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the behaviour of ungulates and its relation to management

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Ungulate Behaviour and Management, with Special Reference to Husbandry of Wild Ungulates on South African Ranches

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ABSTRACT

Nineteen species of wild ungulates, out of a total fauna of 44, are now important in terms of numbers, distribution, or both, on farmed land in South Africa. They have attained this status for a variety of reasons. Factors such as cultural attitudes, legislation, the (real or imaginary) dangerous or harmful attributes of larger forms or of those acting as vectors of disease in domestic livestock, and other economic considerations have been important in determining which species were eliminated and which were not. The paper attempts to show the role played by the behavioural patterns of the successful surviving species in enabling them to adapt to the environment provided by land used for agricultrual and pastoral farming.

The small, solitary species inhabit more or less dense cover in which they are dispersed by their territorial or home range behaviour. They are difficult to eliminate, even when deliberate extermination is attempted, and appear to compete little with domestic livestock. Their sedentary habit assists in making them proof against disturbance by man. Fences, unless they be of netting, are no barrier to the smaller species, while bushbuck are not contained by fences of standard height.

Of the semi-gregarious forms, klipspringer, mountain reedbuck and vaal rhebok occupy hills and mountains where the terrain gives security. Reedbuck shelter in tall grass and reeds. Fences do not hinder free movement while spacing behaviour usually tends to limit density to a level at which competition with domestic animals for food is of little practical consequence. Kudu are wary, difficult to hunt in the dense vegetation they prefer and are able to move freely over fences. Competition with cattle for food appears to be important only in some regions, as for example the Eastern Cape Province and perhaps in South West Africa. The small groups in which kudu occur preclude congregations which might lead to serious competition.

By occupying thick cover, and by extreme wariness, together with a high reproductive rate, bushbuck resist extermination in the face of constant persecution for damage to crops. Warthog tend to be dispersed by low sociability and home range behaviour but may compete with livestock for food to some degree.

The seven social species are behaviourally most closely akin to domestic ungulates, with many of the attributes considered favourable for domestication. Except for eland, they probably all compete, at least to an extent, with domestic livestock for food, although critical studies of the competition have yet to be carried out.

Gemsbok, eland, blue wildebeest and hartebeest are important mainly on large holdings where extensive pastoral farming is practised. Springbok, blesbok and impala are the three dominant farm species, springbok mainly in the arid western part of the country, blesbok in the central and eastern grassland regions, and impala in the northern and north-eastern savannah. Both springbok and blesbok are easily controlled by fencing and all three species are now of some economic importance.

The future of farm ungulates is related to changing patterns of land use and to economic factors. There is a trend to apply sophisticated grazing management in smaller paddocks and the role in these conditions of wild ungulates, which cannot easily be moved to rest the food plants, requires close scrutiny. Their economic value is not determined only by their utility as meat producers, however. Recreational hunting

and game viewing on private land has already become a source of revenue for some farmers. Its value is likely to assume increasing importance in the future and rational management on scientific lines will become increasingly necessary.

INTRODUCTION

South Africa, in this paper taken to comprise the Republic of South Africa and the Territory of South West Africa, had a varied and abundant ungulate mammal fauna in historic times. The orders Proboscidea, Perissodactyla and Artiodactyla were represented by 44 species (Table 1). Development of the country, following its settlement

TABLE 1. COMPOSITION OF LARGER UNGULATE FAUNA OF SOUTH AFRICA IN HISTORIC TIMES

Order	Family	Sub-family	No. of Species
Proboscidea	Elephantidae		1
Perissodactyla	Rhinocerotidae		2
	Equidae		3
Artiodactyla	Suidae		2
	Hippopotamidae		1
	Giraffidae		1
	Bovidae	Bovinae	6
		Cephalophinae	3
		Hippotraginae	15
		Antilopinae	10
			44

by Europeans in 1652, led to a marked reduction in the numbers and restriction of the range of most species (see, e.g., Van der Merwe, 1962; Sidney, 1965). Two, the quagga *Equus quagga* and the blaauwbok *Hippotragus leucophaeus,* became extinct.

Some forms, particularly the largest ones, are now entirely or virtually confined to parks and reserves. These include the elephant *Loxodonta africana;* two species of rhinoceros, *Diceros bicornis* and *Ceratotherium simum;* the hippopotamus *H. amphibius;* the Cape race of the mountain zebra *Equus z. zebra;* the giraffe *Giraffa camelopardalis*; the roan antelope *H. equinus,* and others.

A number are rare and survive only over small portions of their original ranges. Reviews of ungulate status and distribution have been published for the Transvaal by Kettlitz (1962), for Natal by Vincent (1962), for the Orange Free State by Van Ee (1962), for a part of the Cape Province by Bigalke and Bateman (1962), and for South West Africa by Bigalke (1958) and Van der Spuy (1962).

The species of particular interest in the context of this paper, are those which are relatively widespread and abundant on privately owned farm and ranch land at the present time. Private land makes up approximately 69% of the area of the Republic of South Africa (472, 359 sq. miles = 122, 104, 200 ha) and 47% of South West Africa (total area 318, 261 sq. miles = 82, 429, 600 ha). It is for the most part used primarily for crop or live-stock production, although the economic value of wildlife on farms has increased in importance in recent years (Riney and Kettlitz, 1964). The surviving wild mammals are, by and large, those which are adapted to the conditions created by the primary form of land use. The species are listed in Table 2.

The range of several of the commoner farm species has been enlarged and the populations increased by secondary redistribution. This has taken place mainly during

TABLE 2. LARGER UNGULATES OF LOCAL OR GENERAL IMPORTANCE ON FARMED LAND IN SOUTH AFRICA

Family		Species	Main Localities
Suidae	Bushpig	*Polamochoerus porcus*	EC,N,T
	Warthog	*Phacochoerus aethiopicus*	N,T,SWA
Bovidae			
Bovinae	Bushbuck	*Tragelaphus scriptus*	EC,N,T
	Kudu	*Tragelaphus strepsiceros*	EC,NC,T,SWA
	Eland	*Taurotragus oryx*	SWA
Cephalophinae	Blue Duiker	*Cephalophus monticola*	EC,N
	Grey Duiker	*Sylvicapra grimmia*	General
Hippotraginae	Vaal Rhebok	*Pelea capreolus*	C,T
	Reedbuck	*Redunca arundinum*	N
	Mountain Reedbuck	*Redunca fulvorufula*	C
	Gemsbok	*Oryx gazella*	SWA
	Blesbok	*Damaliscus dorcas phillipsi*	T,C
	Hartebeest	*Alcelaphus buselaphus*	SWA
	Blue Wildebeest	*Connochaetes taurinus*	T, some N
Antilopinae	Springbok	*Antidorcas marsupialis*	General except N
	Klipspringer	*Oreotragus oreotragus*	C,T
	Steenbok	*Raphicerus campestris*	General
	Grysbok	*Raphicerus melanotis*	C
	Impala	*Aepyceros melampus*	Mainly T, some N

C = Cape Province; EC = Eastern Cape; NC = Northern Cape; N = Natal; O = Orange Free State; T = Transvaal; SWA = South West Africa.

the last 15 years. Translocation was initiated by enthusiastic farmers and also by some of the conservation authorities which attempted to provide interested landowners with nucleus populations for restocking. All these conservation authorities are now to some extent involved in the capture and translocation of game. In addition many farmers are active in capturing and distributing the commoner species.

SOCIAL BEHAVIOUR

The ungulates listed in Table 2 may be simply classified into three categories according to the size of the groups in which they are normally found (Table 3). The allocation of species to these categories is in some cases somewhat arbitrary. Nonetheless the classes represent increasingly complex types of social organisation which profoundly affect the management of the animals.

(a) Species occurring singly or in pairs

Five species are usually described in older, general works as being essentially solitary. Recent studies of some of these provide quantitative information on group sizes and give some idea of the nature of their intra-specific behaviour. Elder and Elder (1970) report on 167 sightings of bushbuck; lone animals made up 72% of the observations, lone males (55) being seen slightly more often than lone females (50). Only 10 sightings were of groups larger than two and the largest consisted of 5 animals. Verheyen (1955) reports that both males and adult females occupy territories of 2-3 acres, usually pear-shaped, with access to communally used 'neutral' ground.

TABLE 3. SOUTH AFRICAN FARM UNGULATES CLASSIFIED ACCORDING TO SOCIABILITY

Solitary or pairs	Semi-gregarious	Gregarious
Bushbuck	Klipspringer	Eland
Blue duiker	Vaal rhebok	Gemsbok
Grey duiker	Mountain reedbuck	Blesbok
Steenbok	Reedbuck	Hartebeest
Grysbok	Kudu	Blue Wildebeest
	Bushpig	Springbok
	Warthog	Impala

Von Gadow (unpublished) observed 59 blue duiker, of which 78% (46) were single, 17% (10) in pairs and 5% (3) in a group of three. He found dung heaps in the field and suggests that they may indicate behaviour of a territorial nature. In the closely related and possibly conspecific (Ansell, 1968) *Philantomba* (=*Cephalophus*) *maxwelli,* Rahm (1960) has described preorbital gland marking in captive animals. Aeschliman (1963), working with animals of the same species in captivity, describes territorial behaviour involving preorbital gland marking and the utilisation of dung heaps. In captivity, an adult male marked 79 times in 4 hours, an adult mature female 21 times and two younger mature females 8 and 9 times respectively.

