

**THE ECO-ETHOLOGY OF THE KAROO KORHAAN
EUPODOTIS VIGORSII.**

BY

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**SUBMITTED IN PARTIAL FULFILMENT OF THE DEGREE OF MASTER OF
SCIENCE (ORNITHOLOGY)**

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PREFACE

The study of the Karoo Korhaan allowed me a far broader insight in to the Karoo than would otherwise have been possible. The vast openness of the Karoo is a monotony to those who have not stopped and looked. Many people were instrumental in not only encouraging me to stop and look but also in teaching me to see. The farmers on whose land I worked are to be applauded for their unquestioning approval of my activities and general enthusiasm for studies concerning the veld and I am particularly grateful to Mnr. and Mev. Obermayer (Hebron/Merino), Mnr. and Mev. Steenkamp (Inverdoorn), Mnr. Bothma (Excelsior) and Mnr. Van der Merwe. Alwyn and Joan Pienaar of Bokvlei have my deepest gratitude for their generous hospitality and firm friendship. Richard and Sue Dean were a constant source of inspiration throughout the study and their diligence and enthusiasm in the field is an example to us all. Many people were indispensable in showing me around the flora of the Karoo. Of these, Sue Dean, Craig Hilton-Taylor, Timm Hoffman, Bruce Bayer, Richard Cowling and David Shearing deserve my full gratitude as, were it not for each one of them I wouldn't have made any headway at all. Graham Kerley who accompanied me on my first sojourn to the Karoo was always a source of enthusiasm and companionship. My friends Grant Fabian and Wayne Smith both gave indispensable help in the field, as did Jimmy McCrindle, Ali Mohammed and Dave Allan. Peter Steyn and Richard Brooke provided valuable accounts of their observations of korhaans.

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I will always be in the debt of the University of Cape Town and the Council for Scientific and Industrial Research who jointly supported me for the first two years of this study. The FitzPatrick Institute of African Ornithology was a sound base from which to project myself into the Karoo and the staff and facilities of the "Fitz" were, in no small way, really responsible for this project being possible. My thanks are deserved by my supervisor, Dr. Phillip Hockey, who provided valuable criticism of this manuscript.

Finally, I thank my family who have had no experience of the large, dry, open spaces of the Karoo, but who have patiently indulged my absence and encouraged me throughout. I dedicate this work to them.

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CHAPTER ONE

GENERAL INTRODUCTION

The following study was undertaken as part of the Karoo Biome Project (KBP) and sets out to investigate an aspect of karoo ecology that will contribute to a predictive understanding of both biotic and abiotic processes in the region for the development of meaningful management guidelines (Cowling, 1986).

The Karoo is a vast arid to semi-arid region south of 22°S, covering 652 339 km² of southern Africa (Rutherford & Westfall, 1986). In South Africa alone, the Karoo accounts for 427 015 km² or 35% of the land surface area (Cowling, 1986). The karoo biome (*sensu* Huntley, 1974) is an area of extensive pastoralism, the wide ranging non-selective grazing of large migratory herbivores (most typically Springbok *Antidorcas marsupialis*) having been replaced by a profitable small stock industry. The generally lime-rich, weakly developed soils are readily erodable, and, in areas where persistent overgrazing has significantly reduced the natural vegetation cover, gully and sheet erosion have reached advanced stages. Typified by extensive flat to gently undulating plains with characteristic dolerite topped "Mesas" and some mountainous regions, the area ranges from sea level in some western areas to 2000 m above sea level in the interior.

Arid and semi-arid areas generally are defined as areas where potential evaporation exceeds the average precipitation, and are characterized by rainfall that is not only limited, but also extremely irregular, both in timing and the amount it eventually contributes to soil moisture (Noy-Meir, 1973; Mott, 1979). The Karoo is particularly unfavourably placed geographically relative to the rain bearing circulation patterns of southern Africa (Booyesen & Rowsell, 1983). The sub-continent is situated largely within the southern sub-tropical high pressure belt and is skirted to the south by circumpolar westerly airstreams (Weather Bureau, 1950). Rainfall decreases to the west and to the north of the region (Anon, 1957) ranging from 20-290mm in the north-west to 100-520mm in the east (Rutherford & Westfall, 1986). Linked with a decrease in the annual precipitation is a decrease in its reliability. The relative variability of the rainfall is about 25-30%, increasing to 80% in the north-west (Werger, 1978). Precipitation in the summer rainfall areas of the interior of South Africa originates mostly from the extension of thunder storm activity emanating from the north and east. The western regions receive up to 60% of their precipitation from the deep penetration of cyclonic fronts cut off from the low pressure cell in spring and autumn (Cowling *et. al.*, 1986). Although generally divided into summer and winter rainfall regions the whole area experiences summer drought (Cowling, 1987). A more comprehensive review of the physical environment of the karoo biome is provided by Cowling *et. al.*, 1987a,b.

The flora of the Karoo is dominated by members of the Asteraceae, Mesembryanthemaceae, Aizoaceae, Poaceae and Scrophulariaceae (Werger, 1978; Hilton-Taylor, 1987). There is an increasing dominance of dwarf and low succulent shrubs towards the western and southern continental margins associated with a decrease in the likelihood of severe winter frost in these regions (Werger, 1978).

Rutherford and Westfall's (1986) separation of the region into two "biomes" on the basis of floral life forms, an index of summer aridity and moisture regime places emphasis on existing

vegetation and not on supposed climax vegetation and productivity (Acocks, 1975). However, Acocks' (1975) categorization of the vegetation of South Africa remains the most detailed for the region and I refer to his "veld types" throughout. Rutherford and Westfall (1986) divide the area into the Succulent Karoo biome (limited to even, winter and strong winter rainfall with the greatest summer aridity in South Africa) and the Nama-Karoo biome (limited to strong summer, summer and even rainfall). For a detailed description of these biomes and the criteria for their separation see Rutherford & Westfall (1986).

Soil water in arid and semi-arid regions is far from being a single homogenous resource and the availability of soil moisture to different plant growth forms varies according to a suite of physiognomic and edaphic factors. In the summer rainfall areas a large proportion of the moisture does not penetrate beyond the grass rooting zone and therefore these areas are dominated by grasses (Roux, 1966; Werger, 1978). In higher rainfall areas shrubs begin to increase (Werger, 1978). In certain areas degradation due to the effects of overgrazing and poor land management has resulted in the reduction of grass cover, the proliferation of a complex of ephemerals and the subsequent increase in the cover of shrubs (Acocks, 1975; Bosch, 1987). The north-easterly "invasion" of sub-tropical grasslands by karroid vegetation has been estimated to have reached distances of up to 70km since 1953 (Jarman & Bosch, 1973). In the Orange Free State alone some 66 000 km² of grassland have been encroached by "undesirable" plants of karroid affinity.

The avifauna of the Karoo is characterized by a high proportion of endemic species. Of the 166 species endemic to southern Africa, 70% are confined to the south western arid zone with 73 of these occurring in the Karoo (Clancey, 1986; Vernon, 1986). Winterbottom (1968) and Vernon (1986) list 23 species that typify the Karoo avifauna in that they are endemic to southern Africa, are largely confined to the biome and are presumed to have evolved there. One of these species, the Karoo Korhaan (*Eupodotis vigorsii*), is one of 10 species of the family Otidae that occur in the southern African region 5 of which are endemic to the sub-region (for a description of the status of the family in southern Africa see Appendix 3). A common feature of the bustard literature is the allusion to the paucity of knowledge concerning this and other South African species (Clancey, 1973, 1974; Kemp & Tarboton, 1976). The species was first described by Dr. Andrew Smith (Smith, 1830) from a location assumed to be in the vicinity of Beaufort West (Hall, 1954), and forms part of a super-species with Rüppell's Korhaan (*Eupodotis rueppellii*) of Namibia and south-western Angola. These two species meet without apparent intergradation in areas southern Namibia (Clancey, 1959, 1986). The species is highly variable and up to four races have been described (Roberts, 1937; Hall, 1954)

The Karoo Korhaan is a medium sized (1.2 - 1.5kg) bustard with plain greyish-brown to sandy coloured plumage lightly mottled with dark brown above and a delicate pink below. A conspicuous black throat patch outlined with white is puffed out when displaying. The species is endemic to the Karoo (Winterbottom, 1961) and inhabits open, flat, stony shrublands (Horsburgh, 1912; Maclean, 1985), preferring vegetation that is high enough to see over (MacDonald, 1957; Winterbottom, 1968).

Although undertaking localized movements (Quinton, 1948; Maclachlan & Liversidge, 1978; Robinson *et. al.*, 1957; Uys, 1963) the species is not migratory (Roberts, 1952). The Karoo Korhaan is not reliant upon rainfall for breeding. It breeds in the austral summer (August to March), laying a single egg on bare ground with no nest. Most commonly encountered in pairs (Quinton, 1948) Karoo Korhaans defend territories all year round by means of a territorial duet (Anon, 1931; Quinton, 1948). The call of the male and female are distinguishable, though both are loud croaks, and comprise an antiphonal duet for the purposes of territorial display. The sexes can be identified on the basis of the call (McLachlan & Liversidge, 1978) and colouration of the head and neck (Kemp & Tarboton, 1976).

Preliminary observations of Karoo Korhaans in areas of the southern Karoo in 1986 showed that territorial pairs responded well to a taped recording of the duet, and therefore the species was relatively easy to census. It was also observed that the species was absent from various areas that appeared to conform to the understood habitat preferences of the species (Winterbottom, 1968). Although most commonly encountered in pairs, larger group sizes did occur at certain localities.

It was concluded that a study of the Karoo Korhaan would provide an interesting insight in to ecological processes of the Karoo and that the species may have value as an indicator of long term veld "quality".

The following key questions were addressed:

- 1) What is the habitat preference of the Karoo Korhaan and how do physiognomic and floristic attributes of karroid vegetation influence the species' habitat selection?
- 2) What are the dietary preferences of a territorial, non-migratory species in an environment that is characterized by low predictability of rainfall events and widely fluctuating resource availability?
- 3) How do group sizes vary along ecological and habitat gradients?

In order to address these key questions four permanent study sites were chosen, two in the winter rainfall, succulent karoo and two in the summer rainfall Nama-Karoo, each with marked plots that could be re-located for detailed botanical study.

CHAPTER TWO

PHYTOSOCIOLOGICAL CLASSIFICATION OF KAROO KORHAAN HABITATS IN THE SUCCULENT AND NAMA-KAROO BIOMES

INTRODUCTION

Descriptions of karroid vegetation have been, to date, broad regional studies (Acocks, 1975; Werger, 1978; Rutherford & Westfall, 1986). Few detailed phytosociological studies have been made in the Nama-Karoo (Werger, 1973) or the Succulent Karoo (Norton, 1977; Jürgens, 1986). Acocks (1975) describes twelve karoo veld types, with twenty-four variations, and a further nine anthropogenically induced "False Karoo" types. This description of "Veld Types" - areas with similar agricultural potential - is of great value for studies of the karoo biome (*sensu* Huntley, 1984) on a large scale, but belies the high local heterogeneity of areas within the biome (Acocks, 1975). Rutherford and Westfall (1986) identify two karoo "biomes", the Nama-Karoo biome and the Succulent Karoo biome, differing in rainfall regime, level of summer aridity and the life form compositions of the flora. The Nama-Karoo occupies areas of strong summer, summer and even rainfall, but generally receives rain from encroaching storm cell activity from the north and as such has an unpredictable rainfall (Schumann, 1949; Rutherford & Westfall, 1986; Cowling, 1986). The biome is the second largest in southern Africa and incorporates 21 of Acocks' (1975) veld types. The region is dominated by both chamaephytes and hemicryptophytes, having the form of a "grassy, dwarf shrub-land" (Rutherford & Westfall, 1986). The temporal partitioning of resources due to the unpredictability of rainfall allows a co-dominance of grasses with shrubs.

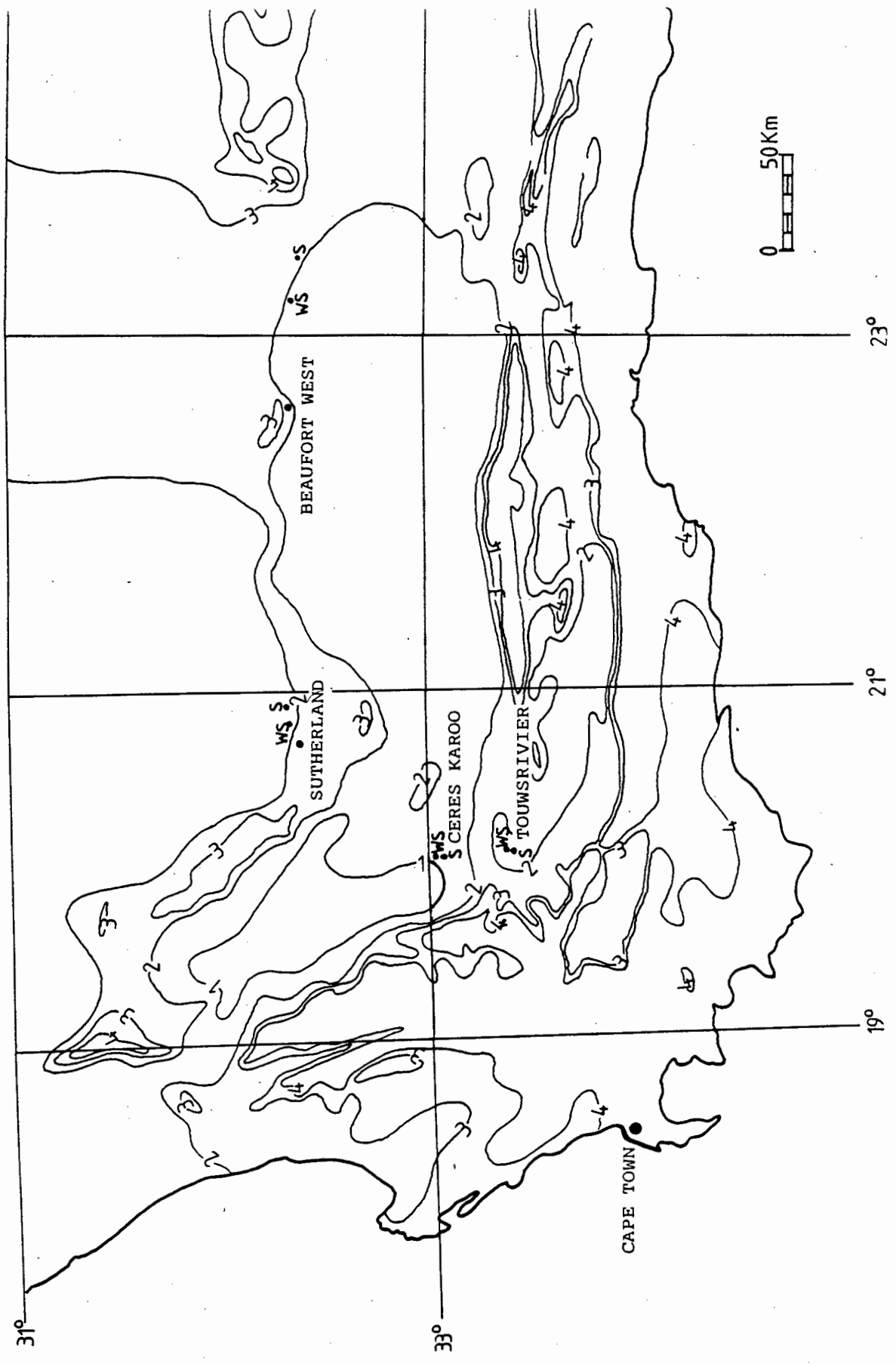
The Succulent Karoo occupies areas of even, winter and strong winter rainfall and has the greatest level of summer aridity in the region. The biome is the fourth largest in southern Africa, incorporating seven of Acocks' (1975) veld types. High summer aridity and the predictable, highly seasonal rainfall results in graminoid hemicryptophytes being rare and the biome is dominated by chamaephytes, mostly succulent in character (Roux, 1966; Rutherford & Westfall, 1986).

In this study the phytosociology of two areas of succulent karoo and two areas of Nama-karoo were investigated in order to describe the habitat of the Karoo Korhaan (*Eupodotis vigorsii*).

METHODS

The method of study was standardized for four areas of karroid habitat. Two areas, Touwsrivier and the Ceres Karoo (Fig. 1) lie within the winter rainfall, Succulent Karoo (*sensu* Rutherford & Westfall, 1986). The remaining two sites, Beaufort West and the site between Sutherland and Fraserberg, lie within the even to strong summer rainfall Nama-Karoo (*sensu* Rutherford & Westfall, 1986). Twenty plots, each comprising two 5x5m sub-plots (quadrats) were located throughout the respective study areas (with the exception of the Ceres Karoo site which had 25 plots) in areas that represented "typical" Karoo Korhaan habitat (*sensu* Winterbottom, 1966; Maclean, 1985). These plots were visited five times at three-monthly intervals between July 1986 to August 1987 so that all species present (especially ephemerals) would be detected. For each of the sub-plots a standardized vegetation form was completed (Fig. 2). Species presence was noted during the study and growth form distribution

Figure 1: Map of the Western Cape Province showing the location of the study sites and weather stations. Isohyets at 100mm intervals; ws = weather station.



and floristic analyses conducted. The plant taxa were identified using a reference collection gathered from the study areas. A data matrix noting the presence (1) or absence (0) of the plant taxa recorded in the area for the twenty plots (replicate quadrats for each plot were combined) was subjected to classification by polythetic, group average sorting using the Czekanowski coefficient (Bray & Curtis, 1957) which excludes double zero matches as a measure of similarity (Field *et al.*, 1982). Communities were identified by arbitrarily selecting a level of similarity from the resulting dendrogram. Plant taxa were identified that differentiated between the communities on the basis of their restricted occurrence. These "indicator" or "differential" species were separated into four categories depending upon their degree of fidelity (see Werger, 1974): exclusive species, occurring in only one community; preferential species, occurring in one community and rarely in others; vague species, indifferent to any particular community and, companion species, common throughout the communities. Each species was further assigned to a growth form category and growth form spectra were constructed for each community. An ordination of the analysis was produced by multi-dimensional scaling using the BMDP programme M-D-SCAL (Field *et al.*, 1982). Floral nomenclature follows Gibbs-Russell *et al.* (1987). For detailed descriptions of genera see Dyer, 1975

TOUWSRIVIER SUCCULENT KAROO.

STUDY AREA

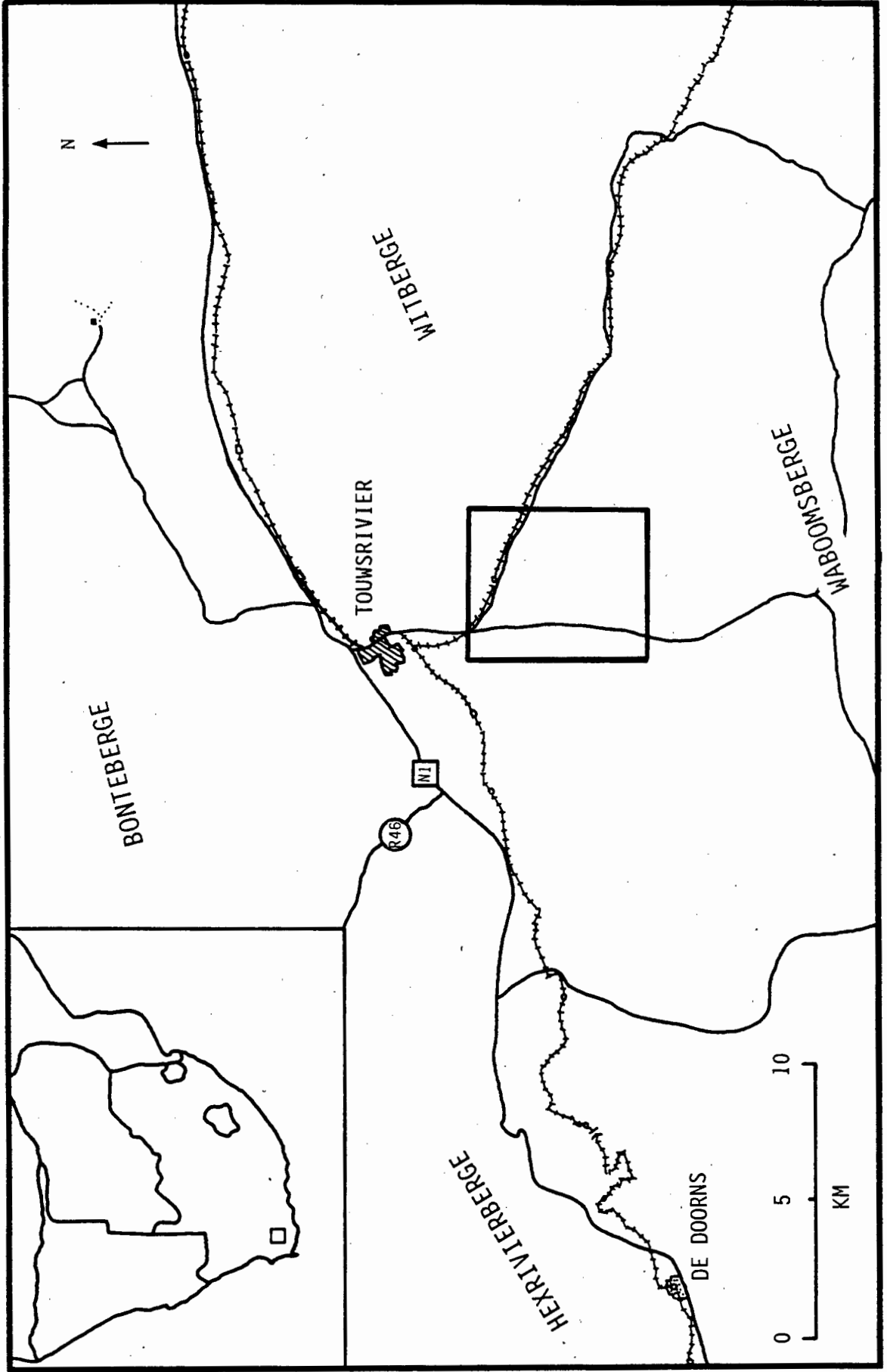
The study area was situated 5km south-east of Touwsrivier in the western Cape Province, and occupied approximately 3000 ha of open flats bounded by the Waboomsberge to the south, the Bontberge to the north and the Witberge to the east (Fig. 3). The open flats are situated on Nougá (33°27'S 20°03'E) and Excelsior (33°26'S 20°06'E) farms. The terrain varies from 780 to 850m a.s.l. with a north-easterly aspect draining into the Touws River via several small ephemeral water courses. The mean annual rainfall of 218mm is concentrated in the winter months, although rain may fall at any time of the year (Weather Bureau, 1950). According to Acocks (1975) the vegetation is Succulent Karoo (VT. 31), with intrusions of Renosterbos Veld (VT. 43) on the flats and at the base of the hills, grading into Western Mountain Karoo (VT. 28) and Fynbos (VT. 69) on the tops of higher hills.

RESULTS

Species composition analysis allowed the delineation of 2 major community groups at the 52% level of group average similarity with 4 outliers (Fig. 4). These 2 major communities (1 & 2) were further sub-divided into 5 communities at the 60% level. The geographical positioning of the communities, as determined by the classification analysis are presented in Figure 5.

Table 1 lists the species recorded in all of the sub-plots grouped according to the classification of the communities. Both succulent and non-succulent taxa are represented. Companion species

Figure 3: Map of Touwsrivier showing the location of the study plots.



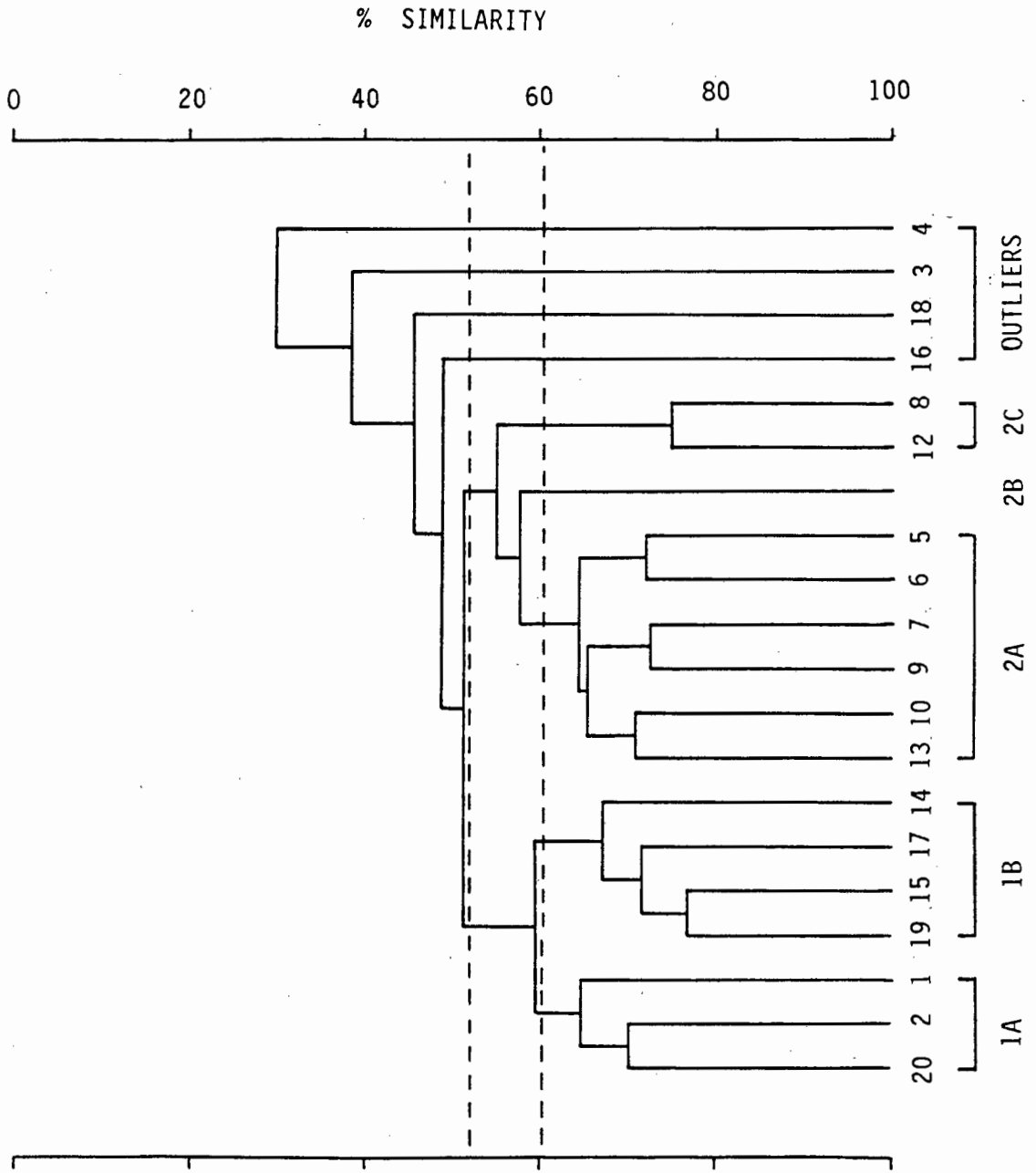


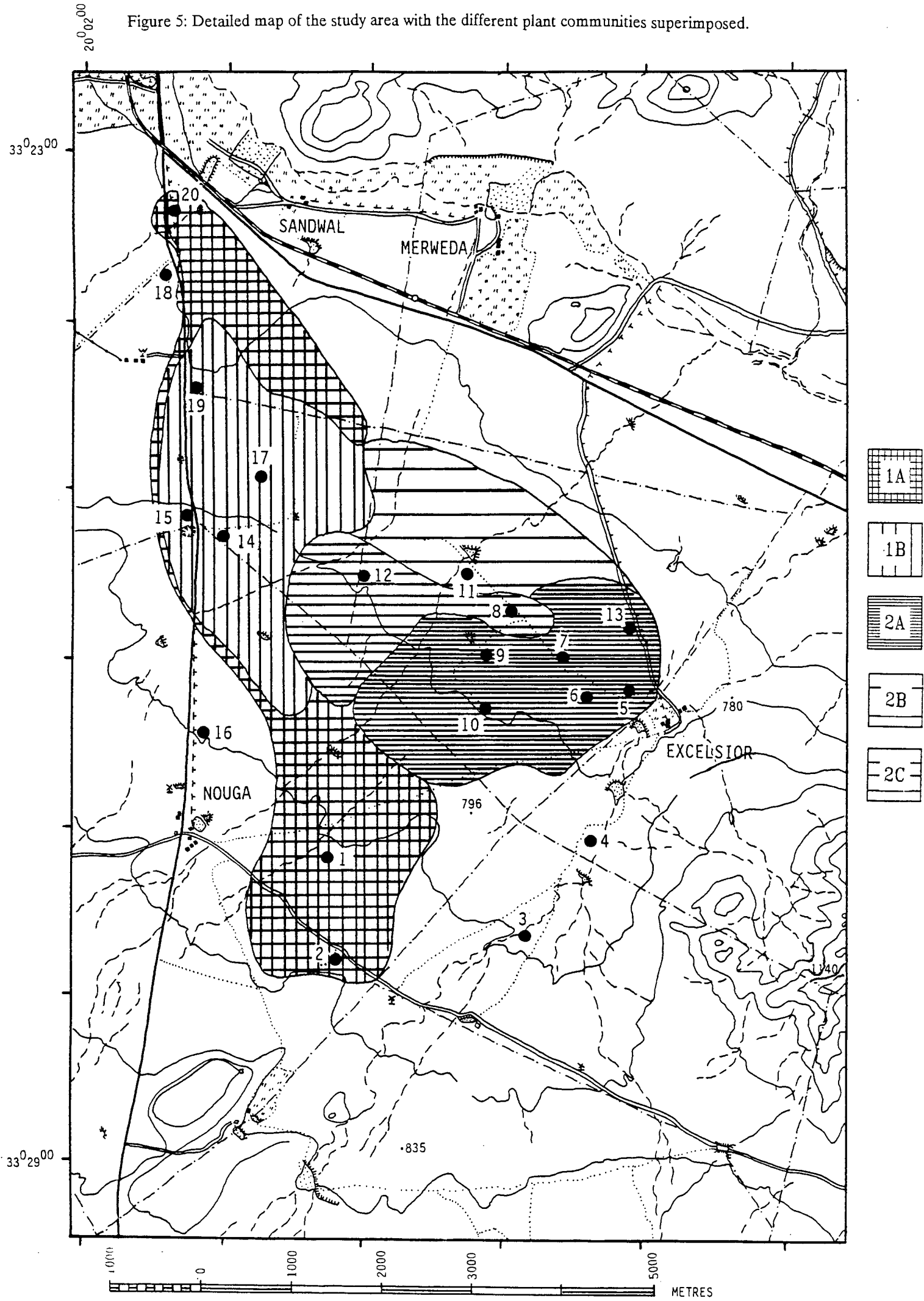
Figure 4: Dendrogram of percentage similarity (Bray-Curtis measure) of plant taxa among the 20 plots near Touwsrivier. Broken lines demarcate cutoff levels for groupings.

TABLE 1: A SPECIES/PLOT MATRIX SHOWING THE CLASSIFICATION OF SUCCULENT KAROO COMMUNITIES NEAR TOUWSRIVIER. VALUES REPRESENT FREQUENCIES OF OCCURRENCE IN THE SUB-PLOTS.

