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Dikdik *Madoqua kirki*^c in South West Africa: Notes on Distribution, Ecology and Behaviour

by

K. L. Tinley

Nature Conservation Branch
South West Africa Administration



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INTRODUCTION

The Angolan or Damara dikdik, *Madoqua kirki* Günther, is the only species of dikdik which occurs in southern Africa. The same species occurs in Tanzania, Kenya, Uganda and Somalia, but with no present-day link between the two populations. Ellerman, Morrison-Scott and Hayman (1953: 189-190) distinguish the northeast African population as the typical species, *Madoqua kirki kirki* Günther, and the western southern Africa population as the subspecies *Madoqua kirki damarensis* Günther. The two populations of *Madoqua kirki* are completely separated today by the forest and moist savanna biomes which extend from the Congo southeast to Mogaambique (Map 1). There is apparently very little difference between the typical race and the subspecies *damarensis*.

In contrast to the single dikdik species occurring in the Southwest Arid Zone, the Northeast Arid Zone contains about seven or eight *Madoqua* (or *Rhynchotragus*) species with their distribution centred about the Ethiopian (Abyssinian) and Somalia broken country (Thomas 1894; Allen 1939: 505-508), which is an important endemic or biotic centre (Glass 1965).

The dikdiks are distinguished by the long nose, which is extensible and slightly bulbous at the base (Plate 1, Fig. 1) similar to that of the Russian steppe antelope the saiga *Saiga tartarica*. Dikdik are small antelope of about 5 kg bodyweight and stand some 42 cm high at the shoulder.

Some of the references dealing specifically with dikdik include their biology in northeast Africa (Drake-Brockman 1911; Kellas 1955), whilst Lamprey (1963, 1964) in his fine research on the ecology of the large wildlife of the Tarangire Game Reserve in Tanzania, deals with *Madoqua kirki* as part of the entire wild ungulate spectrum as well as including some detailed ecology on the species. Published accounts on dikdik in South West Africa are by Shortridge (1931; 1934: 482-487), Roberts (1951: 333-335) and Gaerdes (1966). The only mention of dikdik in southwest Angola that I am aware of is by Dollman (1929) and Hill & Carter (1941).

The vernacular names of the dikdik in South West Africa include: *English* — dikdik; *Afrikaans* — dikdik, neusbokkie, bloubokkie; *German* — blauböckchen; *Herero* (Bantu) — othini or okathini; *Nama Hottentot* — couwib (used by the Heikum Bushmen of the Etosha Basin: the *c* in couwib is a front dental click). The Afrikaans name bloubokkie often used for dikdik is correctly the vernacular name of the blue duiker *Cephalophus monticola* which does not occur in South West Africa.

The dikdik is included on the Specially Protected list of wild ungulates in South West Africa.

The following notes are from observations made over a two year period (October 1965 to March 1968) whilst engaged on detailed ecological surveys of various parts of northern South West Africa (Tinley MS). These notes are not complete as observations were made only whenever the opportunity was available. All photographs are by the author except where otherwise acknowledged.



Plate 1. The Damara dikdik *Madoqua kirki dumirensis* Günther. Adult male. Note the inflated, proboscis-like nose without a rhinarium; preorbital glands and white circumocular ring. (photo: Alice Mertens)

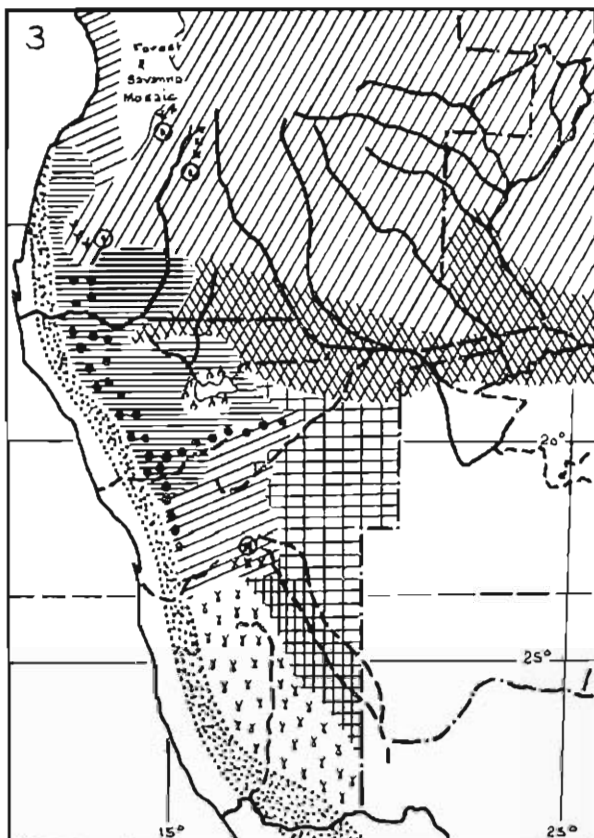
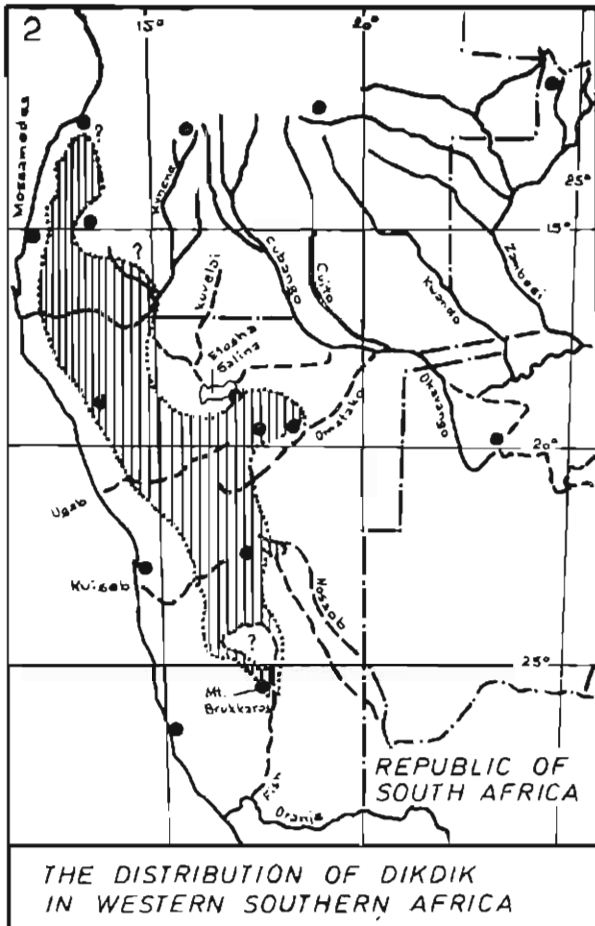
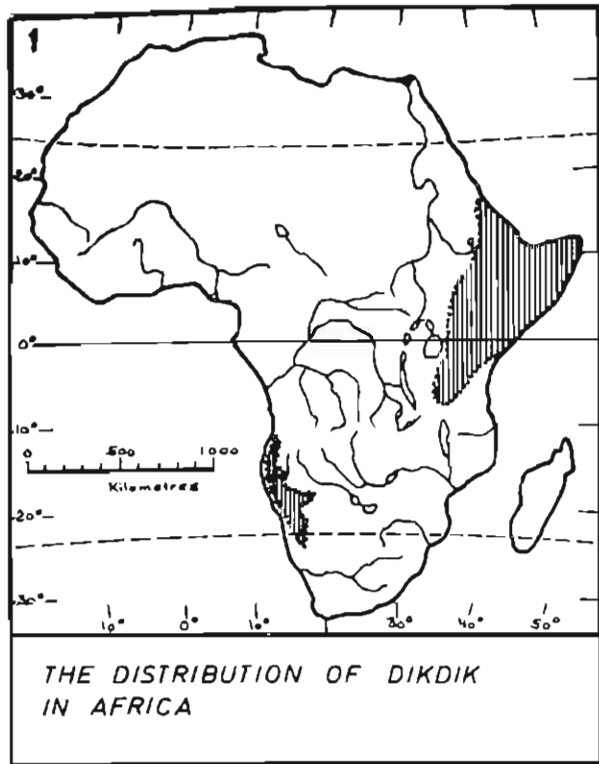
1. DISTRIBUTION

The distribution of dikdik in South West Africa and Angola follows closely that of the broken ground of inselbergs, hill ranges, mountain pediments and the riverine strips between the 75 and 500 mm isohyets which support their typical habitat (Maps 2 & 4). Shortridge (1934: 482—484) gives a detailed distribution of the species in South West Africa. Its northern limit is near Benguela in southwest Angola (Hill & Carter 1941: 157). The eastern limit is near the town of Grootfontein in South West Africa which is within the 500 mm isohyet. In the Kaokoveld of northwestern South West Africa dikdik occur into the Subdesert Namib to within about 45 km of the coast in riverine woodland and thicket of the larger seasonal rivers. These riverine strips are savanna life lines extending deep into otherwise barren desert (Plate 6). The southern distribution limit of dikdik is at Mt. Brukkaros (25°50' S) in southern South West Africa. Shortridge (1934: 482—484) gives the Rehoboth District as the southern limit of the species, but the past Curator of the South West Africa Museum, Mr. E. Zelle, found dikdik in the thickets at the base of Mt. Brukkaros (communicated via the present Curator

Mr. C. G. Coetzee). This extends the southern limit by nearly three degrees latitude. The habitat link between Mt. Brukkaros and the thickets of mountain pediments in central South West Africa would be along the riverine thickets of the Fish River catchment area and probably includes part of the Western Escarpment Mountain Belt.

Dikdik do not extend into the higher rainfall zone in the northeast of South West Africa where suitable habitat is plentiful, but discontinuous, along the clayey drainage lines which cross the wooded Kalahari Sand country and meet the riverine thicket habitats of the Okavango River. In this area there are no other small antelope thicket species. Sharpe's grysbok *Rhaphicerus sharpei* is recorded so far only from the Eastern Caprivi Strip (ie. between the Mashi and Zambezi Rivers). Although the reasons for the absence of dikdik in the sandveld between Grootfontein and the Okavango River is not definitely known, it is suggested that a prime factor may be the specialised hooves of the dikdik which confine them to stony ground (see Limiting Factors and Digital Pads).

Except perhaps very locally, dikdik still show their entire original distribution pattern, unlike the greatly changed distribution of most of the larger wild ungulates which have been eliminated by hunting over the major part of South West Africa.



VEGETATION	
[Hatched pattern]	Acacia
[Dotted pattern]	Mopans
[Cross-hatched]	Montane Forest
[Diagonal lines]	Sclerophyll Desert
[Stippled]	Sub desert
[Horizontal lines]	Brachystegia
[Dotted]	Commiphora / Kirkia
[Small circles]	Halophytic Communities
[Vertical lines]	Acacia haematoxylon
[Diagonal lines]	Burkea, Terminalia
[Vertical lines]	Rhigozum shrubland
[Diagonal lines]	Baikiaea, Pterocarpus, Dialium

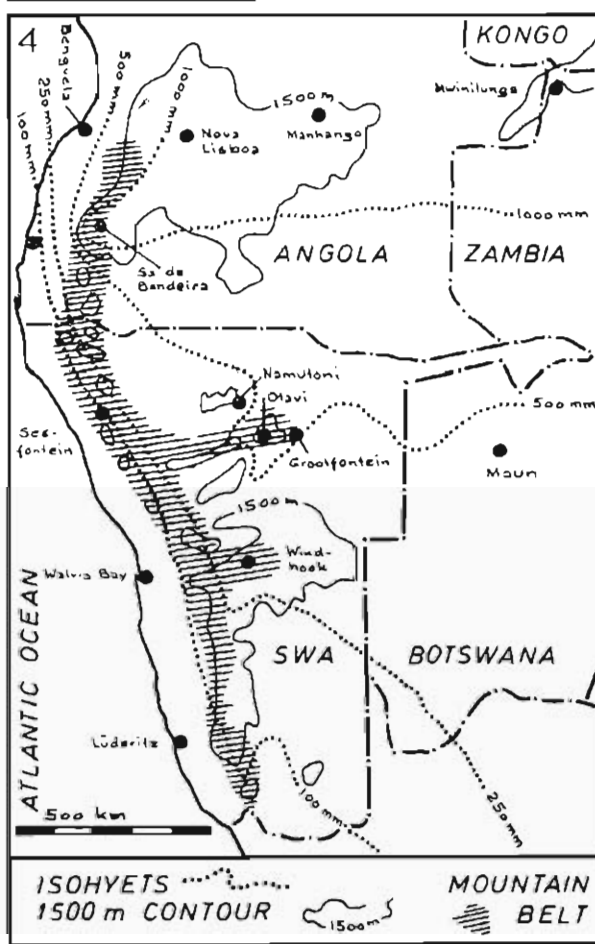




Figure 1. *Dikdik* male. The characteristic long nose of the *dikdik* which is proboscis-like and mobile, shown extended as when whistling. Note also the conspicuous preorbital gland and the erectile crest.

