along the river tributaries, despite these being the channel for cold air drainage. Animals were seldom recorded on top of the catena, which was flat, leafless and exposed during the winter months. Dusk and night distribution, however, always showed animals to be on slightly raised ground where air temperatures were several degrees warmer than in the stream beds. Thus it would appear that the small pockets of warm air, characteristic of broken ground along river tributaries, were more inviting to kudu at this time of year than was the more open country.

Winter observations on Doddieburn ranch and in the Chobe area showed another link between topography and behaviour. The majority of kudu herds seen in the early morning were on east facing slopes, often in the type of bush-free openings usually avoided by this species. Similarly, the majority of late evening sightings were of herds on west facing slopes, where animals were able to get the last rays of the sun before it set. Temperature readings taken at approximately 0700 h and

TABLE 2  
MORNING AND EVENING DISTRIBUTIONS OF KUDU IN THE CHOBE NATIONAL  
PARK IN WINTER TO SHOW ASPECT SELECTION

	<i>East-facing Slopes</i>			<i>West-facing Slopes</i>			<i>Total</i>
	<i>May</i>	<i>June</i>	<i>July</i>	<i>May</i>	<i>June</i>	<i>July</i>	
Days sampled .. ..	5	11	10	5	11	10	26
Mean morning temp. (°C) ..	18,0	14,4	13,6	16,2	9,9	10,0	13,7
Herd sightings (a.m.) .. ..	10	19	14	4	6	3	56
Per cent for month .. ..	71	76	82	29	24	18	—
Days sampled .. ..	6	10	8	6	10	8	24
Mean evening temp. (°C) ..	15,8	12,3	12,6	18,6	16,0	14,4	14,9
Herd sightings (p.m.) .. ..	6	9	5	14	17	20	71
Per cent for month .. ..	30	35	20	70	65	80	—

1700 h on east and west facing slopes in the winter of 1970 showed that the east slopes warmed up more rapidly in the morning, and cooled down more quickly than west facing slopes in the evening (Table 2). This morning and evening slope selection by kudu was not as apparent during the dry season or during the rains; thus it seems that aspect and insolation may play a more significant role in kudu distribution during the cold months than at any other season.

There was an unusually cold spell of weather in the spring of 1968 in Rhodesia, and reports from the lowveld indicated that most kudu populations had suffered a high mortality. Wilson (1970) reported on the kudu killed by this cold snap in the Kyle Game Reserve, and data from Doddieburn ranch showed most of the kudu deaths of this time to have occurred along the major cold air drainage lines (Cowie, personal communication). As kudu were one of the harder hit species during this period, it is reasonable to suppose that they are cold sensitive and that temperature has an important effect on their behaviour, especially in winter months.

### *Vegetation*

Vegetation has two major influences on animal movement. Plants represent the food supply that is available to and maintains the animal population over the year, and vegetation affords animals cover for escape and everyday living requirements.

Some localised food preferences for kudu have been described by Wilson (1965; 1970). And these clearly demonstrate that there are seasonal changes in food selection, concomitant with phenological changes in vegetation. Analysis of the plant species involved is not pertinent to this paper, but the overall changes in vegetation characteristics are useful in understanding population movement. Data collected in the Chobe area over 18 months showed that there was a sequence of phenological changes along the catena, starting on high ground and moving down to the river. As could be expected, there were exceptions to these generalised observations, but most of the more commonly occurring plants conformed reasonably well to the flowering sequence. *Baphia obovata* growing on the sand ridge at the top of the catena flowered during the rains, in mid-December,

while the same species growing at the base of the slope did not flower until the rains were over at the end of March. The flowers of this species are a highly favoured food for kudu and during the flowering period kudu herds spent up to 70% of their observed feeding time in these thickets.

On Doddieburn ranch a similar phenological sequence was noted. The *Baphia obovata* and *Grewia discolor* flowered and set seed before species occurring further down the slope. Kudu on Doddieburn were noted to move around considerably more during the rains (December to March) than at any other season. From stomach contents analysis from both here and the Guluene/Chefu area, it was concluded that a diversity of plants from different habitats were being eaten in a short period of time. Consecutive sightings of identifiable animals at Chobe during the rainy season also indicated greater movement than that at other times of the year.