NUMBER OF QUADRATS TAXA	COMMUNITIES					OUTLIERS				GROWTH FORM
	1A 6	1B 8	2A 12	2B 4	2C 2	3 2	4 2	16 2	18 2	
* <i>Malephora</i> sp. N.E. Br.	4					1				LS
* <i>Osteospermum sinuatum</i> D.C.	3	5								A
* <i>Cotula</i> sp. L.	3	2								A
<i>Chrysocoma ciliata</i> L.	1	3		1			2			PS
* <i>Leysera tenella</i> D.C.	3	2					2			A
<i>Protasparagus capensis</i> Oberm.	4		1							PS
* <i>Glottiphyllum fragrans</i> Schwant	4		7			2				DS
* <i>Leipoldtia</i> sp. L. Bol.	4		9		2	1	2			LS
* <i>Felicia muricata</i> Thunb.	1	7	2			1				A
<i>Oxalis ?purpurea</i> L.	5	5	4		2	1		1	1	G
<i>Zygophyllum microcarpum</i> Licht.	3	4	3			2				SS
<i>Salsola tubercula</i> (Moq.) Fenzl.	4	5	7	2	2	2	2		2	PS
<i>Tetragonia fruticosa</i> L.	2	2	5	2		2			1	PS
* <i>Gibbaeum</i> sp. N.E. Br.	3	2	9	3	2				2	DS
<i>Eberlanzia ?tricroformis</i> L. Bol.	4	8	5	4		2		2	2	LS
<i>Galenia africana</i> L. subsp. <i>africana</i>	5	6	5	4	2	1	2	1		PS
<i>Eriocephalus ericoides</i> (L.F.) Druce	6	8	11	4	2	2		2	2	PS
<i>Pteronia adenocarpa</i> Harv.	6	8	11	4	2	1		2	2	PS
<i>Pentzia incana</i> (Thumb) Kuntze.	4	5	10	3		2		2		PS
* <i>Psilocaulon ?absimile</i> N.E. Br.	1	2	3		2				1	SS
<i>Drosanthemum</i> sp. Schwant.	1	1	6	1		1	2	1		LS
<i>Androcymbium</i> sp. Willd.	1	2	1	1	1		1			G
<i>Massonia depressa</i> Houtt.	1	1	4		1					G
* <i>Pteronia incana</i> (Burm) D.C.		6		2						PS
* <i>Aridaria</i> sp. N.E. Br.		3	9	1	2					LS
* <i>Sceletium</i> sp. N.E. Br.		1	5	3		2		2		SS
<i>Ruschia</i> sp. Schwant.		1	3		1			1		LS
* <i>Rosenia humilis</i> (Less) Bremer.			5							PS
<i>Senecio radicans</i> (L.F) Sch. Bip.			4			1				LS
<i>Zygophyllum</i> sp. L.			2	1	1	1				LS
* <i>Babiana</i> sp. Ker - Gawl.	2		1							G
<i>Euphorbia burmannii</i> E.Mey.	2		1						1	SS
<i>Lycium cinerum</i> Thunb.	1		1			1	1		1	PS
<i>Berkheya spinosa</i> L.F. Druce	1		1			1				A
<i>Felicia ovata</i> (Thunb.) Compt.	1		1							A
<i>Mesembryanthemum</i> sp. L.		1								LS
<i>Hereroa</i> sp. Dinter Ex. Schwant.			1		1	1				LS
<i>Euphorbia esculenta</i> Marloth.				1						SS
<i>Moraea tortillis</i> Goldbl.					1				1	G
<i>Gnidia deserticola</i> Gilg.						1				PS
<i>Dorotheanthus</i> sp. Schwant.						1				LS
<i>Manochlamys albicans</i> (Ait.) Aell.								1		A
<i>Zalunzianskya villosa</i> (Thunb.) F.W. Schmidt									1	A

* = Differential species (see text); LS = leaf succulent; SS = stem succulent; PS = perennial shrub; A = annual; G = geophyte.

Figure 5: Detailed map of the study area with the different plant communities superimposed.



(species of general occurrence; *sensu* Acocks, 1975) included *Eriocephalus ericoides* L., *Pteronia adenocarpa* Harv., *Pentzia incana* (Humb.) Kuntze., *Salsola tubercula* (Moq.) Fenzl., *Eberlanzia triciformis* L. Bol., *Oxalis* sp. L., and *Galenia africana* L. subsp. *africana*, which are widespread Succulent Karoo species (Acocks, 1975). Vague species included *Zygophyllum microcarpum* Licht., *Aridaria* sp. N.E. Br., *Psilocaulon ?absimile* N.E. Br., *Leipoldtia* sp. L. Bol., and *Tetragonia fruticosa* L.

Only one exclusive taxon occurred (*Rosenia humilis* (Less) Bremer). Differential species are shown on Table 1. The differential taxa of community 1 were characterized by asteraceous annuals (e.g. *Osteospermum sinuatum* D.C., *Leysera tenella* D.C., *Cotula* sp. L. and *Felicia muricata* Thunb.) while those of community 2 were characterized by dwarf leaf succulent shrubs (e.g. *Gibbaeum* sp. N.E. Br., *Glottiphyllum fragrans* Schwant., *Sceletium* sp. N.E. Br.) and succulent shrubs (i.e. *Leipoldtia* sp. L. Bol.). Succulence was a good distinguishing feature between the communities (Figs. 6, 7). Communities 1a and 1b had between 15% and 30% succulent taxa, while communities 2a, b and c contained a significantly higher proportion of succulent taxa ($\chi^2=7$, $df=1$; $p<0.05$). The growth-form spectra (Fig. 7) suggest that not only is succulence a distinguishing character of the two major communities but that the proportion of therophytes (mostly asteraceous annuals) is higher in community 1 (although not significantly so; $\chi^2=0.39$, $df=2$; $p>0.05$)

Life form categorization of the entire area indicated a dominance of chamaephytes (79%), with hemicryptophytes (geophytes; 14%) and therophytes (7%) being less common.

DISCUSSION

This classification produced 2 communities with 5 sub-communities, that differed not only in the species present but also in the growth forms of those species present.

The distribution of life-forms was typical of Succulent Karoo (Rutherford & Westfall, 1986) with a dominance of chamaephytes and no phanerophytes. The distribution of growth-forms was less typical of Succulent Karoo, as non-succulent perennial shrubs were co-dominant with succulent shrubs (leaf, dwarf and stem succulents combined). This is undoubtedly due to the fact that rainfall in the region is far more even than more "typical" strong winter rainfall areas of the biome in which succulent shrubs predominate (Acocks, 1975; Werger, 1978; Rutherford & Westfall, 1986).

The higher degree of succulence of community 2 (a,b & c) may in part, be due to the north-easterly drainage of the area. The higher degree of succulence of community 2 (a,b & c) and the higher proportion of annual species in community 1 (a & b; Fig. 7) could also be indicative of different grazing management systems. Annuals are often characteristic of anthropogenically induced disturbance in the Succulent Karoo (Leistner, 1979; Rutherford & Westfall, 1986). Figure 5 shows that the division of the communities conforms to the boundaries of the two farms (Nouga and Excelsior). The grazing regimes of the two farms are not adequately known, but it is interesting to note that the camps that comprise

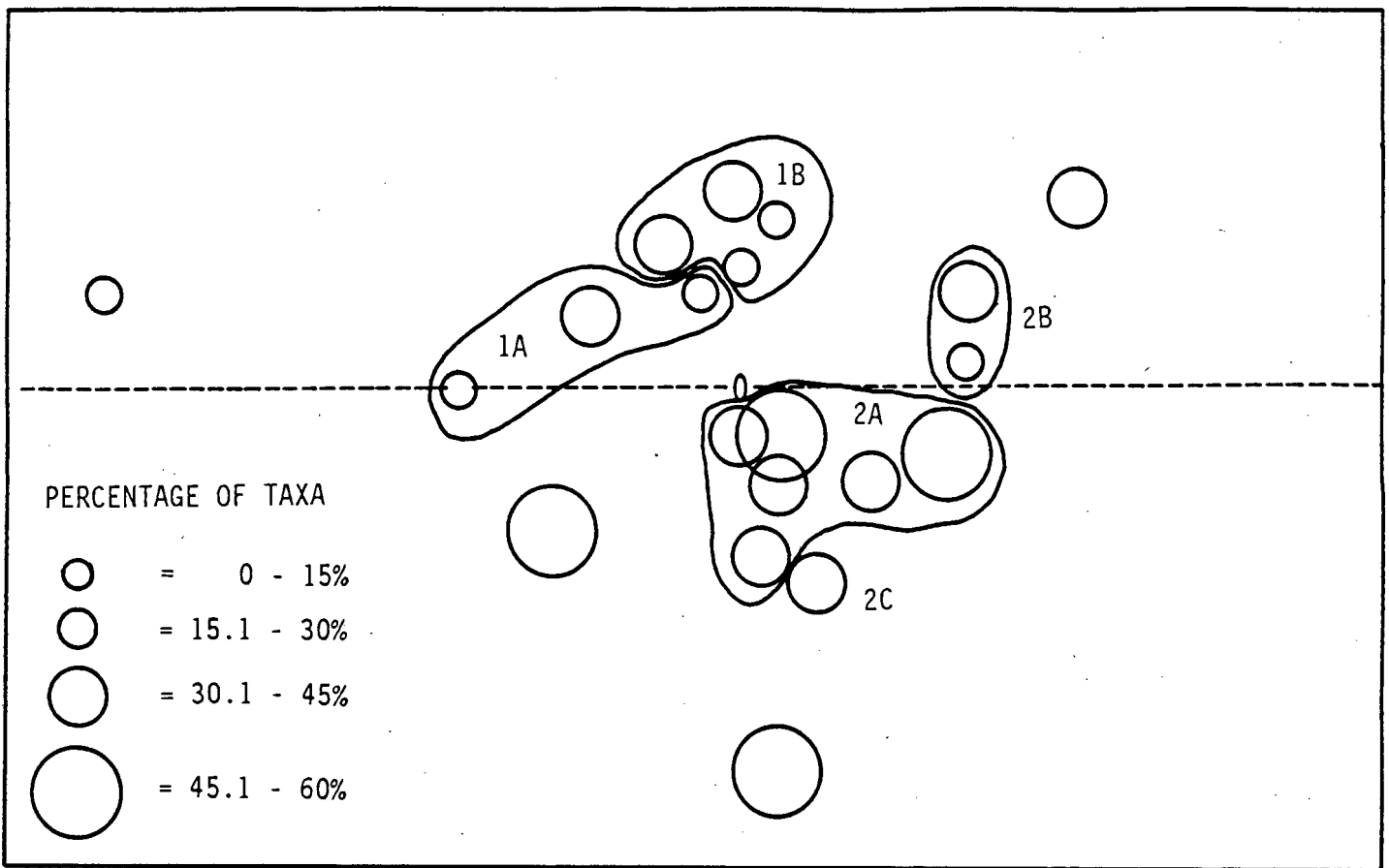


Figure 6: Ordination by MDS of the 20 plots near Touwsrivier. Circles denote the number of taxa in each plot with succulent growth-forms as a percentage of the total taxa in each plot.

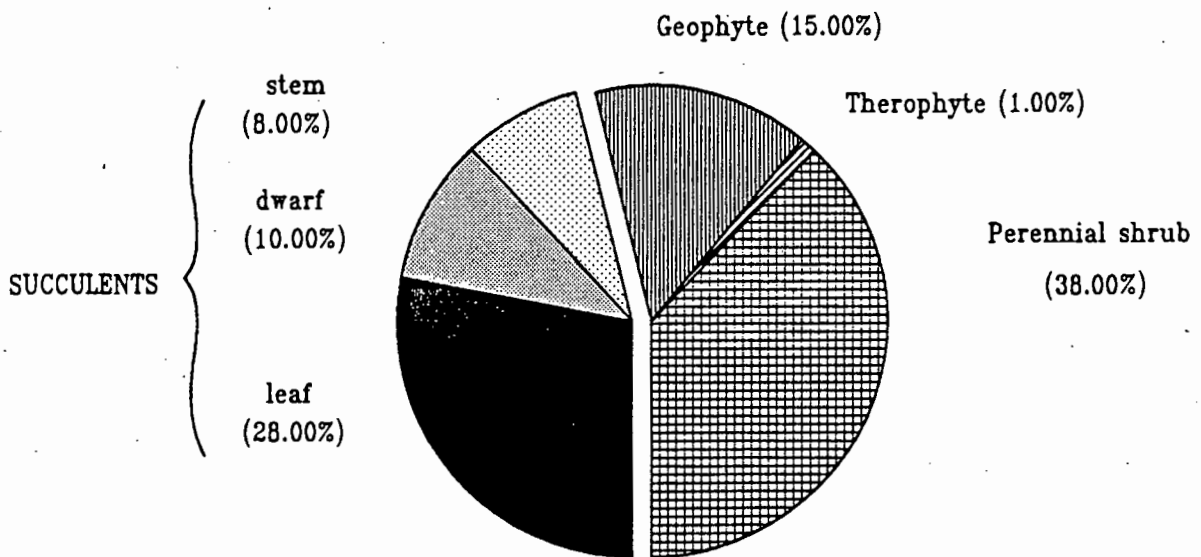
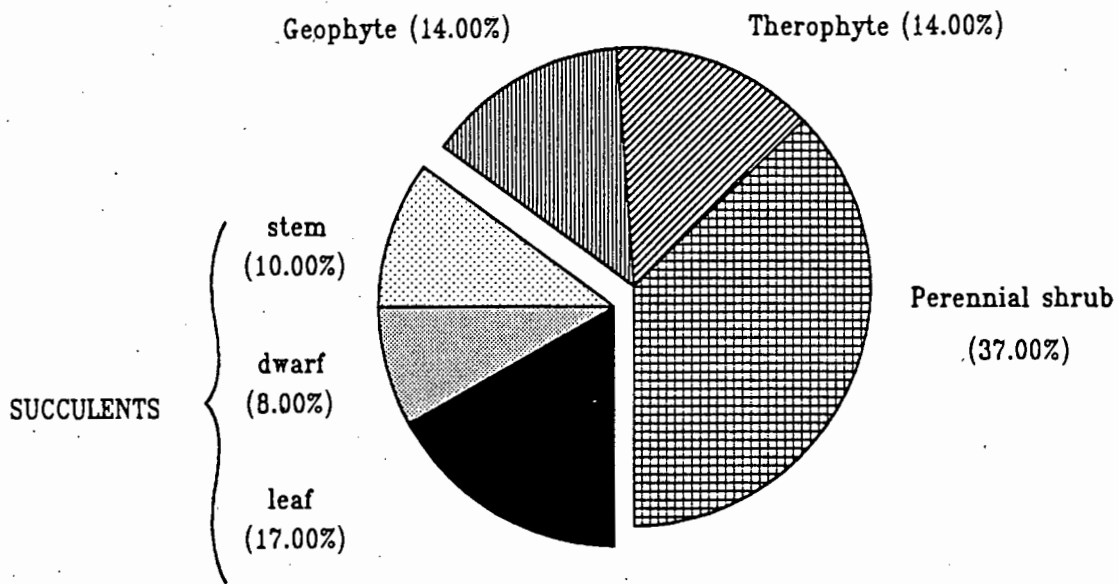


Figure 7: Growth form spectra for two vegetation communities near Touwsrivier.

community 1A had a mixed stock regime with Springbok (*Antidorcas marsupialis*) and Merinos, combining non-selective and selective herbivory.

The outliers (plots 3, 4, 16, 18; see Fig. 6) differ from the other communities in having several unique taxa. The outliers were on the periphery of the study area (Fig. 5), were comparatively species poor and are likely to be affected by influence from the Renosterbosveld and Fynbos affinity communities on the periphery of the flats.

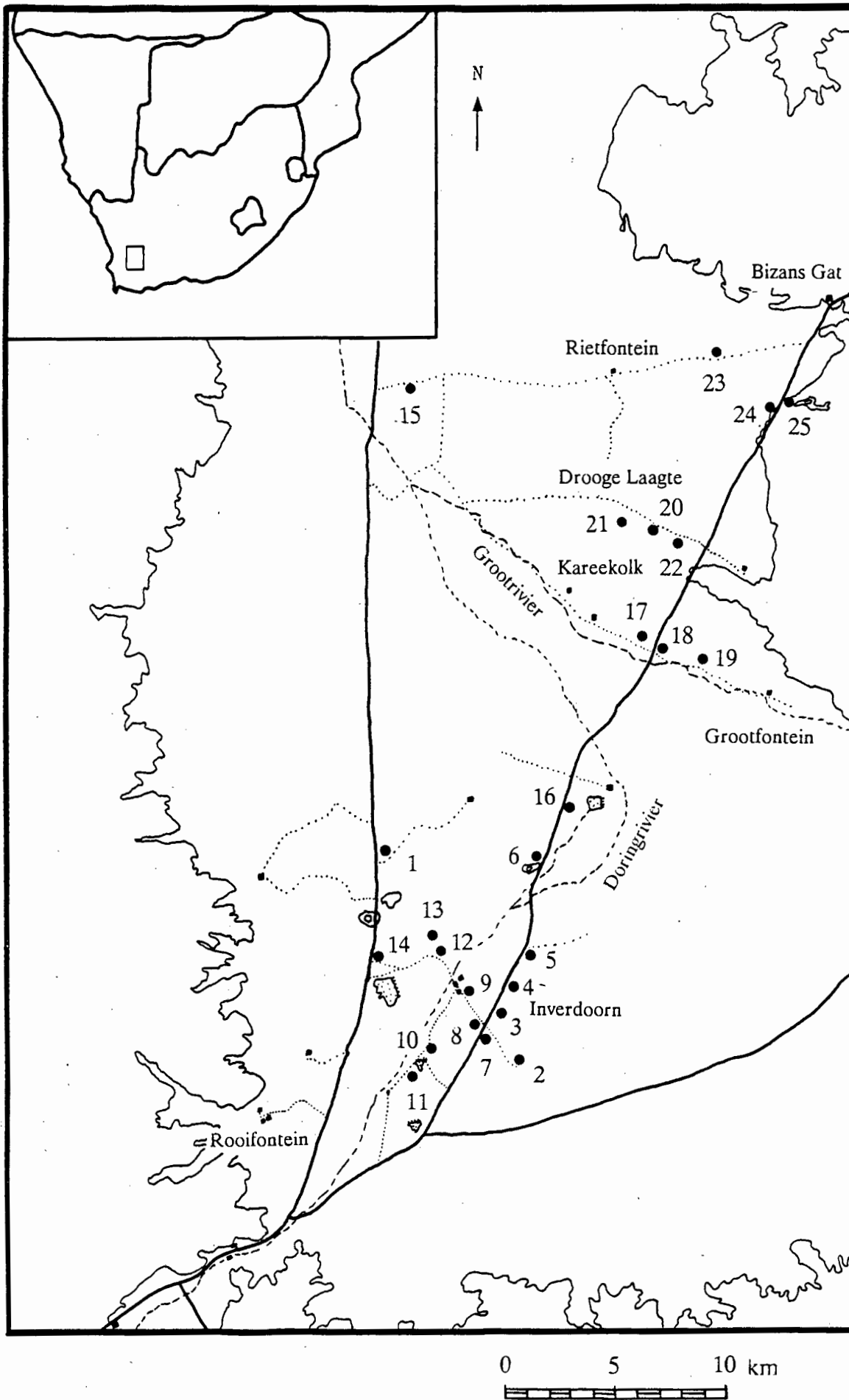
The identification of 2 communities with 2 and 3 respective sub-communities, provides clear evidence of the spatial patchiness of karoo vegetation. Although the communities cannot be mapped on a biome scale (see Rutherford & Westfall, 1986), they illustrate the local heterogeneity of the Succulent Karoo biome in response to variations in climate within the biome and local variations in water availability. No soil characteristics were measured. Although some authors have shown (Norton, 1977) or stated (Hoffman & Cowling, 1987) that soil pH, salinity, depth and texture are all important factors influencing karroid vegetation community structure, others state that soil character is of lesser importance in determining community structure when compared with water availability (Rutherford & Westfall, 1986). However, the soils of the area covered by community 2 were generally deeper than the soils of community 1 (a & b; pers. obs.).

CERES SUCCULENT KAROO

STUDY AREA

The "Ceres Karoo" occupies a wide depression, of roughly 3000 km², to the east of the Swartruggens and Cedarberg mountain ranges and to the south-west of the Koedoesberge and Roggeveld ranges below the south-western limit of the escarpment. The area is the southern extent of the Tanqua Karoo; a vast area of virtual desert that has suffered the combined effects of low rainfall and over grazing (Acocks, 1975; Werger, 1978). The Ceres Karoo is the only portion of the Tanqua Karoo that still supports small stock grazing throughout the year; although many of the farms in the more northerly parts are only seasonally grazed. The climate of the area has a strong orographic influence and as a result, the moisture regime of the central plains is likely to differ from that of the periphery where run-on and increased precipitation have a major effect upon vegetation (pers. obs.). The area of study (Fig. 8) covered some 44000 ha and included the farms Inverdoorn (33°06'S 19°49'E), Karreekolk (32°58'S 19°53'E), Droogte laagte (32°55'S 19°53'E) and Rietfontein (32°52'S 19°53'E). The area is a strong winter rainfall area of the Succulent Karoo Biome (Rutherford & Westfall, 1986), with an average rainfall of 107 mm (average over 29 years; Weather Bureau, 1950). The vegetation is a Tanqua Karoo form of Succulent Karoo Veld (VT. 31; Acocks, 1975). There is also a strong Great Karoo (VT. 26a) influence on the vegetation via the Grootrivier valley between the Witberge and the Kleinroggeveldberge from the area of Merweville and Laingsburg (C. Hilton-Taylor,

Figure 8: Map of Ceres showing the location of the study plots.



pers. comm). In the north-easterly areas a strong Western Mountain Karoo influence can be found near the vicinity of the Pienaarsfontein se berge and Bizansgat (32°50'S 19°59'E; Acocks, 1975). The area has a slightly northerly aspect, ranging in altitude from 520m to 680m with a few isolated tillite outcrops ("koppies") of ca. 700m. There are no perennial water courses but many seasonal drainage channels that drain into the Doringrivier. The Doringrivier enters the "Ceres Karoo" in the south west corner through Karoopoort (where surface flow is present throughout the year) and flows underground, north-east for 25km before changing course and flowing north-west to the edge of the open plains. There it is joined by the Grootrivier and Matjiesrivier before turning north-west again to join the Tanqua river that flows underground in a easterly direction south of the Tanqua Karoo. The combined Tanqua-Doring drainage system is one of the largest in the Karoo (Rutherford & Westfall, 1986) and forms a complex peripheral drainage from the surrounding ranges into the middle of the plains by means of subterranean rivers, resulting in the area being composed of brackish alluvial silts and gravelly sand, with paleosoils that may indicate a previous large perennial water course that used to flow through the area.

RESULTS

Species composition analysis allowed the delineation of 4 communities above the 45% level of similarity (Fig. 9). One of these communities (community 1) was further split into 2 sub-communities at the 50% level of similarity (see Fig. 9).

Table 2 lists the species recorded in the sub-plots grouped according to the classification of the communities. No exclusive differential taxa occurred. Preferential taxa of community 1 were generally leaf succulents (e.g. *Augea capensis* Thunb., *Cephalophyllum* sp. N.E. Br.). A preferential taxon of community 2 was *Tetragonia fruticosa* L. Community 2 had a wide variety of both succulent and non-succulent taxa and had the greatest number of annual taxa. Some of the species found in community 3, although not frequently enough to be considered differential taxa, indicated a Karroid Broken Veld (VT. 26) influence (i.e. *Lycium cinerum* Thunb., *Aptosimum procumbens* (Lehm.) Steud.). The general area was dominated by succulent taxa but had a gradation to co-dominance with non-succulent taxa in the southern region comprising communities 2 and 3. The 4 communities (Fig. 9) can be distinguished on their degree of succulence (Fig. 10) when viewed in conjunction with the growth form profiles (Fig. 11). Figure 11 shows the gradation from succulent dominance in communities 1 and 4 to non-succulent/succulent co-dominance in communities 2 and 3. The northern community (1a & b) was significantly more succulent than the southern communities of communities 2 ($\chi^2 = 7.9$, $df = 1$, $p < 0.005$) and 3 ($\chi^2 = 12$, $df = 1$, $p < 0.0005$). The gradation of succulent dominance is exhibited by a lack of significance in the degree of succulence between communities 1 and 4 ($\chi^2 = 1.1$, $df = 1$, $P > 0.05$; see Fig. 10), 4 and 2 ($\chi^2 = 2.2$, $df = 1$, $P > 0.05$) and 2 and 3 ($\chi^2 = 0.3$, $df = 1$, $P > 0.05$). Figure 11 illustrates the wide variety of different growth forms exhibited by community two.

TABLE 2: A SPECIES/PLOT MATRIX SHOWING THE CLASSIFICATION OF SUCCULENT KAROO COMMUNITIES IN THE CERES KAROO. VALUES REPRESENT FREQUENCIES OF OCCURRENCE IN THE SUB-PLOTS.

NUMBER OF QUADRATS TAXA	COMMUNITIES					OUTLIERS		GROWTH FORM
	1A 10	1B 10	2 14	3 6	4 6	(4) 2	(8) 2	
* <i>Augea capensis</i> Thunb	6							LS
<i>Cylindrophyllum</i> sp.	2							LS
<i>Hereroa</i> sp.	2							LS
* <i>Drosanthemum</i> sp.	6	8	1	1	3			LS
* <i>Psilocaulon utile</i> L. Bol.	10	8	5		2	1		SS
<i>Eberlanzia</i> sp.	10	2	14	6	6	2	2	LS
<i>Salsola tubercula</i> (Moq.) Fenzl.	4			2	4			PS
* <i>Cephalophyllum</i> sp.		3						LS
<i>Spalmanthus</i> sp.	3	1			2			LS
* <i>Aridaria</i> sp.	7	8	5					LS
* <i>Leipoldtia</i> sp.	3	2	3					LS
<i>Oxalis</i> sp.	9	8	8	6	3	1		G
<i>Ruschia</i> sp.	8	7	8	5	2	2		LS
<i>Pteronia paniculata</i> Thunb.	3	8	13	6	4	1		PS
<i>G. chrySTALLINA</i>	3	5	10		5	2	2	PS
<i>Osteospermum sinuatum</i> D.C.	3	4	8				1	A
<i>Galenia africana</i> L. subsp. <i>africana</i>	1		5	3	2		2	PS
* <i>Tetragonia fruticosa</i> L.			11	1		2		PS
<i>Berkheya spinosa</i> (L.F. Druce)			2					A
<i>Pteronia incana</i> (Burm.) D.C.			2					PS
<i>Chrysocoma ciliata</i> L.		2	3					PS
<i>Malephora</i> sp. N.E. Br.		1	2					LS
<i>Mesembryanthemum</i> sp.		2	2					LS
<i>Zygophyllum retrofractum</i> Thunb.			3	1				PS
<i>Protasparagus capensis</i> Oberm.		2	2	2				PS
<i>Cotula</i> sp.		8	3		2			A
<i>O. pes-caprae</i> L.			3	3	1			G
* <i>G. pubescens</i> (Eckl. & Zeyh.)	2		2		4			A
<i>Dorotheanthus</i> sp.	2		2			2		LS
<i>Crassula</i> sp.	5				6	1		LS
<i>C. muscosa</i>	3						1	LS
<i>Eriocephalus africanus</i> L.	1		3					PS
<i>Stipagrostis</i> sp.	1		1					PG
<i>Gazania</i> sp. Gaertn.			2				1	A
<i>Rosenia humilis</i> (Less.) Bremer	1							PS
<i>Indigofera</i> sp.	1							A
<i>Euphorbia burmanii</i> E. Mey. ex Boiss	1							SS
<i>Atriplex lindleyi</i> Moq.		1						A
<i>Gymnodiscus linearifolia</i> D.C.				1				A
<i>Pentzia incana</i> (Thunb.) Kuntze				1				PS
<i>E. esculenta</i> Marloth				1				SS
<i>Lycium cinerum</i> Thunb.				1				PS
<i>Aptosimum procumbens</i> (Lehm.) Steud.				1				PS
<i>Amphibolia</i> sp.					1			LS
<i>Tylecodon reticulatus</i> (L.f.) Toelken					1			DS
<i>Morea polystachya</i> (Thunb.) Ker-Gawl					1			G
<i>Tylecodon wallichii</i> (Harv.)					1		1	SS
<i>Sceletium</i> sp. N.E. Br.					1	2	1	DS
<i>Pteronia adenocarpa</i> Harv.					1	1		PS
<i>Senecio radicans</i> (L.f.) Sch. Bip.						1		LS
<i>Babiana</i> sp. Ker-Gawl							1	G
<i>Felicia muricata</i> (Thunb.)							2	A

* = Differential species. LS = leaf succulent, SS = stem succulent, DS = dwarf succulent, PS = perennial shrub; G = geophyte, A = annual.

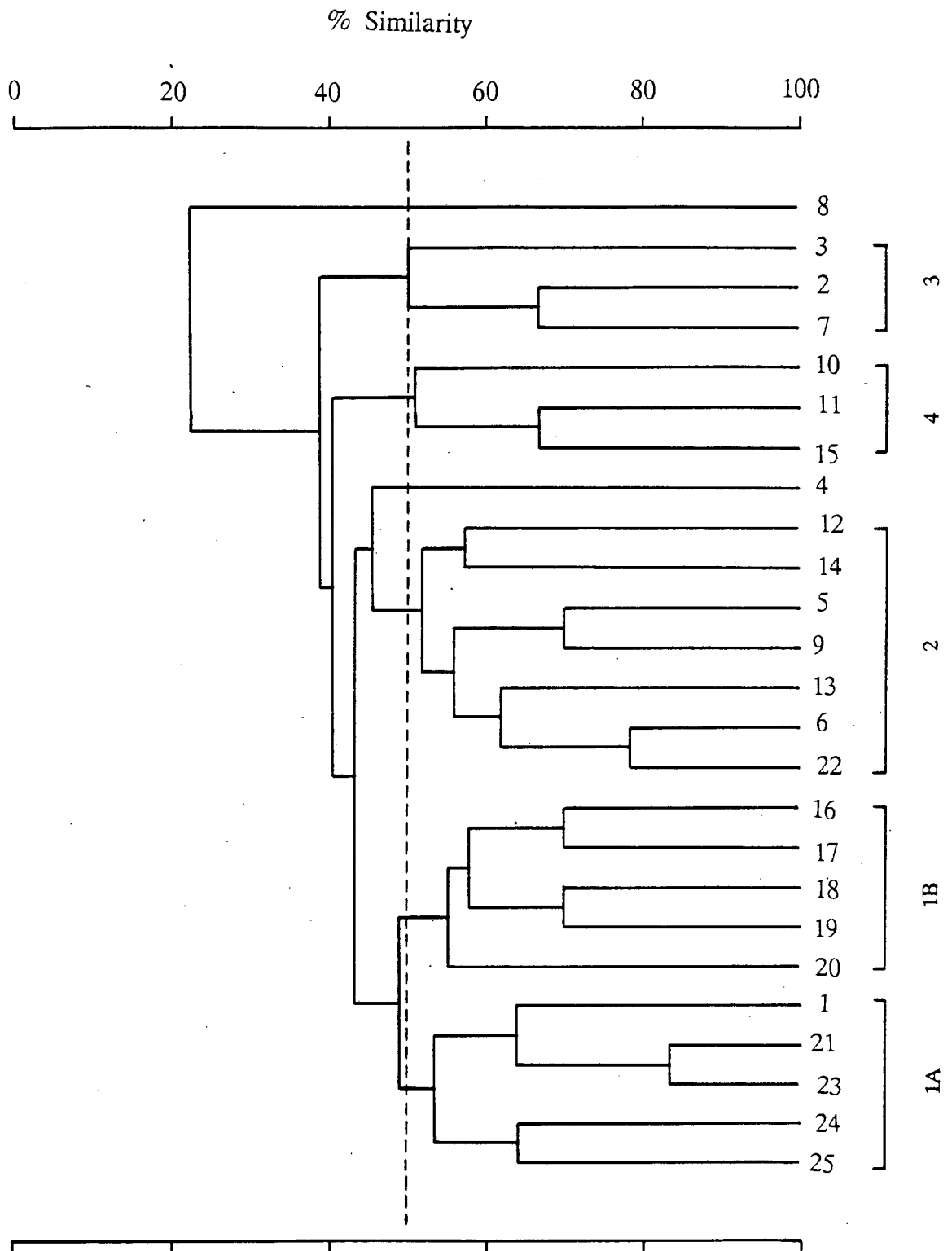


Figure 9: Dendrogram of percentage similarity (Bray-Curtis measure) of plant taxa among the 25 plots from near Ceres. Broken lines demarcate cutoff levels for groupings.