2. ECOLOGY

Habitats

Physiography: Western southern Africa is composed of three main topographical features which are bounded on the west by the Atlantic Ocean and in the east by the Kalahari Endoreic Basin: a coast lowland of some 120 km width comprising desert and subdesert; the Western Great Escarpment composed of a broad deeply incised mountain belt which rises to over 1000 m and gives place to the Interior Continental Plain. On the Interior Plains are isolated mountains and inselbergs some of which attain over 2000 m altitude (Plate 2). In two areas, south of the Etosha Salina to Grootfontein and the Central Highlands around Windhoek, mountain chains link directly with those of the Western Escarpment (Map 4). The plains in the north, north-east and east of South West Africa are covered in Kalahari Sand which supports wooded savanna, and the remainder of the country is composed of vast clayey plains with rocky eminences of various dimensions. *Dikdik* occur in all three topographic zones wherever suitable habitat occurs.

Climate: The climate is characterised by a markedly seasonal rainfall with an erratic occurrence and distribution within the rainy season. This is the prime climatic feature affecting life in South West Africa (Tinley MS). In the north and centre the rainy season occurs during the summer months from November to April, this changes southwest-

wards to a winter rainfall regime. Rains are brought by moist easterly winds in the form of thunderstorms of the continental convectional type. The zonation of the isohyets is shown in Map 4. Evaporation from a free water surface is between 4 and 7 times the annual rainfall over most of the country. An example of the temperature regime in the Arid Savanna moisture province of the Interior Plains is provided by Outjo, and in the Desert moisture province by the Namib Desert Research Station at Gobabeb (Appendix A). Temperature regimes are similar in the coast desert and in the arid savannas of the Interior Plains, except that the latter region experiences frost in winter. The coastal Namib Desert is extremely arid but moderate in its temperature regime because of the ameliorating influences of the ocean and the occurrence of coast fogs which extend inland over the desert at night. For interrelationships of surface, structure, climate, vegetation, wildlife and man in northern South West Africa refer to Tinley (MS).

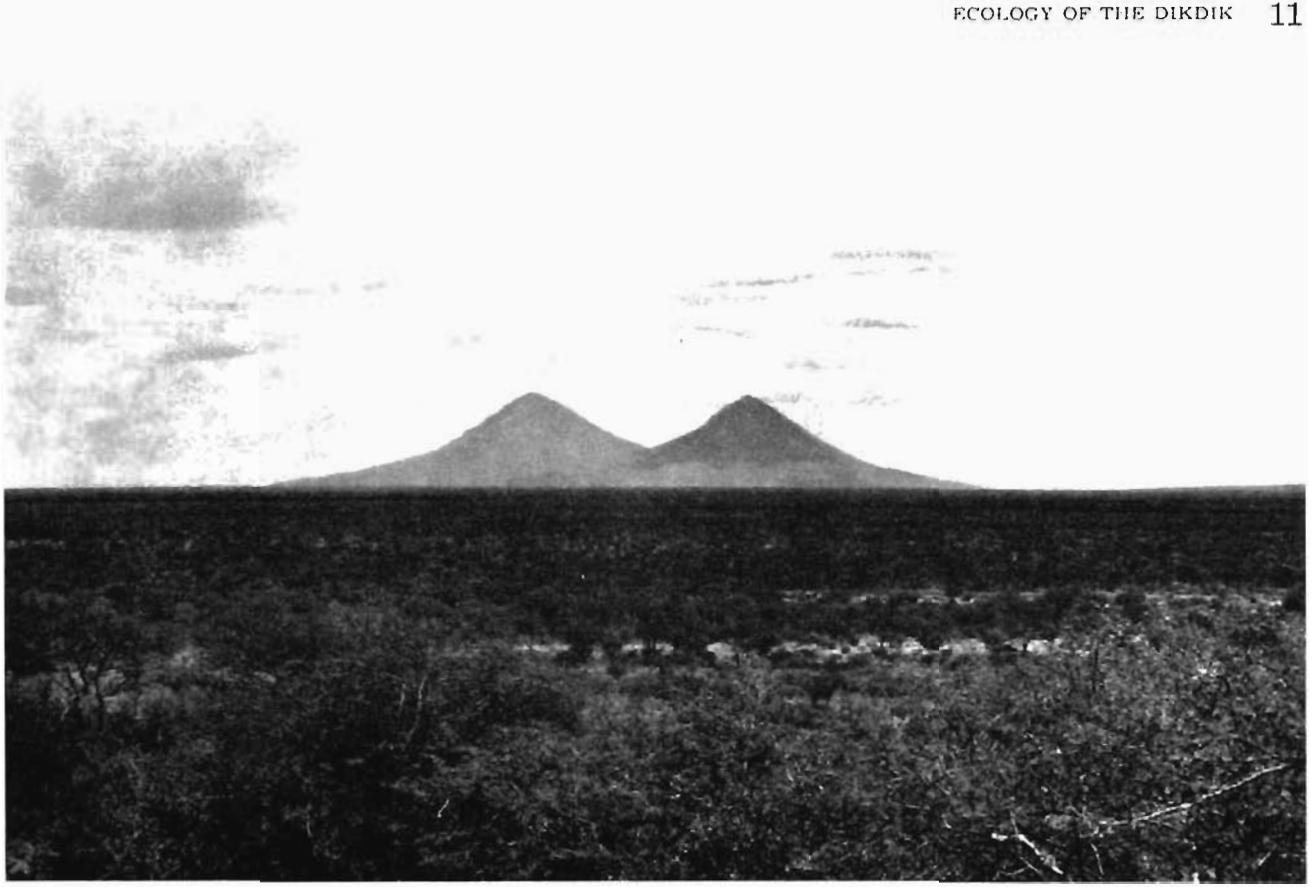
Vegetation: The distribution of the *dikdik* in western southern Africa extends chiefly through two main plant formations: in the north the Caesalpinaceae non-thorny wooded savanna of *Colophospermum mopane* and in the south (south of 20°S lat.) with the Mimosaceae thorny *Acacia* savannas. A third formation, the *Commiphora* dominated savannas are confined almost entirely to the rock outcrop surfaces of eminences (Map 3).

Dikdik occur chiefly in the Arid Savanna Zone of South West Africa and southwest Angola (between the 100 and 500 mm isohyets) but extend into the Desert Zone along well wooded riverine cover of the larger west draining seasonal rivers. As far as I know their distribution extends in only two places into the zone receiving more than 500 mm rainfall; in the Otavi-Grootfontein areas of South West Africa and in the area of the Cuculovar tributary of the Kunene River in Angola.

Their typical habitat is woodland and/or thicket in which the groundlayer is mostly free of grass but with a well developed shrub layer (for physiognomic definitions refer to Appendix B). Viewed from the animal's eye level one can see a considerable distance beneath the midcanopy and between the low shrubs. *Dikdik* do not occur on the actual rock outcrops but in two stony situations which usually support woodland and thicket, (a) on the pediments of hills or at the foot of outcrops, and (b) in riverine woodland and thicket which extend up mountain slopes, cross the open savannas and

Plate 2: (Top) Part of the Interior Continental Plain with towering inselbergs and acacia savanna to the horizon. The twin peaks of Omatako Mountain. *Dikdik* live in the thickets of the mountain pediments and ravines. Except for the riverine strips, *dikdik* are entirely absent over the greater part of the plains. They thus show a discontinuous distribution pattern.

Plate 3: (Bottom) Typical habitat of *dikdik* in the Namutoni area of Etosha National Park. Showing the mosaic of thickets and open glades, the well developed shrub layer and a sparse and short grass cover. Thicket dominated here by *Spirostachys africana* on calcrete rubble of the plains southeast of the Etosha Salina.



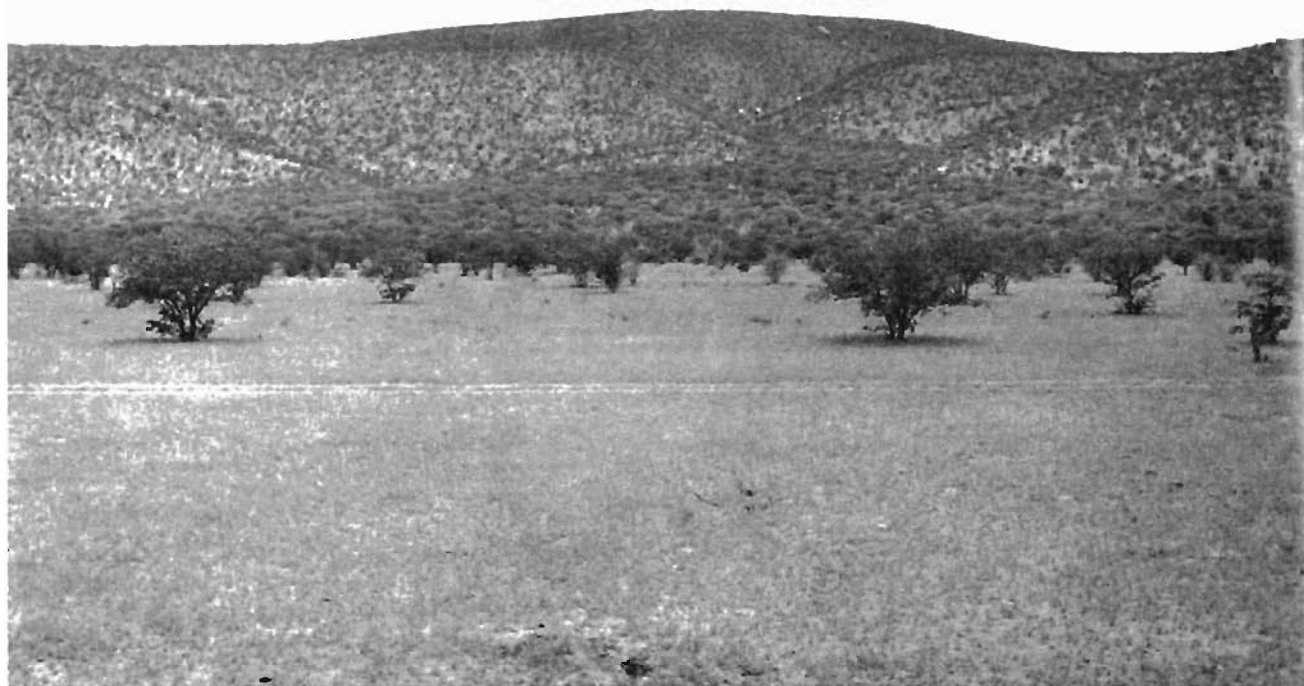




Plate 6. The narrow strip of riverine woodland and thicket of the larger seasonal rivers of the Atlantic drainage, crossing otherwise barren desert. The Huarosib River in the Namib Desert at Purros, looking east into the subdesert margin. Here riverine woodland is dominated by giant *Acacia albida* trees. The riverine strips carry savanna life deep into the desert.

the Namib Desert. In the Kaokoveld, woodland and thicket is also supported by the alluvial fans which occur on the sides of the intermountain valley plains where mountains streams debouch (Plate 4).

Where calcrete appears at the surface to produce very rough ground as between Namutoni, in the east of the Etosha National Park, and the town of Tsumeb, dikdik occur away from the precincts of hills and mountains onto the plains (Plate 3). Clayey plains soils are hard and shed more water than they absorb and here the cover varies as a mosaic from shrub savanna to savanna woodland with a tall grass cover. Thus where plains have been dissected by erosion exposing the calcrete or other

Plate 4. (Top) The alluvial fan of a seasonal stream entering the side of a large intermountain valley plain in the Kaokoveld. The thicket supported by the alluvial fan and the streambanks are typical habitats of dikdik in this area of high mountain ranges and broad valley plains. Here thicket is dominated by mopane, acacia, combretums and *Terminalia prunioides*; the mountains support mostly *Commiphora* savanna.

Plate 5. (Bottom) Interior view of typical dikdik habitat in riverine thicket and woodland of the Kaokoveld. The canopy is dominated by mopane; the understory alternates from dense to open patches and the stony floor is covered in plant litter.

rock surface a dense woodland or thicket usually occurs. This cover can develop because of the increased efficiency of the broken substrate to absorb more rain and the stony surface protects the cover against fire. The plains soils support a large variety of open savanna types where dense woodland or thicket is local and usually confined to depressions or stream banks.

In the Namutoni, Tsumeb and Otavi-Grootfontein area dikdik occur in woodland and thicket dominated by *Spirostachys africana*, *Terminalia prunioides*, *Acacia reficiens*, *Peltophorum africanum* and in the Namutoni area by *Spirostachys africana* and *Colophospermum mopane*. These trees form a woodland and thicket mosaic with a canopy at 8 to 14 m and a shrublayer from near ground level to 2 m in height (Plate 5). The shrub layer is dominated by various species in different localities but the typical components include: *Croton subgratissimus*, *Grewia* species, *Dichrostachys cinerea*, *Securinega virosa*, *Acanthaceae* and the shrub forms of *Spirostachys* which are kept short by the browsing of kudu *Tragelaphus strepsiceros* and dikdik.