Wilson and Clarke (1962) write of the grey duiker—'(it) is generally spoken of as a solitary animal and although this was found on the whole to be true, pairs were also frequently recorded, almost half as many times as single animals'. Bigger groupings were found to be very rare and only five groups of three were noted. These authors also describe aggressive behaviour between males and between females, when placed in the same enclosure. They consider it to be 'strongly suggestive of an animal with a territorial system'. Personal observations (Bigalke, unpubl.) confirm aggression between adult males brought together in a pen, usually resulting in the death of one individual. Shortridge (1934) noted that males in the field 'appear to fight much among themselves'. Preorbital gland marking by a male and a female in captivity has recently been established (Greig and Bigalke, unpubl.) and the existence of dung heaps noted. This latter observation confirms the remark by Shortridge (1934) that duiker 'are in the habit of returning to the same open spots to deposit their droppings, although large massed accumulations.... are not formed'. Wilson (1966) found grey duiker to occupy a very small home range.

No quantitative data is available on the groupings of steenbok and grysbok. Lamprey (1963) gives qualitative confirmation of earlier observations (e.g. Shortridge, 1934) that steenbok are solitary although sometimes seen in pairs. Stevenson Hamilton's (1913) observation that Sharpe's grysbok, *Raphicerus sharpei,* which is closely related to the grysbok *R. melanotis,* is 'very solitary in habit, and, even when a pair are put out of the same patch of bush, they seem generally to have been lying in different parts of it', has been confirmed for both this species and the Cape grysbok by a number of later observers (e.g. Shortridge). All three species of *Raphicerus* use dung heaps (Stevenson Hamilton, 1913; Shortridge, 1934; pers. obs.) and have well developed preorbital glands, suggesting that they display territorial behaviour.

(b) Semi-gregarious species

Klipspringer, sometimes considered to be solitary, are probably best placed in this group. Wilson and Child (1965) give an analysis of 168 groups of klipspringer, totalling 313 animals. The average group size was calculated to be just under two animals, with a range of 1 to 6. Singletons constituted 22.1%, pairs 47. 2% and threes 15. 3% of the sample. Massed accumulations of dung are characteristic of areas inhabited by klipspringer (Shortridge, 1934; pers. obs.) and deposits of preorbital gland secretions have been found near the dung heaps (Walther, 1966; Tinley, 1969). Territorial behaviour thus probably exists.

Reedbuck live in pairs of male and female or female and young, or in family groups of male, female and young (Jungius, 1969). The mean size of 34 groups in Natal was 1. 8, with a range of 1 to 3 (Rowe-Rowe, *in litt.*). Jungius has shown that territories are occupied jointly by a male and a female, although they may not always remain together within these areas. The female rears her young in the territory. It is not known whether the pair bond is permanent or is only important during the mating season. Territories are maintained by the males through a combination of advertising behaviour (display of chinspot, whistling) and the diffuse deposition of dung and urine, and probably also of small quantities of gland secretions, throughtout the territory. Two territories were found to extend over areas of 48 ha and 60 ha respectively in summer. In winter, a shortage of water caused reedbuck to concentrate around available sources and to exert pressure on the two territory holders in question. As a result the extent of each territory was reduced to 35 ha. Temporary congregations of reedbuck, e.g. on good grazing grounds, are often encountered (Jungius, 1969).

Little is yet known of the social behaviour of the mountain reedbuck *Redunca fulvorufula.* Observations by early naturalists, brought together in Shortridge (1934), all show that it is found in small groups. For example, Selous (quoted in Shortridge) stated that herds usually number from three or four to fifteen animals with only one adult male and, sometimes, a few immature males. Records collected by officers of the Natal Parks Board in the Drakensberg show that the mean size of 540 groups is 3. 67, with a range of 1-21 (Rowe-Rowe, *in litt.*). Personal observations confirm that only a single adult male is usually present in the herds, and it would seem that these are small and possibly permanent harem groups. Selous (*loc. cit.*) also notes the occurrence of solitary males, while Shortridge suggests the existence of a territorial system, writing 'the rams are very pugnacious, and, it is said to be impossible to keep two males together in one enclosure without one eventually killing the other'.

The vaal rhebok or ribbok *Pelea capreolus,* has a similar form of social organisation. The mean size of 514 groups seen in Natal is 3.1 and the range 1-9 (Rowe-Rowe, *in litt.*). The herds have one adult male and solitary males occur (Shortridge, 1934; pers, obs.).

Information available on the size and composition of kudu herds has been summarised by Wilson (1970). Some authors have recorded herds of up to 30, but these are apparently exceptional. The biggest group encountered in the course of his study by Wilson numbered 15, while Simpson (1968) found herd size to vary from a maximum of 7 in the dry season to 12 in the winter. Herds tended to be larger in December-January, possibly as a result of females aggregating before calving, and in July, when the rut takes place, than at other times of year (Simpson, 1968). Wilson (1970) found the mean size of 35 herds in Rhodesia to be 5. In a tsetse-fly control area in Zambia, where 185 groups totalling 768 animals were seen, he counted 33 single animals and found the average herd size to be 3. 9 (Wilson, 1965). Males occur singly and in small herds (up to 16—Wilson), females in herds with or without juveniles and sometimes accompanied by one or more males. There is a suggestion that males are only in temporary association with groups of females and young (Wilson, 1970).

In the warthog, the social unit is a small group, often composed of two or more mature females with their half grown young, sometimes accompanied by an adult male. Females go off on their own when about to give birth to a litter and this habit probably prevents the formation of large groups. Each group has its own home range including sleeping holes, resting, feeding, drinking and wallowing places. Ranges overlap with those of other groups; there is no territorial defence and animals may move to a new area if seasonal vegetational changes make this necessary (Ewer, 1968, quoting Frädrich, 1965). Mating by the male accompanying a family group and aggression towards a solitary male in the vicinity is described by Simpson (1964).

Bushpig behaviour has not been studied in detail. The sounders have been described by various authors as containing from 4-20 pigs (Sowls and Phelps, 1968) and are said to include a dominant adult male (Astley Maberley, 1963).

(c) Gregarious species

The system of social organisation in the hartebeest (Backhaus, 1959), blesbok (Du Plessis, 1968), blue wildebeest (Estes, 1968; Watson, 1969), springbok (Bigalke, 1970) and impala (Leuthold, 1970; Jarman, 1970) is similar to that of many other gregarious bovids. Populations are organised into three main classes: herds of females and young, variously called breeding herds, harem herds or nursery herds; herds of adult and sub-adult males, sometimes accompanied by sub-adult females and often called bachelor herds; and solitary adult males.

Backhaus (1959) records herds of hartebeest (*Alcelaphus buselaphus lelwel*) in the Garamba Park numbering 4-15 animals. They are mother-young groups accompanied, apparently permanently, by one adult male, and occupy fixed territories. He also saw male herds but no solitary males. Gosling (1969) has found solitary male Coke's hartebeest (*A. b. cokei*) defending territories of 0.4 km^2 in the Nairobi Park. Solitary males do occur in *A. b. caama* observed in the Northern Cape Province, South Africa (pers. obs.). Of 40 sightings of *A. b. caama* from the air (pers. obs.) 10 were of solitary animals. The remainder were made up as follows:

groups of	2-5	6-10	11-20
number	17	8	5

The largest herd of the same sub-species seen by Eloff (1959b) in the Kalahari Gemsbok Park numbered 35, but he also records an assemblage of 200 seen in the adjacent part of Bechuanaland (now Botswana). Eloff (1959a) also notes that hartebeest, together with eland and springbok, took part in several large scale movements beyond the boundaries of the Park, apparently in search of fresh grazing.

Solitary male blesbok are found throughout the year but the number increases markedly during the rut in March and April (Du Plessis, 1968), when some of them defend harems (or territories within which the harems are herded?) of females, accompanied by six-month-old lambs. Du Plessis did not consider the solitary males to be territorial. However David (1970) has since described well-developed territorial behaviour in solitary male bontebok (*D.d. dorcas*), a closely related sub-species. He also found some evidence of harem herds living on male territories throughout the year. Du Plessis encountered large, mixed aggregations of blesbok during the winter months following the rut, as well as after the onset of the rains, when they congreated on the burnt grassland. For example, on one occasion in November, the entire population studied was distributed in only four herds (numbering 590,299, 72 and 17 respectively) on green burns.