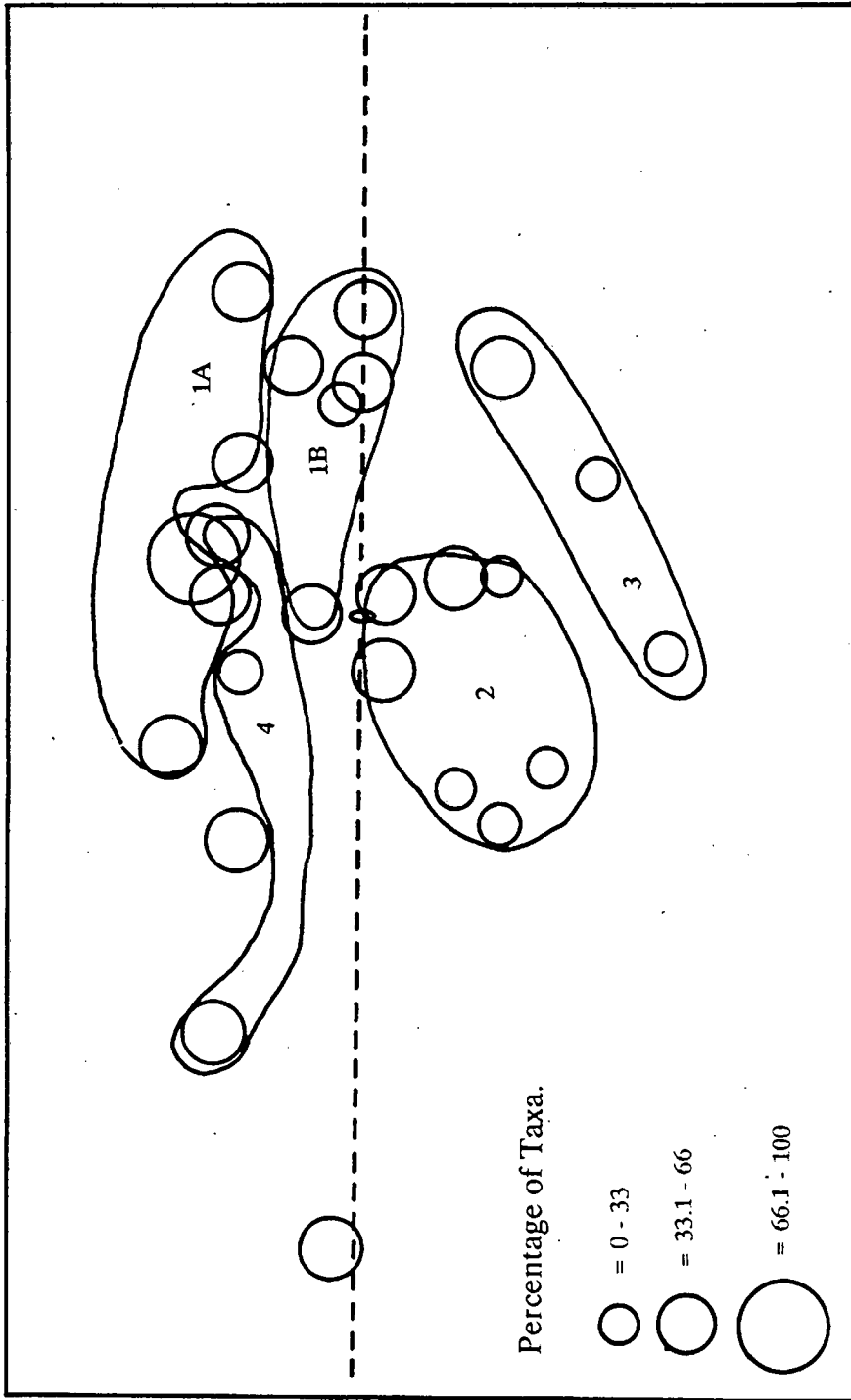


Figure 10: Ordination by MDS of the 25 plots from near Ceres. Circles denote the number of taxa in each plot with succulent growth-forms as a percentage of the total taxa in each plot.

DISCUSSION

Four communities with sub-communities were identified. These differed not only in the species present but also in the growth forms of those species present.

The area exhibited a gradual transition from a perennial, asteraceous shrub-dominated community with a rich mesemb component in the south, to a dwarf succulent mesemb community with a poor non-succulent component in the north. The transition from south to north is further complicated by strong influences of other veld types (especially Karroid Broken Veld; VT. 26). Species such as *Pteronia paniculata* Thunb., *Galenia chrystallina* (Eckl. & Zeyh) and *Chrysacoma ciliata* L. forming community 2, are indicative of such an influence, being species more commonly found in Karroid Broken Veld than in Succulent Karoo (Acocks, 1975). The northern half of the study area, as typified by communities 1a and 1b, resembles the rest of the Tanqua Karoo proper as described by Acocks (1975). The transition is further perturbed by physical and anthropogenic factors. All of the plots of community 1 (a & b) lie within farms producing mutton and wool. Some of these farms are only grazed seasonally due to a steady reduction in their annual sustainable yield over the years. All of the plots in communities 2 and 3 and those of the outliers fall within the boundaries of Inverdoorn which, being a 10 000 ha Merino, Dorper and Ille de France stud farm, has a different stocking practice from those to the north. The southern limit of the study area has deeper soils (pers. obs.) and receives more rain (both as direct precipitation due to the proximity of the surrounding mountains and indirectly as a result of runoff from these higher areas). The synergistic effects of higher rainfall (due to the orographic influence) and different land-use and management practices could be responsible for the lower degree of succulence of the southern area. However, the presence of disturbance indicators in all of the communities (i.e. *Cotula* sp. L., *Tylecodon wallichii* Harv., *Osteospermum* sp. D.C.), indicators of overgrazing (i.e. *Galenia africana* L. subsp. *africana* and the presence of some grazing intolerant species (i.e. *Indigofera* sp. L.) in the more "succulent" communities suggest that moisture availability is the more important factor separating the communities at a gross level and that the effects of disturbance are common to all communities.

WESTERN MOUNTAIN KAROO

STUDY AREA

The study area comprised 2500 ha of undulating land 20 km to the east of Sutherland on the farm "Merino", 32°20'S 20°53'E (Fig. 12). The area varies in height from 1350 m to 1400 m and is characterized by small terrace-like "vlaktes" surrounded by undulating hills. The area drains north and north - west into the Rietrivier that flows north north-west. The management of Merino farm

Figure 12: Map of Sutherland showing the location of the study plots.

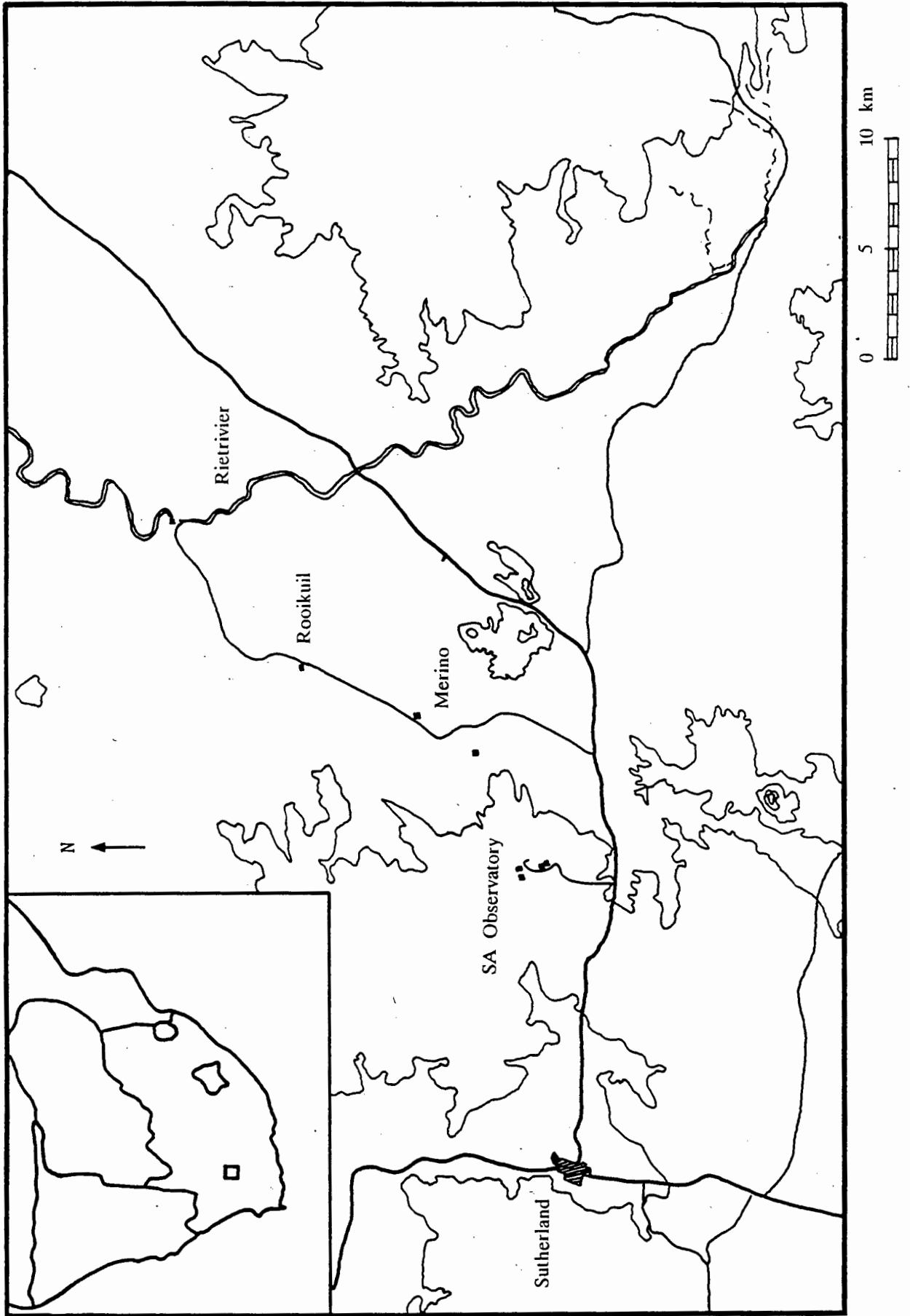


TABLE 3: A SPECIES/PLOT MATRIX SHOWING THE CLASSIFICATION OF NAMA-KAROO COMMUNITIES NEAR SUTHERLAND. VALUES REPRESENT FREQUENCIES OF OCCURRENCE IN THE SUB-PLOTS.

NUMBER OF QUADRATS TAXA	COMMUNITIES			OUTLIERS			GROWTH FORM
	1 16	2 14	3 4	(8) 2	(9) 2	(18) 2	
* <i>P. glomerata</i> L.f.	10					1	PS
<i>Lycium oxycarpum</i> Dun.	10	10			2		"
<i>Chrysocoma ciliata</i> L.	11	14	4	2	2		"
<i>Eriocephalus ericoides</i> (L.f.) Druce	16	14	4	2	2	2	"
<i>Pentzia incana</i> (Thunb.) Kuntze	14	13	4		2	2	"
* <i>Euryops</i> sp.	11	7	2		1	2	"
* <i>Pteronia glauca</i> Thunb.	2	13	4	1		2	"
* <i>Relhania</i> sp.	1	11	3	2		1	"
<i>Hermannia</i> sp.	2	4	1	1			"
* <i>Pterothrix spinescens</i> D.C.	9	5	1			1	"
<i>Salsola zeyheri</i> (Moq.) Schinz.	4	1	1				"
<i>Nylandtia spinosa</i> (L.) Dumort	2	5					"
<i>Eberlanzia</i> sp.	3	1					LS
* <i>Protasparagus burchelli</i> Oberm.	1	5					PS
<i>Stipagrostis</i> sp. Nees.	2	2					GR
<i>Enneapogon</i> sp. Beauv.	2	1					"
<i>Eragrostis lehmanniana</i> Nees.		2	3				"
<i>Drosanthemum lique</i> Schwant.		2	2		1		LS
<i>Themeda triandra</i> Forssk.		2			2	1	GR
* <i>Androcymbium</i> sp. Willd.		2					G
* <i>Leysera tenella</i> D.C.	3						A
<i>Bulbine</i> sp. Willd.	1			2	1		G
<i>E. esculenta</i> Marloth.	1						SS
<i>Indigofera</i> sp.	1						A
<i>Oxalis</i> sp.	1						G
<i>Hyobanche sanguinea</i> L.	1						G
<i>Cotula</i> sp.	1	1					A
* <i>Walafrida geniculata</i> (L.f.) Rolfe		2					PS
* <i>E. mauritanica</i> L.		2					SS
<i>Leipoldtia</i> sp.		1					LS
<i>Felicia muricata</i> Thunb.		1					A
<i>Massonia depressa</i> Houtt.			1				G
<i>Dimorphotheca</i> sp.			1				A
"Fan geophyte"					1		G
<i>Euphorbia braunsii</i> N.E. Br.						1	SS

* = Differential species (see text); PS = perennial shrub, LS = leaf succulent, SS = stem succulent, G = geophyte, GR = grass, A = annual.

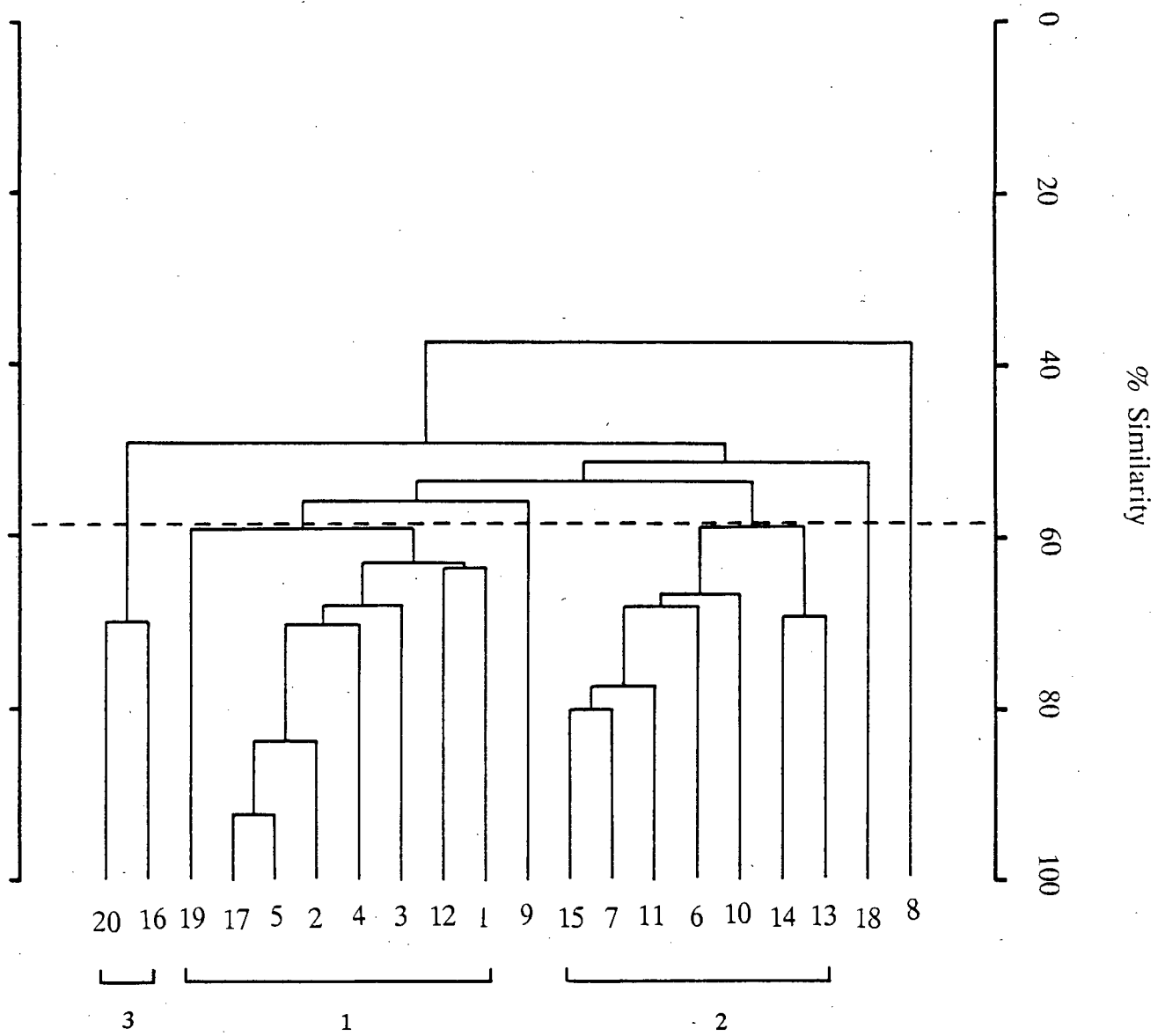
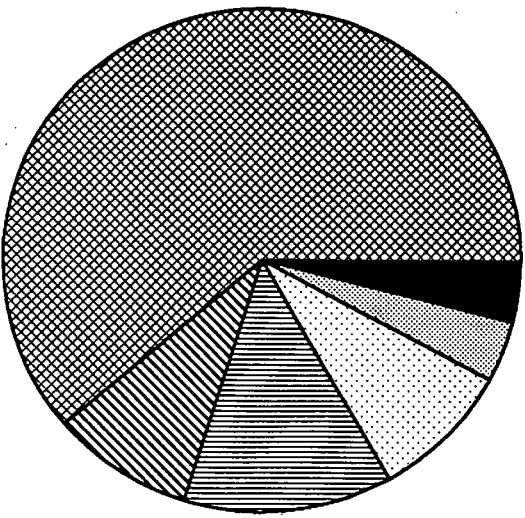
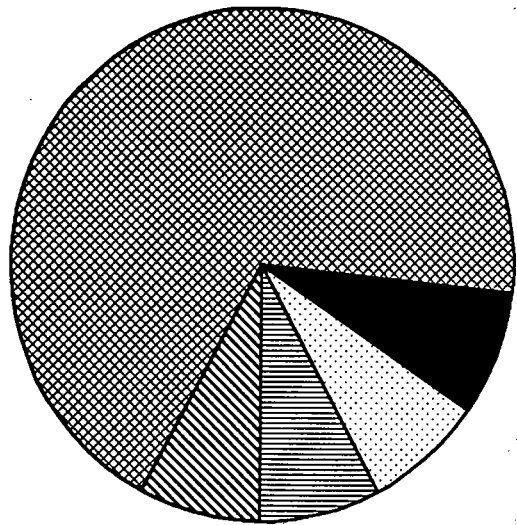


Figure 13: Dendrogram of percentage similarity (Bray-Curtis measure) of plant taxa among the 20 plots from near Sutherland. Broken lines demarcate cutoff levels for groupings.

1



3



2

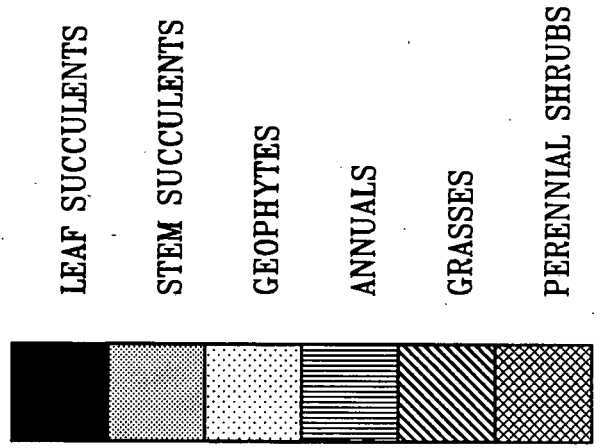
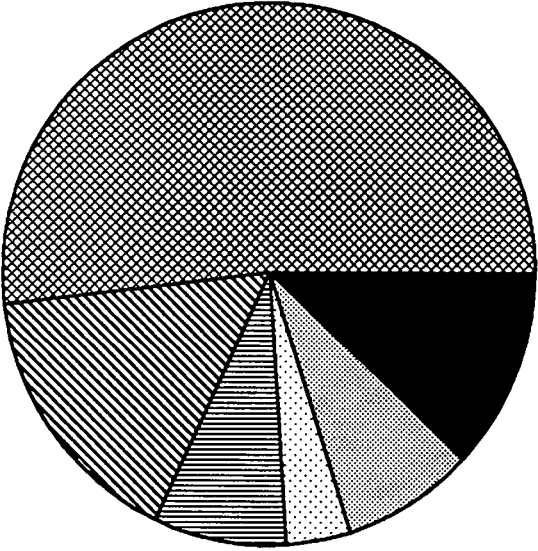


Figure 14: Growth form spectra for three vegetation communities near Sutherland.

comprised a large camp with a mixed stocking regime of Springbok and Merinos and several smaller camps on the lower lying regions containing Merinos only.

RESULTS

Analysis of the species composition of the plots within the study area (Fig. 13) allowed the delineation of 3 plant communities (groups) at the 59% level of group average similarity.

Table 3 lists the species recorded at all of the sub-plots grouped according to the classification of the communities. Companion species were *Eriocephalus ericoides* (L.f.) Druce., *Chrysocoma ciliata* L., *Pentzia incana* (Thunb.) Kuntze., *Pteronia glauca* Thunb., and conform to the species listed as being of general occurrence in Western Mountain Karoo by Acocks (1975). Vague taxa were *Euryops* sp. Cass., *Lycium oxycarpum* Dun., *Pterothrix spinescens* D.C., *Relhania* sp. (L'Herit) and *Hermannia* sp. L. The differential taxa are shown in Table 3. The differential taxa of community 1 were *Pteronia glomerata* L.F. and *Leysera tenella* D.C. The community occupied the lower regions around the main farm and was typified by annuals and species associated with Western Mountain Karoo (Acocks, 1975).

Community 2 occupied the higher more broken ground and was typified by species often associated with Central Upper Karoo (VT. 27; i.e. *Pteronia glauca*, Thunb. and *Nylandtia spinosa* (L.) Dumort), which is to be expected as the whole area is transitional between Western Mountain Karoo and Central Upper Karoo (Acocks, 1975). Community 2 was typified by hardy species and appears to be an altitudinal transition between the two veld types that also contains elements of Mountain Renosterveld (VT. 43; i.e. *Relhania* sp. (L'Herit), *Drosanthemum lique* Schwant.) and may be as a result of greater exposure to frost and sub-zero temperatures. Only two species of leaf succulents occurred in the area. This is most likely due to the high incidence of frost (184 days p.a.; Venter *et. al.*, 1986). *Eberlanzia* sp. L. Bol. occurred in community 1 and a lower sheltered area of community 2. *Drosanthemum lique* Schwant. occurred in communities 2 and 3 but within the canopy of other bushes such as *Eriocephalus ericoides* (L.F.) Druce., thus receiving shelter from the frost. The growth form spectra of the 3 communities (Fig. 14) indicate the grassier nature of the upland area (community 2) and the increased annual component of the low lying areas around the farm (community 1).

DISCUSSION

The use of classification by group average sorting of a species presence or absence data matrix allowed the arbitrary identification of 3 communities that differed in the climatic affinities of their taxa. The Western Mountain Karoo falls in the even rainfall area and as such is situated on the intergrade between the two major karroid biomes. The area exhibits influences from several veld types (*sensu* Acocks, 1975) but generally, the presence of perennial grasses and the dominance of non-succulent chamaephytes indicates affinities with Nama-Karoo vegetation and a strong Central Upper Karoo influence (especially in the higher areas). Frost is an important limitation on the distribution of

succulent species, and those found in the study area were confined to north facing slopes or lower ground and generally were absent from high flat land.

THE GREAT KAROO

STUDY AREA

The study area comprised the farm "Bokvei", 32°25'S 23°21'E, 80km east of Beaufort West and 75km west of Aberdeen on the boundary between the western and eastern Cape Province (Fig. 15). The area covered by the study was 5400 ha of flat to undulating Great Karoo, a variation of Karroid Broken Veld (veld type 26a; Acocks, 1975). High ground of up to 1300 m (Winterberge, Langeberg and Oorlogspoort Berge) lies at the northern edge of the flat land (950 m) and water drains from these "mountains" across the flats by means of seasonal and subterranean drainage channels into the Juriesfontein se Rivier. This river flows south east beneath dry, sandy pans, into the Kariegarivier. The farm stocks predominantly Angora goats but also has Merino sheep and approximately 300 Springbok.

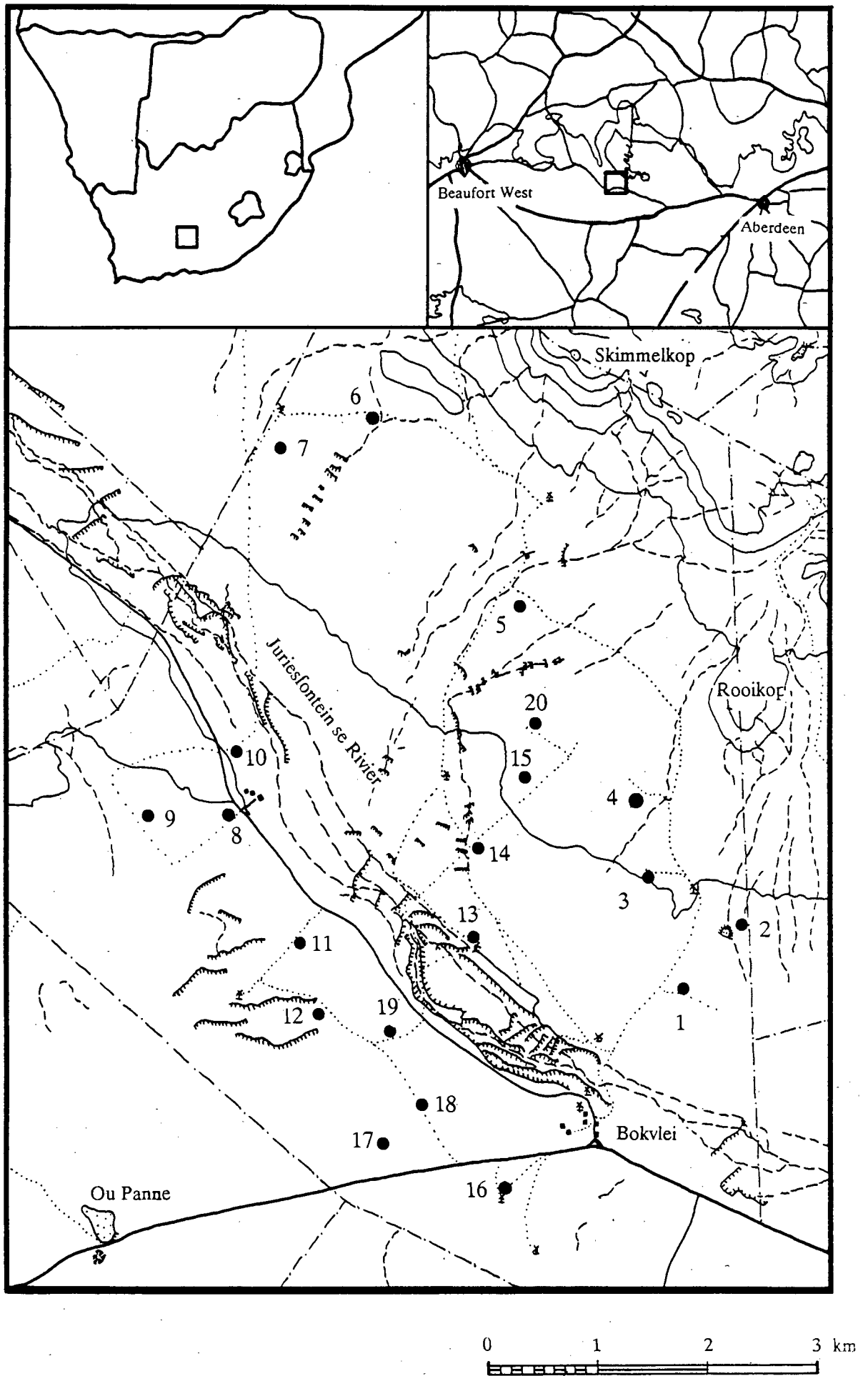
RESULTS

Analysis of the species composition of the plots within the study area allowed the delineation of 5 plant communities (groups) at the 48% level of group average similarity (See Fig. 16). Community 1 was further split into two sub-communities (1a & 1b) at the 52% level of similarity.

Table 4 lists the species recorded at all of the plots grouped according to the classification of the communities. The general area was typified by non-succulent taxa with a few widespread succulent taxa. Companion species were the widespread perennial shrubs *Pentzia incana* (Thunb.) Kuntze, *Eriocephalus spinescens* Burch. and *Hermannia desertorium* Eckl & Zeyh., the succulent shrub *Eberlanzia* sp. L. Bol., and the two thorny shrubs *Lycium cinerum* (Thunb.) and *Protoasparagus burchelli* Oberm. Vague species recorded were *Monechma incanum* (Nees) C.B. Cl., *Felicia muricata* Thunb., *Pteronia glauca* Thunb., *P. viscosa* Thunb. and the perennial grass *Stipagrostis* sp. Nees.

Community 1 had several differential taxa such as the eastern Cape species *Sarcocaulon cambdeboensis* Moffett and the disturbance indicator *Euphorbia ferox* Marloth. A highly selective taxon of community 1a was the halophyte *Zygophyllum gilfillani* N.E. Br. Community 1b was characterized by the occurrence of *Protoasparagus striatus* Oberm. Community 1b had a number of taxa indicative of saline, alkaline and/or disturbed soils such as *Psilocaulon* sp. N. Br., *Zygophyllum retrofractum* Thunb., *Atriplex lindleyi* Moq. and *Galenia africana* L. The communities 1a and 1b had several species commonly associated with Central Lower Karoo (VT. 30; i.e. *Zygophyllum gilfillani*, *Pentzia incana*, *Eriocephalus spinescens*). Community 2 resembled communities 1a and 1b but differed by lacking stem

Figure 15: Map of Beaufort West showing the location of the study plots.



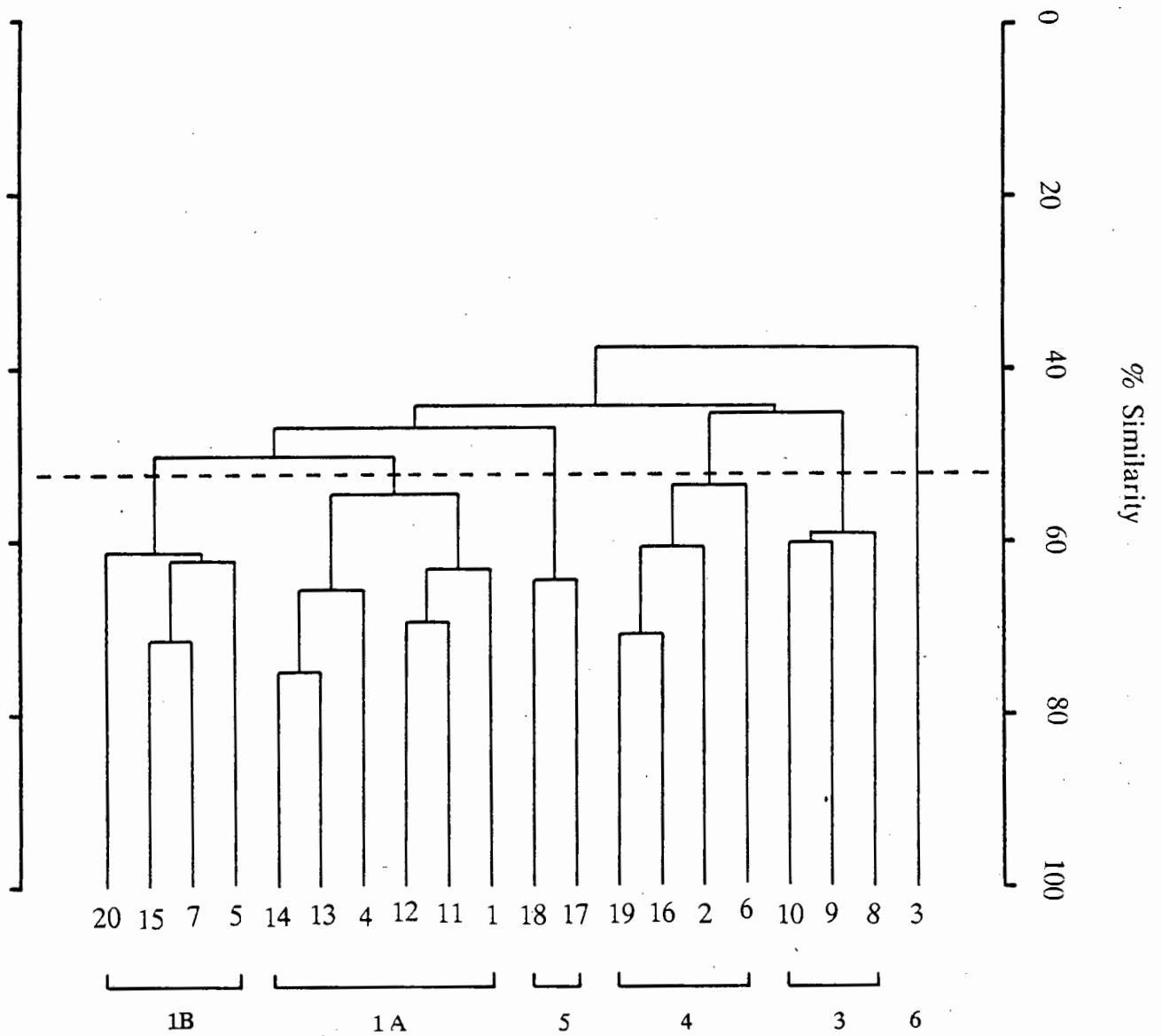


Figure 16: Dendrogram of percentage similarity (Bray-Curtis measure) of plant taxa among the 20 plots from near Beaufort West. Broken lines demarcate cutoff levels for groupings.

TABLE 4: A SPECIES/PLOT MATRIX SHOWING THE CLASSIFICATION OF NAMA-KAROO COMMUNITIES NEAR BEAUFORT WEST. VALUES REPRESENT FREQUENCIES OF OCCURRENCE IN THE SUB-PLOTS.