Habitat preferences, and distinctly differing behaviour in various habitats, gave another indication of the significance of vegetation to kudu distribution. The species was never observed to occupy open grassland for any length of time, and was only seen in open country when going to water or crossing extensive vlei systems. Herds were often recorded in woodland, but on these occasions were usually in transit, and few instances of feeding in this habitat were observed. Kudu herds were frequently seen in small clearings, especially in Riverine Acacia woodland, where they spent some hours feeding on fallen pods or merely resting in the shade; these clearings were always in close proximity to dense cover. In the Chobe area the majority of animals recorded over a 12 month period were either in the Riparian fringe or in thickets (Table 3). Despite the reduced visibility in this latter habitat, the large number of sightings clearly indicated the preference of kudu for denser vegetation. Data from Doddieburn ranch (Simpson & Cowie 1967) showed a similar preference for dense habitat types.

TABLE 3  
KUDU DISTRIBUTION BY SEASONS IN THE FOUR MAJOR HABITATS IN THE  
CHOBÉ NATIONAL PARK, ASSESSED AS PER CENT OF SIGHTINGS

Season	N	Grassland	Riparian	Thicket	Woodland	Total
Rains: Nov. to Mar.	20	0	24	62	14	100
Cold: Apr. to July	202	1	33	52	14	100
Dry: Aug. to Oct.	263	1	43	40	15	100

The flight behaviour and whole demeanour of herds varied, depending on the habitat in which they were observed. In open grassland kudu were constantly on the alert, cautious, and extremely hesitant in their progress. When disturbed, they immediately ran for the nearest cover without any evaluation of the cause for alarm, and even undisturbed herds have been recorded hurrying back to the Riparian fringe after drinking far out on open flats. In woodland habitats herds were less nervous, did not pause as much to appraise their surroundings, and seemed more casual in their movements. On being alarmed, they usually stood long enough to assess the situation before they ran off. The distance run in open woodland was dependent on the available cover but, in the absence of understory vegetation, the animals were usually recorded as still running when lost from view. In the denser vegetation of the Riparian fringe, or in thickets, kudu were more relaxed, feeding or resting without apparently paying much attention to their surroundings. It was here

that animals were most easily approached and several records of flight distances of less than 12m were obtained in these habitats. When animals did run off, they went a short distance into the thicket before stopping and they seemed to take a much shorter time to relax after disturbance when in the relative security of dense vegetation.

#### *Water*

Shortridge (1934) and Smithers (1966) both recorded kudu as occurring in desert areas where the presence of surface water is highly unlikely. Stomach contents from animals in these areas contained a high proportion of succulent plants which were probably used as a compensatory water source. General observation and data from all study areas showed that kudu drank regularly when water was available, although this may have entailed travelling some distance to and from water each day. Quite what influence water availability has on the distribution of these animals is uncertain. However, annual dry season concentrations of kudu around water points, especially in the face of heavy population pressures from other game species, indicated a considerable degree of dependence on water at this time of year (August to November).

The distribution of water in the study area varied. In the Guluene/Chefu area water was widespread during the rains, but supplies had dried up to a few semi-permanent pools by mid-winter, and in dry years even the pools in the two main rivers disappeared. In the Chobe area the river was the only source of water to the kudu population after mid-September, but on Doddieburn, although the only natural water source was again the river, several artificial water points were available to game throughout the year. In the Guluene/Chefu, kudu distribution in the dry season seemed to be random over the whole area, but the other two study areas showed a marked concentration of animals at the river ends of the catena as the dry months progressed. In Chobe, kudu started to concentrate along the river in September and numbers increased until the advent of the rains; when the main rains arrived the kudu moved away from the river *en masse* and very few animals were seen near the river again until early winter. Simpson & Cowie (1967) showed an identical dry season concentration of animals along the river at Doddieburn.

An assessment of the relative values of the environmental factors discussed above has been made for all three areas, and it is shown in Fig. 1. The seasonal shift in population distribution is indicated by arrows, and the approximate percentage of the population occupying the different positions on the catena are shown as histograms for each season.

In the rainy season, kudu were distributed over most of their range, and this wide dispersal indicated that conditions of the environment at this time of year were probably optimal for the species. Temperatures were relatively high but not too hot, there was an abundance of food and cover with the vegetation in full foliage and plenty of water was available in pans and temporary pools. The kudu is a secretive and comparatively non-gregarious animal. Behavioural tendencies to disperse were most clearly shown at this time of year, when conditions were equitable to their requirements in most habitats.