The riverine vegetation of the west draining seasonal rivers is dominated chiefly by tall (25 m) woodland and thicket formed by *Acacia albida*, *Acacia tortilis*, *Acacia giraffae*, *Combretum imberbe* and shorter *Ziziphus mucronata*, *Acacia hebeclada*, *Acacia karroo* and in the north large trees of *Colophospermum mopane* (Plate 6). Small trees and shrubs include *Salvadora persica*, *Tamarix usneoides*, *Euclea pseudebenus* and in the north the en-

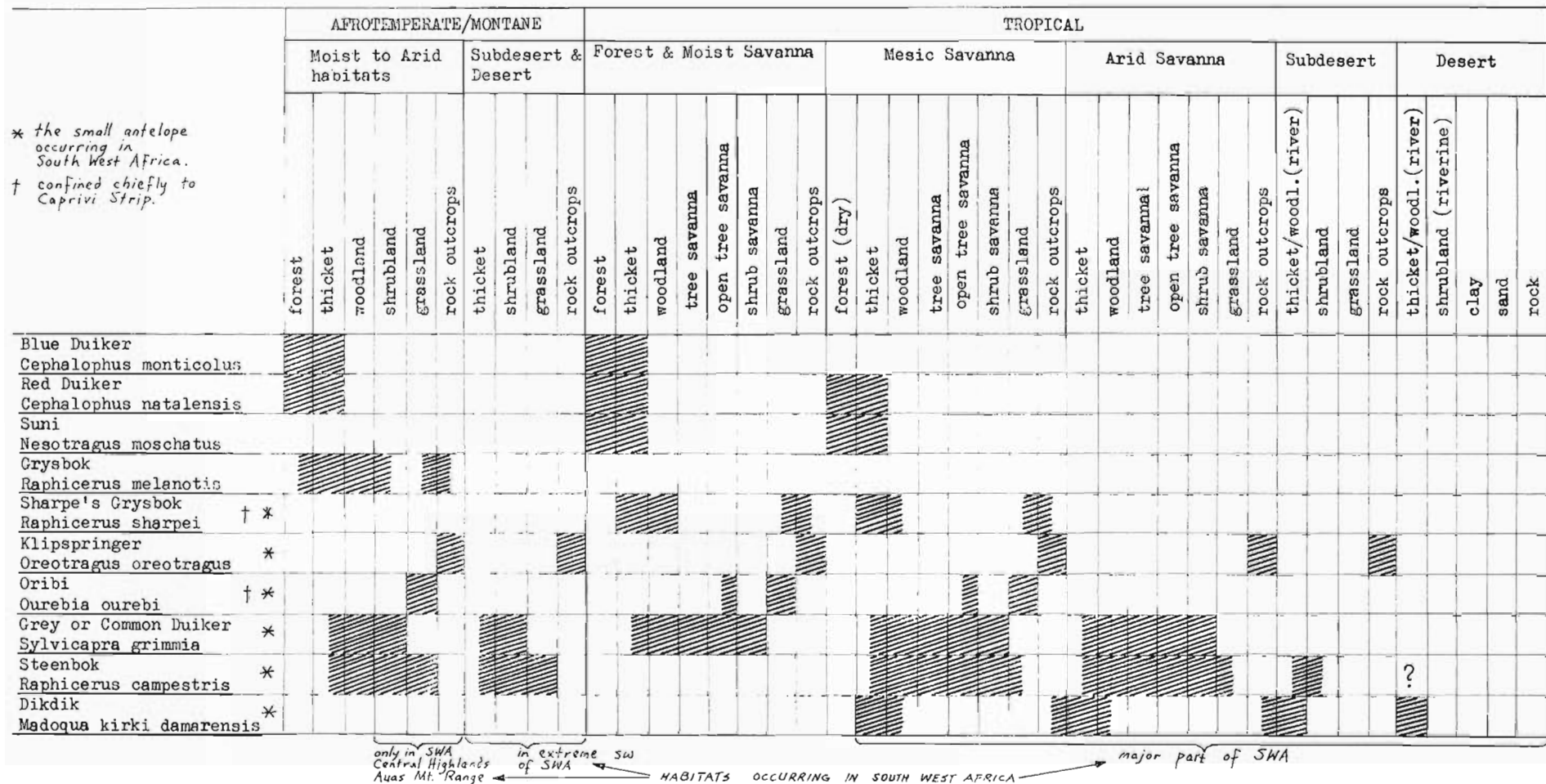


Figure 3. Patterns of habitat use by the small antelope of southern Africa.

demically *Balanites welwitschii*. *Salvadora* also forms large masses of scandent tangles which are much preferred by dikdik. Along the perennial Kunene River the riverine strip also has extensive woodlands of the palm *Hyphaene ventricosa*. See Map 3 for distribution of vegetation in southern Angola and South West Africa (after Gossweiler & Mendonça 1939 for Angola, and Giess & Tinley 1968 for South West Africa).

Feeding

Dikdik are dominantly browsers of leaves, shoot tips and fallen plant material. They feed most actively just after sunrise and in the late afternoons and at dusk. They also feed at night. During the heat of the day they usually rest and stand or lie in shade or beneath dense cover which overlooks open glades. When resting they chew the cud. Whilst watching two dikdik at close quarters for over an hour they showed an activity cycle of feeding followed by rest, another active cycle, and so on. It is possible that this is kept up throughout the 24 hour cycle as individuals can be found feeding in the heat of the day.

The long nose is not used as a prehensile organ but is extended to scent the preferred food whilst the animal is browsing or picking up fallen leaves. Fallen leaves are often picked up then immediately dropped for a fresher specimen nearby. Where browse is out of normal reach dikdik stand on their hind legs to reach up to them, and balance themselves with the front feet against the shrub stems or bend the thinner twigs down (Fig. 2).



Figure 2. Feeding on the upper leaves of a shrub.

Dikdik food plants have been recorded from only one locality in their distribution range and these show a dominance of browsing and litter feeding in both the dry and wet seasons, with a little grazing during the rainy season (Table I). The chief dry season foods are marked with an asterisk. The same dikdik species in the Tarangire Game Reserve in Tanzania shows a dominance of browsing and is classed as primarily a browser with elephant *Loxodonta africana*, black rhino *Diceros bicornis* and giraffe *Giraffa camelopardalis* by Lamprey (1963: 77, Table 5).

The food records were made in the Namutoni area of the Etosha National Park where there is a large concentration of kudu which maintain the shrub layer to within 1 m of the ground. This may be an important contributory factor to the high concentration of dikdik, as an extensive food supply is kept within reach of the small antelope, and at the same time the grass layer is kept down by the grazing ungulates such as plains zebra *Equus burchelli*.

Spirostachys africana which is heavily browsed by kudu and dikdik, and although there are some old plants with a large basal plate, their multiple stems seldom attain a height of more than one metre. In the rainy season many of these shrubs temporarily grow out of reach of dikdik, but with the onset of the dry season kudu browse the shoots back.

A similar situation appears to be at work in the Swartbooi's Drift area of the Kunene River where large numbers of dikdik are associated with heavy concentrations of pastoralists' stock, chiefly cattle and goats (Dr. H. Ebedes *pers. com.*). This concentration increases the woody plant cover and at the same time the large numbers of goats would maintain the browse within reach of the dikdik.

Dikdik are especially common, and do most of their feeding, on the ecotones of the mosaic of thickets and open glades. This mosaic of habitats provides the dikdik with a large amount and variety of browse food, an open understorey at the dikdik's eye level, cover from predation and provision of extensive shade (Plate 7). The life requirements provided by the boundary effect, and quantitative details of ecotone use by the dikdik in the Tarangire Game Reserve in Tanzania are given by Lamprey (1963: 74–76, Fig. 8). Even when feeding in the open glades the animals seem to keep to the areas of shade which might be provided by a large tree some distance away. In these situations they are seen with difficulty unless they move.

The ecotones are provided by microtopographical features, for example: where rock outcrops and plain meet, where a rise may have dense woodland which stops quite abruptly at an open depression which is seasonally waterlogged, or where large bare conical termitaria occur. In the riverine strips the change from riverbank woodland and thicket to the non-riverine vegetation of valley plains is typically sharp. These abrupt changes and the natural breaks in the riverine vegetation provide a multiplicity of ecotones.

Browsing mammals in the Arid Savanna moisture province are provided with nearly perennial shade or cover and food by the mosaic periodicity of the phenology of the various plant communities and their components. Only in extended drought periods

is most of the woody vegetation of the plains bare of foliage for several or more months, otherwise only the vegetation of rock outcrops is completely deciduous during every winter dry season. Dikdik also have the advantage of being provided with

TABLE 1. Food plants of *dikdik* in the Namutoni area of Etosha National Park, South West Africa (recorded between October 1965 and March 1968)

SUMMER RAINY SEASON (November to April)	WINTER DRY SEASON (May to October)
<i>Grasses</i> (Grazing mainly leaf tips) <i>Antheophora schinzii</i> <i>Enneapogon cenchroides</i> <i>Setaria verticillata</i> <i>Tragus racemosa</i>	<i>Grasses</i> none recorded
<i>Herbs</i> (Stems and leaves) <i>Barleria prionitoides</i> <i>Hypoestes forskalii</i> <i>Chenopodium</i> sp <i>Talinum cafferum</i>	<i>Herbs</i> none recorded
(Stems, leaves, flowers, fruit) <i>Commelina forskalii</i> <i>Commelina welwitschii</i> <i>Ipomoea plebeia</i> <i>Ipomoea sinensis</i> <i>Tephrosia dregeana</i> <i>Tribulus terrestris</i>	<i>Herbs</i> none recorded
(Flowers) <i>Abutilon</i> spp	
<i>Trees and shrubs</i> (a) Browse (leaves, shoots or twigs) <i>Acacia mellifera</i> <i>Acacia nebrowonii</i> <i>Acacia nilotica</i> <i>Albizia anthelmintica</i> <i>Dichrostachys cinerea</i> <i>Commiphora calcicola</i> <i>Croton subgratissimus</i> <i>Securinega virosa</i> <i>Spirostachys africana</i> <i>Cyathula deserti</i> <i>Monechma tonsum</i> <i>Opilia campestris</i> <i>Rhus marlothii</i> <i>Ziziphus mucronata</i>	
(b) Fresh litter (fallen plant parts) (Fruit) <i>Ficus petersii</i> <i>Phyllogeiton discolor</i> <i>Salvadora persica</i>	
	<i>Trees and shrubs</i> (a) Browse (leaves, shoots or twigs) <i>Acacia hebeclada</i> <i>Acacia nilotica</i> <i>Acacia tortilis</i> * <i>Dichrostachys cinerea</i> <i>Boscia albitrunca</i> <i>Boscia foetida</i> <i>Croton subgratissimus</i> * <i>Spirostachys africana</i> <i>Grewia</i> spp * <i>Maytenus cymosus</i> <i>Opilia campestris</i> <i>Salvadora persica</i> <i>Terminalia prunioides</i>
	(b) Fresh litter (fallen plant parts) (Fruit) <i>Acacia nilotica</i> <i>Dichrostachys cinerea</i> <i>Ficus petersii</i> <i>Salvadora persica</i>
	(Flowers) <i>Lonchocarpus nelsii</i>
	(Leaves) <i>Combretum apiculatum</i> * <i>Terminalia prunioides</i> * <i>Spirostachys africana</i> <i>Ziziphus mucronata</i>

* chief dry season foods

additional browse by the action of elephant, black rhino, kudu and impala *Aepyceros melampus* (only in the Kaokoveld) and to a lesser extent by giraffe. Giraffe sometimes provide a litter of leaves or flowers which are picked up by the dikdik. Trees and shrubs are broken or bent by elephant and black rhino to within reach of the dikdik, and kudu and impala keep many shrubs low by browsing. Strong and sometimes violent winds associated with thunderstorms, and with the end of the dry season also provide fresh plant litter derived from the canopy which is used by dikdik.

In the mid rainy season there is some movement of dikdik from their usual haunts, apparently in evasive response to the rank growth of annual grasses and herbs which grow higher than the animal (more than 60 cm), and thus temporarily close off areas of preferred habitat. The animals are then found where there are extensive slabs of stone such as calcrete or dense canopied woodland which inhibits the growth of grass understorey, but promotes the shrublayer components. Lamprey (1964: 32-33, Fig 6) notes that the same species in his study area showed seasonal movement during the rains but was not certain of the reason for this. In the Namutoni area of Etosha National Park dikdik are conspicuous in the dry season and the highest road counts were made at the height of the dry period, whilst in the rainy season they are seen much less. This may be due solely to the rank growth of annuals which precludes a clear view and imposes some local movement on some individuals or groups.

Like the klipspringer *Oreotragus oreotragus* (Shortridge 1934: 480) and the steenbok *Raphicerus campestris* (Eloff 1959: 22) dikdik are independent of surface water. But they may drink at rainwater puddles as do oryx *Oryx gazella* and springbok *Antidorcas marsupialis* which otherwise need only occasionally to drink from natural surface water.

Associated animals

Mammals: Large wild ungulates which share the same habitat and feed chiefly on woody plants are: elephant, black rhino, giraffe and kudu. These species are separated by different feeding levels and by movement into different areas, but all of them increase the provision of food for the smallest animal, the dikdik. Mixed feeders which interdigitate with the dikdik habitat are springbok and impala. In the dry season they are chiefly browsers and in the wet season are dominantly grazers and herb feeders. In the woodlands most of the grazing ungulates such as wildebeest *Connochaetes taurinus*, red hartebeest *Alcephalus buselaphus*, plains zebra and mountain zebra *Equus zebra* pass through the understorey and graze.

In the past, buffalo *Syncerus caffer* would have shared the same habitat as dikdik, but they are now extinct over the greater part of South West Africa, and are found only in the extreme northeast of the country outside the dikdik distribution. They may still occur in riverine situations in the dikdik's distribution area in Angola.

Elephant increase the thicket habitat on stony ground to the advantage of dikdik, by felling trees which either continue to grow in a recumbent position or provide shelter for woody plant encroachment.