NUMBER OF QUADRATS TAXA	COMMUNITIES						GROWTH FORM
	1A 12	1B 8	3 6	4 8	5 4	6 2	
<i>Salsola rabieana</i> Verdoorn	3	2				1	PS
* <i>Protasparagus striatus</i> Oberm.	1	3				1	PS
<i>Sarcocaulon camdeboensis</i> Moffett	2	1			1	2	SS
<i>Euphorbia ferox</i> Marloth	3	3			2	1	SS
* <i>Walafrida geniculata</i> (L.f.) Rolfe.	3	1			1		PS
* <i>Aridaria</i> sp. N.E. Br.	8	2		1			LS
<i>Pteronia glauca</i> Thunb.	4	6		2	2		PS
<i>Felicia muricata</i> Thunb.	9	7		6	1	1	A
<i>Pentzia incana</i> (Thunb.) Kuntze.	11	8	6	8	4	2	PS
<i>Hermannia desertorum</i> Eckl. & Zeyh.	5	3	1	5	3	1	"
<i>Protasparagus burchelli</i> Oberm.	6	6	3	3	1	2	"
<i>Eriocephalus spinescens</i> Burch.	9	7	2	4	4	2	"
<i>Eberlanzia</i> sp.	7	7	6	8	4	1	LS
<i>Lycium cinerum</i> Thunb.	9	3	6	6	4		PS
<i>Pteronia viscosa</i> Thunb.	6	3	2	1			"
<i>Monechma incanum</i> (Nees.) C.B.Cl.		5	6	4	3		"
<i>Zygophyllum retrofractum</i> Thunb.		2	1	2			PS
<i>Galenia chrystallina</i> (Eckl. & Zeyh.)		1		4		1	PS
* <i>Aptosimum spinescens</i> (Thunb.) Weber				6			PS
* <i>Osteospermum sinuatum</i> (D.C.)				5			A
<i>Pentzia punctata</i> Harv.	4			2	1	1	PS
<i>Stipagrostis</i> sp.	3		1	2	1	1	GR
<i>Drosanthemum lique</i> Schwant.	1		1	1		1	LS
<i>Senecio radicans</i> (L.f.) Sch. Bip.	2		2	1			LS
* <i>Zygophyllum gilfillani</i> N.E. Br.	8		4				SS
<i>Rhigozum obovatum</i> Burch.	1		1				PS
* <i>Asclepias</i> sp.			2				"
<i>Plinthus karoocicus</i> Verdoorn	2				4		"
* <i>Heliochrysum penzioides</i> Less.	2						"
<i>Morea tortilis</i> Goldbl.	1						G
<i>Leipoldtia</i> sp.	1						LS
<i>Indigofera</i> sp.	1						A
<i>Lachenalia</i> sp.	1						G
<i>Atriplex lindleyi</i> Moq.		1					A
<i>Galenia africana</i> L.		1					PS
<i>G. prostrata fruticosa</i> Eckl. & Zeyh.		1					A
* <i>Delosperma</i> sp.		2					LS
<i>Psilocaulon</i> sp.		2		1			SS
<i>Chrysocoma ciliata</i> L.		1		2			PS
<i>Tetragonia fruticosa</i> L.				1			PS
<i>Aloe arenicola</i> Reynolds				1			LS
<i>Rumex</i> sp.				1			A
<i>Felicia ovata</i> (Thunb.) Compt.				1			A
<i>Garruleum bipinnatum</i> (Thunb.) Less.				1			PS
<i>Euphorbia mauritanica</i> L.				1		1	SS
<i>Morea polystachya</i> (Thunb.) Ker-Gawl.				1	1	1	G
<i>Hermannia spinosa</i> E. Mey ex. Harv.				1	2		PS
<i>Selago</i> sp.					1		A
<i>Cucumis</i> sp.					1		A
<i>Arctotheca calendula</i> (L.) Levyns		1				1	A
* <i>Eragrostis</i> sp.						2	GR

* = Differential species; Ps = perennial shrub, LS = leaf succulent, SS = stem succulent, G = geophyte, A = annual, GR = grass.

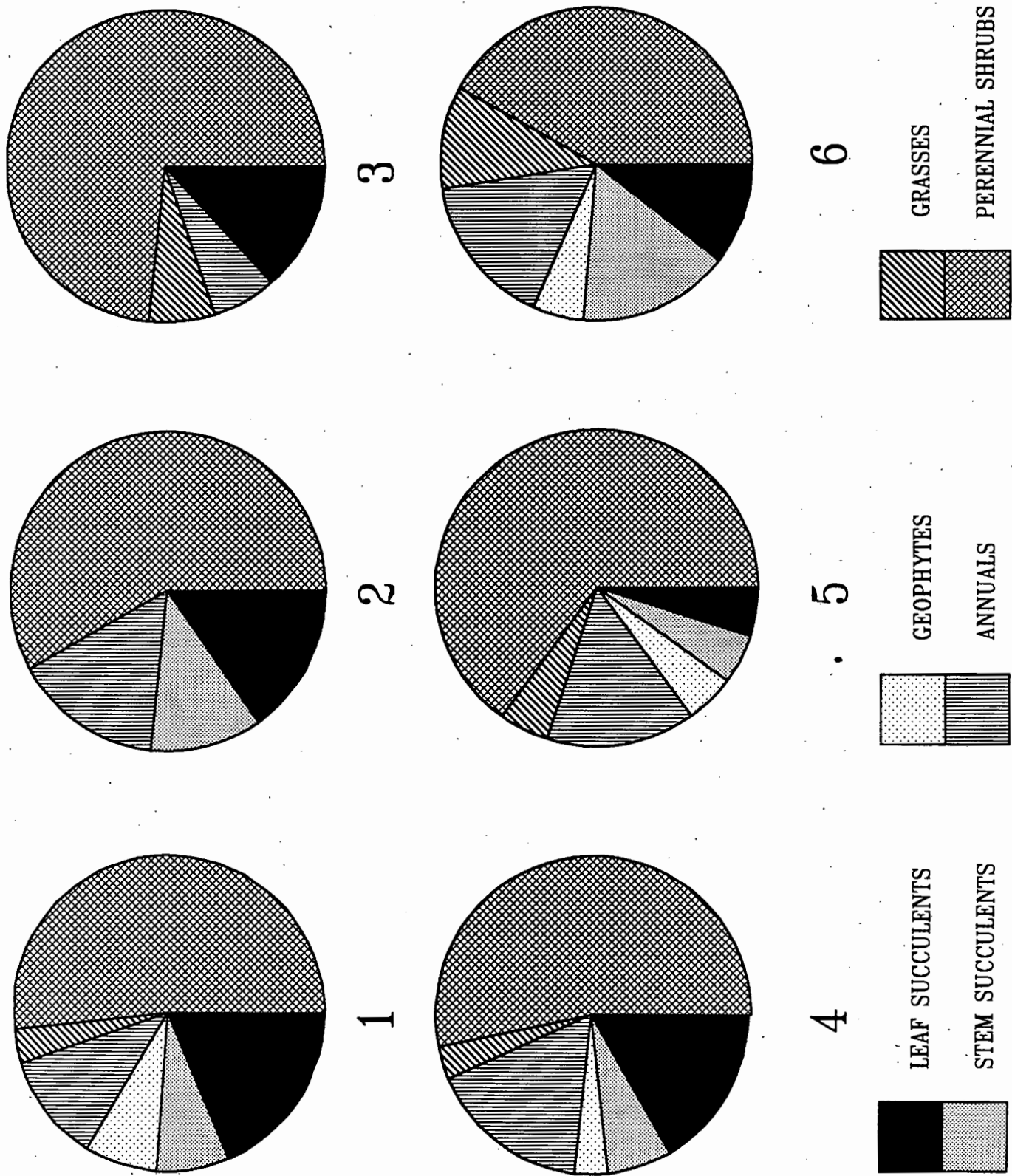


Figure 17: Growth form spectra of six vegetation communities near Beaufort West.

succulents, annuals and generally had a lower species diversity. Community 3 differed markedly from the others and contained several species of annuals and perennial shrubs considered to be invasive in Karroid Broken Veld (i.e. *Osteospermum sinuatum* (D.C.), *Chrysocoma ciliata* L. and *Galenia chrystallina* (Eckyl. & Zeyh.); Acocks, 1975).

Community 4 was distinct, containing many exclusive species. Many of these were either annuals or plants considered to be indicative of disturbance (i.e. *Morea polystachya*, *Galenia chrystallina*) and exhibited strong affinities with Karroid Broken Veld (VT. 26a).

The growth form profiles of the 6 communities (Fig. 17) illustrate the dominance of perennial shrubs in all communities. Grasses were most prevalent in community 6 that also contained a wide variety of other growth forms. Communities 2 and 3 had the poorest variety of growth forms with annuals in 2 being replaced by grasses in 3.

DISCUSSION

The use of classification by group average sorting of a species presence or absence data matrix allowed the arbitrary identification of 6 communities. The area had a wide variety of species, and communities in the area could be distinguished by the occurrence of species normally associated with factors such as soil salinity (i.e. Halophytes such as *Zygophyllum* spp. and *Psilocaulon* sp.) and disturbance (i.e. annuals and stem succulents). The area exhibits transitional influences of both Karroid Broken Veld (VT. 26a; community 4) and Central Lower Karoo (VT. 30; community 1a & b). This transition is perturbed by effects of grazing and other forms of disturbance. Grass was generally rare in all communities except community 5. Succulents were poorly represented in terms of species. One species (*Eberlanzia* sp.) was widespread throughout the area and throughout the communities. Community 1b had two exclusive succulent taxa that dominated an area of high disturbance and had a generally higher incidence of species indicative of over grazing (i.e. *Galenia* spp. and *Chrysacoma ciliata*).

GENERAL CONCLUSIONS

The disadvantages of such an analysis is that a graded series of species communities may be forced into discrete classes. As plots were chosen randomly, in terms of vegetation, they may not be well placed in an area or phytocoenose that best represents the vegetation (Werger, 1974). The delineation of communities at the Touwsrivier site, as superimposed on the map of the study area, are identified more for convenience than as a definitive study. The delineation of communities was only represented for the Touwsrivier site to illustrate the coincidence of the communities with the farm boundaries. The communities are enclosed by contours of inter-group similarity and are likely to include areas that would perturb the analysis if a larger number of plots had been sampled. No soil characteristics were measured and therefore conclusions as to the edaphic factors that may influence

vegetation at the sites can not be made. The purpose of this study was to describe vegetation communities in an area utilized by the Karoo Korhaan. Responses of the Karoo Korhaan to the communities will be discussed in chapter 3.

In general, species commonly associated with the veld types of the respective sites were identified (Acocks, 1975). Delineated communities tended to differ on the basis of the synergic effects of disturbance and the influences of neighbouring veld types. The known encroachment of Succulent Karoo and Arid Karoo forms into Western Mountain Karoo areas is illustrated by vicariant populations in the Ceres Karoo and Sutherland sites. It may be that the Ceres site was historically less succulent and that the presence of species normally associated with other veld types is indicative of remnant populations rather than an external influence. Only further, more detailed study could confirm this and elucidate the historical processes that have occurred in these obviously altered landscapes. The two Succulent Karoo sites had communities separable on the basis of their degrees of succulence but were generally dominated by succulent shrubs. The two Nama-Karoo sites were dominated by a wide range of asteraceous and other shrubs. Succulent shrubs were generally rare (especially at the Sutherland site where the high incidence of frost militates against succulent species' encroachment). At the Beaufort West/Aberdeen site succulents were common but were limited to a few species that were typically resilient to frost (i.e. *Euphorbia* spp., *Aloe* spp. and *Eberlanzia* sp.). Grasses were rarer than expected throughout the four sites but were generally more abundant at the two Nama-Karoo sites than at the two Succulent Karoo sites. These general findings concur with the criteria used to separate the two biomes (Rutherford & Westfall, 1986). However, results also indicate that local heterogeneity is much greater than could be inferred from broad-scale community classifications.

CHAPTER THREE

**PHYSIOGNOMIC CLASSIFICATION OF KAROO
KORHAAN HABITATS IN THE SUCCULENT AND
NAMA-KAROO BIOMES.**

INTRODUCTION

In the Karoo biome (*sensu* Huntley, 1984), the classification of vegetation by growth-form has been considered by several authors to be of greater heuristic value than the use of life-form or floristic characterization (Moll *et. al.*, 1976; Cowling, 1986; Hoffman & Cowling, 1987). The climatic regime of the Karoo biome not only results in low rainfall but also rainfall that is highly unpredictable. The Karoo flora has a variety of functional responses to this unpredictability, including drought evasion, avoidance and drought tolerance (Noy-Meir, 1973; Werger, 1978). Because rainfall is a primary driving force in such ecosystems (Noy-Meir, 1973; Werger, 1978; Rutherford & Westfall, 1986) the relative abundance of tolerators, avoiders and evaders varies from place to place in response to the particular local climatic regime (Noy-Meir, 1973; Hoffman & Cowling, 1987). The physiognomy of the vegetation of a particular site can therefore be considered a good indicator of the local environment and thus demonstrate the biotic potential of that site (Moll *et. al.*, 1977).

Chapter 2 identified major communities at the study sites in terms of their plant species composition. The study also described the communities in terms of growth-forms and identified those species and growth-form characters that were characteristic of the delineated communities. In this study the seasonal changes in growth-form dominance and cover at four sites were classified in order to characterize the structure and seasonality of Karoo Korhaan habitats and to compare the physical characteristics of the four sites over the four seasons.

STUDY AREAS

Four areas of karroid vegetation within the species' range were chosen as study sites that conformed to the known habitat requirements of the species (Winterbottom, 1966). Two of these sites were in the Nama-Karoo and two in the Succulent Karoo (*sensu* Rutherford & Westfall, 1986). For detailed description of the study sites see Chapter 2.

METHODS

Surveys of the physiognomic characteristics of the vegetation at the four study sites within the species' distribution were carried out at three monthly intervals between July 1986 and July 1987. A vegetation survey form was designed in order to standardize the information taken within the four sites (Fig. 2). The growth-form categories used followed Cowling (1986), with certain modifications. No distinction was made between C3 and C4 grasses because of the difficulty in reliably separating the two in the field. No distinction was made between shrubs as to their leaf shedding nature, in light of the controversy surrounding the deciduousness of perennial shrubs (Werger, 1978; Cowling, 1986; Hoffman & Cowling, 1987). Forms were completed for two 5x5m sub-plots within each of the 85 plots and the data combined for the analysis. The floristic data were analysed separately as a description of the phytosociology of each site (Chapter 2). This was done because some species have functionally

different growth-forms in different areas (Hoffman & Cowling, 1987). Data matrices were constructed for each season with nineteen variables, including the total percentage cover of vegetation, the percentage cover of each growth-form, the number of species of each growth-form, the percentage cover of spinescent forms (leaf and stem spinescence combined for the analyses), percentage cover of dead material and an index of both flowering and fruiting activity (percentage of individuals in flower and/or with fruit). The data matrix was root-root transformed and subjected to polythetic group average sorting using the Czezanowski coefficient as a measure of similarity (Bray & Curtis, 1957; Field *et. al.*, 1982). Information statistics (I-tests) were calculated in order to assess which variables differed most between one site and another. The information statistics were calculated for the sites and not the groups as defined by the classification and are presented in tabular form in Appendix 1. The procedure was conducted for each of the four seasons.

The height profile of vegetation at each of the sub-plots was measured along a 10m transect at 0.1m intervals. The presence and abundance (group size) of Karoo Korhaans in the vicinity of the plots was investigated by the use of a taped Karoo Korhaan duet that, when played, elicited a territorial response from individuals in the immediate vicinity of the plot (see Chapter 6).

Graphs of the monthly rainfall for the study period, at each of the sites were constructed using rainfall data taken from the monthly reports of the Weather Bureau of the Department of Environmental Affairs. The term "summer rainfall" is used (*sensu* Werger, 1978; Rutherford & Westfall, 1986) to define areas that receive precipitation from thunder cell activity from the north-east during the summer and autumn months in contrast to "winter rainfall" areas that receive rainfall most commonly from cyclonic fronts in the winter months (Schumann, 1949).

RESULTS

SPRING

Sixteen groups were identified at the arbitrary level of 80% group average similarity (Fig. 18). The two Succulent Karoo sites were grouped, at the 75% level, into two groups, One of which contained all but two of the Touwsrivier plots and all but nine of the Ceres Karoo plots. This group was further split into two groups at the 80% level that contained either Touwsrivier or Ceres Karoo plots. The classification shows the general similarity of the two succulent sites. On the basis of the information statistics (see Tables A1 - A6; Appendix 1), Touwsrivier plots were distinguishable from other plots by having a greater number and percentage cover of annuals, with "dead material" and perennial grass being scarce. The Touwsrivier plots were distinguishable from the Ceres Karoo plots in having a lower total cover, with more annuals (both cover and variety), lower cover of spinescent taxa (especially shrubs such as *Eberlanzia* sp. L. Bol.), much less dead material and in being generally less dominated by succulent taxa. Both Touwsrivier and the Ceres Karoo had an appreciably greater variety and cover of succulent taxa (both leaf and stem succulents) than either of the Nama-Karoo sites. Six of

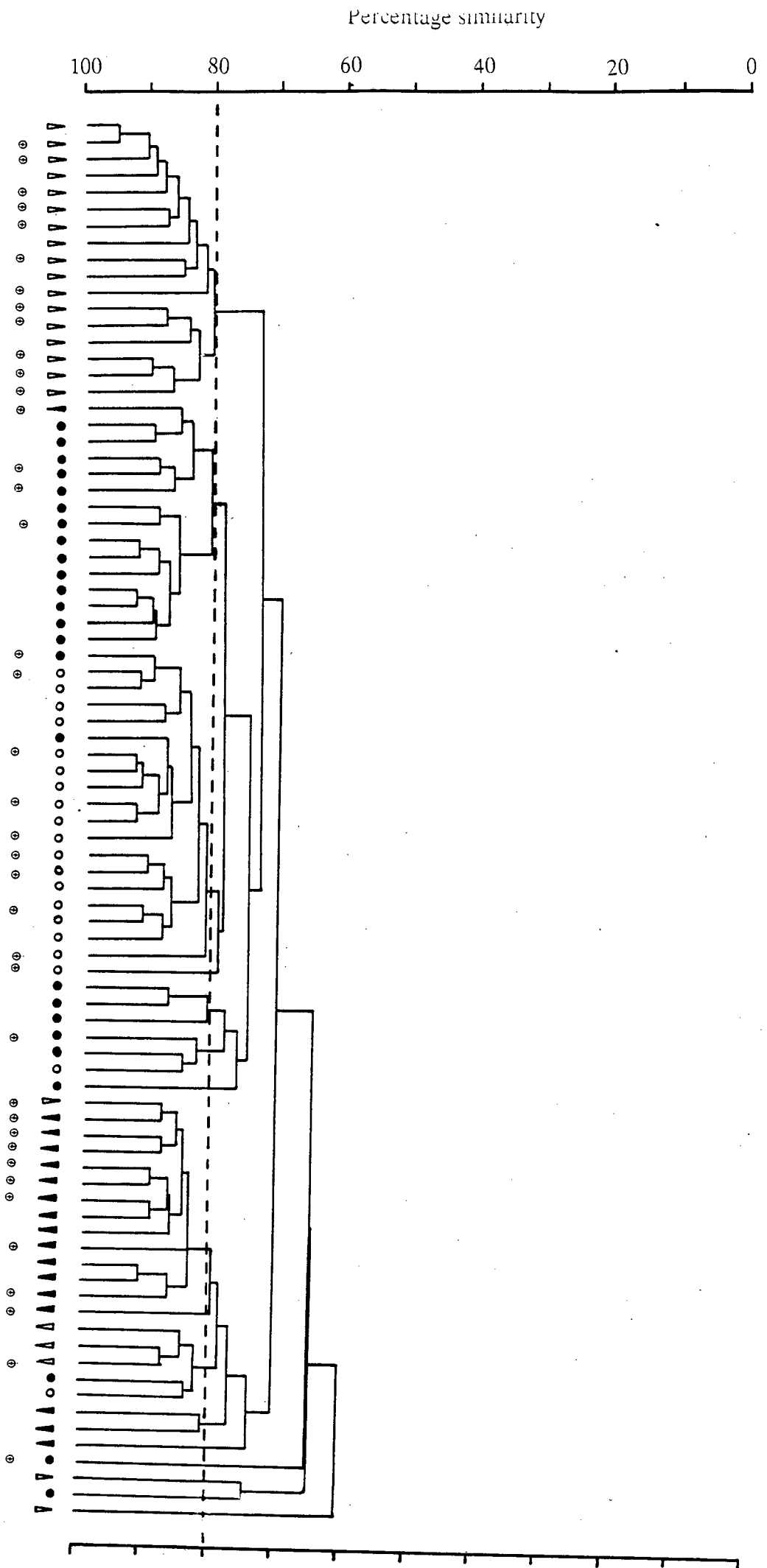


Figure 18: Dendrogram of percentage similarity (Bray-Curtis measure) of growth-forms along 85 sample plots analysed from Ceres (●), Touwsrivier (○), Sutherland (▼) and Beaufort West (▲) in spring. Presence of Karoo Korhaans at the plots is indicated by ⊕.

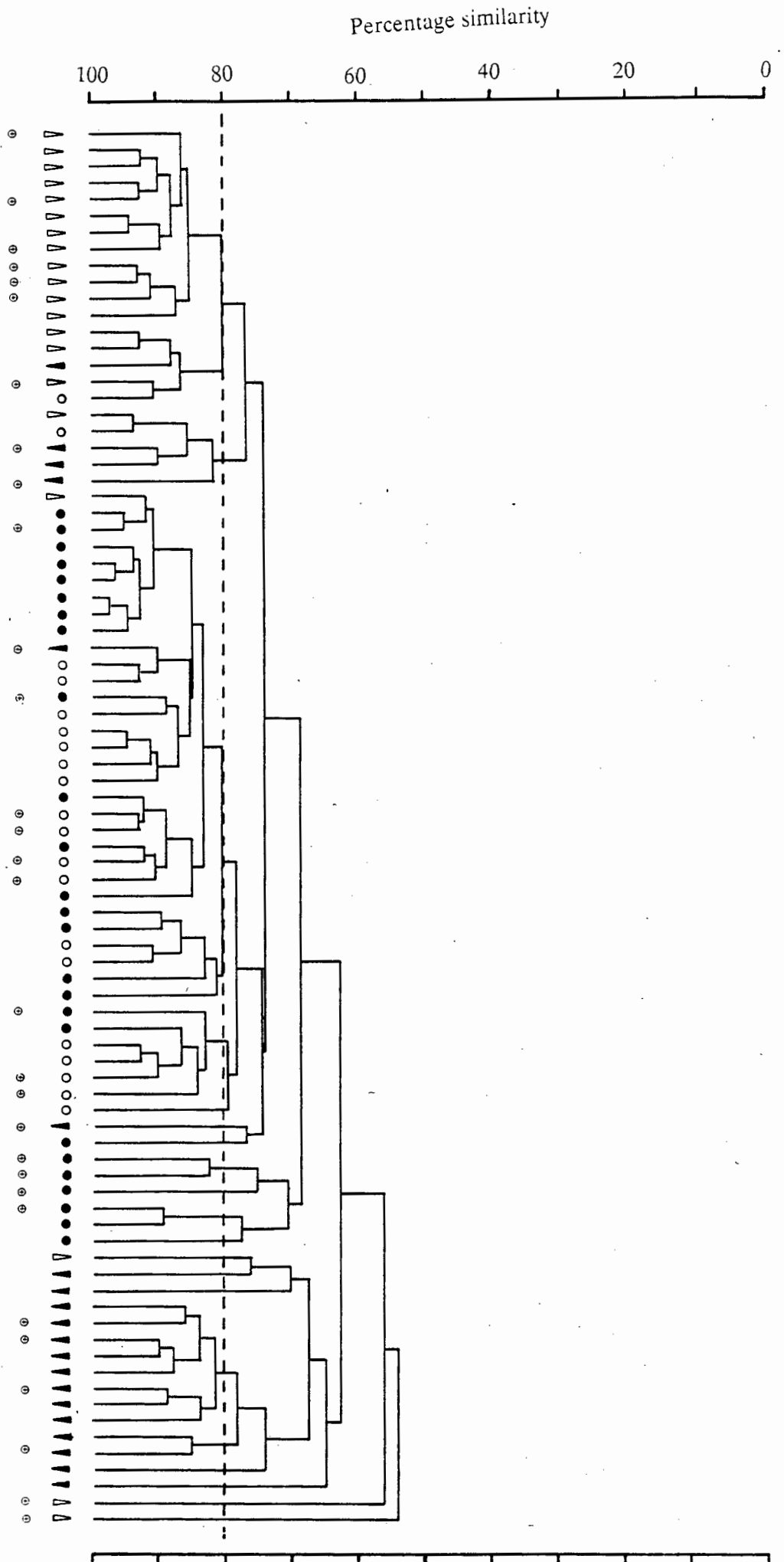


Figure 19: Dendrogram of percentage similarity (Bray-Curtis measure) of growth-forms along 85 sample plots analysed from Ceres (●), Touwsriver (○), Sutherland (▼) and Beaufort West (△) in summer. Presence of Karoo Korhaans at the plots is indicated by ⊙.

the Ceres Karoo plots were placed in groups distinct from the majority of the Ceres Karoo plots. These plots were characterized as having a very low total cover with a large annual component in an area of sandy soil, with large bare "pans" on the farm "Droogte laagte". All but one of the Sutherland plots were grouped at the 74% level, with 12 being grouped at the 80% level (group 8). The Sutherland plots had the lowest mean total percentage cover (mean = $30 \pm 6.9\%$, S.D., N = 20) the greater proportion of which was made up of perennial shrubs (mean = $25.8 \pm 8.45\%$, S.D., N = 20), a strong grass component few succulents and a high cover of dead material. All but three of the Beaufort West plots clustered together, at the 80% level (group 1). The site was characterized by having a high total percentage cover (mean = $42 \pm 7.83\%$, S.D., N = 20), made up of a strong perennial grass component and a wide variety of perennial and spiny shrubs but small succulent and annual components.

SUMMER

The classification of the summer data yielded 20 groups at the level of 80% group average similarity (Fig. 19). The two Succulent Karoo sites were virtually indistinguishable in terms of the classification, except for 6 Ceres Karoo plots grouped at the 71% level but split into 4 groups at the 80% level, and a further 2 grouped with Touwsrivier plots at the 80% level. Most of the Sutherland plots fell into a single group. Most Sutherland outliers were grouped with Succulent Karoo plots, but a few were grouped with plots from Beaufort West. All but 5 of the Beaufort West plots were grouped together.

The information statistics (Appendix 1) showed that the relative levels of spinescence, succulence and number of species did not differ between spring and summer. All sites had a generally low cover of annuals. The cover of dead material increased at Touwsrivier. The Sutherland plots that were grouped with Beaufort West plots were grassier than others. Touwsrivier and the Ceres Karoo resembled each other in total cover and the lack of perennial grasses but differed in the proportion of the cover made up of succulent taxa. Plots from the Ceres Karoo, grouped with those from Touwsrivier resembled the Touwsrivier plots in having low total cover made up of spiny shrubs and dead material. Heterogeneity within most sites in summer was greater due to the death of annuals in Succulent Karoo and the growth of perennial grasses in the Nama-Karoo. The greater level of similarity between the two succulent sites indicates that they differ most in their ephemeral components that are not active during the summer period.

AUTUMN

The autumn classification yielded 13 groups at the 80% level (Fig. 20). The classification separated the two Succulent Karoo sites. All but 2 of the Sutherland plots were grouped together, with 1 plot from Beaufort West, at the 74% level but were split between 5 groups at the 80% level. Only 2 of the Beaufort West plots fell outside the single grouping at 80%. Touwsrivier and the Ceres Karoo differed most markedly in the cover of geophytes, percentage cover of leaf succulents and perennial

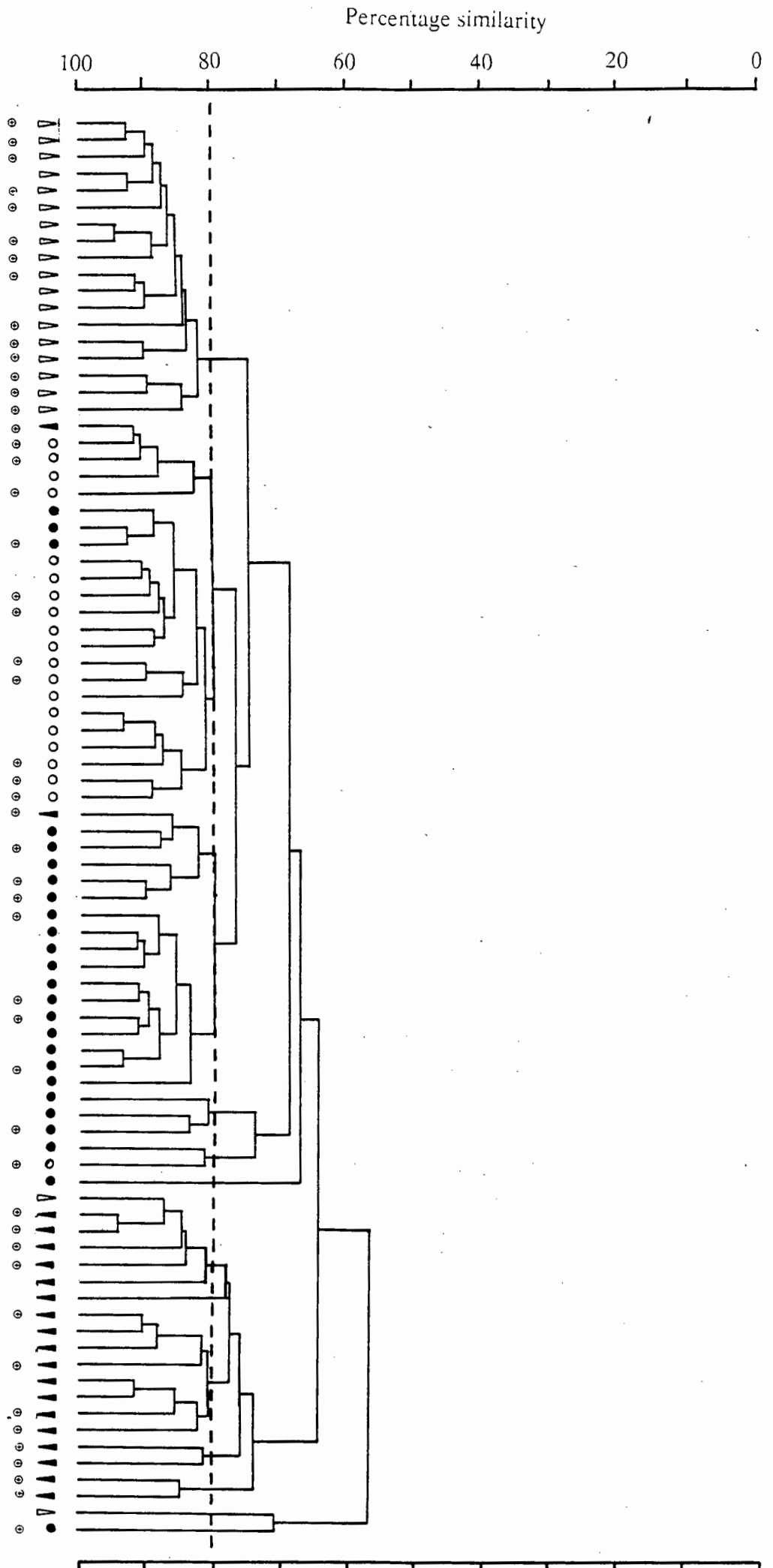


Figure 20: Dendrogram of percentage similarity (Bray-Curtis measure) of growth-forms along 85 sample plots analysed from Ceres (●), Touwsrivier (○), Sutherland (▼) and Beaufort West (▲) in autumn. Presence of Karoo Korhans at the plots is indicated by ⊙.



Figure 21: Dendrogram of percentage similarity (Bray-Curtis measure) of growth-forms along 85 sample plots analysed from Ceres (●), Touwsvier (○), Sutherland (▼) and Beaufort West (△) in winter. Presence of Karoo Korhans at the plots is indicated by ⊙.

