Koedoe 17: 185 – 195 (1974).

HABITAT-PREFERENCE IN SOUTH AFRICAN ANTELOPE SPECIES AND ITS SIGNIFICANCE IN NATURAL AND ARTIFICIAL DISTRIBUTION PATTERNS

U. DE V. PIENAAR
Division of Nature Conservation
Private Bag X404
Skukuza
1350

Abstract – The unequal distribution of species is due to different environmental conditions of the various regions of the globe. The environmental factors governing the occurrence, distribution and abundance of large herbivorous mammals may be divided into physical, historical and biotic. Vegetation is all-important in herbivore biology as it provides habitat, cover and food. Many of the distribution patterns and structural attributes of species are associated with living in and utilizing particular vegetation zones. Africa has an enormous diversity of habitats and animal species utilizing these habitats. An attempt is made to characterize the patterns of habitat preference of South African antelope species and the significance of the habitat requirements of the individual species is discussed in the light of natural and artificial distribution patterns. It is stressed that artificial introduction of species without prior knowledge of the habitat requirements of such species may lead to disastrous consequences.

The total of a million or more distinct species of animals is not evenly distributed on land and in oceans. This unequal distribution is due, above all, to the very different environmental conditions of the various regions of the globe, as well as to the many changes undergone by the earth's surface during the course of time.

The environmental factors determining distribution seem separate in (i) sea barriers and temperature, which are of particular zoogeographical importance since they have historical and phylogenetic consequences, and (ii) rainfall and vegetation, which determine more the contemporaneous pattern of the biomes, and whose effects are evident more in the adaptive ecological types than in the phyletic constitution of the fauna (Poynton 1962).

Factors governing the occurrence, distribution and abundance of large herbivorous mammals may also be divided into physical, historical and biotic categories. Species differ in the ranges of temperatures at which they can function efficiently or comfortably, and this explains latitudinal and altitudinal differences in distribution. Rainfall is important directly in providing surface water and indirectly in its influence on distribution. Limitations to population size imposed by low water supplies has been

described by many workers and the catastrophic effects of droughts on animal populations in Africa are well known. The areas of climatic extremes – the deserts, high mountains and the Arctic regions – are notoriously poor in numbers of herbivorous species, and seasonal movements, dictated by the necessity to maintain minimal living conditions, are well developed in the inhabitants of these places.

Soils exercise a direct on herbivores through the vegetation. In the Kruger National Park the average daily density of grazing herbivores is, for example, significantly higher on soils derived from a doloritic or basaltic substrate than on adjoining granitic soils – climatic conditions being equal (Van Wyk 1972).

Physiography, as well as being important in its influence on rainfall, drainage patterns and vegetation, may limit distribution (e.g. the Great Rift Valley of Africa) or create special habitats such as rocky outcrops, islands, etc.

Biotic factors influencing distribution and abundance of herbivorous species are the destructive and competitive actions of man, the variety and abundance of natural predators sharing the habitat, enzootism of drastic bacterial, viral or parasitic diseases in habitats of susceptible species and the presence and density of other herbivores with complementary or competitive actions in the shared habitat.

Ultimately, however, vegetation is the all-important factor in herbivore biology in that it provides habitat, cover, protection from natural enemies and food (Keast 1968). Many of the distribution patterns and structural attributes of species are associated with living in and utilizing specific vegetation zones. An understanding of distribution in large herbivores is greatly simplified by most species being linked to one or other of the major vegetation formations.

Habitat preference as indicated by herbivorous species may be measured by the frequency of their distribution in the various vegetational zones. In a transect of a particular area characteristic patterns of frequency are apparent for each of the species in the vegetation zones present.

The degree of dependence or attachment to a habitat by a herbivorous mammal, is not only linked with the availability of preferred food plants and required growth stages in a particular region, but the animal also requires a great deal more from its habitat. Important features are (i) whether it affords the minimum sized living area acceptable to the species (territoria and activity zones) for daily and seasonal movements; (ii) adequate shelter to avoid exposure to the elements, predation, etc.; (iii) freedom from excessive competition by competitive associated species; (iv) availability of surface water; (v) the facilities for escape from abnormal climatic phenomena such as floods, droughts, etc.; and (vi) whether it fulfils the requirements for reproduction.