Three other small antelope occur in the same region as the dikdik, and either interdigitate with one another where their preferred habitats form a mosaic, are widespread from one another where preferred habitats are widely separated, or overlap in their habitat use. The other small antelope are the common or grey duiker *Sylvicapra grimmia*, steenbok and klipspringer. The steenbok is the only small antelope which I have seen feeding in the same vicinity as dikdik in a homogenous woodland with a well developed shrub layer. No interspecific antagonism was noted.

In the Subdesert Namib steenbok also occur in the vicinity of the riverine strips of woodland and thicket where dikdik live, but were seen to feed on the margins of the riverine cover and a short way into the Subdesert grassland where small shrubs and herbs were common. In the Kaokoveld and southwest Angola mountain and plains country it may be possible for klipspringer to overlap in habitat use with the dikdik as the latter lives in the dense cover at the foot of rock outcrops. Common duiker also occur in the vicinity of dikdik habitats in northern South West Africa.

The habitat preferences of the four species of small antelope occurring together in northern South West Africa is shown in Figure 3 where overlap is chiefly an ecotonal phenomena. All four species are chiefly browsers (Brynard & Pienaar 1960; Lamprey 1963: 66; Pienaar 1963; Wilson 1966a).

Insects (Biting Flies): A characteristic feature of dikdik in the rainy season and autumn is the constant "nervous twitching" of the feet as the animal stands or feeds. This is due to the persistence of small biting flies which go primarily for the thin haired parts of the body, mainly the legs and the ears. Dikdik also move their ears rapidly and shake the head but the chief movement is the sharp twitching of the legs. The two main biting flies seen feeding on dikdik are a muscid *Stomoxys* species and especially a slightly larger, dark black tabanid which appears to be a *Philoliche* species. The tabanid can be seen hovering next to the legs after every twitch the animal makes. The muscid goes mostly for the upper parts of the dikdik's body including the sides, and the tabanid for the lower parts.

The dikdik do not seem to be irritated enough to have to move to another area although their evasive twitching is quite violent at times. Evasive action taken by other animals against biting flies is recorded by a number of authors (eg. Fraser Darling 1937: 131-140; Fosbrooke 1963: 124-126; Glasgow 1963: 97-99, 105-108; Tinley 1964: 73-75).

Endoparasites: A collection of endoparasites was made from four adult dikdik collected in the Namutoni area of Etosha National Park in February 1968 (see Appendix C for bodyweights and mea-



Plate 7. Adult male dikdik inside its typical habitat in the Namutoni area of Etosha National Park. (photo: Alice Mertens)

surements). The parasites included a tapeworm *Monozia expansa* from the small intestine; a roundworm *Haemonchus contortus* from the abomasum and a cosmocercid (*Cosmocercidae*) from the caecum.

The small antelope spectrum in southern Africa

Figure 3 shows the habitat preferences and patterns of all ten small antelope occurring in southern Africa. The small antelope group are here defined by being much less than 20 kg in weight, except for the oribi *Ourebia ourebi* which can attain 20.5 kg (Shortridge 1934: 492; Wilson 1968).

The relationship of dikdik to the other five small forest and thicket antelopes is as their ecological equivalent in the Arid Savanna and Subdesert zones. Two species, the red duiker *Cephalophus natalensis* and Sharpe's grysbok occur into suitable habitats in the Mesic Savanna moisture province where the rainfall approaches the 500 mm isohyet (see Appendix B for glossary of terms). Of the ten small antelope, six are forest and/or thicket and dense

woodland species, two are most common in the more open savannas, one is chiefly a grassland species and the other confined to rock outcrops and their vicinity (Fig 3). Nine are chiefly browsers, and one the oribi, is mainly a grazer (Ansell 1960: 61) although further investigation may show it to be classed rather as a mixed feeder (*pers. obs*).

There is thus a spectrum of small browsing antelope occupying the whole array of closed woody habitats from rain forest into desert. Dikdik occupy the extreme arid thicket niche, as is also shown by the dikdiks in East Africa (Grimwood 1963). Broken ground and riverine situations carry the thicket habitat with a forest-like interior into the desertic zone (Plates 5 & 7).

All ten small antelope have preorbital glands and most have pedal glands which are used for marking purposes, and in addition some have inguinal glands (eg. common duiker, oribi). There are no pedal glands in the klipspringer and the Damara dikdik.

Figure 3 shows the arrangement of the moisture provinces and habitats into two major life divisions, Afrotropical and Tropical [or, Psychrophilic and Thermophilic (Poynton 1967: 473)]. See Appendix B for glossary of terms.

In southern Africa there is often much confusion about the correct terminology for the Cape flora and the Karroo flora. With increase in latitude and the added effect of the high rainfall zone being confined to the maritime zone, the Afromontane system becomes depressed altitudinally and from Natal to the Cape Peninsula also occurs near sea level. The Cape "region" is actually one of several endemic floral centres in the Afromontane system, here occurring near sea level as well as on the mountains and hill ranges. In this situation the Afromontane system may be best referred to as Afrotemperate. Hereafter the term Afrotemperate is used to include the terms Afromontane and Afroalpine. Other endemic centres in the Afromontane division include Ruwenzori, Kilimanjaro and Mount Kenya. The Afrotemperate forest and tropical forest tension zone in northeastern Zululand and Natal is described briefly by Tinley (1967: 82—85). The forest and thicket small antelope of the two last mentioned areas show the following pattern of distribution.

In Natal, evergreen forest of the Afrotemperate type, with *Podocarpus* as the actual and potential climax canopy tree, occurs from 2014 m altitude in the Drakensberg (montane aspect) to near sea level, as for example near Durban (coast, dune or lowland aspect). Tropical components also occur into the lowland aspect from the north. The red duiker and blue duiker occur side by side with niche differences in the forests near Durban for example, but in the higher altitude and higher latitude coast forest only the blue duiker is present. Northwards into Zululand the blue duiker becomes confined to the forest on higher ground, and the red duiker more to the lowland or coast forests to which the suni antelope *Nesotragus moschatus* is confined (Tinley 1958; Dixon 1964, 1966).

Red duiker also occur in the temperate forest patches along the eastern Transvaal escarpment. In Figure 3 the red duiker thus appears in the forest and thicket habitats of both major life divisions. The blue duiker also appears in the tropical division as it occurs in tropical forest types in Zambia (Ansell 1960) and Mozambique (*pers. obs.*). In East Africa another example of a small antelope occurring in both major life divisions in different localities is the black-fronted duiker *Cephalophus nigrifrons* which is confined to high altitude montane forest and the bamboo zone on Mount Kenya, Elgon and the Ruwenzori Range. West of the Ruwenzori it occurs into West Africa in the lowland equatorial rain forest (Allen 1939: 487; Kenya Wildl. Soc. 1961).

The Karroo flora is both tropical and temperate in origin (Bews 1925, Acocks 1953) but because of its geographical position on the poleward side of a desert (the Namib) is either subtropical, temperate subdesert or subdesert steppe (Stocker 1964). This arid region is thus included in the Afrotemperate life division in Figure 3.

The Karroo vegetation is associated typically with alkali soils or desertic soils (highly alkaline, calcareous, saline or gypsum rich) which occur in a variety of situations, eg. subdesert, desert (where the shrubs are usually confined to washes and del-

tas), internal drainage basins, salinas, estuaries and valleys in arid areas. Examples include the Great Karroo Basin, Etosha Salina, Makarikari Salina, Namib and Sahara Desert washes, Lake Rudolf, Lake Chad, Somalia and the Limpopo River valley. In addition the Karroo has its own endemics plus elements common to both the Sahara and Namib Deserts (eg. the grasses *Stipagrostis* (*Aristida*) *ciliata* and *obtusa*). In southern Africa this subdesert shrubland is referred to as a karroid physiognomy, but this term conceals the essential unity of all the alkali and halophytic shrublands of Africa.

In the Karroo subdesert grey duiker, steenbok and klipspringer occur throughout in suitable localities (Shortridge 1934, Roberts 1951, Ellerman et al. 1953, Bigalke & Bateman 1962). Oribi is primarily a grassland species and occurs in both life divisions in montane grassland, as in the Natal Drakensberg, the Transvaal highveld (Kettlitz 1962), near the coast in the eastern Cape (Bigalke & Bateman 1962), on the Nyika Plateau, Malawi (Cater 1954); as well as on flood plain and drainage line (dambo) grassland in tropical habitats (Mitchell 1953, Ansell 1960).

In conclusion the only small antelope in southern Africa confined to the Afrotemperate/montane life division is the grysbok *Raphicerus melanotis*. Blue duiker, red duiker, grey duiker, klipspringer, oribi, steenbok and Sharpe's grysbok occur in both major life divisions. Sharpe's grysbok occurs into the montane areas of the eastern Rhodesian highlands (Child & Savory 1964, Fig. 16), and although in Zambia the species does not occur in montane cover (Ansell 1960: 60), it possibly occurs into or on the margins of the riverine evergreen forests, known as mushitu, in the Abercorn and Kasama districts which contain many montane forest components such as *Podocarpus milanjanus* (Lawton 1963: 58—59).

Suni and dikdik are the only small antelope confined to the tropical formations in southern Africa. But in East Africa suni occur into montane forest on Mount Kenya (Allen 1939: 499). Klipspringer, grey duiker and to a lesser extent steenbok are the most widespread of the small antelope.

The dikdik is one example of the biotic similarity between the at present isolated Southwest Arid Zone and the Northeast Arid Zone (Kenya, Somalia, Ethiopia). The latter arid area is an endemic biotic centre within the Saharo-Sindic Region. As indicated by the different degrees of differentiation shown by the elements common to both arid zones, the various elements were probably in contact at different times during the Pleistocene. References on this subject include: *plants* — Monod 1957; de Winter 1964: 61—62; Volk 1964; *animals* — Roberts 1936, 1937, 1951; Balinsky 1962: 299—310 + map I; Meester 1965: 87—93; Winterbottom 1967: 77—79 + fig 6; Wells 1967: 480—481.

Today the dikdik population in western southern Africa is separated by some 2100 km from the nearest (southernmost) *Madoqua kirki* population in southwest Tanzania near the 6°S latitude in the Ugogo area (Shortridge 1934: 484) and Ugalla drainage (Vesey-Fitzgerald 1954b: 358). Meester

(1965: 88) remarks on the fossil occurrence of one of the Northeast Arid Zone endemics, the gerenuk *Lithocranius walleri*, in Middle Stone Age deposits at Broken Hill, Zambia. This species occurs today in the same Arid Savanna country as the dikdiks in northeast Africa where it is associated chiefly with *Acacia mellifera* whose foliage is one of its chief foods (Vesey-Fitzgerald 1954a: 286—293; Simon 1962: 233—234).

Parallel to the occurrence of the gerenuk fossil at Broken Hill, is that of its main food *Acacia mellifera*. This acacia occurs today only in the nearby Zambezi and Luangwa River valleys of Zambia (White 1962: 82) which are extensions of the Arid Zone into the forest and moist savanna biomes. In the Southwest Arid Zone, *Acacia mellifera* is again widespread and abundant (and an encroachment problem) as it is in the Arid Savanna of northeast Africa. The Zambezi and Luangwa River valleys are important present day links between the Southwest Arid and Northeast Arid Zones (Winterbottom 1967: 77—79).

TABLE II: Potential predators of the dikdik in South West Africa and southwest Angola.

REPTILES:
Python <i>Python sebae</i>
Dwarf or Angola python <i>Python unchietae</i>
BIRDS
<i>Diurnal raptors</i>
African hawk-eagle <i>Hieraetus spilogaster</i>
Bataleur <i>Terathopius ecaudatus</i>
Black eagle <i>Aquila verreauxi</i>
Brown snake-eagle <i>Circaetus cinereus</i>
Crowned eagle <i>Stephanoaetus coronatus</i> (possibly occurs in densely wooded country of northern Kaokoveld and southwest Angola)
Martial eagle <i>Polemaetus bellicosus</i>
Tawny eagle <i>Aquila rapax</i>
<i>Nocturnal raptors</i>
Giant eagle owl <i>Bubo lacteus</i>
MAMMALS
<i>Primates</i>
Baboon <i>Papio ursinus</i>
* Man
<i>Carnivores</i>
Black-backed jackal <i>Canis mesomelas</i>
Brown hyaena <i>Hyaena brunnea</i>
Spotted hyaena <i>Crocuta crocuta</i>
Wild dog <i>Lycaon pictus</i>
Small spotted genet <i>Genetta genetta</i>
African wild cat <i>Felis silvestris</i>
Black-footed cat <i>Felis nigripes</i>
Cheetah <i>Acinonyx jubatus</i>
* Leopard <i>Panthera pardus</i>
Lion <i>Panthera leo</i>
* Lynx <i>Felis caracal</i>
Serval <i>Felis serval</i>

* the only definite predator records.

Predators

Only three definite records are known to me. Bushman have noted that leopard *Panthera pardus* and lynx *Felis caracal* prey on dikdik. Gaerdes (1966: 83) also records that the lynx is an important predator of dikdik in South West Africa. Hunter-gatherers and pastoralists in the Kaokoveld and southwest Angola sometimes hunt the dikdik for food by means of bows and arrows, or with snares made from acacia or baobab *Adansonia digitata* bark. These snares are set in the small paths used by the dikdik in their thicket habitat. As no other records are available the potential predators of the dikdik are listed in Table II. Included are some small carnivores which may possibly prey on the young of dikdik.