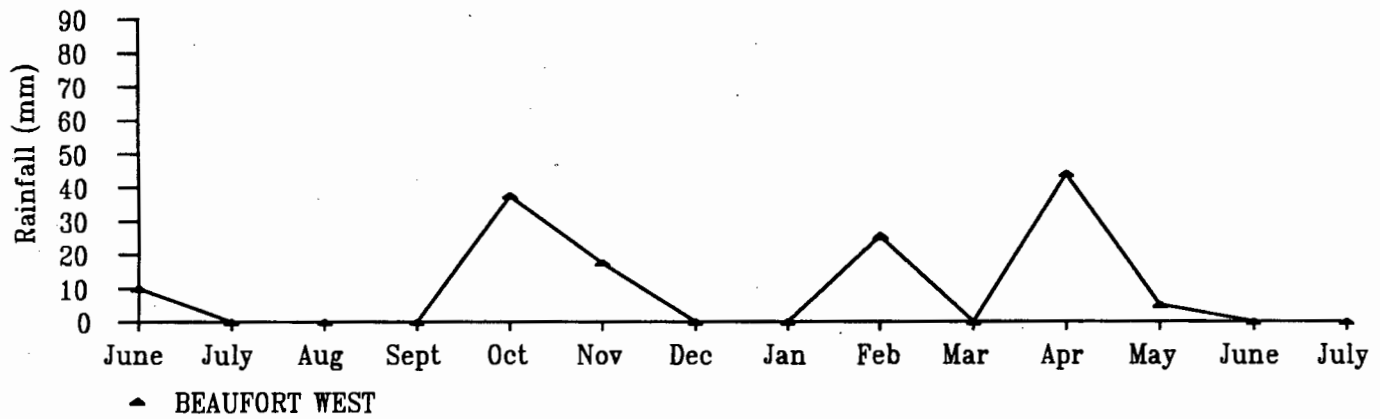
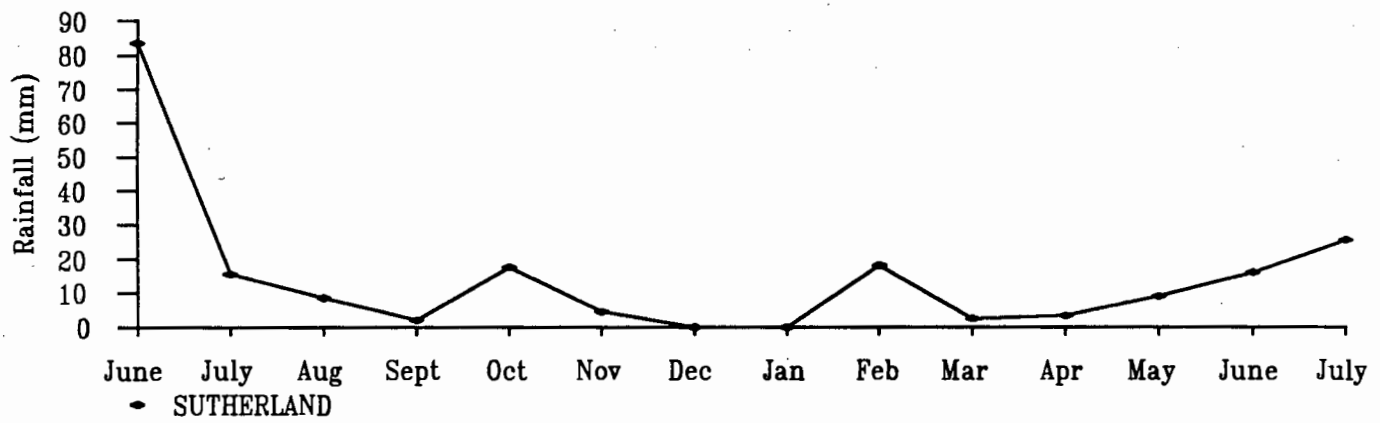
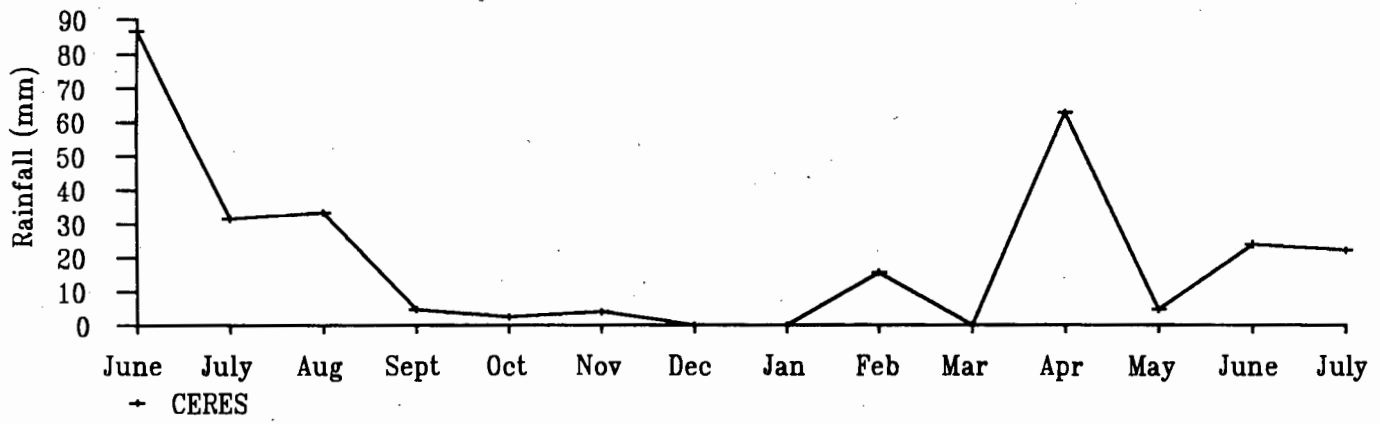
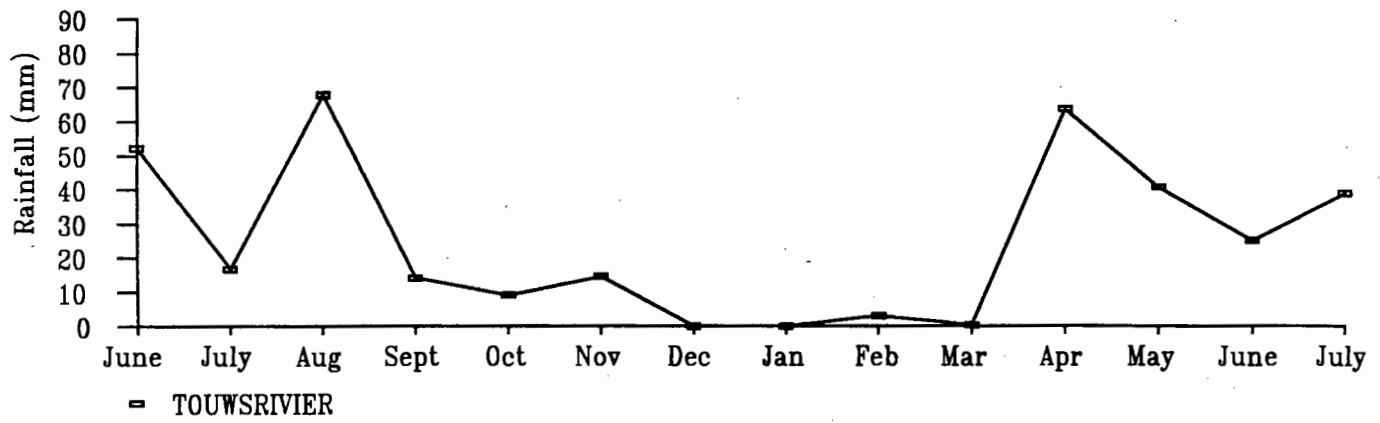


Figure 22: Monthly mean rainfall (mm) of the four study sites.

shrubs. The Ceres Karoo had the highest cover of annuals, succulents and the least perennial shrubs (see Appendix 1, Tables A12 - A18). Sutherland had a generally low total cover, low level of spinescence, low annual cover and few succulents, but had the highest cover and variety of perennial shrubs. Beaufort West had a wide variety and high cover of perennial shrubs, a large grass component but was low in annuals, geophytes and succulents.

Autumn exhibited a high level of flowering and fruiting activity at all of the sites. Differing phenophases of growth-forms, such as annuals, succulent shrubs and geophytes differentiated the two succulent sites, with the Ceres Karoo having the highest level of annual activity and Touwsrivier having by far the greatest level of geophyte activity.

WINTER

The classification of the winter data yielded 17 groups at the 80% level (Fig. 21). The two Succulent Karoo sites were indistinguishable, falling into 7 groups. Touwsrivier plots were grouped into 2 groups, one exclusively Touwsrivier plots and the other mixed with Ceres Karoo plots. The Ceres Karoo plots fell into 8 groups, with the northerly plots being separate from the majority that were grouped with plots from Touwsrivier (as per the spring data). All but two of the Sutherland plots were grouped with one of the Beaufort West plots at the 74% level but were split across 6 groups at the 80% level. All but two of the Beaufort West plots were grouped alone at the 80% level. Touwsrivier differed from all of the other sites in the cover and species diversity of geophytes. Touwsrivier and the Ceres Karoo maintained the highest cover of annuals, which, coupled with geophyte cover, gave Touwsrivier an increased cover relative to the other seasons.

An increased "pulse" of annual growth in the Ceres Karoo, changing from a high cover of a few species (in autumn) to a wider variety of species present (in winter), increased this site's similarity to Touwsrivier.

GENERAL RESULTS

The rainfall data (Fig. 22) giving the mean monthly rainfall for the study period show that none of the sites received precipitation in December and January, and that sites differed most in the amount of precipitation received in winter. It is important to note that Sutherland received far more rain than usual during the winter months of 1986 and 1987, with 613% and 179% of the rainfall averages for June 1986 and July 1987 respectively. The information statistics (Appendix 1) indicated that total cover, annuals, geophytes and perennial grasses were important in differentiating sites. The different sites have distinct growth seasons (Fig. 23). As a rule growth and flowering activity at all sites was low in summer, except for the perennial grass components of the summer rainfall regions. Flowering activity was significantly seasonal across all sites ($F = 237.2$, $d.f. = 3$, $p < 0.0001$; ANOVA) and within sites (see Tables 5, 6).

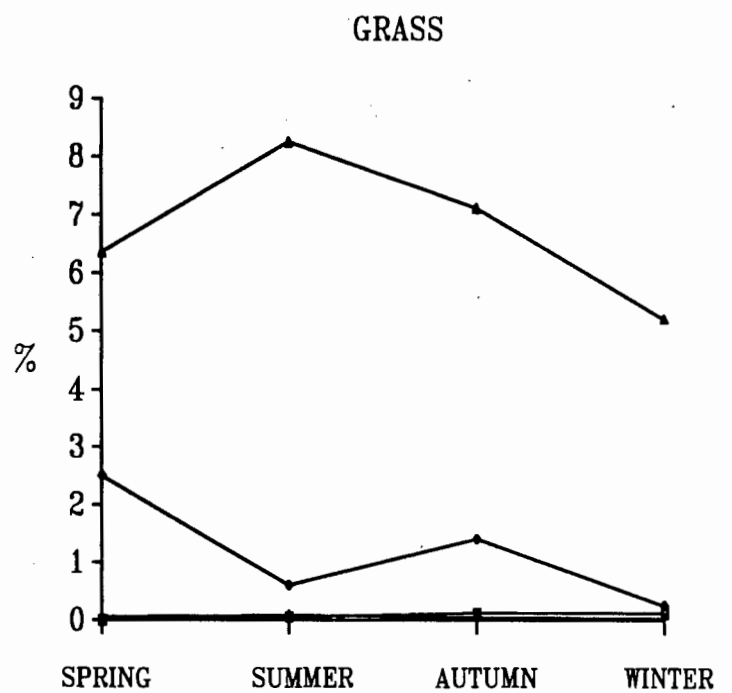
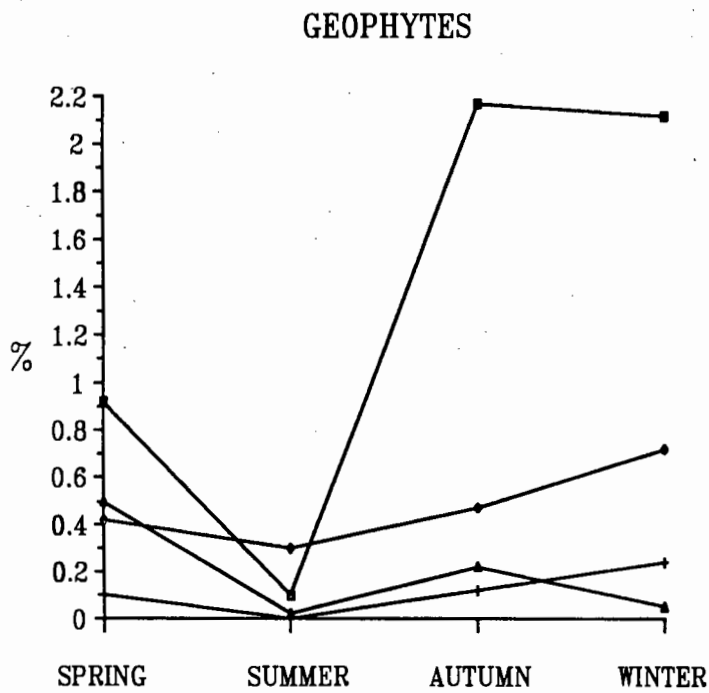
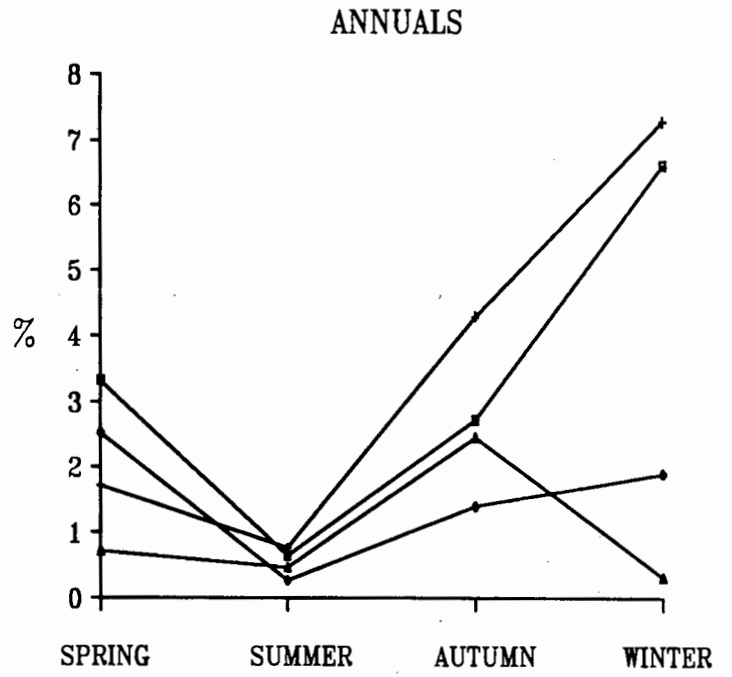
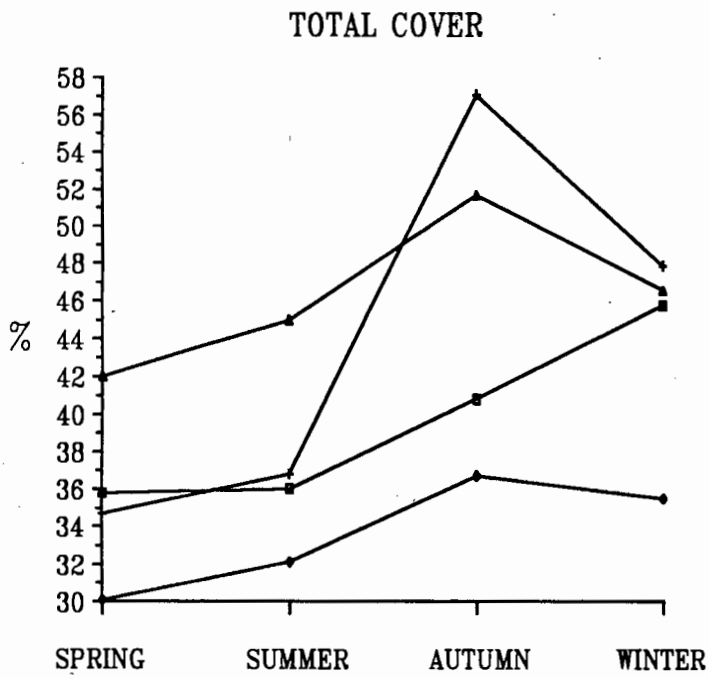


Figure 23: Seasonal variation in the mean percentage cover of those growth-forms accounting for most of the variation in the data set.

◻ Touwsrivier + Ceres • Sutherland ▲ Beaufort West

TABLE 5: ANALYSIS OF VARIANCE OF FLOWERING IN THE FOUR STUDY SITES OVER FOUR SEASONS.

SOURCES OF VARIATION	F-RATIO	D.F.	P<
LOCATION	10.02	3	0.0001
SEASON	237.22	3	0.0001
LOCATION BY SEASON	31.24	9	0.0001

TABLE 6: ANALYSIS OF VARIANCE OF FLOWERING IN THE FOUR STUDY SITES OVER FOUR SEASONS.

SOURCES OF VARIATION	F-RATIO	D.F.	P<
SEASON			
TOUWSRIVIER	53.05	3	0.0001
CERES KAROO	97.95	3	0.0001
SUTHERLAND	76.85	3	0.0001
BEAUFORT WEST	111.63	3	0.0001

TABLE 7: ANALYSIS OF VARIANCE OF FRUITING IN THE FOUR STUDY SITES OVER FOUR SEASONS.

SOURCES OF VARIATION	F-RATIO	D.F.	P<
LOCATION	13.69	3	0.0001
SEASON	95.13	3	0.0001
LOCATION BY SEASON	38.68	9	0.0001

TABLE 8: ANALYSIS OF VARIANCE OF FRUITING IN THE FOUR STUDY SITES OVER FOUR SEASONS.

SOURCES OF VARIATION	F-RATIO	D.F.	P<
SEASON			
TOUWSRIVIER	63.01	3	0.0001
CERES KAROO	97.18	3	0.0001
SUTHERLAND	10.75	3	0.0001
BEAUFORT WEST	32.38	3	0.0001

At Touwsrivier flowering activity was lowest in summer, highest in spring and winter and slightly lower in autumn. Spring flowering activity was dominated by leaf succulents (*Eberlanzia* sp. L. Bol., *Glottiphyllum fragrans* Schwant. and *Aridaria* sp. N. E. Br.), perennial shrubs (i.e. *Pteronia adenocarpa* Harv.) and annuals (i.e. *Cotula* sp. L. and *Leysera tenella* D.C.). Autumn flowering was dominated by geophytes (*Oxalis* sp. L., *Androcymbium* sp. Willd. and *Massonia depressa* Hoult.) and perennial shrubs (*Pentzia incana* (Thunb.) Kuntze and *Zygophyllum microcarpum* Licht.). Leaf succulents began flowering in autumn (*Aridaria* sp. N.E. Br.) with greatest phenophase activity in winter (*Glottiphyllum fragrans* Schwant. and *Gibbeaum* sp. N.E. Br.) with geophytes such as *Oxalis pes-caprae* L. and *Babiana* sp. Ker-Gawl.

In the Ceres Karoo, spring and winter were the most prolific flowering periods, with most species flowering during both. Summer saw no flowering activity although a high cover of *Cotula* sp. (up to 60%) in some plots may have resulted from a localized isolated rainfall event. The main annual activity appeared to be an accumulated response during autumn and winter.

At Sutherland certain species flowered throughout autumn, winter and spring (i.e. *Chrysacoma ciliata* L., *Pentzia incana* (Thunb.) Kunze., *Euryops* sp. Cass. and *Nylandtia spinosa* (L.) Dumort.).

At Beaufort West some species appeared to flower at different times of the year (especially *Pentzia* spp.). The area exhibited a pulsed response in flowering activity (c.f. Noy-Meir, 1973) with most species favouring autumn, *Sarcocaulon cambdeboensis* Moffett favouring summer and *Euphorbia* spp. favouring spring. Whether this is indicative of distinctly seasonal floras (*sensu* Noy-Meir, 1973), which so far have not been identified in the Karoo (Hoffman & Cowling, 1987) is not clear. Annual activity was generally greatest in autumn and low in winter, in contrast to other sites which exhibited an increase in annual activity from autumn to spring. This single peak of annual activity was almost certainly due to the fact that the prospect of follow up rains from late summer to autumn is far better than at other times of the year (Fig. 22)

Fruiting varied significantly in seasonality from site to site (Tables 7 & 8). The measure of fruiting activity is less informative than that of flowering activity. Most of the fruits were accounted for by dry seed heads (i.e. *Eriocephalus* sp.) or capsules (i.e. mesembs). The seasonality of fruiting activity was lowest in the two Nama-Karoo sites. This was mostly due to the abundance of serotinous species that retain the seeds on the plant for extended periods.

DISCUSSION

The classification dendrograms show that the Succulent Karoo sites are relatively homogeneous (grouping at a high level of similarity) and were more similar to each other in terms of the growth-form characteristics than they were to other sites. The Sutherland plots were distinctive, forming groups with few plots from other sites but at a lower level of similarity and thus one can

TABLE 9: Stepwise multiple regression of spring growth-form variables and occurrence of Karoo Korhaans (Only variables included in model are given):

INDEPENDENT VARIABLE	COEFFICIENT	S.E.	t-value	P.
PERENNIAL GRASS (COVER)	-0.034	0.012	-2.8	0.008
SUCCULENT LEAVED (COVER)	0.047	0.010	4.72	0.000
DEAD MATERIAL (COVER)	0.035	0.012	2.96	0.006
SUCCULENT LEAVED (SPECIES)	-0.156	0.048	-3.27	0.003
FLOWERS	0.114	0.057	2.02	0.051

R^2 (ADJ.) = 0.45

TABLE 10: Stepwise multiple regression of summer growth-form variables and occurrence of Karoo Korhaans (Only variables included in model are given):

INDEPENDENT VARIABLE	COEFFICIENT	S.E.	t-value	P.
ANNUAL (COVER)	0.211	0.046	4.58	0.0001
ANNUAL (SPECIES)	-0.468	0.143	-3.28	0.003
SUCCULENT LEAVED (SPECIES)	0.057	0.022	2.58	0.016

R^2 (ADJ.) = 0.46

TABLE 11: Stepwise multiple regression of autumn growth-form variables and occurrence of Karoo Korhaans (only variable included in model is given):

INDEPENDENT VARIABLE	COEFFICIENT	S.E.	t-value	P.
SUCCULENT LEAVED (COVER)	0.011	0.005	2.11	0.041

R^2 (ADJ.) = 0.07

conclude that although distinct from other sites the Sutherland site was, in terms of growth-form, a heterogeneous, non-succulent site with a low cover of a wide variety of perennial shrubs and a strong grass component. Beaufort West also formed distinct groups with few strays and but was less heterogeneous than Sutherland. The two Nama-Karoo sites had a wide variety of shrubs, few succulents and few annuals.

The high levels of cover of each growth-form in all sites in autumn, with a decline in winter and an increase in spring agrees with the generally accepted concept that growth initiated in autumn is suppressed by cold winter temperatures and revived in spring (Noy-Meir, 1973; Werger, 1978; Van Rooyen *et al.*, 1979^a; Rutherford & Westfall, 1986; Hoffman & Cowling, 1987). Due to the unpredictability of the timing, duration and magnitude of precipitation events and follow-up events in the Karoo, plant responses to rainfall have to be cautious in order to avoid wasting reserves (Noy-Meir, 1973). The presence of annuals at the different sites can be related to the likelihood of follow-up rains. In Touwsrivier and the Ceres Karoo rainfall in autumn and spring, with rainfall in winter, resulted in an accumulative level of annual cover. The Ceres Karoo showed an accumulated response to autumn rains during the winter and spring periods. Although the cover of annuals was high throughout this period the species composition changed from a low diversity in autumn (areas being dominated by single species "stands") to a high diversity in winter, indicating that species vary in the level and timing of their response to moisture input. In Beaufort West rainfall occurs in more discrete peaks in spring and autumn with a smaller peak in late summer. This resulted in a pulsed response of annual activity typical of such "summer rainfall" areas (Noy-Meir, 1973). The large annual component of the two succulent sites agrees with the accepted view that predictable seasonal rainfall favours annuals (Westoby, 1980).

Grasses occurred in the winter months in the Succulent Karoo. Summer favours grasses in Beaufort West, whereas the most favourable season for grasses in Sutherland appears to be autumn, which may be due to the fact that the area is within the even rainfall area of the Nama-Karoo and received unusually high rainfall in winter during the study period. Autumn saw a peak in total cover at both of the Nama-Karoo sites.

In terms of resource availability, the less seasonal a site is with regard to flowering and fruiting activity the less temporally clumped the resources. Ceres had the greatest seasonality of resources. Beaufort West was highly seasonal in terms of flowering activity but less seasonal in terms of fruit availability.

The seasonal classification of the physiognomy of four sites of karroid vegetation highlighted the distinction between succulent and Nama-Karoo regions. The high level of similarity between the plots from Succulent Karoo sites and the greater heterogeneity of Nama-Karoo plots agrees with the findings of Rutherford & Westfall (1986). They found that the Succulent Karoo biome was the most distinct biome in terms of the criteria they used to classify the biomes of southern Africa and that

spatial variability of rainfall in the Nama-Karoo biome results in localized patchiness of vegetation. The results also highlight the greater incidence of perennial grasses in the Nama-Karoo region and that this is generally favoured by summer rainfall being unpredictably erratic causing the partitioning of resources (Roux, *et. al.*, 1966; Rutherford & Westfall, 1986).

CHAPTER FOUR

THE DISTRIBUTION OF KAROO KORHAANS IN RELATION TO THE PHYTOSOCIOLOGY AND PHYSIOGNOMY OF KARROID HABITAT

INTRODUCTION

The variation in timing and magnitude of precipitation events in arid and semi-arid regions has a large random component, and organisms living in such areas have developed a wide variety of functional strategies that overcome the rigours of such an unpredictable environment (Noy-Meir, 1973). Many of the animals characteristic of such areas have developed highly opportunistic, adaptive strategies which enable them to exploit the characteristically unpredictable pockets of resource availability (Thomas, 1984; Wiens, 1985). The spatial and temporal unpredictability of the Karoo is evidenced by the proliferation of drought evaders (i.e. annual plants, migratory birds and mammals; Leistner, 1979) and the specialization of drought endurers (i.e. xerophytic evergreen shrubs, succulents and granivorous nomadic birds; Werger, 1978; Vernon, 1986). The phytosociology and vegetation physiognomy of Karoo Korhaan habitats was described in the previous chapters. This chapter examines the influences of habitat structure on the distribution of Karoo Korhaans

METHODS

Detailed descriptions of the four sites and the methods of analysis of their phytosociology and plant growth-form characteristics are detailed in Chapters 2 & 3.

The height profile of the vegetation at each of the sub-plots was measured along a 10 m transect at 0.1 m intervals. The presence and abundance (group size) of Karoo Korhaans in the vicinity of the plots was investigated by the use of a taped Karoo Korhaan duet that, when played, elicited a territorial response from individuals in the immediate vicinity of the plot (see Chapter 6). In order to determine whether or not growth-form characteristics accounted for the presence and abundance of Karoo Korhaans in the vicinity, step-wise multiple regressions of group size against the nineteen variables of growth-form (see Chapter 3) were conducted for each season.

RESULTS

PHYTOSOCIOLOGY

At the Touwsrivier site Karoo Korhaans were most commonly found in areas with few succulent taxa but with a large annual component. During spring groups were more evenly spaced, but generally avoided areas dominated by succulents. In summer, groups were scarce and were found on the periphery of the flats, generally avoiding community 2b which contained mostly dwarf succulent taxa.

In the Ceres Karoo groups spent spring, summer and autumn in areas with a high proportion of annual taxa (1a & 1b; i.e. *Osteospermum sinuatum*, *Cotula* sp., *Leysera tenella*). In winter groups moved and generally were rare in all areas except those with an even mix of growth forms. During

summer groups were not present in areas where succulents or perennial shrubs dominated to the exclusion of all other growth forms (groups 3 & 4).

In Sutherland during winter, groups inhabited communities with the highest variety of taxa. These were generally upland areas with both grasses and annuals. During the summer months groups occupied communities with strong annual components. In autumn groups occupied low-lying areas that were characterized by stronger annual and leaf succulent components than the upland areas.

In Beaufort West groups in spring frequented areas of high species diversity (4,5 & 6). In summer, groups avoided areas of low variety, without geophytes or grasses (2). In autumn groups were evenly spaced avoiding areas of low variety and the annual component was not important in determining distribution of Karoo Korhaans. In winter, by contrast, the annual component was very important with the highest concentration of birds in the areas of low diversity, but high cover, of annuals.

PHYSIOGNOMY

The occurrence of Karoo Korhaans in the study plots is depicted on the seasonal classification diagrams (see Figures 18 - 21)

In spring, Karoo Korhaans were present at 40 of the 85 plots (Fig. 18). A step-wise multiple regression of the nineteen variables of growth-form against korhaan occurrence and group-size showed that the species generally avoided grassy areas, with a variety of leaf succulents. The species favoured areas in flower and with a high cover of dead material (Table 9) and a high cover, but a low diversity of succulent shrubs. The areas with the most individuals were the Nama-Karoo sites which, although generally grassier than the Succulent Karoo sites, also had a far greater variety of perennial shrubs.

During summer, Karoo Korhaans were less common at the study plots with only 30 of the 85 plots having korhaans present (Fig. 19). This was probably due to the low resource abundance, with rainfall, and therefore flowering activity, being low at all sites. The presence and abundance of Karoo Korhaans was positively correlated with the percentage cover of annuals ($t=4.58$, $p<0.0001$; Stepwise multiple regression), but negatively correlated with the diversity of annuals ($t=-3.28$, $p<0.005$; Stepwise multiple regression) suggesting that birds favour monocultures of annual activity.

Forty-nine of the 85 plots contained Karoo Korhaans in autumn (Fig. 20). The greatest concentration occurred at Beaufort West where the percentage cover of annuals, and total plant cover was highest in autumn. Stepwise multiple regression showed that the percentage cover of succulent leaved shrubs was correlated (albeit weakly) with bird presence (Table 10). This was probably due to the flowering of such taxa in response to the autumn rains.

In winter, only 37 of the 85 plots had Karoo Korhaans in the vicinity (Fig. 21). The low densities of Karoo Korhaans probably was due to the high incidence of flowering activity at most of the sites and therefore the widely dispersed nature of resources. Stepwise multiple regression did not indicate that any of the variables measured were correlated with bird distribution.

A stepwise multiple regression of season, location (site) and mean vegetation height against the occurrence of korhaans showed that only location had an effect on bird presence ($R^2 = .015$, $df = 678$; $p < 0.005$).

DISCUSSION

Although the Karoo Korhaans favour areas with little grass this appears to be less deterministic of their habitat choice than preference for variety of perennial shrubs and avoidance of areas dominated by succulents. This accounts for the greater numbers of birds in the Nama-Karoo sites. The avoidance of areas with a wide variety of succulents may account for the relatively low incidence of birds in the Ceres Karoo. However, this may be a secondary effect of temporal, highly patchy resource availability, with low perennial shrub cover and high aridity.

The density of Karoo Korhaans appears to be related to the phenophase activity at the sites. When flowering was limited to annuals of a few species, the densities increased. Conversely, when rainfall was high and a broad, general flowering event occurred (autumn and spring in winter rainfall areas and autumn in summer rainfall areas) and resources were widely available, the Karoo Korhaan appeared to "spread out", possibly into mesic areas. This agrees with the observation that the species has plastic territories that alter in size in response to resource availability (Quinton, 1948). In areas such as the Ceres Karoo, individuals maintained large territories throughout the year because the area was dominated by annuals and succulents, and resources generally were widely spaced, possibly due to the effects of disturbance. The interesting correlations between annual cover and annual variety and bird presence at the Ceres site indicate that the species responds to local pulses in resource availability, favouring almost monoculture therophyte flowering events. This is particularly characteristic of such disturbed areas (Werger, 1978; Leistner, 1979).

That mean vegetation height played no part in determining korhaan presence was not unexpected since vegetation height is one of the most critical determining factors of habitat choice of the species and was accounted for in the location of the study plots. Korhaans do not occur in vegetation with a mean height of greater than 0.5m or lower than 0.1m, and none of the sites had such vegetation. Provided that this basic criterion, essential to the visual component of the display, is met, vegetation height plays little further part in the choice of habitat by Karoo Korhaans.

The Sutherland site area supported the greatest density of Karoo Korhaans in winter and autumn. As birds were absent from surrounding areas in all but summer (pers. obs.) it appears that the

area may serve as a winter refuge for the species, avoiding the greater exposure of the open flats to the south during the winter.

Variety of plant taxa rather than cover appears to be a determinant of habitat choice by the Karoo Korhaan. In the Nama-Karoo sites, the wide variety of perennial shrubs with a large compliment of serotinous species provides a broad resource base. In times of low moisture availability, specific flowering events such as that of mesembs (possibly more responsive to discrete moisture input than non-succulent shrubs) are important features of habitats frequented by the species.