The distribution of herbivores within their selected habitats are also significantly influenced by (i) their tendency to be dispersed uniformly or concentrated where there is a particular fodder species, plant composition or degree of cover; (ii) the degree of europhagia or stenophagia in their

feeding habits; (iii) their link with particular successional growth stages (Vesey-Fitzgerald 1965); (iv) their dependance on surface water, drinking frequency and tendency to keep close to streams, etc.; (v) their degree of tolerance of associated herbivores and place in the social hierarchy of the herbivorous community; and (vi) their response to seasonal changes in the vegetation and fire.

Africa with its great diversity of species, diverse physiography, vegetational and climatic range, portrays greater spatial and habitat subdivisions than the other continents. The striking fact about the ungulate fauna in Africa is the variety, and at one time, the abundance of its antelope species. "This variety does not exist for our amusement or for our contempt; it has evolved as a complex of creatures making the fullest possible utilization of part of a habitat. A characteristic phenomenon in evolution is that species differentiate to states in which they overlap others as little as possible: evolution is, as it were, always probing unoccupied niches or finding possible new niches" (Fraser-Darling 1960).

Success in evolution comprises the exploitation of unoccupied links in the energy conversion cycle. Occasionally a species is successful by its ability to be unspecialized and to exploit several aspects of its environment. Amongst the southern African antelope species the most successful species are probably the kudu *Tragelaphus strepsiceros,* grey duiker *Sylvicapra grimmia* and steenbok *Raphicerus campestris,* all being able to exploit a wide range of ecological situations, even those which have become severely degraded by the activities of man. This can certainly be considered the primary reason why these three species have been able to maintain themselves over such a large area in the face of ever-increasing human and other pressures. On the other hand, there are those species which are adapted and specialized to survive only in particular and localized habitats. Thus one encounters true marsh antelope e.g. the sitatunga *Tragelaphus spekei,* crag-inhabiting antelope e.g. the klipspringer *Oreotragus oreotragus,* dambo- or plains-loving species e.g. the tsessebe *Damaliscus lunatus,* the lechwe *Kobus leche,* black wildebeest *Connochaetes gnou* and the blesbok *Damaliscus dorcas phillipsi,* forest and thicket species e.g. the nyala *Tragelaphus angasi,* the bushbuck *Tragelaphus scriptus* the blue duiker *Cephalophus monticola,* the red duiker *Cephalophus natalensis,* the suni *Neotragus moschatus* and the Damara dik-dik *Madoqua kirki,* as well as distinct lowland and highland grassland species e.g. the reedbuck *Redunca arundinum,* the vaal rhebuck *Pelea capreolus* and the oribi *Ourebia ourebi.*

Certain species show a tendency, sometimes strong, to concentrate along the boundaries between adjoining vegetation zones and in the ecotones between the zones. This is ascribed to a greater diversity of food, availability of shelter from the sun and/or greater protection from predators (Lamprey 1963). Examples in this category are the roan antelope *Hippotragus equinus,* which is a relatively unsuccessful species due to a variety of ethological and other limiting factors (Joubert 1970). In contrast, the impala *Aepyceros melampus* and steenbok, are both highly successful species and are able to thrive even in severely degraded habitats.

Distribution of many species varies seasonally and breeding and non-breeding sections of the population often differ in their distribution and preference for vegetation types (Jarman 1972).

Several schemes have been advanced for describing and formalizing habitat. These take into account such variables as the height of component trees, spacing of trees, ratio of shrub to grass layers. height of canopy, density of canopy and number of strata in the vegetation. The habitat classification and characterization of vegetation zones which are recognized by the majority of ecologists include the entities listed by Tinley (1969) i.e. forest, thicket, woodland, tree savanna, open tree savanna, shrub savanna, grassland and/or swampland and rock outcrops.

In southern Africa there occurs a wide spectrum of antelope species occupying the complete array of habitat types. These vary from moist through mesic and arid savanna to subdesert and desert, and in both the major life divisions of the sub-continent i.e. Afrotemperate/montane and Tropical (Table 1). Tinley (1969) includes the Cape and Karoo subregions in the Afrotemperate/montane life division, and this classification is also followed in Table 1, presenting the patterns of habitat preference of South African antelope species in the various moisture provinces of the two major life divisions.