In northeastern Zululand the forest and thicket suri antelope is preyed on chiefly by the crowned eagle *Stephanoaetus coronatus*. The same observation is made in East Africa (Brown 1963: 7). Also in northeastern Zululand is the slightly larger forest and thicket antelope, the red duiker, and the smallest antelope, the blue duiker, which are also preyed upon by the crowned eagle and the leopard. Red duiker are also preyed on by crocodile (Deane 1960: 36).

The chief predators of the common or grey duiker in the wooded savannas of Zambia are leopard and wild dog *Lycaon pictus* (Wilson 1966b). Steenbok are preyed on by leopard, black-backed jackal *Canis mesomelas* and martial eagle *Polemaetus bellicosus* amongst others. Leopard and lynx also take klipspringer which are also possibly preyed on by black eagle *Aquila verreauxi*. The most ubiquitous and widespread carnivore, the leopard, is the predator common to small antelope in all situations.

Limiting Factors

Dikdik are limited in their overall distribution and local occurrence by several interrelated factors. The coincidence of suitable habitat and suitable substrate ie. of thicket and/or dense woodland with a stony groundlayer which occur typically in an arid zone. The same habitats in higher rainfall zones almost without exception occur on soil without a stony surface. A characteristic of the arid zone are the extensive areas of rough or broken ground. In turn the dikdik appears to be confined mainly to stony surfaces including those in riverine situations by the specialised structure of their feet which have rubbery digital pads (see Digital Pads).

In sum the interrelated factors are (1) Arid climate effect on land surfaces, (2) local soil moisture supporting thicket, and (3) specialised feet. Dikdik are thus limited to some extent to a particular substrate by the specialised hooves as are the klipspringer and mountain zebra; the latter has hooves of a hard rubber consistency (Tinley MS).

Another possible limiting factor is the large nose of the dikdik which has no external rhinarium. This may be an adaption to tropical arid and desertic climates, and possibly a feature which excludes it from higher rainfall and moist environments (for further data see Nose).

3. BEHAVIOUR

Social Structure

Dikdik occur typically in pairs, but can often be seen singly or in threes. Where three animals occur together the unit is composed of the parents and a juvenile or subadult male or female (Plate 8 & 9). But in the dry season up to 6 adult and subadult animals have been seen together, and in the wet season four. It is possible that a territory is defended during the main mating and breeding period, and different groups or related families come together in areas where their home ranges abut or overlap? It would be of great value and interest for a detailed study to be made of dikdik and other small antelope behaviour, especially on the lines of the superb behaviour study on the wildebeest by Estes (1968).

Dikdik are generally widely distributed in suitable localities and are shy, though they will show much curiosity if the observer keeps still. One locality where they are common is the Namutoni area of the eastern end of the Etosha National Park. Here 42 animals are the highest total recorded along a road 6.4 km long with a 20 m visibility into either margin of the road (road count by Dr. H. Ebedes, July 1966). This gives 42 dikdik in 12.8 hectares (linear) or 0.3 ha per pair of dikdik assuming the total to be made up of the social unit of two.

Reproduction

A few records of reproductive activity in dikdik were made in the Namutoni area of Etosha National Park. At the end of February 1968 a juvenile of about one month old was seen; one adult female collected during the same period contained a small foetus of about one month's development and the other adult female collected had a ripe ovarian follicle, an old corpus luteum in the other ovary and a non-pregnant uterus. At the same time courtship behaviour was observed in one pair of dikdik (Fig 4). The detailed study by Kellas (1955) on the reproductive activities and growth rate of the same dikdik species in East Africa established the following patterns which are probably also shown by the western southern Africa population: "the females are perennially polyoestrus with two periods of intense breeding, one at the beginning of the rains and the other at the end of the rains. The gestation period is about 6 months and most females become pregnant twice yearly. Two peaks of high average testes weights correspond with the two periods of intense breeding in the female. The factors responsible for maintaining the seasonal breeding rhythm are not known, as they are probably not maintained by the activity of the primiparous females." Kellas found a close correspondence between the rise and fall of weights of testes, epididymides and seminal vesicles with the fluctuation of solar radiation records (Kellas 1955, Fig 11).

Kellas (1955: 781—782) says that the breeding cycles ensure "that the young of both seasons are dropped when the grass is long". But dikdik hide their young in thicket or under bushes, and from

the data given above on the ecology of dikdik it is far more likely that the criterion is not the long grass but the time of greatest browse availability i.e. during the pre-rain and first rain woody plant flush, and at the beginning of the dry season when there is an abundance of fresh litter.

Calls

Dikdik utter a high quavering whistle with the nostril extended downwards (Fig 1). An observer has to listen carefully for this high airy whistle although when the animal is agitated it is loud. The nose whistling is a communicative call. One female with a month old juvenile when approached by me left the youngster lying beneath a shrub. The mother moved away slowly in a circle whistling loudly every few seconds and making small bounding movements as depicted in Figure 5. When the whistle was imitated she answered immediately as do most dikdik.

Another sound is made if the animal gets a sudden fright or is alerted. The animal bounds away stiff-legged and at each contact with the ground a short explosive whistle is made. The bounding action is like stotting (Fig 5), but at the height of the bound the legs are tucked beneath the body. At other times a single explosive whistle is made and the animal disappears into the shadows and thicket. Shortridge (1934: 485) describes their sudden disappearance very aptly, "... even when running the shadows cast are more conspicuous than the animals themselves, and they vanish like wisps of smoke."

Nose

A characteristic feature of the dikdik is the proboscis-like mobile nose (Plate 1, Fig 1). As noted above the nose is used to make a variety of whistling sounds with the nose extended fully downwards. There is no external rhinarium as is seen in all the other small antelope and the skin hair terminates at the nostril opening. The internal surface of the nostrils is lined with black epithelium which extends as far back as the reduced nasal bone. The small nasal bone is characteristic of the dikdik (Roberts 1951).

The nasal openings cannot be closed or nearly closed as in the springbok and oryx which have slit-like nostril openings similar to the camel *Camelus dromedarius* and are typical arid zone and desert ungulates. In the oryx the external rhinarium is small (or reduced) and absent in the springbok and camel. No external rhinarium or a reduced external rhinarium surface would be advantageous to mammals living in desert regions as an aid in lowering water loss. But two small antelope, the steenbok and klipspringer, have conspicuously large rhinaria and they occur into Subdesert in more exposed habitats than the dikdik! They are however, animals which are adapted to a wide variety of conditions.

The dikdik nose can be extended in any direction to smell potential food or directed downwards for



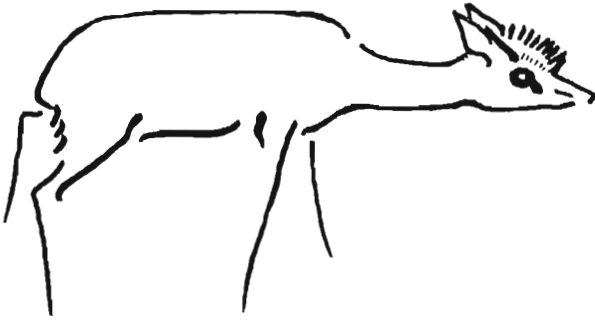


Figure 4. Courtship or intimidatory posture adopted by the male *dikdik*. Stiff-legged walk with head held low, the crest fully raised and the nose extended anteriorly. The female reacts with a crouching supplicatory pose.

whistling. It is not prehensile and cannot be used for pulling forage to the mouth as does the upper lip of the black rhino.

The saiga antelope of the arid and cold Russian steppe has a nose similar to the dikdik though on a larger scale and with a number of unusual and peculiar internal structures. These structures may be an adaptation to warming and moistening inhaled air and for increasing the efficiency of the sense of smell (Walker et. al. 1964: 1465). The dikdik lacks peculiar structures in the nostril but the thin moist epithelium may serve a similar purpose. The dikdik's nose has not been studied in detail.

Crest

Dikdik have an orange-brown or ginger erectile crest of long hairs situated on the forehead, which in the male extends back to between the horns. The females are hornless. This crest is raised when the animal is alarmed or uncertain, and especially by the male in courtship behaviour or when chasing off another male (Figs 1, 4). At other times if the animal is suddenly alarmed the crest is not raised. The crest thus acts as a signal in various situations of excitement. There is no glandular patch associated with the erectile crest as there is in the springbok which has an erectile crest of long white hairs on the rump (the "pronk").

Digital Pads

The hooves have a distinctive rubbery black pad on the post-ventral surface which is in contact with the ground (Fig 6). These naked pads may be the reason why dikdik are to be found typically in habitats associated with broken or stony ground, where they would be of value as non-skid surfaces

Plate 8. (Top) Dikdik adult and subadult males. The female was out of the picture on the left. These are probably one family and shows the late stage to which the offspring remain with the parents or their vicinity.

Plate 9. (Bottom) A group of dikdik composed of two adult females and a male on the right. This photo was taken at the height of the dry season after seven years of less than mean annual rainfall and shows the extreme stark phase of the dikdik thicket and woodland habitat (Namutoni area).



and protection against abrasion and shock. The digital pads could be the factor excluding dikdik from apparently suitable thicket habitats on the Kalahari Sands of northern and eastern South West Africa. These hoof pads seem to be a characteristic of the subfamily *Madoquiniae* and are also especially well developed in the beira antelope *Dorcotragus megalotis* which leaps about on rocks in the stony hills of Somalia and Ethiopia (Walker et. al. 1964: 1455—1456).

The pronghorn antelope *Antilocapra americana* of the arid zone of North America also has well developed digital pads which are protection against the stony substrate (Einarsen 1948: 37, Fig 15).

Glands

The dikdik has one pair of scent-producing skin glands, the preorbital glands, which are used for marking territory or home range and for other social purposes (Plate 1, Fig 1). The glandular secretion is used for marking various parts of their habitat, for example when walking between feeding sites the male marks leaf tips, grass inflorescence tips and twigs on either side of the path taken (Fig 7). After defecating both the male and female wipe off some of the black tarry glandular secretion onto the tip of a low branch or twig on the periphery of the dung heap. Some of these accumulations of glandular secretion on twigs are as large as a pea,



Figure 5. Stiff-legged stotting action repeated three or four times with an explosive whistle uttered at each contact with the ground.



Figure 6. The rubbery digital pad on the post-ventral surface of the hoof (lateral view).

about 8 mm in diameter (Plate 10). Dikdik do not have inguinal glands. Klipspringer also leave pre-orbital glandular secretion marks around all their family communal dung heaps (Plate 11).

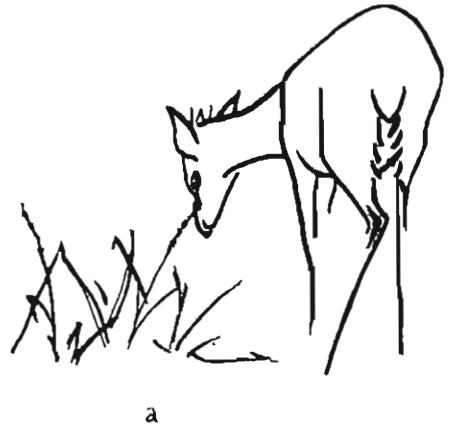
According to Pocock (1910: 876—879) the East African dikdiks *Madoqua phillipsii* and *saltiana* have pedal glands. The pedal glands of *M. phillipsii* illustrated by Pocock show them to be narrow cylindrical tubes unlike that of the Damara dikdik which have a small invaginated fold of skin between the digits of both the front and hind feet. A tuft of slightly longer hairs 15 mm in length extend out of the invagination into the interdigital space. Recent microscopic investigation was unable to locate any functional pedal glands. The skin in this region contained an apparently normal number of normal sized sweat and sebaceous glands (Veterinary Research Institute, Onderstepoort *in litt.*). The klipspringer also has a shallow interdigital invagination with elongate hairs, but there are apparently no functional pedal scent glands (Pocock 1910: 885—886, Roberts 1951: 331).

The function, origin and evolution of sweat glands in ruminants is described in detail by Pocock (1910) and territorial advertising by scent marking is described for other antelope such as Thomson's gazelle *Gazella thomsonii* and wildebeest by Estes (1967, 1968). Talbot & Talbot (1963: 48—49, 60) also describe the wildebeest scent glands and suggest that the pedal gland odour is probably a valuable form of communication in migration.

Defecation

Dikdik usually defecate at family communal dung heaps which are in the vicinity of low branches or twigs (Plate 12). These branches are used by dikdik for marking purposes (Plate 10). It is possible that at times several families share the same communal dung heaps. The dung of other mammals such as elephant, kudu and impala (in the Kaokoveld) also stimulate defecation in the dikdik (see also Shortridge 1934: 485). A few of these communal dung heaps are nearly 2 m in diameter and 10 cm high at the centre, but most heaps are generally smaller.

The behaviour of dikdik when defecating is fairly constant and follows this pattern. A male dikdik approaches the communal dung heap, smells the dung, then walks onto the heap and proceeds to scratch or paw the soil and old dung backwards into a pile with the forefeet; urinates on this pile and sometimes digs again before defecating or defecates directly after urinating (Fig 8). Female dikdik were not seen to dig up the dung. Immediately after using the communal dung heap both the male and female wal kover to a low twig, one that has been much used already, and wipes its preorbital gland deftly on the twig tip. After defecating dik-



a



b

Figure 7. Marking with the preorbital gland. (a) marking the tip of a grass, and (b) the tip of a twig.