Generally the Karoo Korhaan appears to optimise its' habitat choice seasonally in relation to resource provision by certain guilds of plants. The varying responses of annuals, succulents and asteraceous shrubs to erratic precipitation pulses and more predictable seasonal rainfall appear to provide resources throughout the year and korhaan territories appear to be sufficiently plastic to allow them latitude in exploiting these resources.

CHAPTER FIVE

DIET OF THE KAROO KORHAAN

INTRODUCTION

It is often stated in the literature that korhaans and bustards are insectivorous, taking fruits and seeds to a lesser extent (Cramp & Simmons, 1980; Maclean, 1985). This conclusion stems from the investigation of the stomach contents of several species, in which stomachs contained conspicuous items such as whole beetles and grasshoppers. The Karoo Korhaan has been assumed to be overwhelmingly insectivorous (Layard, 1867; Stark and Sclater, 1906; Leighton-Hare, 1915; Maclean, 1985) but the diet has not been studied and no information exists on which to assess the relative importance of insectivory and herbivory in the diet. Detailed and objective studies of the gut contents of certain bustard species have shown that vegetation constitutes a far greater proportion of the bustard diet than was previously thought (Jackson, 1938; Meinertzhagen, 1950; Dementév & Gladiov, 1951; Valverde, 1957; Benson, 1962; Ali & Ripley, 1969; Glutz von Blotzheim, 1973; Palacios *et. al.*, 1975).

In elucidating those aspects of the species' eco-ethology that enable the Karoo Korhaan to survive the unpredictable environment of the Karoo, a description of the habitat favoured by the species was undertaken and is detailed in the preceding chapters. In this chapter a detailed analysis of the species' diet investigates the dietary preference of the species in order to provide information necessary to interpret the species' habitat choice.

Fourteen Karoo Korhaans were collected from the western Karoo (Calvinia, Merweville and Touwsrivier) and one from the eastern Cape near Klipplaat between May 1986 and July 1987 (Fig. 1; Table 12). These birds were collected under licence from the Cape Chief Directorate of Nature and Environmental Conservation and with permission from the landowners in question.

METHODS

Collected in the absence of adequate preservation facilities, the individual collected from the eastern Cape was skinned and the stomach was removed and placed in 70% alcohol. For the subsequent individuals the entire carcass was retained intact and the alimentary organs were left *in situ*. In order to minimize post-mortem degradation of the body tissue and digestion, the collected birds were frozen immediately in polystyrene boxes containing blocks of "Dry-ice". The individuals were later frozen at - 20° C.

The whole digestive tract was removed from the body after ligatures had been tied at the junctions of the proventriculus and stomach, stomach and small intestine and at the ileo-caecal-colic juncture (separating the intestines and colon from the caeca). Ligatures were also tied at the external limits of the oesophagus and the cloaca.

It has been stated (Hartley, 1948) and illustrated (Martin *et. al.*, 1946; Swanson and Bartonek, 1970) that the portions of the digestive tract distal to the oesophagus give increasingly poor indications of the diet. Analyses of portions other than the oesophagus give emphasis to items in the diet that are

TABLE 12: Details of the fifteen Karoo Korhaans collected for the food habits analyses, during the period 1986 - 1987.

Bird #	Time	Date	Gender	M _b ¹	Locality and grid reference
1	13:20	02/12/86	M	1650	Merweville 32°57'S 21°23'E
2	06:30	09/12/86	M	1720	Vaalputs 30°15'S 18°26'E
3	06:30	09/12/86	F	1490	" "
4	07:34	14/01/87	M	1550	Calvinia 31°28'S 19°47'E
5	08:00	14/01/87	M	1560	" "
6	17:00	14/01/87	M	1700	" "
7	18:30	14/01/87	M	1580	" "
8	18:30	14/01/87	F	1270	" "
9	08:22	15/01/87	F	1390	" "
10	10:40	06/02/87	M	1500	Touwsrivier 33°27'S 20°07'E
11	17:30	21/07/87	M	1680	Calvinia
12	12:40	22/07/87	F	1212	" "
13	13:00	23/07/87	F	1395	" "
14	14:00	24/07/87	F	1360	Kraairivier 32°37'S 20°26'E
15	10:00	26/05/86	M	(ND) ²	Klipplaat 33°04'S 24°19'E

1 Body mass in grams

2 No data.

resistant to digestion, have recognisable hard parts and are small enough to pass through the pylorus, thus escaping the milling effects of the pre-pyloral musculature (Hartley, 1948).

In order to minimize the recognised biases of such a study it was decided that the whole digestive tract would be analysed and some measure of the importance of dietary items be inferred through differential representation within the respective sections. The digestive tract was separated, for the purpose of analysis, into five sections; the oesophagus and proventriculus; the stomach (ventriculus); the small intestine (duodenum and ileum); the paired caeca (combined); the colon, coprodeum and cloaca (combined). The respective organs were opened and their contents removed and placed onto glass dishes. The stomach was carefully examined to ensure that seeds and other small items had been removed from the rugose, horny lining. The intestines and the caeca were irrigated with alcohol in order to remove the predominantly "sludge-like" contents. The contents were then examined through a binocular microscope and separated into their constituent food groups. The contents of all sections were separated with respect to a resolution of 1mm (approx. size of isopteran mandibles) which ensured that soft bodied insects were represented as fairly as possible. This method sought to avoid the subjective biases normally associated with conspicuous, recognisable and often less important dietary components.

The separated items were analysed both volumetrically and gravimetrically. Volumetric analysis was achieved by water displacement in a graduated glass cylinder. All items had the surface moisture removed by dabbing with dry paper tissue. For fragments of insect material (other than entire individuals or complete abdomino-thoracic sections that retained quantities of flesh) it was found that the dry mass was equivalent to the volume of the material; for such items that were too small to measure volumetrically, the dry mass equivalent was used in volumetric analyses. The material was then placed on a glass dish and dried in an oven at 80°C for 36 hours, until constant mass was achieved. The drying period maximized water loss from the items, whilst minimizing the loss of volatile oils. The items were weighed to the nearest 0.001mg on an electric balance, immediately on removal from the oven to avoid inhibition of atmospheric moisture. Parasites from the sections were measured volumetrically as outlined above but were not dried for gravimetric analysis as they were sent intact, for identification to the Department of Parasitology at Onderstepoort, Pretoria.

The identification of animal material other than entire individuals, was almost solely dependent on recognition of resistant parts such as mandibles, carapaces and elytra, trunci, petioles, wings, heads and legs. A reference collection of the recognisable remains was made and enabled specific identification of most of the insect remains. A similar reference collection for the plant items was made with recognisable seeds, floral parts and other remains. Plant items in the diet are represented by species and in terms of their origin, grouping plants by the plant organ represented. The representation of seeds and fruits in the analysis is separated into three categories that group seeds according to dispersal mechanism and origin. "Seeds" refers to generally autochorous, dehiscent and passively dispersed, naked seeds, most likely to have been found singly or in numbers away from the

parent plant. "Pods" refers to actively autochorous and often explosively dehiscent capsules usually containing more than one seed and found in association with the parent plant (because the dispersal "event" is generally instantaneous, pods are considered here to be indehiscent at the time of ingestion). "Fruits" refers to fleshy ovaries enclosing several, to many seeds and to seeds of fruit origin which are generally endozoochorally adapted (see Hoffman and Cowling, 1987 for details). This was considered a useful working distinction between types of seeds, giving an indication of their origin, concentration (in the diet and the environment) and nutritive value.

The status of dietary items was recorded as either "important" (occurred in over 30% of the samples and/or represented a large proportion of the individual samples in which they were present); "occasional" (occurred in more than one sample but in small quantities) or "accidental" (very rare or accidentally ingested). The categorization of items as "important" is not meant to imply the actual, qualitative worth of these items but merely their observed, relative quantitative status.

The method outlined above was standardized for all of the sections of the digestive tract. For the purposes of this chapter, only the results of the stomach contents analysis are reported in detail and the major findings of the analyses of other gut sections are briefly outlined.

PRESENTATION OF THE RESULTS

Volumetric and gravimetric analyses were used to give an indication of the relative importance of the different items in the diet. The numerical status of the various food items was also used as an indication of the status of each item in the diet. The methods used to present the volumetric and gravimetric results were adapted from the suggestions of Martin *et. al.* (1946) and Swanson *et. al.* (1974a). The data from the analyses were mathematically weighted in order to represent the importance of the various food items with respect to their status in the total of all samples and in the individual samples. The data from both the volumetric and gravimetric analyses of individual food items are expressed as aggregate volume and mass and aggregate percentage volume and mass. The aggregate volume (AV) was calculated on the basis of the food items ($i=1,\dots,I$) and their volume (V) in the individual samples (birds; $b=1,\dots,B$) as a percentage of the total volume of all food items in all samples, so that;

$$AV_i = \frac{\sum_{b=1}^n V_{ib}}{\sum_{i=1}^I \sum_{b=1}^B V_{ib}} \times 100$$

where AV_i is the aggregate volume of the i th food item.

The aggregate mass (AM) was obtained by substitution of the mass (M) of the food items in the above formula. The aggregate percentages of volume and mass (APV & APM) were obtained by averaging the proportion of each food item ($i=1\dots I$) in each sample ($b=1\dots B$) wherein the item occurred (c.f. Swanson *et. al.*, 1974a). Thus the aggregate percentage (volume) of a particular item (i) was calculated by the equation:

$$APV_i = \left[\frac{\sum_{b=1}^B \frac{V_{ib}}{\sum_{i=1}^I}}{N(B_i)} \right] \times 100$$

The aggregate volume or mass method represents each item of food equally, regardless of which bird ate it, whereas the aggregate percentage (volume/mass) represents each bird feeding on the item equally in the analysis (c.f. Swanson *et. al.*, 1974a). The method of analysis differs from that of Swanson *et. al.* (1974a) in that the aggregate percentages (APV and APM) of any particular item only consider birds that have eaten the item. This method of data representation was chosen as it allows for the practical comparison of two sets of values (AV & APV, AM & APM). The two sets of values, when compared, identify the variation in the status of items between birds that did and birds that did not consume them. The method chosen is regarded as the most expedient use of relative data. The data (for the stomach analyses only) is also presented in graphical form using "Box and Whisker plots" (Appendix 2, Figs. A2.1 - A2.8) to describe the range of the aggregate percentages of the major items (items that contribute >0.5% to AV and AM, or that occur in more than 3 samples). The standard deviation of the aggregate percentages are given in the text. The "actual" number of an item was also recorded. The quantification considered "parts" as representative fractions of an ingested "whole". That is to say that two sections of a three section *Euphorbia* sp. pod represent one pod; nine insect legs represent two insects; seven spider legs represent one spider and so on. The actual numerical value of an item (AN_i) was then tabulated as a ratio of the number of samples containing that item ($AN_i:NJ$). This representation of the data provides some indication of the degree to which some items may be under-represented by the volumetric and gravimetric analyses due to higher digestibility.

RESULTS

OESOPHAGUS AND PROVENTRICULUS

The contents of the oesophagus and the proventriculus generally give the best indication of diet as food items have not been as greatly altered, by mechanical and chemical processes of digestion, as those in the stomach and intestines. As the Otididae in general do not have a functional crop, the proventriculus and the oesophagus are the only parts of the alimentary tract which provide such material.

Karoo Korhaans possess a rudimentary proventriculus (similar to the "spindle" class described by Zisweiler & Farner, 1972) with limited musculature and an unspecialized oesophagus.

Food was present in only seven of the samples. The mean dry mass of the contents of these samples was only 0.086 ± 0.175 g (S.D) and 0.6g in total. Of this material, vegetation made up the main bulk (by dry mass) on average (APM = $96.41 \pm 8.03\%$) but only occurred in five of the samples. The vegetable material was mainly unrecognisable in two of the samples (APM = $69.12 \pm 3.8\%$), but various seeds of annuals and shrubs were present. Flowers accounted for 6.67%, seeds for 1.95% and unidentifiable material for 6.21% in total (AM). Insect material occurred in only two samples (AM = 5%; APM = $57.70 \pm 59.83\%$). Sample 1 contained a large amount of grit (AM = 80.17%). Grit also occurred in sample 4 (APM = 2.56%) but was only represented by a single lith of less than 2mm diameter.

CONCLUSIONS OF THE ANALYSIS OF THE CONTENTS OF THE PROVENTRICULUS AND

OESOPHAGUS.

The use of the contents of the oesophagus for diet analysis theoretically is preferable to the use of those of the more digestive, distal organs of the alimentary tract. However, this is of more relevance to bird species that possess functional crops or that have an expansive oesophagus, allowing for the temporary storage of recently ingested food items (especially the Anatidae; Swanson & Bartonek, 1970; Custer & Pitelka, 1975). The Karoo Korhaan has no pre-stomach storage structure and appears not to retain items in the oesophagus. The items found in the above analysis were not observably less digested than the items found in the stomach. The presence of small quantities of material of an already digested nature implied that the material found in the two proximal sections of the gut were in fact of stomach origin. Regurgitation of material, from individuals collected for food habits analyses, has been observed in Blue-winged Teal *Anas discors* collected by shooting (Swanson & Bartonek, 1970) and captive Mallards *Anas platyrhynchos* killed with sodium pentobarbital (Malone, 1966). There is no published information for the duration of retention of ingested items in the oesophagus of any species of the Otididae, and times vary greatly for species of birds with crops, from

0.6 h to 4.08 h (for a review see Warner, 1981). It was therefore assumed that the material observed in the analysis was mostly present as a result of contamination from the stomach during collection.

ANALYSIS OF THE STOMACH CONTENTS

There was no significant difference in the amount of material present in the stomachs of males and females as a proportion of body weight ($U = 18$; $p > 0.05$; Mann - Whitney "U" test). Females were not significantly more insectivorous ($\chi^2 = 0.552$; $p > 0.05$, $df = 1$) and therefore all samples were pooled for analysis.

ANIMAL MATERIAL

Animal remains were present in all of the samples and made up 6.22% of the aggregate volume and 11.89% of the aggregate mass (APV = $7.34 \pm 1.90\%$; APM = $12.36 \pm 9.08\%$). This represented 3620 individual arthropods.

Of the non-insect arthropods, none contributed more than 0.01% to the aggregate volume (Table 13) or more than 0.001% to the aggregate mass (Table 14) and only the spider *Amoxenus* sp. occurred in more than one stomach sample. This species is a termitivore and is considered "occasional" in the diet of birds feeding on termites.

Insects occurred in all of the samples and constituted 6.21% of the aggregate volume and 11.88% of the aggregate mass. The ratio of the actual number of individuals to the number of samples containing insects (3616:15; see Table 15) highlights the importance of insects in the diet. The average number of insects per bird was 241.1 ± 309.12 ($n = 15$). The marked disparity between the volumetric values (AV and APV) and the gravimetric values (AM and APM) is due to the higher water content of the vegetable material. This disparity is also indicative of the already partially digested state of the main bulk of the insect material. The occurrence of Thysanoptera in two of the samples was coincident with floral material (especially Mesembryanthemaceae) and they were undoubtedly, incidentally ingested along with the flowers and are not thought to represent anything other than an "accidental" dietary component.

Orthopteran remains occurred in over half of samples but contributed less than 0.5% to AV, APV, AM or APM. The disparity between AV and APV, and AM and APM is due to the presence of a single, entire grasshopper in one sample (sample 8). In the other samples in which they occurred, orthopterans were represented by a few recognisable remains such as mandibles, tibiae, heads and in one case, wings. The data in Table 15 shows however, that orthopterans occurred in a ratio of 10:8 (that is ten individuals represented in eight samples). A single orthopteran is likely to represent a considerable intake in terms of energy and essential nutrients.

TABLE 13: A comparison of the aggregate volume, aggregate percentage volume and percentage occurrence of arthropod food items represented in the stomachs of Karoo Korhaans collected during the period 1986 - 1987.

	AGGREGATE VOLUME ¹	AGGREGATE PERCENTAGE	PERCENTAGE OCCURRENCE ²
Arachnida (indet.)	tr ³	0.01	13.33
Acari	0.01	0.20	6.67
Myriapoda	tr	0.02	6.67
INSECTA (Total)	6.21	7.33	100.00
Orthoptera	0.07	0.25	53.33
Isoptera	0.71	0.72	86.66
Thysanoptera	tr	0.01	13.33
Coléoptera (Total)	3.61	5.06	93.33
Curculionidae	3.14	4.47	86.66
Buprestidae	0.06	0.51	13.33
Coccinellidae	0.01	0.24	6.67
Tenebrionoidea			
Tenebrionidae	0.26	4.62	13.33
Zophosidae	tr	0.02	13.33
(indet.)	0.14	0.41	33.33
Diptera	0.01	0.08	6.67
Lepidoptera	0.03	0.35	13.33
Hymenoptera			
Apioptera	tr	tr	6.67
Formicoidae	0.42	0.66	80.00
<i>Messor capensis</i>	0.32	0.64	66.67
<i>Campanotis</i> spp.	0.07	0.39	26.67
<i>Ophthalmopone</i> sp.	0.03	0.19	40.00
<i>Crematogaster</i> sp.	tr	tr	33.33
<i>Tetramorium</i> sp.	tr	tr	13.33
<i>Anaplolepis</i> sp.	tr	tr	6.67
INSECTS (indet.)	1.36	1.65	100.00
TOTAL	6.22	7.34	100.00

1 Wet volume (c.c.) as a percentage of the total wet volume

2 N = 15

3 Trace = <0.01%

TABLE 14: A comparison of the aggregate dry mass, aggregate percentage dry mass and percentage occurrence of arthropod food items represented in the stomachs of Karoo Korhaans collected during the period 1986 - 1987.

	AGGREGATE DRY MASS ¹	AGGREGATE PERCENTAGE MASS	PERCENTAGE OCCURRENCE ²
Arachnida (indet.)	tr ³	0.02	13.33
Acari	tr	0.05	6.67
Myriapoda	tr	0.05	6.67
INSECTA (Total)	11.88	12.35	100.00
Orthoptera	0.12	0.37	53.33
Isoptera	1.04	0.97	86.66
Thysanoptera	tr	0.02	13.33
Coleoptera (Total)	7.06	8.63	93.33
Curculionidae	5.86	7.68	86.66
Buprestidae	0.12	1.14	13.33
Coccinellidae	0.01	0.25	6.67
Tenebrionoidea			
Tenebrionidae	0.79	6.65	13.33
Zophosidae	tr	0.05	13.33
(indet.)	0.27	0.67	33.33
Diptera	0.02	0.29	6.67
Lepidoptera	0.01	0.10	13.33
Hymenoptera			
Apioptera	tr	tr	6.67
Formicoidae (Total)	0.69	0.76	80.00
<i>Messor capensis</i>	0.52	0.74	66.67
<i>Campanotis</i> spp.	0.14	0.43	26.67
<i>Ophthalmopone</i> sp.	0.03	0.25	40.00
<i>Crematogaster</i> sp.	tr	tr	33.33
<i>Tetramorium</i> sp.	tr	tr	13.33
<i>Anaplolepis</i> sp.	tr	tr	6.67
INSECTS (indet.)	2.94	3.19	100.00
TOTAL	11.89	12.36	100.00

1 Dry mass (g) as a percentage of the total dry mass

2 N = 15

3 Trace = <0.01%

TABLE 15: The numerical representation of the occurrence of arthropod food items in the stomachs of Karoo Korhaans collected during the period 1986 - 1987.

	MEAN ¹ (S.D)		OCCURRENCE RATIO (ANi:NJ)	REPRESENTED INDIVIDUALS
Arachnida (indet.)	1.5	(0.71)	3: 2	5,14
Acari	1.0	(0.00)	1: 1	7
Myriapoda	1.0	(0.00)	1: 1	5
INSECTA (Total)	241.1	(309.12)	3616:15	1-15
Orthoptera	1.3	(0.46)	10: 8	1,2,5,6,8,9,10,14
Isoptera	222.3	(305.73)	2890:13	2-11,13-15
Thysanoptera	22.5	(26.16)	45: 2	11,14
Coleoptera (Total)	15.1	(9.13)	211:14	1-14
Curculionidae	12.5	(5.98)	163:13	1-7,9-14
Buprestidae	1.0	(0.00)	2: 2	9,14 ²
Coccinellidae	6.0	(0.00)	6: 1	14
Tenebrionoidea				
Tenebrionidae	8.5	(9.19)	17: 2	2,3
Zophosidae	1.5	(0.71)	3: 2	12,14
(indet.)	3.3	(2.50)	20: 6	1,5,8,9,10,14
Diptera	3.0	(0.00)	3: 1	1
Lepidoptera	4.0	(1.41)	8: 2	3,15
Hymenoptera				
Aplioptera	1.0	(0.00)	1: 1	5
Formicoidea	37.3	(55.57)	447:12	1-6,8-10,12,14,15
<i>Messor capensis</i>	36.4	(50.82)	364:10	1-6,8-10,15
<i>Campanotis</i> spp.	2.0	(1.41)	8: 4	2,3,4,12
<i>Ophthalmopone</i> sp.	2.8	(1.51)	16: 6	1,3-6,10
<i>Crematogaster</i> sp.	9.4	(8.56)	47: 5	2-5,12
<i>Tetramorium</i> sp.	4.0	(4.24)	8: 2	4,6
<i>Anaplolepis</i> sp.	3.0	(0.00)	3: 1	10
TOTAL OCCURRENCE				
BY ITEM³	157.43	(601.00)	3621:23	1-15
BY BIRD⁴	241.40	(309.31)	3621:15	1-15

1 The actual number of individuals as determined by fractions of the identifiable remains

2 Ratio ANi:NJ is inaccurate due to unquantifiable remains in 9 (see text).

3 Average number of individuals of each item

4 Average number of individual items per bird.

By far the most dominant insect items in the diet belonged to the Coleoptera. Ninety-three percent of the samples contained coleopteran remains of which 92.86% were identified as members of the Curculionidae (weevils). Over 12 species of weevils from four families were represented. The family represented most commonly was the Brachycerinae (8 *Brachycerus* spp. and 1 *Synthocus* sp.). Both genera develop in the bulbs of monocotyledonous plants and are diverse in arid areas. All of the species encountered were apterous, terrestrial weevils, abundant in karroid habitats although nothing is known of their biology. Weevils occurred in 87% of the samples and contributed over 3% to the aggregate volume and over 5% to the aggregate mass (APV = $4.47 \pm 6.91\%$, n=13; APM = $7.68 \pm 7.87\%$, n=13). It is clear from the small disparity between the AV and the APV, and the AM and the APM that weevils are regular and important dietary constituents. The numerical ratios (Table 15) support the above conclusion that weevils are important in the diet. Other Coleoptera were represented by Buprestidae (Jewel-beetles), Coccinellidae (Lady-birds) and Tenebrionoidea.

The Buprestidae, thermophilous and generally most active during the warmest part of the day (Holm & Bellamy, 1985), were most prevalent in sample 14 that was collected at 13:00h. Mostly represented by fragments of elytra, buprestids were not quantifiable numerically other than the identification of two heads. The disparity between the AV and AM is due to the low water content of the mainly elytral remains and the disparity between AV and APV, and AM and APM is due to the concentration of most of the remains in only one sample (sample 14). Coccinellidae were also found in sample 14, which contained predominantly floral material. Both these families are associated commonly with flowers.

The poor representation of Tenebrionoidea in the diet, considering the diversity of species and their abundance in the Karoo is most likely due to the speed at which they move. Those members of the Tenebrionidae ingested most frequently were *Psammodes* sp. which are large, sluggish and conspicuous. Two individuals of the Zophosidae were found in two separate samples. These beetles are common throughout the Karoo and although fast moving, they seek shelter beneath bushes during the heat of the day (pers. obs.). None of the analyses gave undue representation of this beetle which is likely to be an "occasional" item, taken by chance.

The low values of APM ($0.97 \pm 1.59\%$, n=13) and APV ($0.72 \pm 1.26\%$, n=13) for Isoptera, are due to their being represented, in nearly all cases, by the paired molar-like mandibles. The species present in 87% of the stomach samples was the common, Karoo species - *Microhodotermes viator*. Most of the mandibles were from worker castes with a few soldier castes being present (Ruelle, 1985). Entire (and therefore recently ingested) termites were found in samples collected in the late afternoon. Numerically the Isoptera dominated the insect portion of the diet with an average number of 223 ± 305.73 individuals in 87% of the samples.

Members of the Formicoidae occurred almost as frequently as isopterans, being present in 80% of the samples and contributing $0.66 \pm 0.78\%$ of APV and $0.76 \pm 0.82\%$ of the APM to the

samples on average (Tables 13 & 14). Although several entire individuals were present in some of the samples, the various species of ants were identified by means of their trunci, petioles and mandibles (Arnold, 1926). Most ants eaten belonged to the Myrmicinae (including the harvester species). The most frequently encountered species in the samples was *Messor capensis*, a common, widespread species throughout the Karoo, occurring as castes of several sizes. The species occurred in 67% of the samples. Another myrmicine was the much smaller *Crematogaster melanogaster*. None of the methods of analysis suggest that the species is anything more than "occasional" in the diet. Two species of ant very similar to *C. melanogaster*, but distinguishable by the structure of ridges on the truncus (Arnold, 1926) were the myrmicine *Tetramorium* sp., and the formicine, black pugnacious ant *Anaplolepis cf. steingroeveri*. Both contributed negligibly to the diet (Tables 13, 14 & 15) and are considered as "occasional" prey.

Of the non-myrmicine ants *Campanotis* sp. is a common genus of the Formicinae in the Karoo. Although a highly social, aphidicolous ant with definite castes (Prins, 1985), the most commonly encountered individuals are solitary foragers. As such they did not contribute greatly to the aggregate volume or mass. The low values of AV and AM are due to the representation of individuals by mandibles and trunci in only four samples. This belies the fact that, being several times larger than any of the other species of ant eaten, individuals of this species represent a greater energy intake than individuals of the other species. Two species were recognised in the samples. One, *Campanotis fulvopilosus* is a solitary foraging member of the genus, widespread throughout the Karoo. The other species *Campanotis mystaceus* is a photophobic species and could only be encountered by foraging crepuscularly (W.R.J. Dean pers. comm.). The species was only encountered in birds collected between the hours of 06:00 a.m. and 07:30 a.m. suggesting that these birds began foraging at first light (or that the remains represent feeding activity of the previous evening. The presence of the termitivorous ant *Ophthalmopone hottentota* is probably due to its presence at centres of termite activity. Their low representation in those samples wherein they occurred is due to their non-gregarious nature; they are found singly or in small numbers at sites of termite activity.

Lepidopteran larvae are likely to be important food items during "outbreaks". However, only eight individuals occurred in two samples (Table 15). Similarly, dipteran larvae were poorly represented in the diet; occurring only as three individuals in one sample. The occurrence of dipteran larvae in sample 1 was coincident with the presence of the flowers of *Pteronia* sp. Data collected on the seed predation of *P. pallens* by a dipteran Tephretid parasite has shown that these parasites have a considerable effect on the seed production of the plant (Milton & Boobyer, unpublished data). Parasitised flower heads are retained on the plant due to the effects of the larvae burrowing into the capitulae. The dipteran larva is, in turn, host to a parasitoid hymenopteran and survivors (non-parasitised larvae) reparasitise the flower heads throughout the season. Karoo Korhaans may select the parasitized flowerheads of *Pteronia* sp. merely because at certain times of the year they are the only flowerheads available, but in doing so receive seed, dipteran and hymenopteran food items.

PLANT MATERIAL

Both the volumetric and the gravimetric analyses highlight the importance of vegetation in the diet (Tables 16 & 17; Figures A2.1 & A2.2) with vegetation making up 90% of the total volume of each sample (APV = $88.58 \pm 8.05\%$, n=15) on average and nearly 80% of the total mass (APM = $78.94 \pm 14.60\%$, n=15) on average. The use of the two methods of quantifying the importance of plant material in the diet of the Karoo Korhaan (AV and AM), gives two quite different indications of the status of various items in the diet. The loss of water between the volumetric and the gravimetric analyses decreases the proportional representation of those items that have a high water content.

Asteraceae occurred in 13 (87%) of the samples and contributed $13.91 \pm 14.15\%$ to the APV and $7.24 \pm 7.99\%$ to the APM (Table 16 & 17; Figs. A2.3 & A2.4, Appendix 2). There is a slight disparity between the aggregates (AV & AM) and the aggregate percentages (APV & APM) due to the large concentrations of the flowers of some species in some samples (Figs. A2.3 & A2.4). *Osteospermum* spp. contributed little to the aggregate volume or mass (AV = 0.16; AM = 0.23) or the aggregates on average (APV = $0.36 \pm 0.51\%$, n=8; APM = $0.34 \pm 0.324\%$, n=8) and were abundant in only two samples (see Figures A2.5 & A2.6 and Table 18). Both species (*Osteospermum sinuatum* and *O. acanthospermum*) have highly drought tolerant pods and have a low water content (as seen from the disparity between AV and AM in Tables 16 & 17). Numerically they provide a ratio (ANi:NJ) of 101:8. All of the other species of the Asteraceae were represented by their flowers and individual florets. Several widespread species of annuals (*Cuspidia cernua*, *Leyssera tenella*, *Ursinia cf. cakilefolia*) and perennial shrubs (*Rosenia humulis* and *Sonchus* sp.) were represented by large numbers of flowers in only a few individuals. This led to large disparities in the values shown in Tables 16 and 17. Their representation by mostly floral remains also caused a marked difference in their relative "importance" as inferred by the volumetric and gravimetric analysis due to the high water content of such organs.

Both *R. humulis* (a perennial) and *Cuspidia cernua* (an annual) are serotinous species (there is a canopy storage of seeds and the seeds are usually retained in the capitulum until favourable conditions; Hoffman and Cowling, 1987) and as such are likely to be sources of food for longer than the extent of the active flowering period.

The majority of the Asteraceae represented in the diet were annuals or other plants commonly associated with disturbed soils (Tables 16 & 17).

The Mesembryanthemaceae (mesemb family) is a predominantly southern African family of about one hundred and twenty genera, with several thousand described species (Dyer, 1975), and is represented by a large number of species in the Karoo that are important sources of food and water for a wide range of herbivores, especially livestock. They were represented in the diet of the Karoo Korhaan by a large number of flowers in sample 14, leaves in samples 4 and 15 and several of the distinctive seed capsules in samples 1, 3 and 9. The seed capsules resembled the characteristic, globular

TABLE 16: A comparison of the aggregate volume, aggregate percentage volume and percentage occurrence of plant food items represented in the stomachs of Karoo Korhaans collected during the period 1986 - 1987.

	AGGREGATE VOLUME ¹	AGGREGATE PERCENTAGE VOLUME	PERCENTAGE OCCURRENCE ²
Asteraceae (Total)	10.79	13.91	86.67
<i>Osteospermum</i> spp.	0.16	0.36	53.33
<i>Ursinia</i> sp.	3.41	10.99	26.67
<i>Rosenia</i> sp.	1.85	8.65	26.67
<i>Cuspidia</i> sp.	0.06	0.27	26.67
<i>Dimorphotheca</i> sp.	0.02	0.13	13.33
<i>Sonchus</i> sp.	1.85	12.95	13.33
<i>Pteronia</i> sp.	0.16	1.78	6.67
<i>Leyssera</i> sp.	1.04	8.74	13.33
<i>Felicia</i> sp.	0.55	3.56	13.33
<i>Dicoma</i> sp.	1.56	10.41	13.33
Asteraceae (indet.)	0.14	2.43	6.67
Mesembryanthemaceae	0.44	1.75	40.00
<i>Trichodiadema</i> sp.	0.14	3.47	6.67
(indet.)	0.30	1.32	33.33
Chenopodiaceae			
<i>Atriplex</i> sp.	4.99	10.52	66.67
Solanaceae (Total)	6.56	7.93	73.33
<i>Solanum</i> sp.	2.23	7.78	33.33
<i>Lycium</i> sp.	3.97	10.77	26.67
(indet.)	0.36	2.60	20.00
Fabaceae (Total)	0.07	0.41	26.67
<i>Melolobium</i> sp.	0.01	0.15	20.00
<i>Crotularia</i> sp.	0.05	0.59	6.67
Legume (indet.)	tr ³	0.07	6.67
Cucurbitaceae			
<i>Kedrostis</i> sp.	0.03	0.30	6.67
Zygophyllaceae (Total)	0.88	3.70	20.00
<i>Z. retrofractum</i>	0.85	10.71	6.67
<i>Tribulus terrestris</i>	0.02	0.18	6.67
(indet.)	0.01	0.22	6.67
Asclepiadaceae (Total)	1.07	5.56	13.33
<i>Microlomma</i> sp.	0.11	0.71	6.67
(indet.)	0.96	10.40	6.67
Brassicaceae			
<i>Lepidium</i> sp.	0.28	0.72	33.33
Euphorbiaceae			
(indet.)	0.22	0.95	33.33
Scrophulariaceae			
<i>Aptosimum</i> sp.	0.01	0.11	26.66
Aizoaceae			
<i>Tetragonia</i> sp.	0.01	0.46	6.67
Sapindaceae			
<i>Pappea</i> sp.	0.03	0.69	6.67
Labiatae			
<i>Leucas</i> sp.	0.19	1.45	40.00

continued overleaf..