It will be noted that the eland *Taurotragus oryx* is, like the greater kudu, able to exploit successfully a wide variety of habitats in both life divisions and ranging from relatively moist savanna regions to subdesert and desert. In view of their large size and preference for more open habitats they have proved more vulnerable to human exploitation than kudu and have become extinct in many regions, such as the moist grasslands and woodlands on the sandy coastal plains of northern Natal. Apart from certain protected areas they have also disappeared from the mesic and arid savannas of the Cape, the Orange Free State and the Transvaal. Natural populations have managed to survive in some of the more remote arid savanna sub-desert and desert regions of South West Africa, Botswana and Rhodesia. The nyala is a tropical species and is an inhabitant of dry forest, thicket and denser woodlands of the moist and mesic moisture province and, marginally, also of certain adjacent more arid regions. This limits its range of distribution to the Limpopo Valley, the northern riverine, deciduous forests and the sandveld thickets of the Kruger National Park, and the denser woodlands, thickets and dry forest of northern Zululand and southern Mocambique (Pienaar 1963). Bushbuck, have a much wider range of distribution and inhabit suitable forest and thicket conditions in both the Tropical and Afrotemperate/ montane life divisions of the sub-continent.

The sitatunga is a highly specialized antelope species, inhabiting tropical swamplands such as those in the Caprivi Strip and along the Okavango River in northern Botswana, but adapts itself surprisingly well to captive or artificial conditions – such as zoological gardens and private game farms far removed from its natural range of distribution (*vide* Amsterdam Zoo and certain game farms in the Orange Free State).

Blue wildebeest *Connochaetes taurinus* occur marginally in the Afrotemperate region of the northern Cape Province (Kalahari Gemsbok National Park) and in southern Africa have adapted themselves to survival in bush encroached habitats presenting rather dense woodland aspects. Thev attain peak abundance on the open grassland plains of Central and East Africa (as on the Serengeti and Athi plains). Although they are partial to water and will drink regularly when surface water is available, they have adapted surprisingly well to survival in arid and semi-desert conditions, e.g. the Kalahari, Botswana and northern South West Africa. Blue Wildebeest and many other grass-eating African antelopes show a marked inclination to move onto range that has recently been burnt.