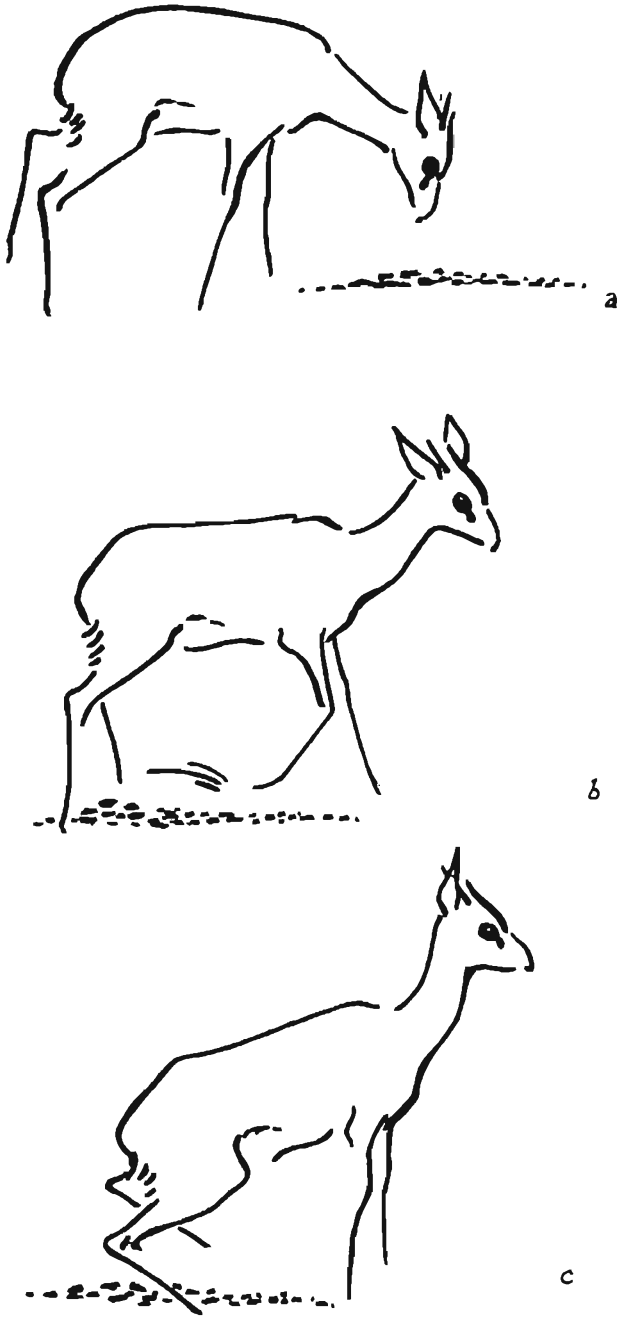


Figure 8. Behaviour at the communal dung heap. (a) male approaches and smells. (b) digs up heap, and (c) urinates then defecates.

dik have not been seen to cover their dung as steenbok sometimes do.

A steenbok male was seen to scratch the ground with the forefeet making a small depression. Into this it urinated, scratched the wet ground again with the forefeet and then defecated. After defecation the dung was dug over with the forefeet and covered with soil (Plate 13). At other times (or it may be the females) they do not cover their dung. Steenbok have not been seen to use communal dung heaps. Klipspringer have an extensive system of family communal dung heaps on the mountain ridges. Some of their heaps are 3 m in diameter (Plate 14) and are spaced some 50 to 100 m apart, but in some places are much closer together.

Dikdik droppings are slightly larger than those of rats. The habit of using species specific (family) communal dung heaps is also a character common to the *Madoqua* species in northeast Africa (Shortridge 1934: 485–486). Communal dung heaps are used by other species such as the lone males of herd mammals, for example wildebeest and oryx, and on the other hand by some or most members of a group as in klipspringer, impala and white rhino *Ceratotherium simum*. Sharpe's grysbok also have communal dung heaps (Shortridge 1934: 496).

The purpose of the dikdik males pawing the dung heap before voiding and sometimes after urinating, may be to mark the forefeet with their own or the communal dung heap's faecal and/or urinary odour which is then left wherever the animal goes and can be picked up by other dikdik. Digital glands in other animals have the function of leaving a scent trail. The same faecal or urinary scent trail laying might have been the purpose of the male steenbok's behaviour. But steenbok have well developed pedal glands in both the front and hind feet (Pocock 1910: 880–881) so not only would this provide a combined scent trail but the particular dung heaps would be marked by the individual male's own pedal gland scent. Similar faecal and urinary scent trail laying is also reported for the black rhino (Goddard 1967: 143) which in addition has pedal glands on the soles of the feet. Estes (1968: 51) in his fine research on the wildebeest says that: "Dung and urine are perhaps the commonest, and no doubt the oldest forms of territorial demarcation in ungulates and in mammals in general".

Beard (1965: 103) relates a delightful African fable from East Africa on the origin of the dikdik communal dung heap, which paraphrased reads: At the beginning of time the king of the dikdiks was running through the bush without looking and in his exuberance fell in a pile of elephant dung. In indignation and anger he called all the dikdik together to decide on a plan to trip up an elephant themselves. Since then dikdik have been working together to make a dung heap large enough to trip a passing elephant.

SUMMARY

(1) The paper is based on random observations made over a two year period.

(2) The relationship between the western southern African and northeast African dikdik population is noted. Only one dikdik species occurs in western southern Africa - *Madoqua kirki damarensis*, which is completely separated from the typical species in northeast Africa and the other six or seven dikdik species endemic to that area.

(3) The distribution of the dikdik in South West Africa and southwest Angola is described and illustrated. Its distribution pattern follows closely that of the broken country where thicket is supported by mountain and hill pediments and the riverine strips. The northern limit is near Benguela (13°S) in southwest Angola and its southern limit at Mt. Brukkaros (25–50°S) in southern South West Africa.

(4) The physiography, climate and vegetation of the area occupied by dikdik in western southern Africa is briefly described. There are three main topographical features: a coast lowland of desert and subdesert; a broad, deeply incised mountain escarpment belt; and the



Plate 10. Dikdik preorbital glandular secretion mark on a bush at the family communal dung heap. The black shiny accumulation from many markings can be seen in the centre of the picture.

Interior Continental Plain which extends across the subcontinent to the Eastern Great Escarpment.

The climate is arid with a markedly seasonal and erratic rainfall. Rainfall is the prime climatic feature affecting life in South West Africa. The temperature and humidity regime in the coast desert and in the arid savannas of the Interior Plain are similar (Appendix A). The main plant formations through which dikdik occur are the non-thorny *Colophospermum mopane* and *Commiphora* savannas, and the thorny *Acacia* savannas.

(5) The dikdik's typical habitat in South West Africa is thicket and dense woodland on stony and hard clayey ground in which there is a well-developed shrub understorey but little to no grass.

(6) Dikdik are dominantly browsers of leaves, twigs and fallen plant material. Some grazing is done during the summer rainy season. Food plants are recorded from one locality only in their distribution range, in the eastern part of the Etosha National Park. Forty-two plant foods are recorded (Table I).

(7) Dikdik are especially common on the ecotones between thicket and open glades. The use of ecotones provides them with a large variety of food, cover from predation and shade. Additional food is provided by the rough feeding of elephant and black rhino; and other species such as kudu and impala browse shrubs heavily and keep them within reach of dikdik.

(8) Dikdik are independent of surface water.

(9) In the mid-rainy season there is local movement of dikdik apparently in evasive response to the rank growth of annuals (see also 11 below).

(10) Browsing mammals which share the same habitat are elephant, black rhino, giraffe and kudu. Mixed feeders such as impala and springbok also occur into the dikdik habitat, and grazing mammals feed in the open glades and woodland. On stony ground elephant-felled trees increase the thicket cover to the advantage of dikdik. Three other small antelope — the grey duiker, steenbok and klipspringer occur in the same country as dikdik. Overlap of habitat use is mostly an ecotonal phenomenon.

(11) Other associated animals include blood sucking flies, chiefly a tabanid (?*Philoliche* sp.) and a muscid *Stomoxys* species. The irritation by these flies was not sufficient to induce movement of dikdik, but may be a factor inducing movement in other areas. Endoparasites include a tapeworm, roundworm and a cosmocerid.

(12) An outline of the small antelope spectrum in southern Africa, and their habitat preferences is given, with a figure of the patterns of habitat use in the Afrotemperate/montane and Tropical life divisions. There is a spectrum of small browsing antelope occupying the whole array of closed woody habitats from equatorial forest to desert (in riverine situations).

There are ten small antelope species which are defined here by being less than 20 kg in weight. They are blue duiker, red duiker, suni, grysbok, Sharpe's grysbok, klipspringer, oribi, grey duiker, steenbok, dikdik. Six are forest and/or thicket species, two are open savanna species, one in grassland and another confined to rock outcrops.

(13) The dikdik is the Arid Savanna and Subdesert ecological equivalent of the other five forest and thicket inhabiting small antelope.

(14) The ten small antelope all possess preorbital scent glands and most have pedal glands which are used in marking their habitat for communication and territorial advertisement.

(15) The patterns of distribution shown by the vegetation of the two life divisions in southern Africa is described briefly, with an analysis of the distribution and overlap of the small forest antelope. The only small antelope confined to the Afrotemperate/montane life division is the grysbok *Raphicerus melanotis*. Except for suni and dikdik all the other species occur in both life divisions in southern Africa, especially in the transition forests of Natal. In East Africa suni and dikdik also occur into the Afromontane division.

(16) The dikdik is one of many examples of the biotic similarity between the Southwest Arid Zone and Northeast Arid Zone in Africa, which is today separated by the forest and moist savanna biomes.

(17) Dikdik are definitely preyed on by three species — the leopard, lynx and man. A list of the potential predators is given in Table II.

(18) Limiting factors are discussed. Dikdik are limited in their occurrence by several interrelated factors: (i) arid climate effect on land surfaces, producing stony ground, (ii) local soil moisture supporting thicket, and (iii) specialized feet which confine them to rough ground.

(19) Dikdik behaviour is associated with several unique external anatomical features which are described — these are the mobile nose, crest, digital pads and preorbital skin glands.

(20) Dikdik occur typically in pairs. Up to six animals have been seen together.

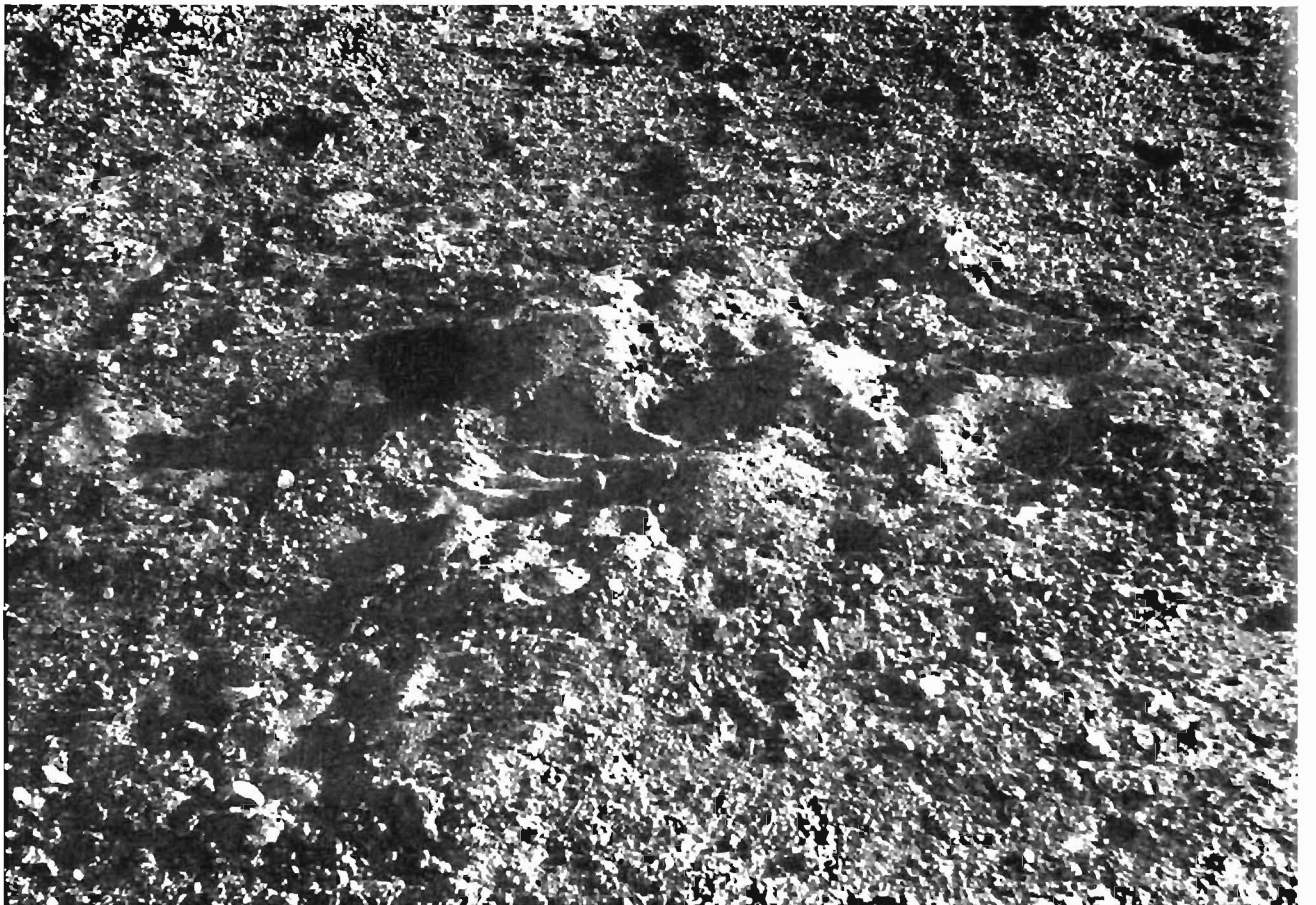
(21) The typical species of Kirk's dikdik in East Africa produces two young per year, with one breeding peak at the beginning of the wet season and the other at the end of the wet season.