TABLE 16:cont.

	AGGREGATE VOLUME ¹	AGGREGATE PERCENTAGE VOLUME	PERCENTAGE OCCURRENCE ²
Poaceae (Total)	0.44	1.79	13.33
<i>Eragrotis</i> sp.	0.33	2.14	6.67
<i>Zea mays</i>	0.11	1.44	6.67
Iridaceae (indet.)	8.62	52.41	13.33
Asparagaceae	tr	tr	6.67
Polygalaceae	tr	tr	6.67
Sterculiaceae	tr	tr	6.67
Seeds (indet.)	0.32	0.93	86.67
Vegetation (indet.)	55.21	55.98	100.00
TOTAL VEGETATION	90.26	88.58	100.00

1 Wet volume (c.c) as a percentage of the total wet volume

2 N = 15

3 Trace = <0.01%

TABLE 17: A comparison of the aggregate dry mass, aggregate percentage dry mass and percentage occurrence of plant food items represented in the stomachs of Karoo Korhaans collected during the period 1986 - 1987.

	AGGREGATE DRY MASS ¹	AGGREGATE PERCENTAGE MASS	PERCENTAGE OCCURRENCE ²
Asteraceae (Total)	6.30	7.24	86.67
<i>Osteospermum</i> spp.	0.23	0.34	53.33
<i>Ursinia</i> sp.*	1.20	6.28	26.67
<i>Rosenia</i> sp.	1.24	5.38	26.67
<i>Cuspidia</i> sp.*	0.05	0.18	26.67
<i>Dimorphotheca</i> sp.*	0.03	0.23	13.33
<i>Sonchus</i> sp.	1.23	7.98	13.33
<i>Pteronia</i> sp.	0.22	3.00	6.67
<i>Leyssera</i> sp.	0.69	3.31	13.33
<i>Felicia</i> sp.	0.60	5.06	13.33
<i>Dicoma</i> sp.*	0.73	4.97	13.33
Asteraceae (indet.)	0.07	0.62	6.67
Mesembryanthemaceae	0.77	3.80	40.00
<i>Trichodiadema</i> sp.	0.02	0.44	6.67
(indet.)	0.75	4.64	33.33
Chenopodiaceae			
<i>Atriplex</i> sp.*	10.00	19.01	66.67
Solanaceae (Total)	10.98	14.38	73.33
<i>Solanum</i> sp.*	5.68	17.10	33.33
<i>Lycium</i> sp.*	4.63	16.25	26.67
(indet.)	0.67	3.85	20.00
Fabaceae (Total)	0.03	0.26	26.67
<i>Melolobium</i> sp.	0.01	0.07	20.00
<i>Crotularia</i> sp.	0.02	0.33	6.67
Legume (indet.)	0.01	0.12	6.67
Cucurbitaceae			
<i>Kedrostis</i> sp.	0.01	0.17	6.67
Zygophyllaceae (Total)	0.60	2.94	20.00
<i>Z. retrofractum</i> *	0.55	8.24	6.67
<i>Tribulus terrestris</i> *	0.01	0.20	6.67
(indet.)	0.03	0.38	6.67
Asclepiadaceae (Total)	0.83	5.23	13.33
<i>Microlomma</i> sp.	0.20	1.72	6.67
(indet.)	0.63	8.75	6.67
Brassicaceae			
<i>Lepidium</i> sp.*	0.53	1.78	33.33
Euphorbiaceae			
(indet.)	0.36	1.34	33.33
Scrophulariaceae			
<i>Aptosimum</i> sp.	0.01	0.07	26.66
Aizoaceae			
<i>Tetragonia</i> sp.*	0.01	0.41	6.67
Sapindaceae			
<i>Pappea</i> sp.	0.04	0.90	6.67
Labiatae			
<i>Leucas</i> sp.*	0.39	1.19	40.00

continued overleaf..

TABLE 17:cont.

	AGGREGATE DRY MASS ¹	AGGREGATE PERCENTAGE MASS	PERCENTAGE OCCURRENCE ²
Poaceae (Total)	0.77	3.62	13.33
<i>Eragrotis</i> sp.	0.50	4.22	6.67
<i>Zea mays</i> *	0.27	3.03	6.67
Iridaceae (indet.)	7.32	42.50	13.33
Asparagaceae *	tr ³	tr	6.67
Polygalaceae	tr	tr	6.67
Sterculiaceae	tr	tr	6.67
Seeds (indet.)	0.36	0.93	86.67
Vegetation (indet.)	40.11	40.49	100.00
TOTAL VEGETATION	79.60	78.94	100.00

1 Dry mass (g) as a percentage of the total dry mass

2 N = 15

3 Trace = <0.01%

* Annuals or perennials associated with disturbance.

capsules of *Aridaria* spp. Karoo Korhaans have been observed pecking at plants of this species for the capsules (pers. obs. and W. R. J. Dean pers. comm.) which, being fleshy, are likely to be more palatable than the capsules of other species. The leaves (of sample 4) and flowers (of sample 14) were unrecognisable, but contributed the majority of the mesemb material. The distinctive, succulent leaves of the mesemb *Trichodiadema cf. barbaratus* certainly have a high water content as can be seen from the difference between APV and APM in Tables 16 and 17. Mesembs contributed $3.8 \pm 6.41\%$ to the APM and $1.75 \pm 1.51\%$ to the APV.

The seed capsules of the naturalized alien fodder plant, *Atriplex semibaccata* (Chenopodiaceae), were numerous in the diet. The mainly arid and semi-arid distribution of the species makes it important to livestock in disturbed and over-grazed areas. The winged, spongy, triangular and extremely fibrous seed-case encloses a single brownish, lenticular seed. These seeds were found in large numbers in several of the samples and were common throughout the samples (Table 18). Like the seeds of other plants which recruit readily able to disturbed sites, the seeds of this species, when available, are abundant.

The family of plants that contributed the most to the dry mass and numerical analyses (Tables 17 & 18; Fig. A2.4) were the Solanaceae. The family contributed an APV of $7.93 \pm 13.53\%$ ($n=11$) and an APM of $14.38 \pm 12.96\%$ ($n=11$) and was represented by two distinctive genera. Seeds and fruits of *Solanum* sp. were found in five samples. The *Solanum* genus contains a wide variety of herbs and shrubs and several have become widespread weeds in South Africa (Henderson and Anderson, 1966). *Solanum* spp. accounted for a large proportion of the total and individual samples (Tables 16, 17 & 18). *Lycium* spp. are widespread dwarf to medium-high spinescent shrubs that are generally unpalatable to livestock, although the berries are an important food source for many birds. Only represented in four samples, the disparities between the figures in Table 16 and those in Table 17 are due to the concentration of over 100 fruits in sample 1 (see also Figures A2.5 & A2.6). Both species are characteristic of disturbed and slightly to seriously overgrazed habitats. The numerical analysis (Table 18) is based on an assumption, 15 seeds per fruit (the approximation was made from investigation of fruits found in sample 1).

The poor representation in the diet of economically important families such as the Fabaceae (i.e. *Melolobium* sp.) and the Cucurbitaceae (i.e. *Kedrostis* sp.) is probably because they are amongst the first plants to disappear from a plant community subjected to long-term selective grazing (B. Bayer, pers. comm.). The red fruits of the perennial cucurbit, *Kedrostis* sp. are thought to be well adapted for avian dispersal (Dean W.R.J., pers. comm.). However, only one ovoid, beaked fruit of this species was found in the stomach samples.

The small 4-5 winged capsules of *Zygophyllum* spp. contributed little to the overall analysis. However the leaves of *Z. retrofractum* dominated sample 3, in which 1400 leaves were present, constituting a substantial proportion of the contents of that sample (APV = 10.71% and APM =

TABLE 18: The numerical representation of the occurrence of plant food items in the stomachs of Karoo Korhaans collected during the period 1986 - 1987.

	MEAN (S.D) ¹		OCCURRENCE RATIO (ANi:NJ)	REPRESENTED INDIVIDUALS
Asteraceae				
<i>Osteospermum</i> spp.	12.6	(25.13)	101: 8	1,2,4,5,8,9,11,12
<i>Ursinia</i> sp.	10.0	(8.49)	40: 4	11-14 ¹
(72.7	(117.22)	218: 3	12-14) ²
<i>Cuspidia</i> sp.	24.7	(17.04)	74: 3	1,2,5
<i>Dimorphotheca</i> sp.	4.0	(2.83)	8: 2	7,8
<i>Felicia</i> sp.	36.0	(48.08)	72: 2	9,11
<i>Dicoma</i> sp.	19.0	(18.39)	38: 2	2,3
Asteraceae (indet.)	57.0	(0.00)	57: 1	2
Mesembryanthemaceae				
<i>Trichodiadema</i> sp.	23.0	(0.00)	23: 1	15
Chenopodiaceae				
<i>Atriplex</i> sp.	769.1	(886.15)	7691:10	2-10,15
Solanaceae				
<i>Solanum</i> sp.	744.4	(1045.57)	3722: 5	4-7,9
(3.0	(0.00)	3: 1	5) ³
<i>Lycium</i> sp.	776.5	(1428.43)	3106: 4	1,12,13,15
(52.3	(95.22)	209: 4) ⁴
(indet.)	230.3	(216.64)	691: 3	2,3,11
Fabaceae				
<i>Melolobium</i> sp.	4.3	(1.53)	13: 3	1,2,6
<i>Crotularia</i> sp.	8.0	(0.00)	8: 1	1
Legume (indet.)	2.0	(0.00)	2: 1	15
Cucurbitaceae				
<i>Kedrostis</i> sp.	1.0	(0.00)	1: 1	1
Zygophyllaceae				
<i>Z. retrofractum</i>	1400.0	(0.00)	1400: 1	3
<i>Tribulus</i> sp.	9.0	(0.00)	9: 1	1
(indet.)	10.5	(8.58)	42: 4	1,3,4,9
Asclepiadaceae				
<i>Microlomma</i> sp.	98.0	(0.00)	98: 1	11
Euphorbiaceae				
(indet.)	16.6	(11.78)	83: 5	4,6-9
Scrophulariaceae				
<i>Aptosimum</i> sp.	5.8	(5.5)	23: 4	8,9,10,12
Aizoaceae				
<i>Tetragonia</i> sp.	1.0	(0.00)	1: 1	10
Sabindaceae				
<i>Pappea</i> sp.	1.0	(0.00)	1: 1	15
Labiatae				
<i>Leucas</i> sp.	16.7	(21.44)	106: 6	4-7,9,10

continued overleaf..

TABLE 18: cont.

	MEAN (S.D) ¹		OCCURRENCE RATIO (ANI:NJ)	REPRESENTED INDIVIDUALS
Poaceae				
<i>Zea mays</i>	1.0	(0.00)	1: 1	8
Iridaceae (indet.)	24.0	(31.11)	48: 2	5,6
Asparagaceae	1.0	(0.00)	1: 1	14
Polygalaceae	1.0	(0.00)	1: 1	6
Sterculiaceae	2.0	(0.00)	2: 1	11
Seeds (indet.)	13.3	(17.25)	133:10	3-5,7,8,11-15
TOTAL (BY ITEM)⁵	539.7	(1537.05)	17811:33	1-15
TOTAL (BY BIRD)⁶	1187.4	(1039.22)	17811:15	1-15

- 1 Mean number of items with standard deviations in parentheses
- 2 Whole flowers (not including separate, individual florets)
- 3 Entire fruits (one fruit contains >20 seeds)
- 4 Number of fruits calculated from number of seeds.
- 5 Average number of individual items
- 6 Average number of individual items per bird.

8.24%). The other recognisable member of the Zygophyllaceae, *Tribulus terrestris*, with its strongly spined seed capsules, is a species characteristic of disturbed ground.

Unrecognisable Asclepiadaceae remains were present in sample 1 and dominated that sample (Table 16 and 17). Because of their representation in only two samples, asclepiads contributed little to the overall analyses but were important components items in those samples in which they occurred.

Members of the Brassicaceae can dominate disturbed landscapes (Leistner, 1979). Although not contributing greatly to the diet (Tables 16 and 17) the flowers of *Lepidium cf. desertorium*, an annual (and sometimes biennial), were abundant in one sample (Figures A2.3,c and A2.4,c) contributing 1.60% to the volume and 3.76% to the mass of that sample (sample 11) but were not quantifiable numerically. The genus is considered to be a widespread weed (Henderson and Anderson, 1966).

The tri-locular, capsular pods of *Euphorbia* sp. were found in five samples and had an APV of $0.95 \pm 0.45\%$ and an APM of $1.34 \pm 0.7\%$. The pods were mostly found as single (similar sized) locules containing a single pendulous ovule. These explosively autelochorous pods are persistent and would most likely have been obtained from the parent plant. Another plant species with an autelochorous pod, found in one of the samples, was the widespread perennial shrub, *Tetragonia* sp. The large, hard, dry terete pod of this species was found in sample 10, but contributed little to the diet (Tables 16 and 17).

An important dietary component in terms of the aggregate percentages shown in Tables 16 and 17 was *Leucas capensis* (Lamiaceae). The dry, ovoid, triquetrous "nutlets" (four to a fruit) were found in large numbers in samples 4 and 6 (224 and 106 respectively), and contributed an APV of $1.45 \pm 2.26\%$ and an APM of $1.19 \pm 1.22\%$. The numerical analysis (as explained for *Euphorbia* sp.) divided the number of "nutlets" by four. Although a widespread species, it is less common in the western portion of the Cape Province and therefore must be considered an item of interest; but with no knowledge of its true distribution in the area of collection, it is impossible to conclude that the species is "selected" in dietary terms. This species, considered to be "passively" dispersed (Hoffman and Cowling, 1987), may be endozoochorously adapted for dispersal by such species as the Karoo Korhaan by virtue of the resistant nature of the nutlets.

The large amount of *Eragrostis lehmanniana* in sample 11 illustrates the problem of representing an item fairly when it dominates one sample and is absent from all other samples. This common grass of the Central Upper Karoo (VT. 27) and Arid Karoo (VT. 29) is a perennial "white grass", an important fodder plant in the Karoo and responds well to rain. Another member of the Poaceae, *Zea mays* was conspicuous in sample 8. The individual was collected from fallow lands on a farm in summer. The maize seed could have been a remnant of cultivation or of stock feed-supplementation, a widespread practice in such areas during summer drought.

The most important items in terms of the aggregate percentage analyses (see Tables 16 & 17) were the corms of a member of the Iridaceae. Korhaans may have obtained these by scratching at the ground with their powerful nailed feet or they could have been obtained from the remnants of digging by another species (e.g. Porcupines *Hystrix africaeaustralis* or Aardvarks *Orycteropus afer*). The corms of this species dominated samples 5 and 6 (APV = $52.41 \pm 56.14\%$; APM = $42.50 \pm 53.68\%$) and, as such, the overall importance of this item in the diet is over-estimated.

The high concentrations of certain items in a few samples increases their importance in the overall analyses. Tables 19 and 20 (and the Figures A2.7 and A2.8) show a breakdown of the major categories of the items in the diet. The importance of plant items in the diet was reduced after drying because of the high water content of items such as flowers (see Tables 19 & 20). Flowers, seeds and fruits dominated the recognisable vegetable fraction (see Figures A2.7 & A2.8). The division of seeds into seeds, pods and fruits illustrated that seeds and fruits are of equal importance. Pods are not so important, probably due to the scarcity of legumes in the Karoo. The importance of seeds must be further elevated because they are, generally, widely dispersed. The seeds of *Atriplex semibaccata* are often available in abundance and the occurrence of large quantities of them - in 66% of the samples (see Table 18) - represents an "important" item in all of the analyses.

GENERAL RESULTS

The stomach contents accounted for $68.94 \pm 13.55\%$ of the total dry mass of the gut contents on average and had an average dry mass of $8.96 \pm 3.86\text{g}$ (n=15).

Galls were found in 40% of the samples (see Tables 19 & 20; Figures A2.7,g & A2.8,g). Neither the host plant nor the parasite could be identified. Many species of insects produce galls and constitute some of the most important pests of cultivated crops (Scholtz and Holm, 1985). Some of the numerous gall-producing species are hymenopterans. It is interesting to note that the Tephritidae, found parasitising the flowers of *Pteronia* sp. are also known to form galls. No definition of the larvae was observable and therefore it was not possible to determine the type of parasite. The ingestion of galls may be incidental; korhaans mistaking them for fruits. Although the hard structure of the gall itself is indigestible, the larvae in most cases were decomposed. Galls have also been found in the stomach of a Black Korhaan (*Eupodotis afra*; pers. obs.).

Gastroliths occurred in all of the samples (see Tables 19 & 20; Figures A2.1 & A2.2) and occurred in all sections of the gut but not consistently throughout each individual. The most commonly occurring gastroliths were fragments of shale and grains of sand smaller than 1mm which are likely to represent mainly "accidental" ingestion. The mean size of particles was similar in all portions of the gut: stomach = $1.67 \pm 0.82\text{mm}$ (n=15); small intestine = $1.26 \pm 0.67\text{mm}$ (n=10); Caeca = $1.77 \pm 0.22\text{mm}$ (n=5) and rectum = $1.32 \pm 0.46\text{mm}$ (n=14). The stomach contained some sizeable stones (the largest being in excess of 10mm in diameter). The mean size of gastrolith did not vary

TABLE 19: A comparison of the aggregate volume, aggregate percentage volume and percentage occurrence of the major categories of food items represented in the stomachs of Karoo Korhaans collected during the period 1986 - 1987.

	AGGREGATE VOLUME ¹	AGGREGATE PERCENTAGE ² VOLUME	PERCENTAGE OCCURRENCE ³
Animal	6.22	7.34 (1.90)	100.00
Vegetable	90.26	88.58 (8.05)	100.00
Seeds, Pods & Fruits	12.92	13.71 (13.09)	100.00
Seeds	5.78	7.25 (8.91)	100.00
Pods	0.52	0.79 (0.64)	86.67
Fruits	6.61	8.12 (13.54)	66.67
Flowers	12.14	15.88 (13.37)	93.33
Leaves	1.18	5.75 (4.30)	40.00
Bulbs	8.62	52.41 (56.41)	13.33
Galls	0.11	0.48 (0.67)	40.00
Misc. Veg	55.29	55.95 (21.38)	100.00
Gastroliths	1.52	1.81 (2.79)	100.00
Parasites	2.00	2.43 (2.45)	93.33
TOTAL	100.00		

1 Wet volume as a percentage of the total volume.

2 Standard deviations in parentheses

3 N = 15

TABLE 20: A comparison of the aggregate dry mass, aggregate percentage dry mass and percentage occurrence of the major categories of food items represented in the stomachs of Karoo Korhaans collected during the period 1986 - 1987.

	AGGREGATE DRY MASS ¹	AGGREGATE PERCENTAGE ² MASS	PERCENTAGE OCCURRENCE ³	
Animal	11.89	12.36	(9.08)	100.00
Vegetable	79.60	78.94	(14.60)	100.00
Seeds, Pods & Fruits	23.02	23.97	(23.27)	100.00
Seeds	11.20	12.62	(17.96)	100.00
Pods	0.68	0.90	(0.74)	86.67
Fruits	11.13	14.66	(21.78)	66.67
Flowers	7.81	11.44	(7.45)	93.33
Leaves	0.86	4.02	(3.94)	40.00
Bulbs	7.32	42.50	(53.68)	13.33
Galls	0.16	0.63	(1.07)	40.00
Misc. Veg	40.45	40.64	(19.58)	100.00
Gastroliths	8.51	8.71	(14.41)	100.00
TOTAL	100.00			

1 Dry mass as a percentage of the total dry mass.

2 Standard deviations in parentheses.

3 N = 15

significantly between the sexes ($U = 20$; $p > 0.05$; Mann-Whitney U-test) nor did the number of gastroliths ingested ($U = 19$; $p > 0.05$). No correlation existed between the amount (dry mass) of gastroliths found in the stomachs of all samples and the presence of seeds ($r_{15} = -0.11$, $p > 0.05$; Spearman's correlation) or insects ($r_{15} = 0.186$, $p > 0.05$). There was no correlation between the amount of *Atriplex semibaccata* seeds (with a dry, fibrous seed case) and the amount of gastroliths ($r_{15} = -0.225$, $p > 0.05$).

There was a significant correlation between the dry mass of the stomach contents as a proportion of the total body weight and the time of collection ($F = 4.428$; $p < 0.05$, $n = 14$; Polynomial regression analysis; Fig. 24). Feeding peaks appeared to occur in the early morning and late afternoon (Fig. 24).

The caeca of the Karoo Korhaan had internal "lamellae", that presumably serve to increase the internal surface area for absorption, and were variable in length (130 ± 21.60 mm; SD).

There was no significant correlation between the weights of the caecal contents and the time of collection ($r_{11} = -0.19$, $p > 0.05$; regression analysis). This is to be expected in view of the known long retention times of material the caeca of other species of birds (Gasaway *et. al.*, 1975; Warner, 1981).

The combined structure of the rectum (colon, coprodeum and cloaca) was pouch-like and very little definition was present between the coprodeum and the cloaca. No cloacal bursa was evident and the general structure of the region was unspecialized. The rectum contents of the Karoo Korhaan contained mainly vegetable material; seeds and vegetable fibre that is indigestible or avoided digestion by virtue of bulk. The dominant plant and animal species found in the stomach were present in the rectal samples. The seeds of fruits (endozoochorous seeds) and woody or fibrous pods (actively autochorous) were found more commonly than naked seeds (passively autochorous seeds). Some seeds were present that one would consider to be highly digestible and consequently valuable food items (i.e. *Osteospermum* sp. and *Rosenia humilis*) due to their high relative abundance in the diet of some individuals.

Animal material consisted of indigestible fragments of termites, ants and weevils. The only occurrence of *Trinervitermes* sp. (Isoptera) and Bristle-tails (*Thysanura*) in any of the sections of the gut was in the rectal contents of sample 5. *Thysanura* are photophobic and must have been collected crepuscularly.

The proportion of animal to non-animal contents did not differ between the stomach and the rectum. This implies that most of the animal material is already well digested in the stomach.

There was a significant negative correlation between the dry mass of the rectal contents and the time of collection ($r_{14} = -0.470$; $p < 0.05$; regression analysis), but no significant relationship

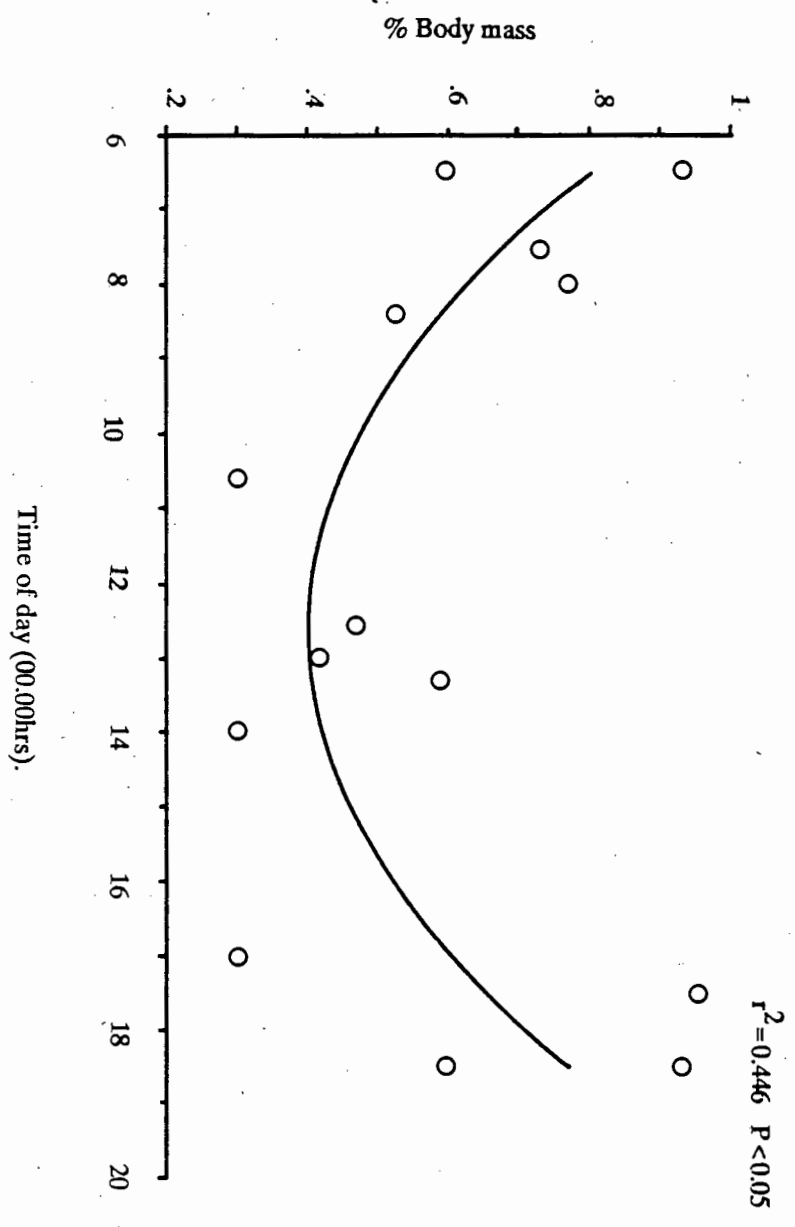


Figure 24. Polynomial regression analysis of gut mass as a proportion of total body mass, against time.

between the weights of the rectal contents and either the stomach contents ($r_{14} = 0.248$; $p > 0.05$) or the contents of the small intestines ($r_{14} = 0.273$; $p > 0.05$). This is to be expected as the rectum plays an important role in storing undigested matter awaiting egestion, retaining about a third as much material as the stomach holds ($APM = 32.174 \pm 31.80$, $n = 14$), and is likely to be out of phase with the filling cycle of the stomach due to the "lag" caused by the intestine in between.

DISCUSSION

The diet of the Karoo Korhaan has not previously been investigated and it has been assumed, as for most bustards, that the species is mainly insectivorous, whilst eating flowers and fruits to a lesser extent (Layard, 1867; Stark & Sclater, 1906; Leighton-Hare, 1915; Maclean, 1985). This assumption is usually based on observations that ignore the main bulk of unrecognisable plant matter found in the stomach of such birds which do not possess a crop. The analyses highlight the fact that vegetation is by far the most prevalent dietary component of this species. This conclusion agrees with the diet analyses of some other bustard species (Dementév & Gladiov, 1951; Valverde, 1957; Pineau, 1964; Palacios *et al.*, 1975).

The flowers of certain species of Asteraceae, Brassicaceae and Mesembryanthemaceae were found in all but one of the samples and are likely to be an important source of energy and water to many species of omnivorous desert birds (e.g. Asteraceae flowers in the diet of the Namaqua Sandgrouse *Pterocles namaqua*; Thomas, 1984). The flowers and seeds of many annual species were also important dietary items. Ephemeral plants can dominate the diet of some bustards (e.g. the Little Bustard *Tetrax tetrax*; Dementév & Gladiov, 1951).

The presence of large numbers of seeds of the alien *A. semibaccata* may indicate a digestive "bottle-neck", where the individual is unable to digest sufficient of these fibrous items to maintain body mass. This has been illustrated for Wood pigeons *Columba palumbus* (Kenward & Sibly, 1977) and for Chukar Partridges *Alectoris chukar sinaica*; Degen & Prinshow, 1984) when forced to subsist on "poor-quality" items. This indicates that items that are considered to be "important" in the analyses may be of limited dietary importance as they are poor quality foods.

Fruits, when available, are generally available in large numbers and are conspicuous, whereas many of the seeds represented in the diet would have been found by searching the substratum for accumulations and therefore are likely to involve a greater effort on behalf of the individual. Corms occurred in two males from the same area, collected on the same day some distance apart. The occurrence of corms in the diet was lower than expected, as geophytic species (especially Iridaceae) were common in the areas of collection (pers. obs., this study). Corms are important dietary constituents for some species of bustards (Meinertzhagen, 1954; Benson, 1962) and Guinea Fowl *Numida meleagris* (Angus and Wilson, 1964; Skead, 1972; Mentis *et al.*, 1975). Leaves contributed

significantly to 40% of the samples (see Tables 19 and 20; Figures A2.7 and A2.8) and are thought to be an important source of water to bustards (e.g. *Parahylia* sp.; White, 1919) and other desert birds (Thomas, 1984; Alkon *et. al.*, 1985). The domination of sample 3 by the leaves of *Zygophyllum retrofractum* could be due to the high water requirements of that individual collected in mid-summer. This species is a halophyte, and korhaans may address a salt requirement by concentrating on the leaves of this species. The leaves of *Zygophyllum* sp. have also been recorded in the diet of other desert birds such as the Namaqua Sandgrouse (Thomas, 1984).

By far the most prevalent arthropod items in the diet belong to species of gregarious insects that, when found, are usually present in large numbers. The most important in terms of numbers are the harvester termite *Microhodotermes viator* and the harvester ant *Messor capensis*. The most important items in the animal fraction, in terms of bulk, were weevils. Weevils are generally found in the canopy or around the bases of plants. They represent an important and predictable prey that would often be encountered by a bird that feeds predominantly on plant material. Species known to develop in the bulbs of monocotyledonous plants (Brachycerinae; R. Oberprieler, pers. comm.) occurred in large quantities in samples from Calvinia. Iridaceous plants were conspicuously common in disturbed veld at this locality and may not only be indicative of overgrazing in such areas but also may be an important source of weevils for the Karoo Korhaan. There was a rather unexpected lack of Orthoptera in the diet, considering the wealth of species and their abundance in the Karoo and their importance in the diet of many species of bustards in the southern African sub-region (Leighton-Hare, 1915; Bell-Marley, 1933; Chapin, 1938; Vesey Fitzgerald, 1955; Benson, 1962; Wilson & Ball, 1978; Van Ee, 1987; Earlé, *et. al.*, 1988).

The limitations of the different methods of representing the data in Tables 13 and 14 are illustrated most effectively by the way in which they represent termites in the diet in comparison to the numerical data presented in Table 15. The representation of such "ephemeral" items in the diet is difficult. The body of a termite is an extremely fragile, lightly sclerotized and highly digestible structure. Several authors (Swanson & Bartonek, 1970; Coleman, 1974; Custer & Pitelka, 1975; Lifjeld; 1983) have shown that similar soft-bodied insects have extremely low residence times in the alimentary system of birds. From their conclusions one could predict a "survival" time of between 30 and 60 minutes for termites. Taking this into account and using the numbers of mandibles in the stomach samples, it was clear that termites are an exceedingly important food source. The volumetric and gravimetric analyses, although showing little disparity within and between them, give a much lower importance to termites in the diet than did the numerical analysis. This illustrates the inherent biases of the various methods and how the various sources of bias can be reduced when the results from the different analyses are considered in concert.

The quantitative and qualitative findings of this study indicated that the species feeds most actively in the early morning and the late evening. This complements behavioural observations of "nonchalant" feeding around mid-day (this study). The results indicated that the feeding activity of

Karoo Korhaans is such that the greatest transfer of matter to the lower intestine occurs during the night or early morning, as rectal weights decrease throughout the day. This may be due in part to an increase in the water turnover rate as the day progresses.

Although few conclusions can be made as to their function, it is obvious from the analyses that gastroliths are frequently and regularly ingested. The presence of gastroliths in all sections of the gut and the similarity between the amounts present in the stomach and the rectum (both storage organs) indicates that they are lost (and therefore compensatorily ingested) at a regular rate. Gastroliths are known to aid the mechanical digestion of sclerous items in the diets of birds (Spitzer, 1972; Welty, 1982)

The presence of well developed caeca are often associated with species that feed preferentially (in terms of bulk) on plant matter (Zisweiler & Farner, 1972; Richardson & Woller, 1986). The development of long caeca in the Karoo Korhaan may also be an adaptation to living in an arid environment. In the Karoo, fibrous vegetable food predominates, evaporation exceeds precipitation and water is therefore scarce and there are wide fluctuations in temperature. The advantages of having efficient caeca are therefore adaptive for both dietary (Leopold, 1953; Lewin, 1963; Moss, 1972), physiological (Thomas, 1982) and possibly thermoregulatory (McBee & West, 1969) processes for a species of omnivorous bird in the Karoo.