In sedentary blue wildebeest, Estes (1968) found a permanently established territorial network. Approximately 25-50% of the adult males occupied territories which were closely spaced, on average a distance of 130-160 yards apart. Territorial activity was much lower during the dry season (June-October) than after the onset of the Short rains (November-December) and reached a peak during the rut in May and June. Females and young occurred in separate, small nursery herds with an average size of approximately 10 animals, of which 6 were adult females. They occupied small home ranges of 1 sq. mile or less. Bachelor herds were separated. In nomadic wildebeest there were large, mobile aggregations of 100-1000 females and young with attached bachelor herds. Males established temporary territories or 'pseudo-territories' (Watson, 1969) when the aggregations remained stationary. The mean size of 'pseudo-herds' held by bulls in their 'pseudo-territories' in the Serengeti region is 28. 4 (Watson, 1969). About half of these animals may be adult cows.

In the springbok (Bigalke, 1970 and in press), solitary territorial males are encountered throughout the year but there is evidence for an increase in their number during the rut in April and May. At this time, harem herds of up to 35 females and lambs are tended, although larger groups with several rutting males are also occasionally seen. In the succeeding months of the dry season, mixed herds of up to several hundred predominate. Females and newly born lambs form separate groups, the lambs resting together in sub-groups in the vicinity of the females. Large, mixed aggregations of up to several thousand animals occur during the rainy season. Non-territorial males associate in fairly loosely knit bachelor herds throughout the year.

Adult male impala have also been shown to be territorial (Leuthold, 1970; Jarman, 1970) and remain within areas of 0. 2-0. 9 sq. km in the Nairobi National Park. Other males run in male herds, most of which number from 2-15, or in the rarely encountered mixed groups of both sexes and all ages. Herds of females and young are basically independent of the territorial males but may stay with the same male for long periods. The size of these groups was generally smaller—up to 25 in most cases—in a region with fairly dense vegetation, than in a more open environment when herds of over 35 were common (Leuthold, 1970).

All animals are fairly sedentary under the stable and favourable environmental conditions of the Nairobi Park, home ranges of individual males and females measuring 2-6 sq. km (Leuthold, 1970). In the more arid Serengeti Park, Jarman (1970) found sedentary behaviour of a similar kind during the dry season, but in the rainy season, animals moved to areas of green flush and formed feeding concentrations of large, diffuse herds of both sexes and all ages. Territoriality was then at a minimum. Seasonal changes of range in response to food are also reported by Lamprey (1963). Leuthold (1970) emphasizes the flexibility of the social organisation which enables the species to meet the exigencies of the various habitats throughout its wide range.

The eland has quite a different pattern of social behaviour. Large mixed herds of 100-150 or more occur during the summer (Lemon, 1964:Martin, 1968), probably associated with rutting and with a good food supply. In winter, smaller herds of 10-50 predominate (Lemon). Martin records groups as small as 3-5 in April. Small male parties and solitary males occur in the valleys of the Natal Drakensberg during winter while the rest of the population is dispersed in small groups at higher altitudes (pers. obs.). Large herds contain several adult males (Lemon; pers.obs.) and a social hierarchy appears to exist, reducing intraspecific aggression and ensuring the cohesion of the groups. A rank hierarchy was well developed in a semi-domestic herd (pers. obs.). No evidence exists for territorial behaviour of any kind.

The social behaviour of gemsbok has not been studied in detail. Shortridge (1934) gives the usual size of groups as 3-12 and occasionally up to 25, although larger, presumably temporary, feeding aggregations, are on record. Solitary males occur.

INFLUENCE OF SOCIAL BEHAVIOUR AND HABITAT REQUIREMENTS ON POPULATION DENSITY

The density at which ungulates normally occur and can be maintained, is basically dependent on the productivity of the vegetation. The availability of water and of cover are further important factors while social behaviour influences the manner in which the resources of the environment are shared amongst members of the population.

(a) Solitary species

Social behaviour is of greatest importance as a determinant of density in solitary species. According to Ewer (1968) 'In solitary species the predominant function of territory is the primary one—spacing out of individuals and ensuring an adequate area for the rearing of each family'. The secondary, male competitive function is simply integrated with the primary one by means of a contest which decides who shall be allowed to enter the female's territory and mate with her.

Densities are influenced by spacing behaviour. This can be said in spite of the fact that the precise nature of the behaviour is not yet known in many cases. Whether either, or both, sexes occupy territories 'where each individual is exclusively dominant over all others of the same sex at a particular site or area, but not elsewhere' (Watson and Moss, 1970, referring to the definition by Tinbergen, 1957), or whether they inhabit home ranges, the species are spaced out.

There is little information on the sizes of territories or home ranges inhabited. Bushbuck have been found to occur at densities of approximately 2. 8 per square mile in Rhodesia (Dasmann and Mossman, 1962), 1. 3 per square mile in the Rwindi-Rutshuru area of the Congo (Hubert, 1947), and 0. 6 per square mile in the Nairobi Park (Foster and Coe, 1968). An average of 6. 4 bushbuck per square mile per annum was shot in the Umfolozi area of Zululand for 7½ years, without apparently reducing the population significantly (Mentis, 1970). These density figures are probably not indicative of territory size, since bushbuck habitat is usually of local occurrence in savannah. Verheyen (1955) suggests that bushbuck in the Albert Park, Congo (now Zaire), spend most of their time in territories of only 2-3 hectares.

Bourliere (1963, quoted in Owen, 1966) gives a figure of 0. 8 *Cephalophus maxwelli* (closely related to or conspecific with *C. monticola*) per square mile in a forest in Ghana.

Dasmann and Mossman (1962) calculated the densities of grey duiker in four different areas in Rhodesia to be 0. 3, 1. 0, 1. 6 and 5. 5 per square mile respectively. In at least one case their figure was subsequently found to be too low. Wilson and Roth (1967) report a density of 2 to 3 per square mile instead of 1. 6 per square mile on one ranch where Dasmann and Mossman worked. Child and Wilson (1964) saw an average of 1. 5 per mile along 60 miles of road where visibility was approximately 100 yards on either side. The density would seem to have been of the order of 13 animals per square mile. This higher figure approaches that suggested by tsetse control figures from the Umfolozi reserve area in Natal. Mentis (1970) records that the average duiker offtake was 5. 9 per sq. mile over 7½ years and as in the case of the bushbuck offtake did not appear to reduce the population significantly. If the offtake for sustained yield is about one third of the total population, as Wilson and Roth (1967) imply, then the Umfolozi population may have been as dense as 18 animals per square mile. At 2-3 per square mile, the average territory size would be 86-129 hectares, at 18 per square mile, only 14 hectares.

Eloff (1959a) encountered steenbok at from 1 per 2.4 miles to 1 per 7.6 miles along roads and tracks in the Kalahari Gemsbok Park. He presents separate counts for each four-mile segment of the distance covered. In 22 such segments in which steenbok were seen, 10 had 1 each, 7 had 2, 2 had 3, 1 had 4 and 2 had 5 steenbok. Lamprey (1963) mentions a density of 1 per 10 square miles in the Tarangire reserve. Much higher densities, of the order of 1 animal per 5 ha, are suggested by observations in fynbos on the west coast of the south-western Cape Province (Cape Nature Conservation Department, unpubl.). Dasmann and Mossman (1962) encountered Sharpe's grysbok at a density of 0. 3 per square mile in Rhodesia, but grysbok in the Western Cape Province appear to be much more closely spaced (pers. obs.).

Clearly social behaviour is not the only spacing factor. Food, water and cover must all be expected to influence the sizes of territories or home ranges occupied. There is however no published information on the relative importance of these factors in determining population density.

Water is of little or no importance in the case of steenbok (Eloff, 1959a) and grey duiker (Wilson, 1966) and possibly also grysbok. In South Africa, blue duiker and bushbuck inhabit vegetation which is confined to moist areas so that it is difficult, and of no great importance, to separate the influence of cover and water on their distribution and density.

The solitary habit is closely associated with the occupation of closed environments where it is difficult for animals to maintain contact with one another. Adequate cover is necessary for all five species, only the steenbok tolerating somewhat more open conditions than the others. There is no information on whether variations in the density of cover as such influence carrying capacity.

All five species are essentially browsers (Wilson and Child, 1964; Wilson, 1966; Lamprey, 1963; Dorst and Dandelot, 1970) and thus utilise plants with a nutritive value which remains fairly consistently high throughout the year, in contrast to the grass on which grazers depend. Seasonal changes in the availability of food do not therefore appear to exercise much influence on their distribution. The animals tend to be sedentary and seasonal shifts of populations are unknown. Thus Wilson (1966) and Wilson and Roth (1967) found only minor changes in the activity and feeding behaviour of grey duiker from wet to dry season. The animals were markedly sedentary in the rainy season but quite mobile in the dry season when they fed on a greater range of plant species. However even the dry season movements were still local. There are no data to show how territory size is related to food supply, although the large differences in the density of e.g. grey duiker in different areas mentioned above, suggest that a correlation is to be expected.

(b) Semi-gregarious species

In klipspringer, the density limiting effect of the small social groups is reinforced by specialised habitat requirements. As is well known, the species inhabits rocky hills and mountains. The animals are mainly browsers and are not water dependent (Wilson and Child, 1965). Reedbuck, also occurring in small groups, have equally specialised but different habitat requirements. For example, in the Kruger National Park (Pienaar, 1963; Jungius, 1969) they are common in open and semi-open parts of the long-grass savannah woodland and treee savannah; elsewhere they are confined to the islands of suitable habitat provided by the long-grass and reed communities of vleis, dambo-like depressions and rivers. Reedbuck are mainly grass eaters and are water dependent (Field, 1970).