(22) Their communicative call is a high, quavering whistle made through the nose.

(23) The long proboscis-like nose is characteristic of dikdik. The nose has no external rhinarium, and is not prehensile.



Plate 11. Klipspringer preorbital glandular secretion marks on a bush at their family communal uung heaps. (photo: W. H. zur Strassen)



(24) Dikdik have an erectile crest of long hairs on the forehead which is raised in various situations of excitement. No glandular area is associated with the crest.

(25) Digital pads are present on the post-ventral surfaces of the hooves. They act as protective and non-skid surfaces on stony ground.

(26) Dikdik possess one set of scent-producing skin glands, the preorbital glands. The black tarry secretion from these glands is used for marking their habitat. There are no functional interdigital glands in the Damara dikdik; but the shape, size and position of these glands in the East African dikdik have been used as a distinguishing feature of the subfamily *Madoquinac*.

(27) Communal dung heaps are used by dikdik. Males, but not females, were seen to scratch or dig up the dung and urine with their forefeet. This behaviour may be for laying a fecal or urinary scent trail. Both sexes wipe their preorbital gland on a twig after defecating. Defecatory behaviour in some other mammals is mentioned.

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APPENDIX

A

Meteorological data from Arid Savanna and Desert in South West Africa

	ARID SAVANNA <i>Ouljo</i> 20°07'S, 16°09'E, 1265 m alt.	DESERT <i>Gobabeb</i> 23°34'S, 15°03'E 407 m alt.
JANUARY (mid-summer)		
<i>Temperature °C</i>		
Abs. Maximum	37.3	40.4
Abs. Minimum	9.7	10.4
Mean Maximum	32.5	31.9
Mean Minimum	17.1	15.2
Average	24.8	23.5
<i>Relative Humidity %</i>		
0800	61%	82%
1400	33%	33%
<i>Wind</i> (dominants only)	W, SW	NW, SW
JULY (mid-winter)		
<i>Temperature °C</i>		
Abs. Maximum	29.0	34.8
Abs. Minimum	-3.9	2.2
Mean Maximum	24.9	26.3
Mean Minimum	5.7	9.7
Average	15.3	18.0
<i>Relative Humidity %</i>		
0800	56%	56%
1400	22%	23%
<i>Wind</i>	E, N, NE	E, S, SW, SE
YEAR		
<i>Temperature °C</i>		
Abs. Maximum	39.6	41.9
Abs. Minimum	4.4	2.2
Mean Maximum	29.7	30.0
Mean Minimum	12.6	12.7
Average	21.1	21.4
<i>Relative Humidity %</i>		
0800	59%	68%
1400	26%	25%
<i>Wind</i>	E, N, SW, W	SW, NW, S
<i>Temperature Range</i>	17.1	17.3
<i>Rainfall</i> (mean annual)	410.0 mm	23.0 mm
<i>Days Rain</i>	43.0	18.0
<i>Days Fog</i>	0	102.0

(all figures courtesy of Weather Bureau, Windhoek, South West Africa)

Plate 12. (Top) Dikdik communal dung heap. Note how the dung has been pawed or dug up into mounds; the preorbital glandular secretion mark can be seen on the lower right twig of the bush (silhouetted against the white stone). The lense cap of a camera is the lay figure (5 cm in diameter).

Plate 13. (Bottom) The dung heap of a male steenbok showing how it has dug up the dung and urine into mounds. The pawing marks can be seen next to the camera case (black object). No evidence of preorbital marking was found around steenbok male dung heaps.

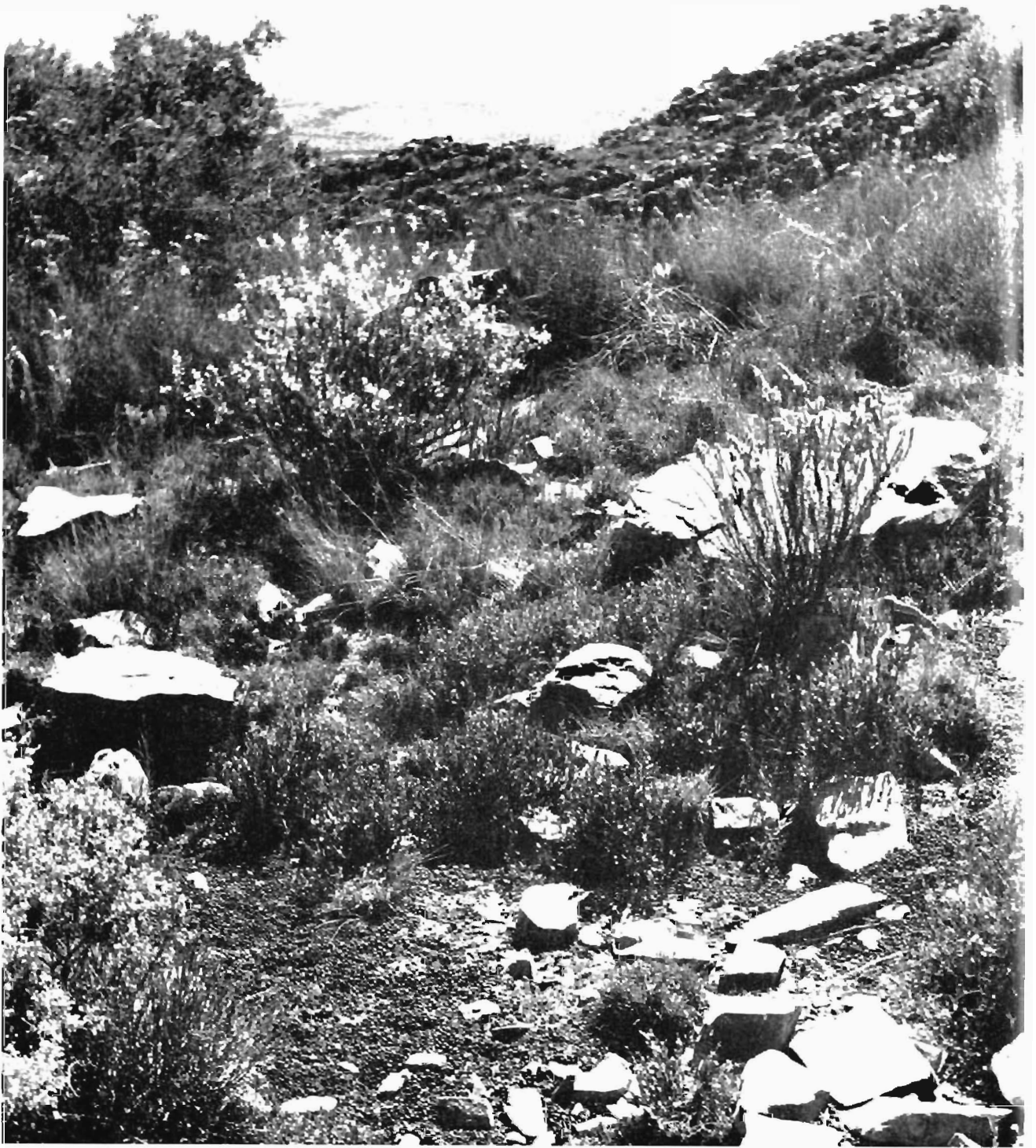


Plate 14. Communal dung heap of klipspringer on the crest of the Awas Mountain range (2300 m alt.) south of Windhoek. This dungheap was 3 m in diameter. Many preorbital gland marks are made on plants surrounding the dung heap. This shows the same behaviour pattern as dikdik but klipspringer do not paw the dung and urine into mounds. (photo: W. H. zur Strassen)

B

Glossary

VEGETATION PHYSIOGNOMY (after Tinley 1966, with modifications and additions)

Forest: stratified, closed woody plant community dominated by trees, usually with more than two woody plant strata including the upper canopy of trees, and containing many synusiae. Seedling stages of canopy trees, subordinate tree and shrub layers, and understorey including some specialised grasses are typically sciophytes. Mostly evergreen but Dry Forest types are semideciduous. Fire does not pass through forest. (eg. Tropical and Afrotropical/montane Rain Forests and related types).

Thicket: usually stratified, very dense almost impenetrable tree and/or large shrub community. Climbing and scandent plants are often common. Grass is usually discontinuous or absent. Thicket can be primary or secondary, tall or short, nonthorny (eg. coast bush) or thorny (eg. acacia). Thicket shorter than 3—4 m should be referred to as *scrub-thicket*. Secondary thicket is the typical mature cover on post-cultivation sites and on areas that have been subject to overstocking. In moist areas thicket is seral to forest. Fire passes through deciduous thicket but not through evergreen thicket. (eg. (1) Tropical and subtropical examples include: discontinuous, tall, island-like thickets on termitaria, and in depressions in arid savanna (see *Clump Savanna*). Continuous or extensive thicket occurs on post-cultivation sites, (2) Afrotropical examples include: Erica-coous thicket, ravine thicket, post-cultivation thicket etc.).

Woodland: stratified, stands of trees with crowns spaced from about one crown diameter apart to crowns overlapping. With shrubs, grass and/or herb groundlayer.

Components of this and the following types are mostly heliophytes. Fire passes through most of these types. (eg. (1) Tropical and subtropical examples include: Brachystegia Savanna Woodland, Mopane Savanna Woodland, (2) Afrotropical examples include: Hage-nia Montane Woodland, Philippia Woodland, Arundi-nella Woodland).

Tree Savanna/Treeveld: stratified, stands of tree spaced from about three crown diameters apart to crowns overlapping where aggregations occur. With shrubs, grass and/or herb groundlayer. The spacing of trees is intermediate between Woodland and the following type. The term *Savanna* is used for tropical and subtropical communities, and *Veld* for Afrotropical/montane communities.

Open Tree Savanna/Open Treeveld: stratified, stands of trees spaced more than three crown diameters apart. With shrubs, grass and/or herb groundlayer. In Afrotropical areas this spacing can be referred to as *Open Treeveld* (eg. Protea Open Treeveld).

Shrub Savanna/Shrubveld and *Scrub*: open short woody and/or suffrutescent plant cover from about 30 cm to 3—4 m in height. Plants may be single or multiple stemmed, scattered or aggregated with a grass ground-layer. The term scrub will be used for shorty woody or suffrutescent growth which usually occurs in relatively small patches. In tropical and subtropical communities the term *shrub savanna* is preferred where the woody cover, whether of a primary or secondary nature, occurs over relatively large area (eg. Mopane Shrub Savanna). In desert areas the community can be referred to as Desert Shrubland. In Afrotropical areas the terms *shrubveld* and *scrubveld* can be used. Where the community is secondary, eg. as a result of fire, cultivation or overstocking, scrub may be composed of normally single-boled, large tree species, here maintained

C

Weights and measurements of 4 adult dikdik*

WEIGHTS (Kg)	MALE	MALE	FEMALE	FEMALE
Liveweight	5.0	4.6	5.5	5.2
Dressed carcase	3.0	2.7	3.0	3.1
Carcase yield (% of liveweight)	60.0%	58.7%	54.5%	58.7%
Hind leg (average of two)	0.65	0.57	0.62	0.67
Stomachs (full), spleen, liver, kidneys, intestines	—	0.84	—	—
Liver, heart and lungs	0.23	—	—	0.24
Heart and lungs	—	0.11	—	—
Stomachs full	0.50	—	0.62	0.58
Stomachs empty	0.14	—	—	0.15
MEASUREMENTS (Cm)				
Head length (tip of nose to atlas joint)	17.7	17.4	16.5	15.8
Head length (tip of nasal bone to atlas joint)	15.3	14.5	13.0	13.8
Tail length (coccygeal-lumbar junction to tip)	4.7	3.4	5.4	4.6
Body length (atlas joint to base of tail)	48.8	46.6	48.5	50.2
Total body length (nose tip to tip of tail)	71.2	67.5	70.4	70.6
Heart girth (circ. of chest behind front legs)	35.2	36.5	36.5	35.0
Shoulder height (to hoof tip)	44.5	42.7	44.2	43.0
Ear length (frontal base notch to tip)	7.7	8.2	8.0	8.1
Horn length (base to tip along frontal surface)	7.7	8.8	—	—
Horn diameter (basal)	4.0	4.0	—	—
Distance between horn tips	3.7	5.2	—	—
Hind leg (point of hock to hoof tip)	21.8	20.4	20.9	20.1
Hind foot (proximal edge of dewclaw to hoof tip)	5.7	5.7	5.6	4.8
Head crest hair length		4 to 5 cm		
Small intestine length	374.5	315.0	346.4	349.0
Large intestine and rectum	174.5	114.0	184.0	179.0
Total length of intestines	548.0	429.0	530.4	528.0

(the standard body weights and measurements used are as described by Ledger 1963)
 * (1) Specimens collected on 24 February 1968 in the Namutoni area of Etosha National Park, South West Africa.
 (2) Shortridge (1934, vol. 2: 765—766) gives measurements of 15 adult dikdik, recording (a) head and body length, (b) tail length, (c) hind foot length, (d) ear length. Kellas (1955) gives a detailed account of the measurements and growth rate of the same species in East Africa from 412 specimens. The mean body weight of the East African dikdik was: males 4.5 kg and females 5.5 kg. See also R. Sachs (1967).

in a shrub-like growth form by one or more of the above factors. A similar physiognomy can be due to primary factors such as fire, frost, drought and over-protection of grassland with subsequent invasion of woody plants. If effects of these factors are removed shrub or scrub may develop into thicket or one of the other tree communities defined above. Scrub species are often in pure stands.