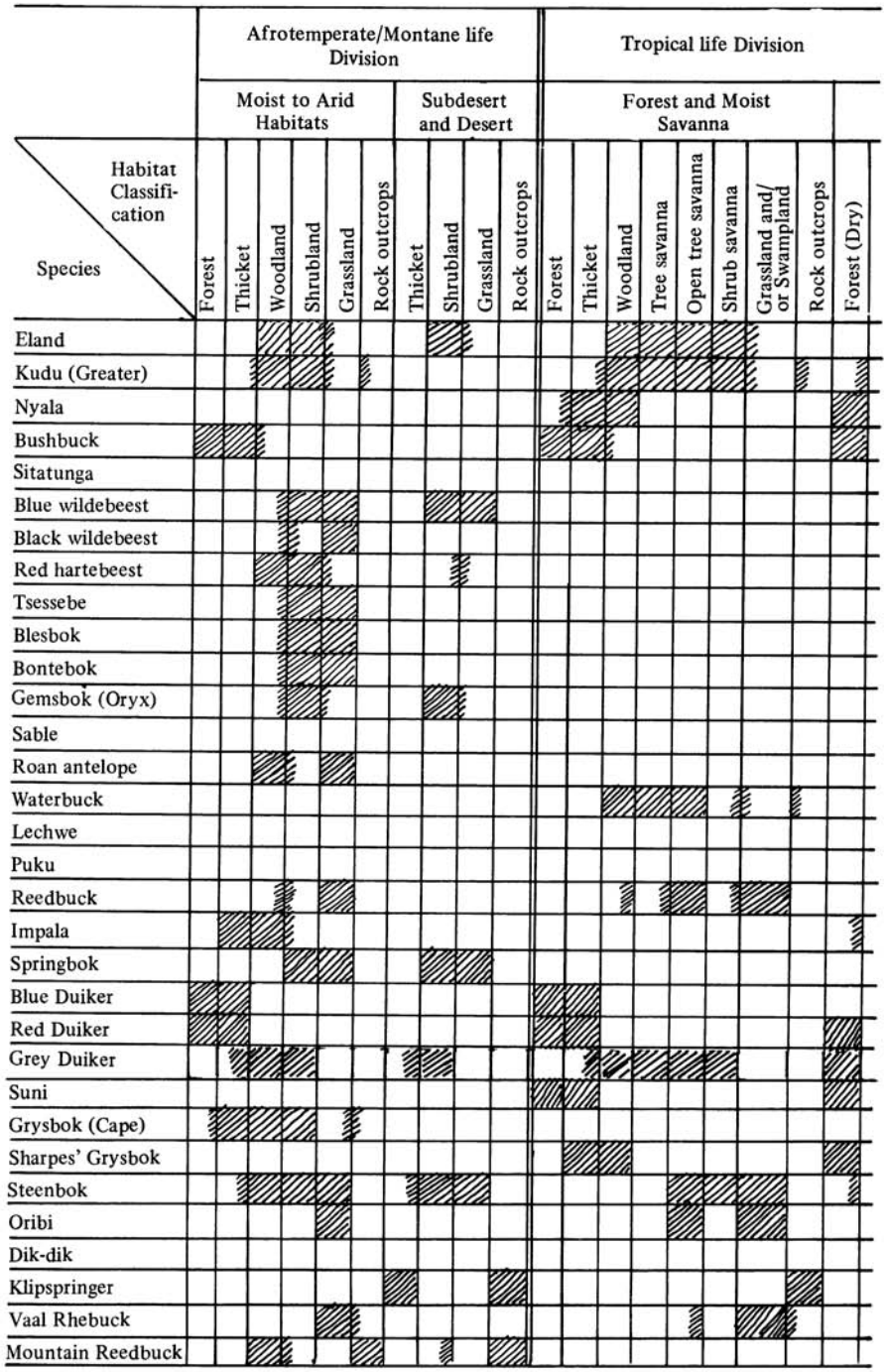
The black wildebeest has a much more limited range of distribution, and although it has become extinct over much of its former range, there is no evidence to suggest that it ever occurred outside the limits of the open grassland and shrubland plains of the Afrotemperate region of the sub-continent. There was probably also only marginal, and perhaps, slight seasonal overlap with the range of habitat of the blue wildebeest, and in view of the fact that these species interbreed under artificial conditions, it is unwise of game farmers or ranchers to introduce both these species simultaneously. It would appear from their rather similar habitat and other preferences, that the red hartebeest *Alcelaphus buselaphus* is the ecological equivalent in the arid savanna and sub-desert zones of southern Africa, of the mesic – to moist savanna inhabiting tsessebe. The latter has become extinct in the Afrotemperate regions of the sub-continent (Kuruman region of North West Cape) as well as from the coastal plains of northern Zululand.

Phylogenetically and ecologically the blesbok and the bontebok *Damaliscus d. dorcas* are closely related plains-loving antelope, with the latter confined to the southwestern Cape sub-region of the Afrotemperate region and separated from the areas inhabited by the blesbok by a system of high mountain ranges.

The gemsbok *Oryx gazella* is the ecological counterpart in arid and sub-desert regions in southern Africa of the mesic savanna-inhabiting sable *Hippotragus niger* and roan antelope. In the sub-desert and desert regions of its range it can subsist independent of surface water by feeding on tsammas *Citrullus lanatus* and water storing plants. It is particularly well adapted for life in arid regions and on a predominantly sandy substratum. There is no concrete evidence of its natural occurrence, in historic times, within the borders of the Orange Free State, and attempts at artificial introduction here have proved disastrous in most instances. The sable antelope is a typical inhabitant of woodland savannas, particularly *Combretum* and *Brachystegia* associations in the Transvaal Lowveld and Rhodesia, and the southern distribution limit of the species was the Komati River in the east and the Magaliesberg range in the west. Attempts at artificial introduction outside these limits will probably also fail in many cases because of the selective food and habitat requirements of this antelope.