Density figures must be treated with reserve because of the restricted habitat occupied. Dasmann and Mossman (1962) give a figure of 0. 2 klipspringer per square mile. Bourlière (1955) records reedbuck occurring at a density of approximately 4. 5 per square mile in the Congo while Foster and Coe (1968), working in the Nariobi Park found 0. 24 per square mile. The two reedbuck territories measured by Jungius (1969) and found to extend over 48 and 60 hectares in summer, reduced to 35 hectares in winter, have already been mentioned.

Mountain reedbuck and vaal rhebok are also rather specialised in their habitat requirements since they are essentially animals of hilly and mountainous country. Cover is of some importance for mountain reedbuck and both species appear to be, at least in many parts of their range, water dependent (Shortridge, 1934). Little is known of their food preferences, Dorst and Dandelot (1970) describing the mountain reedbuck as a grazer which also browses on leaves and twigs and the vaal rhebok as a grazer only. The social behaviour suggests that the harem herds may occupy fixed home ranges or territories so that some behavioural limitation of density occurs.

Kudu do not appear to show territorial or home range behaviour. Simpson and Cowie (1967) and Simpson (1968) have reported marked seasonal differences in distribution on a ranch in Rhodesia. During the wet season the animals were widely dispersed and distribution appeared to be random. Food, cover and water are then widely available. In the cold season, more animals occupied habitats at intermediate altitudes and in the dry season the majority were concentrated in low lying riverine and *Acacia* thickets. The seasonal change in range was more clearly defined in females than in males, perhaps because of the increased physiological demands of pregnancy. Concentration in the riverine *Acacia* thickets in the dry season was thought to be mainly related to the availability of both food and cover, the leafy vegetation providing browse and shelter. The presence of water may have been a contributory factor since, although not dependent on water, kudu drink regularly when it is available. These findings suggest that environmental factors may have more influence than social behaviour on the spacing of kudu.

We have already noted that warthog family groups occupy home ranges and that these overlap with the ranges of other groups. Warthog feed mainly on short grass (Lamprey, 1963) but take some non-graminaceous plants and roots. They move readily if the food supply requires it. Warthog are dependent on free water and usually wallow when visiting water holes. The preferred habitat is open woodland but quite dense closed woodland may also be tolerated (Lamprey, 1963).

Bushpig inhabit dense cover in moist regions and feed on a variety of monocotyledonous and dicotyledonous plants as well as roots, fruits and carrion (Sowls and Phelps, 1968). They are serious pests of agricultural crops in many areas. Whether or not they are dependent on free water has not been discovered and we do not know if seasonal movements take place.

(c) Implications for management

1. *Control of numbers*

Where spacing behaviour is one of the factors determining population densities, overutilisation of the habitat does not seem to occur. It is a matter of experience that the numbers of the solitary antelope discussed, as well as those of klipspringer, reedbuck and vaal rhebok among the semi-gregarious forms, have not required control in South

African parks and reserves. Mountain reedbuck numbers were however judged to be excessively high and control measures were instituted in the Mountain Zebra National Park, near Cradock, several years ago. Similarly, warthog have had to be heavily controlled in some Natal reserves. Complaints of over-browsing by kudu are heard from farmers in the Eastern Cape Province from time to time, but kudu have not yet been controlled in any parks and reserves, possibly because habitat utilisation is kept at a low level by seasonal movements of the kind mentioned above.

The mechanism of density limitation in solitary species has not been described. It is likely to be akin to that known to operate in roe deer. Watson and Moss (1970), summarising the findings of several workers who have studied this territorial species, write that dominant roe deer expel subordinate individuals into less favourable habitats where they suffer a higher mortality rate. When a population was fenced, reproductive performance, body weight and antler size decreased. The fenced deer had apparently reached a higher population level than would have been the case if emigration followed by predation had occurred. 'Obviously, food is important, but behaviour and predation may also limit deer populations in a natural situation'.

In fenced reserves where predators are absent and emigration is impossible, death of 'excess' animals may be expected among solitary species and control measures may be advisable to maintain the animals in good condition. Introductions of solitary species into populated regions are not likely to increase the population density.

2. *Cropping*

Some, and perhaps all, solitary species can tolerate quite heavy cropping. Presumably removal at the optimal rate, once this has been determined, takes the place of expulsion and subsequent losses to predators in maintaining a stable population. Examples of the effect of exploitation are available for grey duiker and bushbuck.

During the course of tsetse control operations in Eastern Zambia, 422 grey duiker were shot in an area of 200 square miles in two years. The population was not apparently significantly reduced. Shooting seemed merely to remove the annual increment, estimated to be of the order of 1-2 duiker per square mile (Wilson and Roth, 1967).

As previously noted, Mentis (1970), discussing the tsetse control campaign in the Umfolozi reserve and surrounding land, reports that grey duiker and bushbuck populations were not much affected by 7½ years of shooting. In an area of 462. 8 square miles, 20, 461 duiker were shot, an average of 2, 728 per annum of 5. 9 per square mile per annum. The bushbuck kill was 22, 232, averaging 2, 964 per annum or 6. 4 per square mile per annum. At the end of the campaign, both species were reported to be 'very numerous'. Du Toit (1954) assessed the degree of eradication achieved and wrote 'game observers reported large numbers of the smaller species of antelope and evidence of the presence of considerable numbers of the nocturnal bushpig, when to the casual observer, all game appears to have been eliminated. In fact, a balance appeared to have been struck whereby natural increase in the thicket-inhabiting species balanced the rate at which they were being destroyed'.

While the rate of cropping sustained is a function of the reproductive capacity, the behavioural response is of particular interest here. Wilson and Roth (1967) found that the duiker responded to continuous hunting by a gradual shift in the period of maximum activity, from the early morning and noon hours to the late afternoon and early evening. This diminished hunter success. Despite heavy hunting pressure and other major distrubances associated with tsetse control operations, the duiker population did not emigrate from the area. This sedentary behavioural trait seems, from casual observation, to be common to all the solitary species and many of the semi-gregarious forms discussed here. There are numerous examples of these animals surviving at the outskirts of quite large South African towns, while the fact that they are important farm species shows the adaptation to agricultural activity and disturbance. The sedentary trait is an important attribute fitting these species for survival and exploitation in inhabited regions.

The dense cover preferred is an important element in this ability to survive. Management must ensure that cover is provided. Their habitat, coupled with the dispersal of the animals, makes cropping by conventional hunting difficult however. The 422 grey duikers mentioned above were shot by 26 hunters stationed in the 200 square mile area, a density of one hunter to 5-6 square miles (Wilson and Roth, 1967) and an average annual bag of only 8 duiker per hunter. By and large, the behavioural attributes of the solitary and semi-gregarious species make them better suited to sport hunting than to exploitation for meat production.

(d) Gregarious species

Group formation is associated with the occupation of open habitats, where grass is an important source of food, fluctuating seasonally in quantity and more particularly in quality. Seasonal movements activated by changes in food supply, and in some cases by the availability of water, are often necessary for survival. Territoriality is more important as 'an agent of male selection' (Ewer, 1968) in social species with a harem, system than as a factor leading to spacing out. However Ewer has emphasised that social organisation is fluid in gregarious forms, not 'something the species has got in the same way as it has got characteristic anatomical and behavioural attributes' but an adaptable response to environmental conditions.

The densities of the gregarious ungulates dealt with here are, in general, more directly governed by the productivity of the environment and by behavioural responses to food and water, than by the presence of cover or by spacing behaviour and the sedentary habit.

1. *Food and habitat*

Blesbok are grazers of open grassland (Du Plessis, 1968); hartebeest and wildebeest are mainly grazing species of grassland and open woodland (Lamprey, 1963; Leistner, 1967). Gemsbok are essentially grass feeders which also dig for roots and tubers and do a fair amount of browsing (Leistner, 1967); they occupy open or lightly wooded country. Eland are mainly browsers (Van Zyl, 1965; Leistner, 1967; Kerr *et al.*, 1970) which live in plains country, savannah and montane grassland. Impala are by preference primarily grass-eaters, although able to utilize a wide variety of other plants (Stewart, 1971); they inhabit open woodland. Springbok are mixed feeders (Van Zyl, 1965; Skinner *et al.,*, 1971; Bigalke, in press), which seem to use grasses mainly in the rainy season and shrubs in the dry season. They prefer open plains and sparse savannah.

2. *Water*

Blesbok and wildebeest are water dependent and hartebeest are generally also considered to be so (Eloff, 1959a; Lamprey, 1963;pers.obs.) although Shortridge (1934) described them as occupants of waterless areas in South West Africa. Springbok (Bigalke, in press) and impala drink where water is available but even then impala drink relatively little and infrequently (Young, 1970). Both species have the capacity to survive in the absence of free water (Shortridge, Lamprey, *op. cit.*). Gemsbok also drink, but their very low requirements enable them to live independently of surface water. Survival of eland in waterless areas is achieved not by low requirements but by selecting succulent food, resting in the shade, forming dry faeces and by possessing a narrow thermal neutral zone (Taylor, 1969).