Clump Savanna/Clumpveld: primary, secondary or relic island-like patches of the above defined types. Physiognomy due to fire, available ground above flood levels, waterlogged ground or cold/frost hollows, to shifting cultivation or a combination of these factors. *Clumpveld* is used for Afrotropical areas. (eg. Tree-Clump, Bush-Clump, Shrub-Clump, Palm-Clump, Forest-Clump etc.). (refer also to Rattray 1962; and Hopkins 1965, p. 44 fig 20, p. 70 fig 29.)

MOISTURE PROVINCES (from Tinley MS)

In northern South West Africa the temperature regime between the highest rainfall zone and the lowest is not very different. The Namib Desert (like the Atacama) is an extremely arid but mild desert, as temperature extremes are damped by proximity to the sea and by the sea fogs which extend inland at night. The most striking feature effecting the distribution of the vegetation and consequently of many animals, is the rainfall zonation. For examples of rainfall importance in other tropical areas see Hopkins (1965) and Owen (1966).

In northern South West Africa and southern Angola the vegetation comprises Tropical Savanna and Desert Formations in which 5 main moisture provinces are recognized. These moisture provinces can be applied to the remainder of southern African tropical areas (as used in Fig. 3 above).

- (1) *Moist or Wet Savanna* (more than 900 mm mean annual rainfall) eg. *Brachystegia*, *Isoberlinia*, *Julbernardia* Savanna Woodlands. Often a mosaic with forest or contains forest remnants or precursors. Absent from South West Africa; the closest is in southern Angola.
- (2) *Mesic Savanna* (500 to 900 mm)
- (3) *Arid Savanna* (100 to 500 mm)
- (4) *Subdesert* (50 to 100 mm)
- (5) *Desert* (0 to 50 mm)

(These categories seem to fit quite closely the divisions in northern Africa: ie. Desert, Subdesert, Sahelian Zone, Sudanian Zone, Guinean Zone.)

REFERENCES

- ACOCKS, J. P. H.
1953 Veld types of South Africa. *Bot. Surv. S. Afr. Mem.* no. 28.
- ALLEN, G. M.
1939 A checklist of African mammals. *Bull. Mus. Comp. Harv.* 83
- ANSELL, W. F. H.
1960 *Mammals of Northern Rhodesia*. Govt. Printer, Lusaka
- BALINSKY, B. I.
1962 Patterns of animal distribution on the African Continent (summing-up talk). *Ann. Cape Prov. Mus.* 2: 299—310
- BEARD, P. H.
1965 *The end of the game*. London, Paul Hamlyn
- BEWS, J. W.
1925 *Plant forms and their evolution in South Africa*. London
- BIGALKE, R. C., and J. A. BATEMAN
1962 On the status and distribution of ungulate mammals in the Cape Province. South Africa. *Ann. Cape Prov. Mus.* 2: 85—109
- BROWN, L. H.
1963 Observations on East African birds of prey. *E. Afr. Wildl. J.* 1: 5—17
- BRYNARD, A. M., and U. de V. PIENAAR
1960 Annual report of the biological section of the Kruger National Park. *Koedoe* 8: 1—205
- CATER, J. C.
1954 The Nyika Plateau, Nyasaland. *Oryx* 2 (1): 298—302
- CHILD, G., and C. R. SAVORY
1964 The distribution of large mammal species in Southern Rhodesia. *Arnoldia (Rhodesia)* 1 (1): 1—15
- DARLING, F. FRASER
1937 *A herd of red deer*. (1963 edition) Oxford
- DEANE, N. N.
1960 Red duiker preyed on by crocodile. In: "Short Notes" of *Lammergeyer* 1 (1): 36
- DE WINTER, B.
1964 Remarks on the distribution of some desert plants in Africa. In: *Palynology in Africa — Eighth Report*, pp. 61—62. (E.M. van Zinderen Bakker editor)
- DIXON, J. E. W.
1964 Preliminary notes on the mammal fauna of the Mkuzi Game Reserve. *Lammergeyer* 3 (1): 40—58
1966 Notes on the mammals of Ndumu Game Reserve. *Lammergeyer* 6: 24—40
- DOLLMAN, J. G.
1929 Angolan dikdik. *Nat. Hist. Mag. London* 3 (24): 253—255
- DRAKE-BROCKMAN, R. E.
1911 On antelopes of the genera *Madoqua* and *Rhynchotragus* found in Somaliland. *Proc. Zool. Soc. London* pp. 977—984
- DUNDAS, L. M.
1926 Dikdiks fighting. *Field*. London vol. 148, p. 205
- EINARSON, A. S.
1948 *The pronghorn antelope and its management*. Washington. The Wildlife Management Institute
- ELLERMAN, J. R., MORRISON-SCOTT, T. C. S., and R. W. HAYMAN
1953 *Southern African mammals: A reclassification*. London, Trustees British Museum (Nat. Hist.)
- ELOFF, F. C.
1959 Observations on the migration and habits of the antelopes of the Kalahari Gemsbok Park. Parts I & II. *Koedoe* 2: 1—51
- ESTES, R. D.
1967 The comparative behaviour of Grant's and Thomson's gazelles. *J. Mamm.* 48 (2): 189—201
1968 Territorial behaviour of the wildebeest (*Connochaetes taurinus* Burchell, 1823). Ph. D. thesis. Cornell University, USA. 151 pp.
- GAERDES, F.
1966 *Tiere im Veld: Lebensbilder aus der Tierwelt Südwesafrikas*. Windhoek, S.W.A.
- GIESS, W., and K. L. TINLEY
1968 Conservation of vegetation in South West Africa. In: "Conservation of vegetation in Africa south of the Sahara". Uppsala Symposium. Proceedings of the 6th plenary meeting of AETFAT.
- GLASGOW, J. P.
1963 *The distribution and abundance of Tsetse*. London, Pergamon Press
- GLASS, B. P.
1965 The mammals of eastern Ethiopia. *Zoologica Africana* 1 (1): 177—179
- GODDARD, J.
1967 Home range, behaviour and recruitment rates of two black rhinoceros populations. *E. Afr. Wildl. J.* 5: 133—150

- GOSSWEILER, J., and F. A. MENDONÇA
 1939 *Carta fitogeográfica de Angola*. Edicao do Governo Geral de Angola. 242 pp. and vegetation map of 1:2 million. Lisboa
- GRIMWOOD, I. R.
 1963 The fauna and flora of East Africa. In: Conservation of nature and natural resources in modern African states. *IUCN Publ. new series* 1: 179--188
- HILL, J. E., and T. D. CARTER
 1941 The mammals of Angola, Africa. *Bull. Amer. Nat. Hist.* vol. 78
- HOPKINS, B.
 1965 *Forest and Savanna*. Ibadan and London, Heinemann
- KELLAS, L. M.
 1955 Observations on the reproductive activities, measurements and growth rate of the dikdik (*Rhynchotragus kirki thomasi* Neumann). *Proc. Zool. Soc. London* 124: 751--784
- KENYA WILDLIFE SOCIETY
 1961 East African duikers: identification series no. 3. *Wild Life* 2 (4): 49--52
- KETTLITZ, W. K.
 1962 The distribution of some of the larger game mammals in the Transvaal (excluding the Kruger National Park). *Ann. Cape Prov. Mus.* 2: 118--137
- LAMPREY, H. F.
 1963 Ecological separation of the large mammal species in the Tarangire Game Reserve, Tanganyika. *E. Afr. Wildl. J.* 1: 63--92
 1964 Estimation of the large mammal densities, biomass and energy exchange in the Tarangire Game Reserve and Masai Steppe in Tanganyika. *E. Afr. Wildl. J.* 2: 1--37
- LAWTON, R. M.
 1963 Palaeoecological and ecological studies in the northern province of Northern Rhodesia. *Kirkia* 3: 46--77
- MEESTER, J.
 1965 The origins of the southern African mammal fauna. *Zoologica Africana* 1 (1): 87--93
- MITCHELL, B. L.
 1953 Game preservation in Nyasaland. *Oryx* 2 (2): 98--110
- MONOD, Th.
 1957 Les grandes divisions chorologiques de l'Afrique: Rapport présenté à la Réunion de Spécialistes sur la phytogéographie (Yangambi, 29 juillet-8 août 1946). CCTA/CSA Publ. no. 24, London
- OWEN, D. F.
 1966 *Animal ecology in tropical Africa*. Oliver & Boyd. Edinb. & London
- PIENAAR, U. de V.
 1963 The large mammals of the Kruger National Park -- their distribution and present-day status. *Koedoe* 6: 1--37
- POCOCK, R. I.
 1910 On the specialized cutaneous glands of ruminants. *Proc. Zool. Soc. London*. June: 840--986
- POYNTON, J. C.
 1967 Santa Rosalia in Africa or why are there so many African birds? *S. Afr. J. Sci.* 63 (11): 471--479
- RATTRAY, J. M.
 1962 Vegetation types of Southern Rhodesia. *Kirkia* 2: 68--93
- ROBERTS, A.
 1937a The South African antelopes. *S. Afr. J. Sci.* 33: 771--787
 1937b The old surviving types of mammals found in the Union. *S. Afr. J. Sci.* 34: 73--88
 1951 *The mammals of South Africa*. Trustees of "The mammals of South Africa" Book Fund, Johannesburg
- SACHS, R.
 1967 Liveweights and body measurements of Serengeti game animals. *E. Afr. Wildl. J.* 5: 24--36
- SHORTRIDGE, G. C.
 1931 Field notes on two little known antelopes: the Damaraland dikdik (*Rhynchotragus damarensis*) and the Angolan impala (*Aepyceros petersi*). *S. Afr. J. Sci.* November, 28: 412--417
 1934 *The mammals of South West Africa*. vol. 2; London, Heinemann
- SIMON, N.
 1962 *Between the sunlight and the thunder: The wildlife of Kenya*. Collins
- STOCKER, O.
 1964 A plant-geographical climatic diagram. *Israel J. Bot.* 13: 154--165
- TALBOT, L. M., and M. H. TALBOT
 1963 The wildebeest in western Masailand, East Africa. *Wildl. Monogr.* no. 12, 88 pp.
- THOMAS, O.
 1894 On the dwarf antelopes of the genus *Madoqua*. *Proc. Zool. Soc. London*. April 3rd, pp. 323--329
- TINLEY, K. L.
 1958 Preliminary reports on the ecology of north-eastern Zululand (Tongaland): (1) Lake Sibayi, (2) Pongolo and Mkuze Flood Plains, (3) Kosi Lake System. (Unpubl. MSS + maps, figures -- roneoed) Natal Parks Boards records
 1964 Some observations on certain tabanid flies in North-Eastern Zululand (*Diptera: Tabanidae*). *Proc. R. ent. Soc. Lond.* (A) 39 (4--6) pp. 73--75
 1966 An ecological reconnaissance of the Moremi Wildlife Reserve, northern Okavango Swamps. Botswana. Okavango Wildl. Soc. Cape Town. 146 pp.
 1967 The moist evergreen forest -- tropical dry semideciduous forest tension zone in northeastern Zululand & hypotheses on past temperate/montane rain forest connections. In: *Palaeoecology of Africa*. no. 2: 82--85 (E. M. van Zinderen Bakker editor)
 -- Ecology and life patterns of man, wildlife and vegetation in northern South West Africa. (MS in prep. for *Madoqua*).
- VESEY-FITZGERALD, D. F.
 1954a Wild life in Kenya. *Oryx* 2 (5): 286--293
 1954b Wild life in Tanganyika. *Oryx* 2 (6): 357--365
- VOLK, H. O.
 1964 Die afro-meridional-occidentale Floren-Region in S. W.-Africa. In: *Beiträge zur Phytologie*. (Kreeb, K. ed.), E. Ulmer, Stuttgart, 16 pp.
- WALKER, E. P., WARNICK, F., LANGE, K. I., UIBLE, H. E., HAMLET, S. E., DAVIS, M. A., and P. F. WRIGHT
 1964 *Mammals of the World*. Volume II. Baltimore, The John Hopkins Press
- WHITE, F.
 1962 *The forest flora of Northern Rhodesia*. Oxford University Press
- WILSON, V. J.
 1966a Notes on the food and feeding habits of the common duiker *Sylvicapra grimmia* in eastern Zambia. *Arnoldia (Rhodesia)* 2 (14): 1--9
 1966b Predators of the common duiker *Sylvicapra grimmia* in eastern Zambia. *Arnoldia (Rhodesia)* 2 (28): 1--8
 1968 Weights of some mammals from eastern Zambia. *Arnoldia (Rhodesia)* 3 (32): 1--20
- WINTERBOTTOM, J. M.
 1967 Climatological implications of avifaunal resemblances between South Western Africa and Somaliland. In: *Palaeoecology in Africa* no. 2: 77--79 (E. M. van Zinderen Bakker editor).