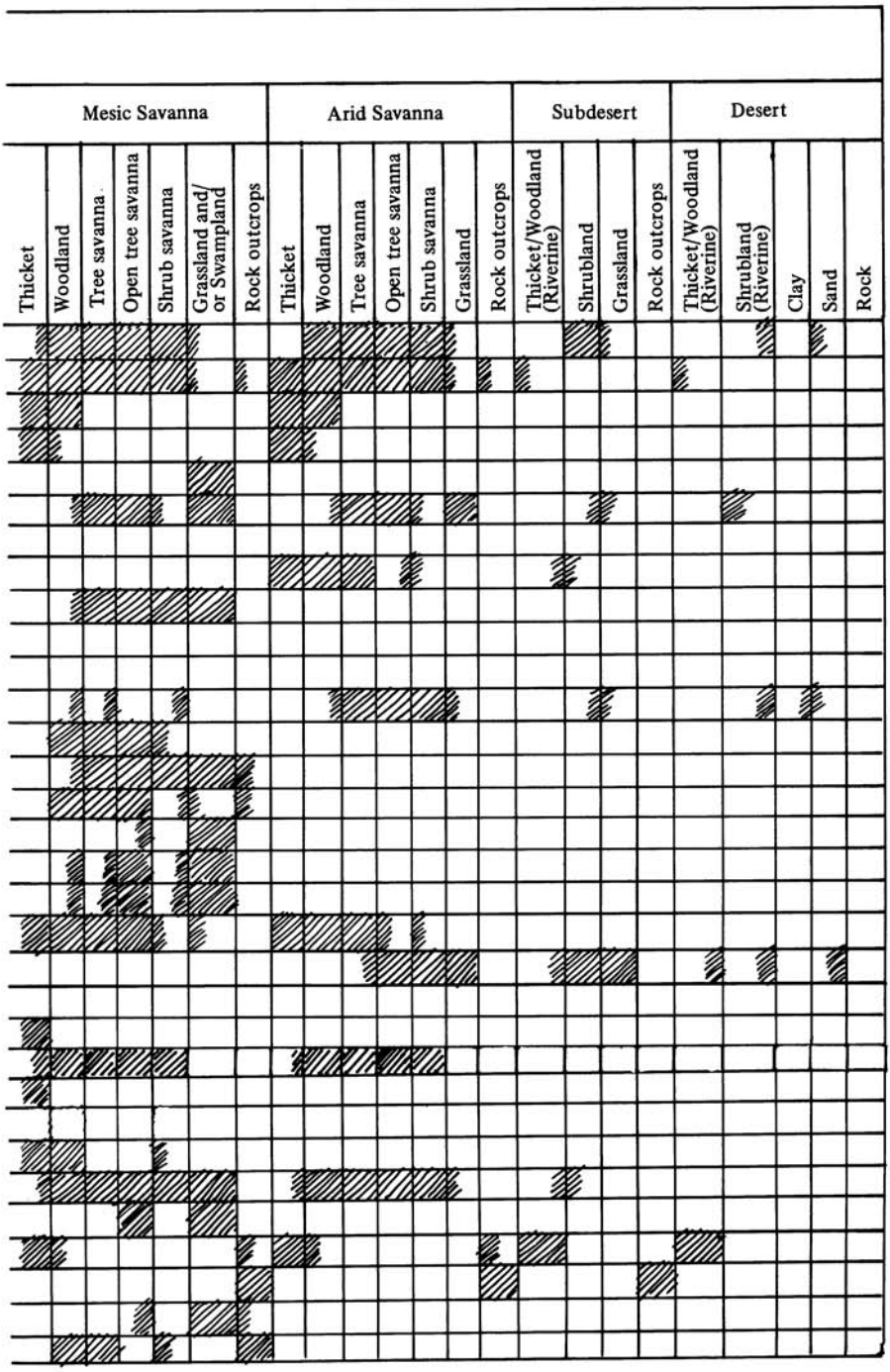
Table 1

Patterns of habitat preference of South African antelope species



(Adapted from Tinley 1969)

Table 1


Mesic Savanna
Arid Savanna
Subdesert
Desert
Thicket
Woodland
Tree savanna
Open tree savanna
Shrub savanna
Grassland and/ or Swampland
Rock outcrops
Thicket
Woodland
Tree savanna
Open tree savanna
Shrub savanna
Grassland
Rock outcrops
Thicket/Woodland (Riverine)
Shrubland
Grassland
Rock outcrops
Thicket/Woodland (Riverine)
Shrubland (Riverine)
Clay
Sand
Rock

Roan antelope, on the other hand, did occur in the Afrotemperate region within historic times, but have become extinct in Natal, Swaziland the Orange Free State and the eastern and northwestern Cape regions of its former range. It is an ecotonal species, which is particularly partial to open 'dambo-like' grasslands and adjoining woodland fringes. In view of its selective feeding habits and certain ethological limiting factors, it has never been particularly abundant even in the prime habitats, and it has also bee shown to be particularly vulnerable to anthrax (Joubert 1970).