3. *Density*

Social behaviour may have an important influence on spacing in some gregarious species under certain conditions. Thus the harem herds of hartebeest which Backhaus (1959) observed in the Garamba Park appeared to remain in their territories throughout the year. One territory which he measured had an area of 3 sq. km. It must be presumed that food and water supplies were adequate all year round. In contrast, Eloff (1959a) found that hartebeest in the Kalahari Gemsbok Park were seasonally mobile and there were occasional large scale shifts of the population, the animals apparently moving to regions where local rain storms had produced fresh green grass. The observations of David (1970) and Du Plessis (1968) show comparable differences between bontebok and blesbok in different areas. In the Bontebok National Park some territorial bontebok males maintain their territories throughout the year and appeared always to be associated with the same harems. This sedentary behaviour may be associated with the relative constancy of environmental conditions. The park is situated in a region where rain falls throughout the year with a maximum in spring (Grobler and Marais, 1967). There are no drastic or spectacular seasonal changes in the vegetation comparable in magnitude with those near Pretoria where Du Plessis worked. He studied blesbok in a 'sour' grassveld region where the pasture is of very poor quality in the winter. After burning, there is a flush of succulent grass when the summer rains start. The blesbok were only dispersed in harem herds during the rut. In early winter they moved about in large, mixed herds, changing to smaller groups in late winter. When the rains started they congregated on the burns.

Wildebeest provide the most striking example of the different roles which social behaviour may play in spacing gregarious animals under different environmental conditions, Sedentary wildebeest in the Ngorongoro Crater have permanent grazing and water. As we have already seen, 25-50% of the males occupy territories while females and juveniles are found in small groups which move about restricted home ranges.

Bachelor herds occupy peripheral unfavourable habitat. Migratory wildebeest in drier environments move about in large mixed aggregations, following grazing and water and not spaced by social pressures (Estes, 1968). Only when migration comes to a halt do males take up temporary territories.

Large mobile assemblages of springbok (Bigalke, 1961 and in press) and impala (Jarman, 1970) congregate on green flush produced by localised rain showers, and the spacing effect of social behaviour is only clearly apparent during the rut.

Gemsbok are seasonally mobile (Eloff, 1969a; Bigalke 1961) and gather on patches of fresh pasture, but very large herds comparable with those of wildebeest, for example, have not been recorded. This may be partly the result of smaller populations, but seems also to be related to less highly developed sociability.

Eland are nomadic (Eloff, 1959a, Bigalke 1961) and this behavioural trait is probably very important in such an ecologically tolerant animal. We have already noted that herds tend to be larger in summer and smaller in winter when dispersal is probably an important means of obtaining enough food.

Implications for management

The influence of the large, gregarious and mainly grazing species on the vegetation is, clearly, much more marked than that of small, solitary and semi-gregarious forms, dispersed by their pattern of social behaviour and in many cases, limited by specialised habitat requirements.

We have shown that green flush attracts large congregations. In arid regions where rainfall is often local, these assemblages of animals may crop the grasses of small areas very heavily at the time when the growing plants are most susceptible to damage. Only where good food, and water, is abundant throughout the range, do social interactions tend to have a spacing effect which serves to spread the pressure on the food plants. In most cases the spacing effect of intra-specific intolerance is usually only marked during the rut. Too many animals, even if they are dispersed and sedentary, can also lead to overgrazing. The distribution of water affects dispersal mainly in the dry season, when the animals have only dry food.

Management of these gregarious ungulates on farms involves careful control of numbers in the first instance. Too many animals set undesirable patterns of plant succession in train, leading to deterioration of the range and to phenomena such as the encroachment of woody plants in grassland. The animals are difficult to move at will, so that the systems of grazing control which can be applied with domestic animals, cannot be used.

Fencing farms into paddocks makes it easier to manage some species (see below). Where paddocks are large and climate and vegetation permit the use of fire, block burning is a useful method of attracting concentrations of animals to different areas in rotation. Manipulation of water points can also assist in moving animals, but this is usually only successful in the dry season.

Social species living in herds in relatively open country can be more easily and economically cropped in large numbers than solitary and semi-gregarious forms. However constant hunting quite soon leads to behavioural adaptations and techniques must be varied. Shooting from hides at water-holes or with the aid of strong lights at night, are methods which may be successfully employed in many cases.

CONTROLLING THE COMPOSITION OF POPULATIONS

Where natural populations are managed merely to keep the numbers within the carrying capacity of the vegetation, control should have the aim of maintaining natural age and sex ratios. Our main interest is however in populations which are managed for trophy hunting and those cropped for maximal production.

In the first case, it is necessary to know what proportion of mature males can be shot without disrupting the social organisation to the extent that reproduction is affected. When cropping, the sex and age composition of the kill which will produce the highest sustained yield must be known. These are not purely behavioural questions. The answers depend on whether a species is polygamous or monogamous, and also on the age at which males and females become sexually mature, and whether sexually mature males are also behaviourally adequate for successful mating. In many cases the basic information required to provide the answers is not yet available.

(a) Solitary species

It is generally assumed that solitary species are monogamous and the fact that the sex ratio in natural populations often approaches unity supports this view. Wilson and Roth (1967) found a unit sex ratio in 422 grey duiker shot in Zambia. There were almost equal numbers of each sex among 324 steenbok shot in Zululand (Mentis, 1970). However Wilson and Kerr (1969) counted 67 males and 35 females in 102 steenbok foetuses and Van Bruggen (1964) saw 47 males, 10 females and 10 unsexed animals in the Kruger National Park. In Sharpe's grysbok, Dasmann and Mossman (1962) report a proportion of 100 females: 81 males, but the sample was not large. Elder and Elder (1970) recorded virtually equal numbers of male and female bushbuck in 167 sightings. However Mentis (1970) reports that 59.9% of 2, 535 bushbuck shot in Zululand were females and Wilson and Child (1964) found a ratio of about 80 males: 100 females among adult bushbuck (shot) although the overall sex ratio of all age groups approached equality.

If it is assumed that dominant individuals of both sexes occupy territories, resulting in the presence of a 'floating reserve' of subordinate animals which are normally lost by emigration or fall prey to predators, disease or starvation, then the removal of territory holders would be expected to 'make room' for subordinates. If adult males are shot, they should be replaced by younger animals. Since the small antelope appear to be quick maturing, reproduction should not be affected by a shortage of fertile males. Assuming monogamy, unselective cropping of both sexes should theoretically produce the highest yield.

Unselective hunting has in fact been shown to stimulate increase in a population of grey duiker (Child and Wilson, 1964) and it is probably safe to assume that this is the best management technique for solitary species. It is in any event the only practicable one, for it is exceedingly difficult to select one sex or the other when hunting small antelope in thick cover.

There is some evidence suggesting polygamous mating in bushbuck. We have already noted the preponderance of females reported by some authors. Verheyen (1955) describes both male and female bushbuck as territorial, but he observed as many as 10 animals together on a communal grazing ground. A particularly fine male had only to appear to be immediately joined by one or other of a pair of females. He would then return to his territory with the female. Mating was not observed however. This observation and the unequal sex ratio suggest the unusual combination of polygamy with territoriality of both sexes. If further work shows this to be the case, cropping for the greatest yield should be planned to take both males and females in the proportion in which they occur. Selective removal of dominant males as trophies, which is easy in this sexually dimorphous species, may simply permit sexually mature but normally subordinate, non-terriorial males to take over the mating functions of the animals which have been shot. However the age of sexual maturity in male bushbuck is not known and until it is, little more than speculation is possible. A 'buck law' has been in operation for bushbuck in the Cape Province and Natal for many years and populations seem little affected by hunting on this basis.

(b) Semi-gregarious species

Wilson and Child (1965) found a sex ratio close to unity in klipspringer, counting 44 males and 52 females. In a reedbuck kill of 840 animals shot in Zululand, the ratio was not significantly different from unity (Mentis, 1970). The same author reports unit ratios for mountain reedbuck (n = 31) and bushpig (n = 179) and a slight excess of females (52.4%; ratio significantly different from unity) among 4, 681 warthog, all shot in Zululand.

Simpson (1968) records 61 males: 100 females in kudu (n = 289), which is in agreement with the figure of 64: 100 (n = 305) from Zululand (Mentis, 1970). Dasmann and Mossman (1962) found a ratio of 46 : 100. Only Wilson (1965) shows more males than females (119 : 100) in the sample collected by shooting, although on his sight records he obtained a ratio of 42 males per 100 females. Simpson (1968) considers that Wilson's non-conforming kill figures are the result of a higher hunting mortality in males, or a lower visibility in sight counts. In any event, kudu have a sex ratio not significantly different from unity at birth, and male mortality thereafter is higher than that of females (Simpson, 1968; Dasmann and Mossman, 1962).