With the coming of winter, environmental conditions changed. Leaf fall started at the top of the catena, resulting in a reduction in the availability of both food and cover. Temporary pools of water dried up and kudu were forced to share the existing water points with other game species. Temperatures dropped, and cold air drained down to the lower end of the catena at night, forming cold air pockets. With the loss of cover and a high daily range in temperature, wind became a

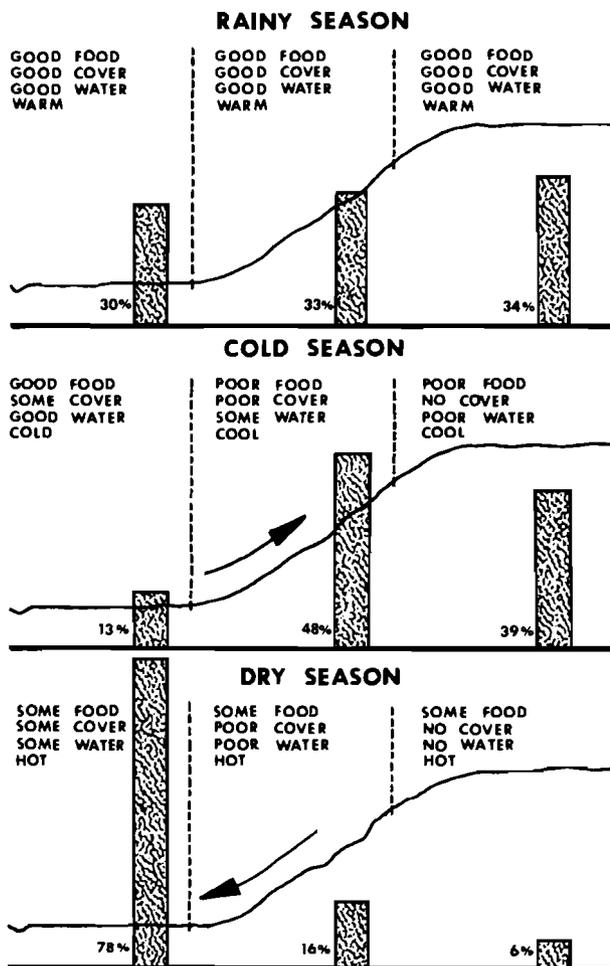


FIGURE 1

Diagrammatic summary of environmental situation at each of three seasons. Distribution of animals for each period shown as a percentage of total data and movement direction indicated with arrows.

factor of some importance on higher ground, and these areas probably became inhospitable to kudu. A similar situation occurred on the catena slopes, but with the more broken ground, the tops of the ridges above the cold air pockets tended to remain fairly warm at night. At the bottom of the slope, food was available from the evergreen riparian plant species, which also offered some cover, and water remained plentiful in permanent pools along the river. However, temperatures fluctuated more widely with conditions becoming extremely cold at night, although maximum day temperatures were about equivalent to those elsewhere at this time of year.

The heavy cold kill in Rhodesia, and winter slope selection by kudu, both indicated that the

species is sensitive to cold. If this is the case, the cold season movement up the catena was probably directly influenced by temperature changes. Examination of the required environmental factors showed the best food, cover and water conditions available at this time of year to be at the bottom of the catena, but this area had the lowest temperatures at night and the highest daily range. The kudu population movement to higher ground in winter, where food, cover and water resources are poorer, but night temperatures are warmer and there is less of a daily range, verified that temperature was significant in limiting kudu distribution during the cold season.

In the dry months, some food is available to kudu from the spring flush of leaves on the deep-rooted trees, but the low-growing shrub and thicket species remain leafless until the coming of the first rains. Cover was poor away from the river and even along the Riparian fringe; heavy animal use had reduced the quality of cover available to kudu. Virtually the only source of water was scattered permanent pools in the river at the base of the catena and these water points became the focus of large game concentrations as the dry season progressed. Days were hot and dry, with negligible humidity and no wind, while night temperatures were only slightly lower.

Kudu populations were concentrated on low ground during the dry season and comparison of the relative availability of environmental factors over the whole catena showed this area to be the most equitable. There was a gradient in both water and cover availability away from the river indicating that one of these two features was probably limiting in kudu distribution. From the early appearance of kudu in the lower catena in poor rainfall years, and the overnight disappearance of this species after the first good rains at the end of the dry season, water, rather than cover, seems to be the primary factor at this time of year.

#### CONCLUSIONS

From the above data it was apparent that kudu distribution and movements were influenced by environmental factors at each season, although the degree of effect cannot be assessed quantitatively. Conditions seemed optimal during the rainy season from December to March, with kudu widespread over their whole range. In winter (April to July) temperatures were probably limiting in distribution and animals concentrated on higher ground. As the dry season advanced water appeared to become more significant in animal distribution and kudu populations showed an overall movement down the catena towards permanent water.

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