Waterbuck *Kobus ellipsiprymnus* are water-loving antelope which, more often than not, frequent broken, lightly wooded country near permanent water. Their range of distribution is confined to the Tropical life division of the sub-continent as is also that of the related lechwe, and the puku *Kobus vardoni.* Ecologically, however, the latter species are separated from waterbuck by their partiality for moist, seasonally inundated flood-plain grasslands. In the Caprivi Strip and Okavango portions of their range of distribution, lechwe inhabit the open grassy flood plains between the major water courses, whereas puku frequent the open woodland and reed fringes of the main rivers and drainage lines.

Reedbuck are still found in a variety of habitats (particularly stands of tall grassland or vleis) within the Afrotemperate region, but are more commonly found in similar situations of the Tropical regions of the subcontinent. The related mountain reedbuck, *Redunca fulvorufula* also occurs in both major southern African life divisions, but this species inhabits the light woodlands or shrub savannas along slopes of mountains or rocky outcrops.

Although the impala *Aepyceros melampus melampus* and A.m. *petersi* is a highly adaptable species, able to exploit a variety of habitats in both the mesic and arid moisture provinces of the subcontinent, and can be extremely prolific in its preferred habitats, it is not partial to particularly moist or forested regions and has also become extinct within the Afrotemperate portion of its former range (Kuruman district). Impala are often particularly abundant in degraded *Acacia* woodlands or thickets along rivers and this is probably due to their ability to switch *ad lib* from a grazing to a browsing diet. The encroachment of shrubs leads to a dimunition of competitive influence of other herbivorous species. Springbok *Antidorcas marsupialis* prefer more open habitats than impala, but could, in many respects, be considered the ecological counterparts of impala in the more arid regions of both the Afrotemperate and Tropical life divisions. They are also capable of existing in the total absence of free surface water.

The vaal rhebuck is a typical inhabitant of montane grasslands in the moist and mesic moisture provinces of both major life divisions. In certain situations they are found in association with both mountain reedbuck and oribi, but they are separated ecologically by dietary differences and their occupation of different portions of the habitat.

Of the South African mini-antelope species i.e. those with an adult mass of less than 20 kg, there are 10 species in southern Africa. The habitat preferences and patterns of these small antelope are depicted in Table 1.

Of the 10 species of small antelope, six are forest and/or thicket and dense woodland species (blue, red and grey duiker, Suni, Sharpe's grysbok *Raphicerus sharpei* and dik-dik), two are common in the more open savannas (steembok, Cape grysbok *Raphicerus melanotis*), one is chiefly a grassland species (oribi) and the other is confined to rock outcrops and their vicinity (klipspringer). Nine are chiefly browsers, and one, the oribi is mainly a grazer, although further investigation may show it to be classed rather as a mixed feeder (Tinley 1969). The only small antelope in southern Africa confined to the Afrotemperate/montane life division is the Cape grysbok. Blue duiker, red duiker, grey duiker, klipspringer, oribi, steenbok and Sharpe's grysbok occur in both major life divisions (the latter only marginally into the montane areas of the eastern Rhodesian highlands) (Smithers 1966). Suni and dik-dik are the only small antelope truly confined to the tropical formations in the subcontinent.

Grey duiker, klipspringer and steenbok are the most widespread of the mini-antelope species and the dik-dik is the ecological equivalent of the other five small forest and thicket antelopes in the arid savanna and subdesert zones i.e. they occupy the extreme arid thicket niche. Broken ground and riverine fringes carry the thicket habitat with a forest-like interior into the desertic zone. The habitat preferences and niche structure amongst southern African mini-antelope species are demonstrated in an unique and remarkable manner by the situation in a narrow strip of country bordering the southern bank of the Lundi River in the Gona-re-Zhou Game Reserve in Rhodesia (Petrides and Pienaar 1970). Here it is possible to find in close and sympatric association the suni in the riverine thickets and forest patches, steenbok and oribi on the open grassland areas adjoining the river banks, grey duiker in the woodland areas and wooded kloofs further afield, Sharpe's grysbok in tongues of mopani woodland penetrating towards the river from higher-lying regions, and klipspringer on the rocky faces and outcrops of the Chilojo cliffs, which bound the Lundi Valley on the south.