Management techniques for klipspringer and reedbuck are affected by their specialised habitat requirements. Where they are sparsely distributed in isolated islands of suitable country, selective removal of males may be undesirable because the chances of replacement from the 'floating reserve' are slight. Where good habitat is widespread and the animals common, and assuming monogamy, which seems to be the case, it should be possible to manage them like solitary species. Removal of dominant males for trophies should not depress reproduction, since they would be replaced by younger males which probably mature quite quickly. It must however be noted that the age of sexual maturity has not been determined for either species. Unselective cropping at a rate determined by population dynamics of the species might be expected to be as suitable as for solitary species. The only evidence available concerns the effect of tsetse control hunting in Eastern Zambia (Wilson and Child, 1965). Klipspringer proved difficult to eliminate, probably because of their specialised habitat and high reproductive potential. Indeed the authors suggest that hunting may have stimulated an increase in the population studied.

In the polygamous mountain reedbuck and vaal rhebok male herds may be expected to provide replacements for mature males shot from harem herds. Unless cropping of males is very heavy, a shortage seems unlikely to develop since these fairly small antelope, by analogy with others of comparable size, probably become sexually mature by the age of about two years. The question of how many apparently excess males, which do not seem necessary for reproduction in polygamous species, should in fact be kept, will be discussed under the heading of 'gregarious species' below.

Child *et al.* (1968) have discussed the implications of the apparently monogamous mating behaviour of warthog, and of delayed attainment of sexual maturity in males, for the management of the species. In a dry area of Rhodesia, they found that females matured as yearlings, but males a year later. The sex ratio was unity, so that there were more sexually mature females than males among animals of 24 months or older. In one sample collected there were 122 sexually mature males, and of 173 mature females, only 124 had bred. Thus the number of females breeding in any season would appear to depend on the number of mature males. Selective hunting of males will therefore depress reproduction. A maximum sustained yield can only be obtained by harvesting correct proportions of males and females, taking into account the existence of a pool of sexually mature females which do not take part in reproduction.

Too little is known of the social behaviour and sex structure of bushpig populations to comment on management.

The mating behaviour of the kudu has not been described[1]. They rut in winter, with maximal development of the testes in June (Skinner, 1971). Simpson (1968) found a peak in herd size in July and associated this with the rut. Wilson (1970) encountered one or more bulls with herds of cows and calves on 10 occasions during May. Kudu

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[1] But see Walther 1964. *Z.J. Tierpsychol.* 21: 393-467.-eds.

are certainly polygamous but males probably do not mate with large numbers of females. The mean July herd size recorded by Simpson was only about 3. 5 (over 20 herds) and the maximum 12. Selective shooting of adult males carrying trophy heads is unlikely to disrupt reproduction since fully developed horns with 2½ twists probably take 6-6½ years to develop (Simpson, 1968). At the age of two yours horns only have one twist. The age of male sexual maturity is not known but since females may mate at about 17 months (Simpson), males, even if they mature later, must be expected to be sexually mature long before their horns attain desirable trophy size.

Exclusive cropping of horned males of all ages must be expected to lead to a shortage, particularly since, as we have noted, the male mortality rate is higher than that of females. Cropping must therefore take both sexes, but it is not possible to suggest an optimal ratio from available information.

(c) Gregarious species

We have seen that competition among males of most of the gregarious species for access to females, results in the formation of harem herds. Comparison of the size of the harem herds with sex ratios found in wild populations, makes it clear that relatively few male hartebeest, blesbok, wildebeest, springbok and impala succeed in mating.

The number of hartebeest cows in harem herds varies from 2-14, according to Backhaus (1959), and this author quotes D'Elzius (1957) who found the population to contain slightly more cows than bulls. Among 3, 457 adult hartebeest, males and females were almost equally represented (Foster and Kearney, 1967). Du Plessis (1968) counted 2-25 blesbok females in harems and calculated a mean of 7. 6 in one year, and 10. 4 in the next. Since there are no longer any wild blesbok, the sex ratio in natural populations is unknown, but an adult ratio of about 1 male : 2. 6 females is reported by du Plessis.

Bigalke (1970) found the mean size of springbok herds during the rut to be 18. 7. Impala harems are similar according to Leuthold (1970); in one area, 54% of the harem herds contained 6-25 animals while in another where the vegetation was less dense, they were somewhat larger, 69% of the groups varying in size between 26 and more than 35. These authors found an adult male: female ratio of roughly 1 : 2 in both species.

Only for wildebeest has the proportion of the male population which copulates been estimated. Estes (1968) found the year-round average size of nursery herds in Ngorongoro to be 10, including 6 adult females. With a sex ratio of 40 males: 50 females, he calculated that adult, territory-holding bulls constituted some 7-14% of the total population and perhaps 25-50% of the adult males. He writes: 'up to 50 per cent if not more of the adult males may be relegated to bachelor herds at any time, not because they are unfit, but simply because they are supernumerary'. Only some of the territorial individuals were successful in mating. The proportion of reproductively active males may be still smaller in other populations, since several authors have reported a preponderance of males:-52 males: 42 females in Serengeti (Talbot and Talbot, 1963) and about 58 males: 42 females in the Nairobi Park (Foster and Kearney, 1967) and in Zululand (Mentis, 1970). Talbot thought that only 8% of his animals, and 16% of the adult males, were lone (i.e. territorial and reproductive) bulls.

The few data available for eland show an adult sex ratio of 14-16% males in Malawi (Martin, 1968) and about 25% males in Natal (Natal Parks Board, unpublished). Foster and Kearney (1967) report 69. 8% males in a sample of 172 adults from the Nairobi Park but this figure is so different from the others that it must be treated with suspicion. The only information on gemsbok sex ratios known to me is a figure of 35 males: 65 females among 302 animals counted in the Etosha Park (Bigalke, unpubl.). The proportions of male eland and of gemsbok which play an active part in mating has not been determined.

The removal of adult males by trophy hunting is unlikely to depress reproduction. The males of all species for which data are available, attain sexual maturity and are physiologically capable of mating, long before they become sufficiently dominant to have access to females. Dominance by older males leads to an 'inhibition of effective puberty' (Sadleir, 1969) or 'psychological castration' (Altmann, 1960) and removal of these older animals must be expected to give younger ones the chance of mating, normally denied them.

Rowe-Rowe and Bigalke (in press) observed successful mating by a male blesbok only about 19 months old. Blesbok of this age are easily distinguishable in the field and are never seen in harem herds. It is of interest that this animal did not appear to be able to mate during the usual rutting season, when he was about 27 months old, but managed to do so later with the result that the young of his three adult female partners were born about three months later than usual.

Skinner *et al.,* (1971), found spermatozoa for the first time in testes of springbok aged 48 weeks. They state that 'Sexual maturity is rapidly achieved after 50 weeks of age'. Impala males are capable of fertilization from the age of about 13 months and an animal of 17-18 months mated successfully (Kerr, 1965). In neither species do males of these ages participate in the rut.

Wildebeest bulls appear to be physically capable of reproduction as two-year-olds, yet few become territorial before the end of their third year (Estes, 1968). The few animals seen to participate in the rut at 28-29 months were subjected to intense psychological, and physical, pressures. Estes writes: 'of half a dozen that were kept under observation, not one withstood the battering of his neighbours for more than a few hours before abandoning his place'. A male eland of 18 months mated successfully with a female of the same age, but other males of this age played no part in mating in a semi-domestic herd where adult males were present (pers. obs.).

The most important question from the point of view of management is: what proportion of males to females is needed for optimal reproduction? The non-copulating segment of the male population seems so obviously unnecessary that there is a strong tendency to dispense with it. There is a suggestion that a normal 'wild' sex ratio may even depress the conception rate under conditions of semi-confinement, because the males interact so vigorously. When the apparently excess males were shot in a herd of black wildebeest (*C. gnou*) on a reserve, the calf crop increased markedly (Van Zyl, pers. comm.). Even in a wild population—of kob (*Adenota kob*)—Leuthold (1966) has suggested that reproduction may be more efficient at low densities where males defend territories of 100-200 m diameter, than at high densities where their territories or leks are only up to 30 m in diameter and male interactions are very frequent.

On the other hand, the presence of supernumerary males ensures selection for the most vigorous animals. It is difficult to imagine any other practicable way of maintaining the genetic quality of managed populations. The role of male stimulation in synchronising oestrus is well known in domestic artiodactyls and other mammals (Sadleir, 1969) and is likely also to be important in the species under discussion. These, at least outside the tropics, have short and distinct lambing seasons, as Bigalke (1970) has shown for springbok, Fairall (1971) for impala, and Du Plessis (1968) for blesbok; remarkable synchronisation within the tropics for wildebeest in the Serengeti has been recorded by Watson (1969), who states that 80% of the calves are born within a three-week period. Oestrus is therefore well synchronised and the 'excitement' provided by male interactions may play a significant part in achieving this. The role of odours has not been studied at all, but it can also be expected to be important. Sadleir's (1969) comment is relevant 'it would seem more than likely that future research will demonstrate that odours act as pheromones and can influence the reproduction of wild animals at high densities in exactly the same way as occurs in the laboratory'.

For the purposes of practical management, the best solution possible in the present state of knowledge is probably to strike a compromise between the normal sex ratios of wild populations and the male: female ratio observed in harem herds during the rut.

REACTIONS TO CONFINEMENT

So far, we have attempted to describe the behavioural attributes of our species as observed in wild and more or less undisturbed populations. Management on farms and ranches, most of them fenced, is concerned with the behavioural reactions to confinement. This is clearly a relative term, but for the purposes of this paper, confinement in areas so small that the animals require artificial feeding will not be considered. Behaviour under these circumstances is the province of the zoo biologist. It is also clear that the size of enclosed areas *per se* is of little interest; it is size in relation to the productivity of food plants and the presence of cover and water that is important. In general, farms tend to be larger and more extensively managed in areas of low productivity, and smaller, with smaller and more intensively managed paddocks in highly productive regions. Game populations are greatest and of most importance on the large, extensive pastoral holdings where they range over fairly big areas in a more or less natural state and are not closely confined. The techniques of managing them more effectively under such conditions are not yet well understood.

1. Reaction to fences

Farm fences in South Africa are usually 4 ft.-4 ft. 6 in. high. In sheep farming regions, most are made of netting wire and are commonly called 'jackal-proof fences. Cattle ranches are enclosed with fairly simple fences of plain or barbed wire. The effectiveness of these barriers in holding wild ungulates is related to the size, behaviour and locomotory abilities of the animals. However, as Hediger (1950) has pointed out, 'excitement weakens all a barriers' and enclosures which are normally adequate, may fail to hold excited and disturbed animals, or those strongly motivated by hunger or thirst. The size of the enclosure also affects the adequacy of the fence, and Kettlitz (1962), urges a policy of 'the smaller the enclosure the stronger the fence'.

The small solitary antelopes do not jump fences and are contained by netting, but slip easily between strands of plain or barbed wire. Bushbuck jump well however and according to Astley Maberley (1963) can clear fences less than 7 ft. high.

Of the semi-gregarious forms, the kudu, a tragelaphine like the bushbuck, is a prodigious jumper and an 8 ft. fence is necessary to keep them out of croplands. Reedbuck, mountain reedbuck and vaal rhebok jump fences of standard height. Nothing appears to have been recorded of the response of the klipspringer. Warthog burrow and can only be contained by netting with the lower end buried.

Blesbok are easily confined by simple fences but crawl beneath or between the lowest strands if these are too far apart. (Kettlitz, 1962). Hartebeest also use regular creeps but do occasionally jump over (pers.obs.). Springbok crawl through or under wire strands but very rarely jump fences unless hard pressed, in spite of their spectacular leaping abilites. Walther (1968) has drawn attention to the fact that none of the gazelles are behaviourally equipped to overcome vertical obstacles—in complete contrast to the tragelaphine bovids. Impala jump normal fences with ease and need a 7 ft. barrier to hold them, although they can clear 8 ft. when pressed (Kettlitz, 1962). Gemsbok creep through or under stranded fences but do not, as far as I am aware, jump over them. Eland, like kudu, are spectacular jumpers in spite of their large size and are capable of jumping 6-7 ft. fences (Skinner, 1967), although a 6 ft. 6 in. barrier successfully contained a semi-domestic herd in Natal (pers.obs.).

Animals which have become accustomed to a fence, tend to accept it as an insuperable barrier. Even when it is removed, farmers often find it difficult and usually impossible to drive springbok, blesbok (pers.obs.) and impala (Kettlitz, 1962) across the line of a known fence. This behaviour thwarts efforts to drive animals from one paddock to another in order to apply rotational grazing systems, and adds to the practical difficulties of efficient game management.

2. Social behaviour in confinement

Ewer (1968) considers an increase in aggressiveness to be a normal feature of captive behaviour among mammals. Under farm conditions, it would seem to be the lack of space for victims of aggression to escape, rather than an increase in aggression as such, that poses problems in small paddocks.

We have already suggested that the weaned young of solitary territorial species may be expected to be killed, or to die from harassment and lack of a place to live, if they cannot disperse because of the presence of fences. There is not yet any clear evidence to support this view. We do not know to what extent territories may be compressible and behaviour capable of modification by confined conditions. That some modification is possible is suggested by casual observation of captive grey duiker (Greig and Bigalke, unpublished). Females, like males, tend to occur singly and are probably territorial, or at least occupy individual home ranges in the wild. In a group consisting of an adult male and three females living in a small zoo paddock, the largest female A is clearly dominant over the other two females B and C. She marks with her preorbital glands almost as frequently as the male. Female C, probably the youngest, is often virtually confined to a kennel by the aggressive behaviour of A. It is interesting that A tolerates B, who is probably her daughter; perhaps sociability is well enough developed to permit establishment of a ranking order of two, but not of three. Much more work is needed to find the greatest densities at which solitary species can be maintained.

The social species are all, except perhaps the gemsbok, seasonal breeders in South Africa. Male aggressiveness reaches a peak during the rut and in species with territorial males and a harem system, rivals are often vigorously pursued. Aggression of dominant males towards yearlings has also been reported in blesbok (Rowe-Rowe and Bigalke, in press) and wildebeest (Estes, 1968), at the time when the next crop of young are born. This rather surprising behaviour may be related to excitement induced by the smell of parturient females. In any event, yearlings are chased with tremendous vigour.

In small paddocks, blesbok males frequently kill other males and even females and lambs (Kettlitz, 1967). It is clear that behavioural responses of this kind influence the density at which social species can be maintained, but no exact information is available on the densities and sex ratios necessary to maintain normal behaviour.

The hierarchical system within eland herds seems to be similar to that of the Bovini which Ewer (1968) discusses. The fact that it successfully reduces aggression, makes eland easy to keep and has certainly been an important, and perhaps hitherto unrecognised, reason for the success of domestication experiments such as those described by Treus and Kravchenko (1968) and Pesselt (1963).

3. Response to herding

When social species are hunted or captured, they are often driven to the guns or catching pens. Horsemen, motor vehicles or aircrfat may be used. Herding from the air does not generally seem to be very successful in the case of springbok and blesbok in open country, but experienced horsemen can move the animals quite efficiently. A helicopter has been shown to be highly suited to driving wildebeest, impala, kudu, warthog and other species (Oelofse, 1970).

Animal catchers and hunters believe that a study of the routes which the animals usually follow when they are alarmed, is a prerequisite if they are to be successfully driven to a pen or on to a line of guns. When arranging drive hunts of springbok and blesbok, farmers often position the guns in a fixed place and drive in a standard pattern. This suggests the existence of favoured routes with which the animals are familiar. Well-worn paths are indeed a familiar feature of all areas where wild ungulates are found and Hediger (1950) in particular has emphasised the fact that animals tend to move between 'biologically significant points connected in a characteristic manner by means of definite tracks or beats'.

4. Temperament

While it is difficult to discuss an attribute as vague and ill-defined as temperament, there is little doubt that the species under discussion differ considerably in this regard. The differences have significant implications for handling and management. It is a matter of experience, and well known to farmers who work with them, that blesbok are docile, and easy to capture and transport (Kettlitz, 1967; Visagie, 1968). Impala and springbok are nervous and difficult to catch and transport, often resulting in high losses (Kettlitz, 1962) unless they are treated with skill and care. Eland have a reputation for docility (Bigalke and Neitz, 1954) and have been successfully domesticated in several trials (Posselt, 1963; Treus and Kravchenko, 1968). Gemsbok and vaal rhebok have a reputation for aggressiveness (Shortridge, 1934) and gemsbok may be captured with ease by using trained dogs to bay them. The animals are so intent on the dogs that they pay no attention to the approach of people (pers. obs.).

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for land had not yet reached a peak, but only after a great deal of shooting had taken place, resulting in the extinction in the areas chosen for the reserves of several species of large ungulates. After their establishment, pressures from settlers increased rapidly with the opening up of nearby land, and the situation today is that nearly all of the reserves comprise mere 'islands' surrounded by intensive settlement.

The result has been that, whereas before, the large game populations had been able to range extensively (and indeed there is clear evidence that seasonal migrations took place), today they are confined for 12 months of the year to only a remnant of their former range. The future management implications are obvious in that the habitat is subjected to year-round utilization—a situation which has, as we shall soon see, had diametrically opposite effects on ungulate population behaviour in two different habitats in Natal.

Coupled with this fact is that of the destruction of predators, in the belief that it was only by doing this that the herbivorous ungulates could be preserved. So was manifest stage 3 of the evolution of game management, and whilst it was not sound policy in the eyes of modern conservationists, the practice must not be too heavily criticised. This control of predators, embracing not only the large cats such as lion and leopard, but also hunting dog, jackal and baboon, continued until after 1950, before wisdom prevailed.

It is too much to hope that the situation will revert to that pertaining before the interference of man, and it must remain a basic tenet of conservation in almost any area throughout the world that some form of management in the form of habitat manipulation or population control will always be necessary.