A knowledge of the habitat preferences and other ecological requirements of herbivorous animals is basic to any management program (Dassman 1964). It is also a pre-requisite to the understanding of the distribution and abundance of animals and to the proper prediction of what species may be introduced into a given area.

The haphazard restocking of game farms or ranches often has calamitous results. Introduction of new species has often been carried to unwise extremes, and farmers eager to encourage large animals on their lands have introduced species unsuited to the area because of a basic lack of knowledge of the habitat requirements of these animals. Even totally foreign types, such as fallow deer, dromedary, water buffalo, nylgai, Barbary sheep, hog deer and llamas have been introduced to some South African game farms. In some instances, there has been an undesirable mixing of species with resultant crossbreeding, as in the case of black and blue wildebeest on some farms in the Harrismith district. More distressing is the mortality which sometimes occurs. Of the gemsbok introduced by farmers in the Orange Free State, nearly 90 per cent died, and the

remainder are not doing well. In areas with sufficient woody growth and cover, impala fared satisfactorily, but amongst lechwe, reedbuck and giraffe the casualties were sometimes as high as 100 per cent (Van Ee 1962).

It is well to remember that no matter how successful an introduced foreign species appears to adapt itself and thrive, it is bound to compete in a detrimental manner with some or other of the naturally occurring herbivorous species of an area. Habitat dependence is also so highly developed in certain species that when these animals are taken out of their natural environment, factors which might seem innocent enough at the time, could bring about a derangement of its protective mechanisms and cause an increased susceptibility to disease conditions, predation and other mortality factors (de Vos 1973). It is also very possible that such displaced animals may fail to digest the food they eat in such foreign environments, in view of a total lack of the appropriate rumen-flora. Unless remedial measures are taken this inevitably leads to starvation and death of the animals involved.

REFERENCES

DASSMAN, R.F. 1964. *Wildlife Biology.* New York: John Wiley and Sons.

DE VOS, V. 1973. Common infectious and parasitic deseases of captured wild animals. *In:* E. YOUNG *(ed). The capture and care of wild animals.* Cape Town: Human and Rousseau.

FRASER-DARLING, F. 1960. *Wild life in an African territory.* London: Oxford Univ. Press.

JARMAN, P.J. 1972. Seasonal distribution of large mammal populations in the unflooded middle Zambezi Valley. *J. appl. Ecol.* 9: 283–299.

JOUBERT, S.C.J. 1970. A study of the social behaviour of the roan antelope, *Hippotragus equinus equinus* Desmarest, 1804 in the Kruger National Park. M.Sc. Thesis. University of Pretoria.

KEAST, A. 1968. The response of herbivores to vegetation. *In: 'A practical guide to the study of the productivity of large herbivores'.* GOLLEY, F.B. and H.K. BUECHER *(Eds).* Oxford & Edingburgh: Blackwell Scientific Publ.

LAMPREY, H.F. 1963. Ecological separtion of the large mammal species in the Tarangire game reserve, Tanganyika. *F. Afr. Wildl. J.* 1: 63-93.

PETRIDES, G.A. and U. DE V. PIENAAR. 1970. *Report of the Wild Life Commission, 1969.* Salisbury: Govt. Printer.

PIENAAR, U. DE V. 1963. The large mammals of the Kruger National Park, their distribution and present-day status. *Koedoe* 6: 1-37.

POYNTON, J.C. 1962. Geographical and ecological determinants of distribution patterns. *Ann. Cape prov. Mus.* 2: 32-35.

SMITHERS, R.H.N. 1966. *The mammals of Rhodesia, Zambia and Malawi,* London: Collins.
TINLEY, K.L. 1969. Dik-dik, *Madoqua kirki* in South West Africa: Notes on distribution, ecology and behaviours. *Madoqua* 1: 7-33.
VAN EE, C.A. 1962. The distribution of ungulates in the Orange Free State. *Ann. Cape prov. Mus.* 2: 53-55.
VAN WYK, P. 1972. *Trees of the Kruger National Park.* Vol. 1. Cape Town; Purnell & Sons.
VESEY-FITZGERALD, D.F. 1965. The utilization of natural pastures by wild animals in the Rukwa Valley, Tanganyika. *E. Afr. Wildl. J.* 3: 38-48.