This 'nettle' has been firmly grasped by the Natal Parks, Game and Fish Preservation Board, which is the body responsible in the province for the control of all wildlife—not only inside game and nature reserves.

THE PAST AND PRESENT

Firstly, a brief explanation of conditions in Natal is necessary. The altitude varies from over 3000 metres to sea level, with a wide range of habitats from Subalpine to truly tropical. Game reserves are so situated as to embrace these extremes, although regrettably there is little reservation in the intervening life zones. However these conditions, when considered in relation to the fact that game populations are restricted, have led to interesting problems which are far from being properly solved, and a good deal of improvisation has had to be employed with, so far, adequate results.

The Highveld Area. Only one major reserve is situated in this zone, namely Giant's Castle Game Reserve. It consists of very open grassland on rugged terrain, and is subjected to severe winters. During the winter the grass has a very low nutritional value and is unpalatable. Few ungulate species are endemic to the Drakensberg, although of those occurring in Giant's Castle, the blesbok *Damaliscus lunatus,*the black wildebeest *Connochaetes gnou.* and the vaal rhebok *Pelea capreolus* are typically highveld forms.

The first two mentioned are re-introductions to the reserve, whilst the third is a smaller antelope and has always occurred there. Little is known of the past habits of the blesbok and black wildebeest, before they were exterminated from Natal, but because of the nature of the vegetation, it is unlikely that the latter species could successfully have existed in the Giant's Castle area on a permanent basis. Certainly von Richter (1971) has shown that the area is very probably marginal to its distribution, as evidenced by the poor reproductive and survival rates. The same can be said of the blesbok population, which has shown a poor performance since its introduction.

Liebenberg (1964) quotes several early travellers, indicating that migration into the highveld grasslands in summer was a feature of the vast herds of game that inhabited the interior of South Africa. In winter they moved back towards the 'lowveld'.

Another important species which occurs in Giant's Castle is the eland *Taurotragus oryx.* This is a mixed feeder, although in this area it has adapted to an almost purely grazing habit. There are many people alive today who recall the fact that eland migrated to lower altitudes in the winter months, returning to the open plains and grasslands when the grass became palatable. Today this movement is restricted, and the animals can only repair to the lower ground within the reserve where limited browse is available. The results had been that the population has not increased to any extent, having remained very stable since it was first censused by air in 1962. Estimates made by residents prior to this date confirm this fact, as shown in Table 1. It would appear again that the rates of reproduction and survival are severely impaired by this existence—a result of management in the form of artificial restriction.

TABLE 1. ESTIMATES OF NUMBERS, AND CENSUSES OF ELAND IN THE NATAL DRAKENSBERG.

(Figures marked * are estimates, the remainder are results of aerial censuses)

Year	Number
1916	600*
1921	700-800*
1926	1, 000*
1962	703
1963	650
1964	817
1965	709
1966	777
1969	536
1970	682
1971	870

Those smaller ungulates species which occur in the area do not pose problems in management: there is no evidence of any serious decline in numbers or of over-utilisation of the habitat, and it must be concluded that they have achieved a reasonable balance with the habitat. Research is needed to establish whether the stability is due to spatial or nutritional reasons—or both.

Thus it is that highveld conditions impose a restrictive effect on population performances, whilst it will now be shown that the reverse is true of the lowveld.

The Lowveld Area. The vegetation of the lowveld is of the form of woodland of varying density, generally with a grass understorey. Severe winters are not a feature of this biome, and the grasses retain their nutritional value throughout the year, being of a different species composition to that in the highveld. The consistent high level of palatability has lent the general term 'sweetveld' to it, as opposed to the 'sourveld' which is applied to the higher altitude areas.

The presence of both grass and woody plants has meant that a wide range of ungulate species has evolved along with this habitat, to include pure grazers, mixed feeders and browsers. Traditionally, it is the lowveld which has become known as the main game area of Africa, the same—or similar—grass species occurring throughout most of the continent.

Because of the nature of the vegetation, the main problem in management of the low-veld reserves, including Umfolozi, Hluhluwe, Mkuzi and Ndumu Game Reserves, has been one of over-utilisation caused by overpopulations of game.

This fact became very evident in the 1950's after rigid protection had been enforced for some years. It resulted in the introduction of a policy of population control which initially took the form of shooting, although small numbers of impala *Aepyceros melampus* were caught alive for distribution to a few interested farmers. Prior to this time, one of the main reasons for there not having been any such problem was the policy adopted by the veterinary authorities in an effort to eradicate the tsetse fly, which was responsible for the transmission of a disease fatal to domestic stock and carried by game animals. Tremendous numbers of game animals were destroyed, as described by Vincent (1969) and Mentis (1970), particularly in Umfolozi Game Reserve.

Thus it was that in 1954, probably one of the first planned ungulate population control programmes in Africa was put into motion in Hluhluwe Game Reserve—planned that is with the benefit of the habitat as the ulterior motive. During the period August 1954 to May 1955, 729 wildebeest *Connochaetes taurinus* and 494 zebra *Equus burchelli* were shot in the area. Then in 1958 it was resolved that population control in Hluhluwe and Umfolozi Game Reserves should become an established management technique, and efforts were directed initially at wildebeest and zebra, but later also at warthog *Phacochoerus aethiopicus* and impala *Aepyceros melampus.* It was clear at this stage that the step was an essential one if habitat deterioration was not to continue, and the benefits thereof were soon evident. It is interesting to note that there was no real problem in so far as browsers were concerned. Furthermore, the control was based largely on estimated populations, and not on census and calculation of annual increments. The numbers of animals destroyed to date, including those shot specifically for rations are shown in Table 2.

TABLE 2. NUMBERS OF ANIMALS SHOT IN THE HLUHLUWE AND UMFOLOZI GAME RESERVES SINCE THE INCEPTION OF THE POLICY OF NUMERICAL CONTROL OF UNGULATES

	Species				
Year	Warthog	Wildebeest	Impala	Nyala	Zebra
1957	39	309	146	16	
1958	580	199	124	21	
1959	4,353	1,325	1, 330	501	577
1960	2,769	732	566	228	246
1961	1,154	741	441	5	9
1962	2,371	894	455	49	84
1963	2,408	954	456	15	73
1964	3,390	835	427	5	45
1965	1,811	1,209	1,283	176	333
1966	1,059	979	1,153	146	16
1967	827	694	586	1	1
1968	782	332	453	0	21
1969	1,842	274	438	0	18
1970	1,222	267	418	0	0

In Mkuzi Game Reserve, the predominant species has for many years been the impala. In the early 1950's small numbers of these animals were caught alive for redistribution to other reserves and to local farmers, who were already recognizing the advantages of having small herds for sport hunting and domestic use. This in fact was the start of an ever-increasing demand in Natal for live animals, and culminated in 1966 in the establishment of the first game ranch in the province.

The numbers of animals shot in Mkuzi Game Reserve are shown in Table 3. The large numbers controlled in the period 1963-1965 followed the realisation of the need for a drastic reduction in the population. Carcasses were sold on the open market.

TABLE 3. NUMBERS OF ANIMALS SHOT IN MKUZI GAME RESERVE SINCE THE INCEPTION OF THE POLICY OF NUMERICAL CONTROL OF UNGULATES.

	Species		
Year	Warthog	Wildebeest	Impala
1960	5	205	118
1961	17	307	237
1962	38	375	346
1963	32	201	1, 567
1964	7	267	4, 360
1965	138	506	3, 045
1966	159	191	845
1967	26	2	624
1968	109	1	691
1969	140	185	559
1970	103	193	284

In order to provide for the game ranching movement, the Natal Parks Board modified its game control policy to allow for the larger scale capture of ungulates, and to this end employed one man to develop satisfactory methods. Regrettably, the evolution of the capture technique has not been documented, so that it will not go amiss if it is described here very briefly.

At first it was done by means of nets, into which animals were driven, and in which they became entangled. This technique involved a good deal of manhandling of animals, often resulting in injuries to both captors and captives. Variations of this method included driving on foot, on horseback, and by vehicle. A significant breakthrough was the discovery that a blue plastic material provided sufficient of a barrier to the animals' movement to enable them to be trapped in a 'boma' or corral, constructed of the material, and enabling them to be subsequently brought down by sheer force of numbers and manhandled into travelling crates.

This method proved good for wildebeest and zebra, whilst impala continued to be caught by hand at night, with the aid of spotlights. Oelofse (1969) describes the method of catching with the use of blue plastic. Initially it was considered that blue had some 'magical' property, but it was subsequently found that the mere presence of a sufficiently high, opaque barrier, whatever colour—was sufficient to prevent animals from attempting to escape; this despite the fact that any animal could simply walk through the material. Bomas so constructed have been known to contain square-lipped rhinoceros for over 24 hours without water (Oelofse, pers. comm.).

The technique has been further perfected, so that at no stage are the animals handled, but are separated into manageable groups and driven up a ramp into waiting lorries carrying a wooden superstructure. Up to 15 wildebeest or zebra may be transported at once in this way.

The latest major development has been the introduction of a helicopter for use in