The above study suggests that there is no sexual dimorphism in the diet. However, it may be possible to predict that females will tend toward greater insectivory whilst raising young, which are primarily insectivorous in the early stages of life (Osborne *et. al.*, 1984).

The contents of the rectum contained the same proportions of animal to vegetable items as were found in the stomach. Therefore, faecal material could be useful in determining the diet of the Karoo Korhaan (and other bustards).

The results of this diet study indicate that the Karoo Korhaan is a highly opportunistic omnivore, responding to the highly unpredictable availability of both animal and plant foods by feeding on whatever resources are abundant. The Karoo, and indeed many similar, semi-arid environments, are characterised by extreme seasonal fluctuations in primary productivity (Noy-Meir, 1973). These fluctuations are particularly pronounced in annual plants, which are highly successful pioneers of disturbed soils (Werger, 1978). The dominance in the diet of the Karoo Korhaan of species that favour or are tolerant of disturbed ground and the large number of species that are associated with intensive grazing and other forms of disturbance, indicates that the Karoo Korhaan itself is a highly successful species of such areas. Whether the sample studied is representative of the population as a whole, is not known. However, this sample is sufficient to illustrate the opportunism of the species. With a more comprehensive knowledge of the phenology and life-history traits of the plants and animals of the Karoo, it would be possible to "predict" the diet of Karoo Korhaans in an area by surveying resource

availability. The high incidence of endozoochorous seeds in the diet may indicate that the Karoo Korhaan is an important disperser of seeds; especially of species such as *Lycium* spp. that are considered to be important "nurse plants" (W. Bond pers. comm). Karoo Korhaans may thus play a role in the reclamation of degraded areas and the spread of certain "invasive" Karoo pioneers into vegetation types bordering the Karoo biome.

Considering the results of the diet study in conjunction with the analysis of habitat preference, it is clear that the presence of annual plants in areas of unpredictable rainfall is very important. Chapters 2 and 3 concluded that the variety of perennial shrubs was an important factor in habitat choice of the species and that mesembs were important on a local scale (although not favoured at the landscape level). These findings tie in with dietary analysis in that the flowers and fruits of a wide variety of perennial shrubs are important dietary components and that the leaves and flowers of mesembs can dominate the diet of individuals.

CHAPTER SIX

GROUP SIZE IN THE KAROO KORHAAN

INTRODUCTION

Karoo Korhaans are endemic to the xerophytic, dwarf shrublands of southern Africa (Winterbottom, 1961) and are most commonly encountered in groups of two (Quinton, 1948) in vegetation not exceeding 0.5m in height (MacDonald, 1957). All indications point to a sexual strategy of strict monogamy, with the male and female pair bond lasting throughout the year and from year to year (Quinton, 1948). The male and female defend a territory throughout the year, excluding conspecifics, by use of a song. The song is a territorial, epideictic, duet. The duet is usually initiated by the male in response to intrusion by conspecifics, to the duet of neighbouring conspecifics, and at twilight in the morning and evening (Anon, 1931).

The Bustard family (*Otididae*), to which the korhaans belong, generally exhibits delayed maturity of up to six years, with females reaching sexual maturity earlier than males (Osborne *et al.*, 1984). Although groups of Karoo Korhaans are most frequently pairs, groups of three, four and, rarely, five individuals do occur. The composition of the groups of more than two individuals is generally thought to represent family groups (Quinton, 1948). This is comparable to closely related species such as the Rüppell's Korhaan of Namibia (Viljoen, 1983) and the Blue Korhaan of South Africa *Eupodotis caerulescens* (Maclean, 1983; Vernon, 1983). It is generally assumed that the Karoo Korhaans' offspring remain in the natal territory for an extended period (Quinton, 1948). However this cannot be taken as a general rule, otherwise groups of more than two birds would be more common than they in fact are. This study aims to test the hypothesis that the group size in Karoo Korhaans is a function of particular habitat parameters and that groups of more than two represent "group territories", wherein each individual accrues benefits from an increase in group size. The assumption that young "sometimes" remain with their parents infers that parent groups defend territories large enough to support one or more additional individuals, and therefore the extra group members make few competitive demands upon that territory. Were this the case, the original pair would be seen as "area maximisers" (Hixon, 1980, 1982) defending an area greater than that necessary to minimize foraging time, in order to maximise reproductive success. The previous chapters have shown that groups favour areas with a wide variety of species and are opportunistic in exploiting a wide variety of both animal and plant resources. I wish to argue therefore, that because the species feeds on a broad range of resources that are widely distributed within their territories, Karoo Korhaans may be "energy maximisers" (Davies & Houston, 1981; Brown, 1982; Stamps, 1985) which respond to increased intruder pressure by augmenting the group size from within, therefore keeping defence costs at a minimum. I hypothesize that habitat quality is a determinant of group size in the Karoo Korhaan and therefore that optimum group size varies from place to place.

METHODS

The study was conducted from March 1986 to August 1987, with seasonal observations in July and October 1986, February, May-June and July-August 1987 in the western Cape Province. Most of the

data were collected at permanent study sites near Touwsrivier, the Ceres Karoo, Sutherland and between Beaufort West and Aberdeen (Fig.1). Additional data were collected on numerous road censuses in other areas of the western and eastern Cape Province. The group size and, when possible, the group composition were recorded.

The sizes of Karoo Korhaan groups were noted by initiating a territorial dispute, using a tape-recorded "male-female" duet. The taped duet was recorded on a loop tape, with a cycle time of 45s and was played through a megaphone loud-speaker. The tape was effective in eliciting a response from Karoo Korhaan groups over a distance of 1000m on wind-free days.

The territorial boundaries between neighbouring groups were difficult to delineate, as individuals respond from within the territorial boundaries and do not move to the limits of the territory as do some other territorial species (e.g. Pied Wagtails *Motacilla alba*, Davies & Houston, 1981). Territory size was estimated by plotting the location of territorial individuals on a map of the respective areas and calculating the spacing density of groups. This does not take into account the possibility of vacant territories but indicates the spacing density of territorial groups and gives an indication of the territory sizes. However, the areas measured corresponded to clumps of territorial groups, isolated groups being omitted from the calculations and it is thought that this method gives a fairly accurate indication of territory size.

Meteorological data were difficult to obtain for the exact localities of the study sites, many of the local weather stations having long been closed. The data used in Table 21 were taken from old records of local stations before their disbandment, or from the nearest station of similar altitude (Fig. 1).

The sexes were distinguished by: relative size (the weights of fifteen individuals collected between March 1986 and July 1987 showed a significant difference in mean weight between the sexes; t test, $t=5.03$, $p<0.01$; Table 22); extent of the throat-patch (an important visual component of the territorial display); the colouration of the wing coverts (more heavily mottled in the female); but most reliably by the part each plays in the duet.

RESULTS

The duet is considered to be a spacing mechanism of territorial defence and is supplemented visually by the display of a black throat-patch in both males and females (although the extent of the patch and therefore its visibility over distance, is greatest in the male). In prolonged territorial disputes, in areas of high density, fighting between groups occurs (albeit rarely).

The response to the taped duet varied from a reply by both male and female and additional members of the group, to an active approach by the group to the source (if the tape was played within the territory of the group).

TABLE 21: Mean annual rainfall for the study sites using the nearest appropriate Weather station of similar altitude.

STATION CODE	COORDINATES	RAINFALL	BASED ON
CERES	0043/516 33°06'00" 19°48'00"	109.7	31yrs
BEAUFORT WEST	0093/200 32°20'00" 23°07'00"	180.8	6yrs
TOUWSRIVIER	0044/50 33°20'00" 20°02'00"	218.2	63yrs
SUTHERLAND	0088/293 32°23'00" 20°40'00"	247.6	64yrs

Rainfall is in millimetres.

TABLE 22: A comparison of the weights of individual Karoo Korhaans collected between July 1986 and July 1987.

	MEAN	S.E	N	t=	
MALES	1597.5	27.18	8	5.03	**
FEMALES	1352.8	40.3	6		

Weights in grams with standard errors. Sample size (N) is the number of individuals of each sex collected. Two-tailed significance level determined by t test; **, $p < 0.01$

BEHAVIOURAL OBSERVATIONS OF KAROO KORHAANS -

DEFENDING TERRITORIES

At Touwsrivier a pair of Karoo Korhaans was observed closely during each visit to the site. The male of the pair was recognisable by a featherless scar on the left side of his neck on the throat patch. This pair remained, for the duration of the study, in the vicinity of a pole that marked the first sighting. Observations of this pair showed that the male was always the first to respond to the recorded duet. In one 30 minute observation period, both called for 10 minutes in response to the tape played at 2 minute intervals. After 10 minutes the tape was not played, the female resumed feeding after one minute whilst the male remained vigilant. The male frequently gave a gruff call and scanned the area and the sky. After 15 minutes the tape was played, giving two duet sequences. The male immediately responded and continued to call alone for five minutes. The female did not call but scanned the area and approached the male. The male generally spent more than twice the time calling in territorial disputes than the female did and took three times as long to resume foraging. Two groups of three birds observed on the farm "Vereniging" (32°57'S 21°23'E), were observed fighting after both groups replied to and approached the taped duet. The adult male of one group and both males of the other group engaged in "fighting-cock"-like conflict, flapping their wings and kicking with their feet. The females of both groups remained *circa* 5m away. The conflict ended with all members of the two groups walking silently but rapidly away from the site of the dispute.

GROUP SIZES

Of the 344 groups observed between March 1986 and August 1987, 87% were pairs. Only 10% of groups contained more than two individuals of which 75% were groups of three (Fig.25). All groups of two contained one male and one female (n=300 groups). The groups of three (n=20) and four (n=7) contained male/female pairs with one or two additional males. One of the groups of five contained two females, one of which was adult and contributed to the territorial display, the other was a subadult that called out of phase with the other members and did not continue to reply after an initial response to the taped duet. The remaining birds in the group were one adult and two sub-adult males. It was not possible to determine the composition of the other group of five other than to observe that the group consisted of two adults and three smaller individuals. The sex ratios for the different areas are given in Table 23. Extra males in groups of four and five were of different ages. The extra male in groups of three was often difficult to distinguish from the dominant male but in general was smaller in size and had a slightly less extensive throat-patch. The extra male was, however, readily distinguishable from the female, being intermediate in size between the two adults. The extra males in groups of four were of obviously different ages, the third male being considerably smaller than the other individuals, but was recognisably male by call.

GROUP SIZE OF THE KAROO KORHAAN RECORDED AT THE MAJOR STUDY SITES

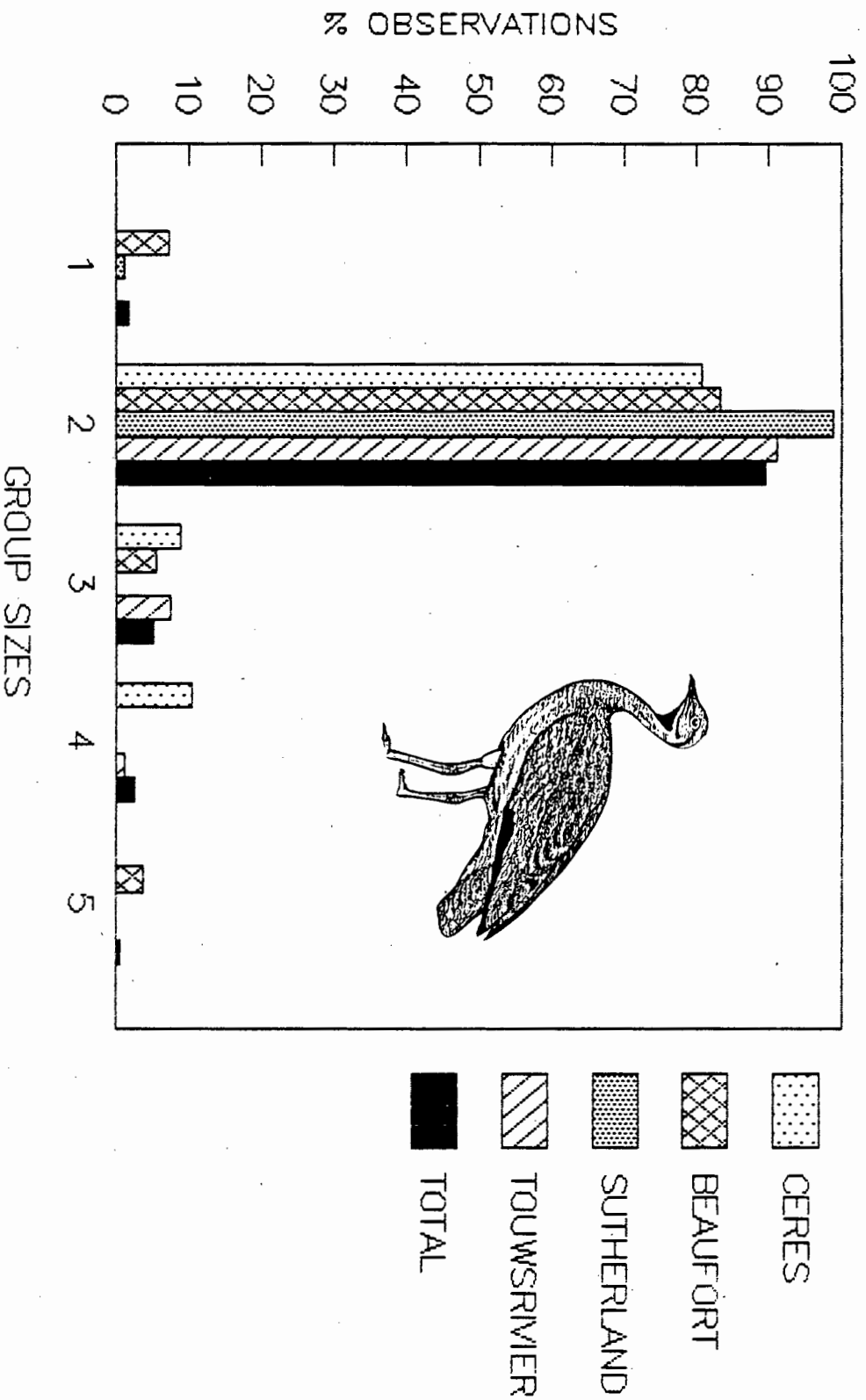


Figure 25.

TABLE.23: Mean number of Karoo Korhaans per group in the study sites recorded from March 1986 - August 1987.

AREA	MEAN	S.E	N	RANGE	RATIO(M:F)
CERES	2.30	0.087	57	2 - 4	1:0.77
BEAUFORT WEST	2.10 (2.17)	0.093 0.083	54 54	1 - 5 2 - 5)	1:0.85
TOUWSRIVIER	2.10	0.039	79	2 - 4	1:0.91
SUTHERLAND	1.99 (2.00)	0.013 0.000	79 79	1 - 2 2 - 2)	1:0.99
TOTAL	2.11	0.026	344 344	1 - 5 2 - 5	1:0.88

Sex ratios and the range of group sizes. Values with groups of one corrected to groups of two are shown in parentheses.

The mean group size for all areas was 2.11 ± 0.3 (S.E), ($n=344$ groups, range = 1-5; Table 23). The mean group size of the Karoo Korhaan is significantly lower than that recorded for the Blue Korhaan (Vernon, 1983; Maclean *et al.*, 1983) and Rüppell's Korhaan (Viljoen, 1983; Table 24). The mean group sizes differed significantly between areas although group sizes at Beaufort West were similar to both Touwsrivier and Sutherland (Table 25).

As the species only maintains territories in groups of two or more it was assumed that the solitary individuals (males) replying to the recorded territorial duet must represent pairs in which the female did not respond. All single birds were recorded during the breeding season and in one instance, one of the groups of two was recorded as a single individual until a female was flushed (although no nest was found). Groups of one were corrected to pairs in further analysis (the absence of more than one adult female from all but one of the 344 groups encountered indicated that Karoo Korhaans are not polygamous). With this correction, there was a more significant variation in group size between sites (Kruskal-Wallis $H=16.04$, $p<0.05$). Group size at Sutherland was significantly smaller than at Beaufort West, and both Beaufort West and Touwsrivier showed similarities with Ceres (Table 25).

Although there was a significant location effect upon group size (Tables 25, 26), there were no significant seasonal differences in group size from site to site (Table 27). The average rainfall for each of the sites is shown in Table 21. There is a highly significant negative correlation between group size and rainfall, (Fig. 26) with the largest group sizes occurring in low rainfall areas.

Table 28 shows the spacing density of territorial groups in the respective areas. There was a significant negative correlation between spacing of territorial groups and rainfall with territorial groups occurring at low densities in low rainfall areas (Table 28; Figs. 26, 27). The highest density of Karoo Korhaans occurred at Touwsrivier, with a mean density of 1.85 groups Km^{-2} . There was significantly greater seasonal variation in group spacing at Sutherland than at all other sites (Table 28). Touwsrivier exhibited similar variation in seasonal spacing to both Ceres and Beaufort West. There was a significant positive correlation between spacing and group size (Fig.28).

DISCUSSION

Causes of variation in group size have been studied extensively in many taxa and a plethora of ecological correlates have been identified (for reviews see Brown, 1964; Caraco, 1979a,b; Brown, 1981, 1982; Pulliam & Caraco, 1984; Stamps, 1985). The advantages of an increase in group vigilance (for predator detection), is, perhaps, the best-supported example of a positive benefit to an individual joining a large group (Hamilton, 1971; Treseman, 1975; Siegfried & Underhill, 1975; Lazarus, 1978). The decrease in time spent scanning for predators due to the increased vigilance of the group allows the individual to spend more time foraging (Berger, 1978; Caraco, 1979; Pulliam & Caraco, 1983). Living in large groups may increase the foraging efficiency of individuals (Krebs *et al.*, 1972; Krebs, 1974; Drent & Swierstra, 1977), who are able to see where others are feeding profitably. Large groups

TABLE 24: Comparison of the mean group sizes of the Karoo Korhaan and two other closely related species of korhaan endemic to the southern African region.

	MEAN	S.E	N	RANGE	H	
Karoo Korhaan (<i>Eupodotis vigorsii</i>)	2.11	0.03	344	1 - 5		
Rüppells Korhaan ¹ (<i>Eupodotis rueppellii</i>)	2.35	0.08	189	1 - 8	8.77	**
Blue Korhaan ² (<i>Eupodotis caerulescens</i>)	3.39	0.07	572	1 - 11	199.37	**

Two-tailed significance levels determined by Kruskal-Wallis one-way ANOVA: ** = $p < 0.01$.

¹ After Viljoen, 1983.

² After Maclean (*et al.*), 1983; Vernon, 1983.

TABLE.25: Comparison of the mean number of Karoo Korhaans per group at the study sites.

	MEAN	S.E	N	RANGE	H	LEVEL
ALL AREAS	2.11 (2.13)	0.029 0.028	269 269	1 - 5 2 - 5	15.87 16.04	** **)
<u>PAIR-WISE COMPARISONS</u>						
BEAUFORT WEST vs SUTHERLAND	2.03 (2.06)	0.038 0.034	133 133	1 - 5 2 - 5	0.41 7.54	N.S **)
BEAUFORT WEST vs TOUWSRIVIER	2.09 (2.08)	0.044 0.033	133 133	1 - 5 2 - 5	1.11 1.84	N.S N.S)
BEAUFORT WEST vs CERES	2.20 (2.23)	0.064 0.060	111 111	1 - 5 2 - 5	4.64 2.17	* N.S)
TOUWSRIVIER vs CERES	2.18	0.044	136	2 - 4	3.53	N.S
TOUWSRIVIER vs SUTHERLAND	2.04 (2.05)	0.021 0.020	158 158	1 - 4 2 - 4	8.18 7.28	** **)

Sample size (N) is the total number of groups. Values with groups of one corrected to groups of two are shown in parentheses. Two-tailed significance levels determined by Kruskal-Wallis one-way ANOVA: N.S, $p > 0.05$; *, $p < 0.05$; **, $p < 0.01$.

TABLE 26: Two - way analysis of variance of the effects of season and location on group size in the Karoo Korhaan.

SOURCE	df	F Value	PR > F
SEASON	4	0.89	N.S
LOCATION	3	5.19	< 0.005
SEASON BY LOCATION	11	0.27	N.S

Number of observations = 200.

TABLE 27: Mean group sizes recorded at the four study sites during the five seasonal surveys from July 1986 (Winter) to July 1987 (Winter).

	WINTER	SPRING	SUMMER	AUTUMN	WINTER
CERES	2.50(0.185) N=18	2.33(0.333) N=6	2.09(0.091) N=11	2.31(0.208) N=13	2.11(0.111) N=9
BEAUFORT WEST [CORRECTED]	NO DATA	1.92(0.137) 2.08(0.077) N=13	1.91(0.091) 2.00(0.000) N=11	2.25(0.215) 2.31(0.198)] N=16	2.214(0.214) N=14
TOUWSRIVIER	2.14(0.097) N=14	2.11(0.105) N=19	2.12(0.081) N=17	2.07(0.067) N=15	2.07(0.071) N=14
SUTHERLAND [CORRECTED]	2.00(0.000) N=20	2.00(0.000) N=20	1.93(0.071) 2.00(0.000)] N=14	2.00(0.000) N=15	2.00(0.000) N=10
<u>PAIR WISE COMPARISONS</u>					
			χ^2		
CERES VS					
	BEAUFORT WEST		4.20	N.S	
	TOUWSRIVIER		5.44	N.S	
	SUTHERLAND		6.67 [4]	N.S	
BEAUFORT WEST VS					
	TOUWSRIVIER		0.18	N.S	
	SUTHERLAND		5.25 [3]	N.S	
TOUWSRIVIER VS					
	SUTHERLAND		2.62 [4]	N.S	
ALL AREAS COMBINED			2.66 [1.35]	N.S	

Standard errors are in parentheses. Values with groups of one corrected to groups of two are shown in [..] parentheses. Sample size (N) is the total number of groups. Two-tailed significance levels determined by Friedmans test, χ^2 approximation: N.S, $p > 0.05$.

Figure 26: Regression of mean Karoo Korhaan group size on rainfall

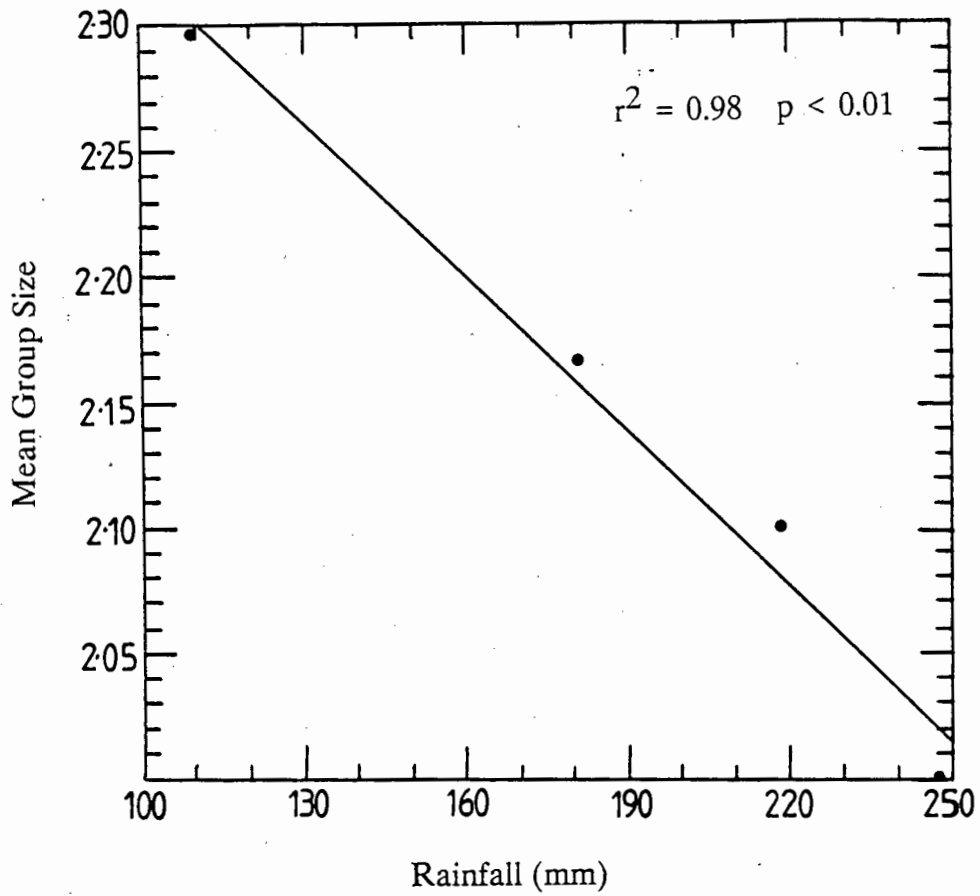


Figure 27: Regression of mean Karoo Korhaan density on rainfall at the study sites.

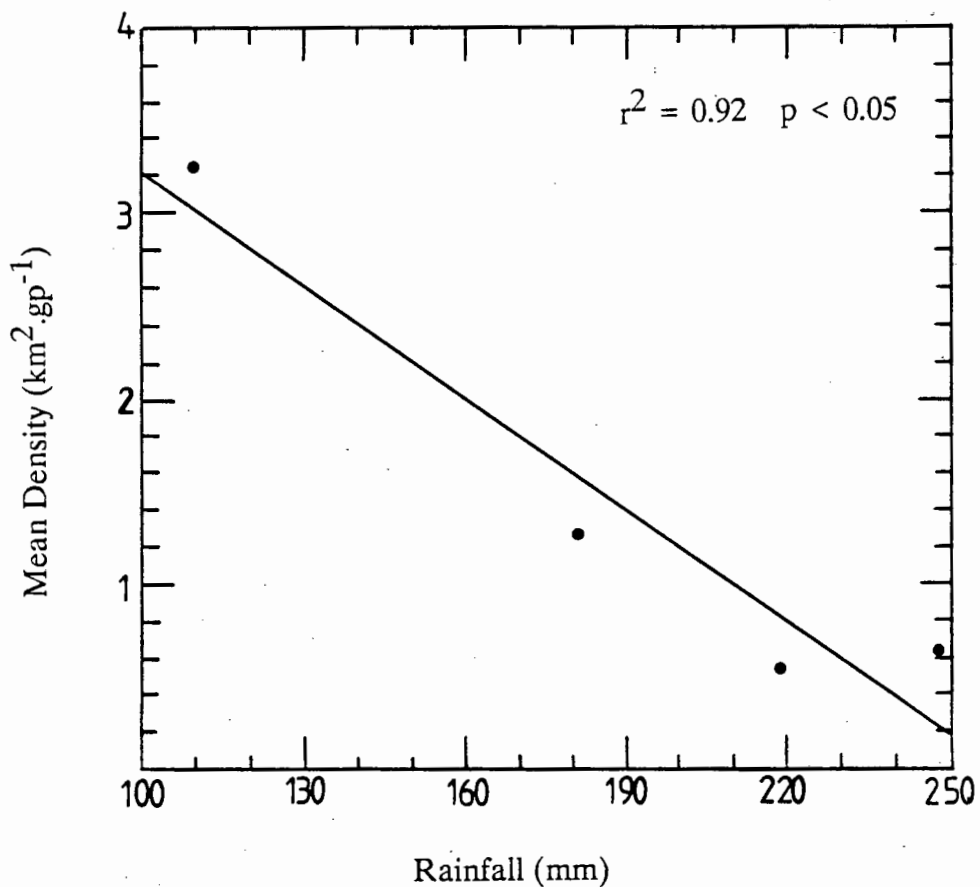


Figure 28: Regression of density of Karoo Korhaan groups on mean group size.

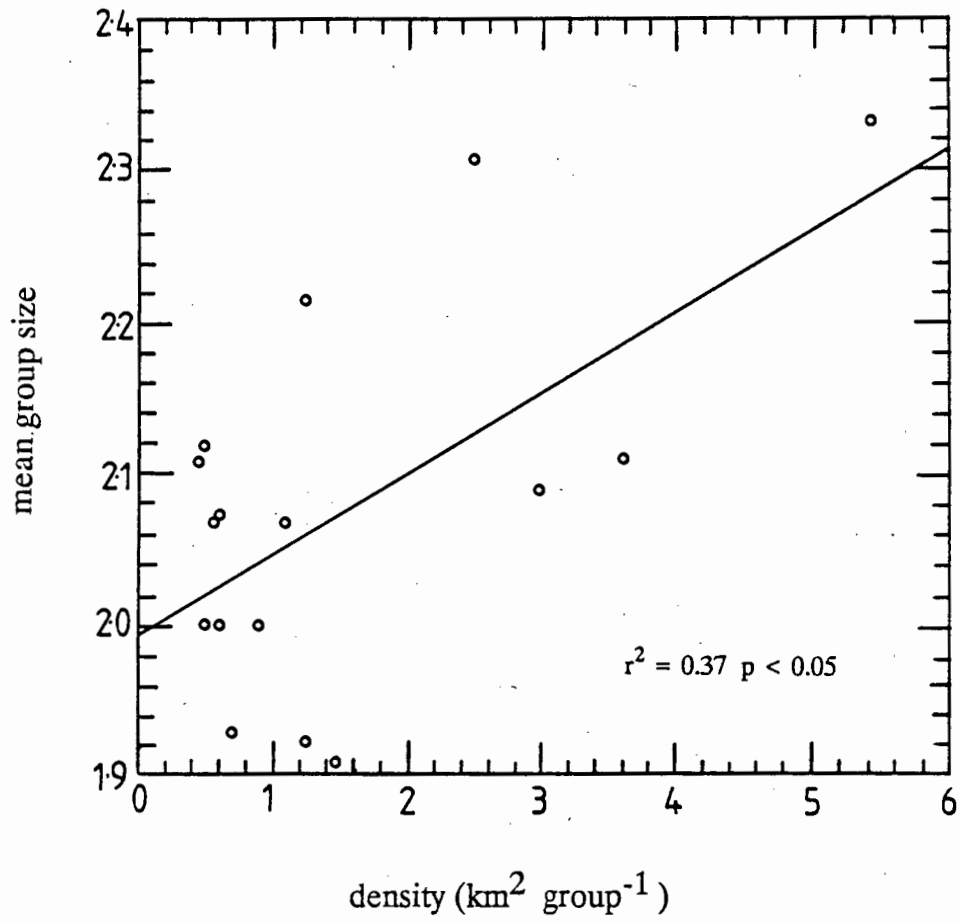


TABLE 28: Spacing of territorial groups in the four main study sites, from July 1986 (Winter) to July 1987 (Winter).

	Groups km ⁻¹						Mean area group ⁻¹
	Total area (km ²)	Winter	Spring	Summer	Autumn	Winter	
CERES	32.6	0.55	0.18	0.34	0.40	0.28	3.26 (0.690)
BEAUFORT WEST	16.3	N.D	0.80	0.68	0.92	0.80	1.27 (0.093)
TOUWSRIVIER	8.5	1.67	2.22	2.00	1.75	1.67	0.54 (0.035)
SUTHERLAND	9.9	2.00	2.04	1.41	1.67	1.11	0.64 (0.085)
<u>PAIR WISE COMPARISONS</u>							
CERES VS			χ^2				
BEAUFORT WEST	BEAUFORT WEST		8.75	*			
TOUWSRIVIER	TOUWSRIVIER		6.80	N.S			
TOUWSRIVIER	TOUWSRIVIER	VS	6.95	N.S			
SUTHERLAND	SUTHERLAND		10.70	**			
TOUWSRIVIER	SUTHERLAND	VS	10.40	**			
ALL AREAS COMBINED			1.28	N.S			

Standard errors are in parentheses. N.D, no data available. Two-tailed significance level determined by Friedmans test, χ^2 approximation: N.S, $p > 0.05$; **, $p < 0.01$; *, $p < 0.05$.

may even enhance the prey availability (Bartholomew, 1942). These benefits are often thought to occur simultaneously and reach an asymptote at a point where group depletion of resources outweighs the benefits of increased vigilance or foraging efficiency. Groups are not always constant in size and quite often form in response to changes in predation and/or food availability during the year. Some species may form temporary groups in response to predation pressure (Hamilton, 1971; Powell, 1974; Siegfried, 1984; Myers *et al.*, 1979). However all these studies concern species that either do not defend territories at all, do not defend territories in the area of flocking or form temporary aggregations in response to predator pressure. Furthermore, the examples listed above, that illustrate an increase in foraging efficiency with an increase in group size, relate to species that feed on patchily distributed resources that generally are economically indefensible.

In territorial species the benefits of an increase in group size have to be considered in relation to the resource being defended and the ability of the territory holder to either alter the territory size, increase the degree of home range overlap with neighbours or to abandon territoriality altogether. These options, usually, are considered to relate to increased intrusion from conspecifics (Davies & Houston, 1981; Stamps, 1985).

The habitat of the Karoo Korhaan is composed of a variety of plant and animal taxa that vary in their availability as resources to the Karoo Korhaan. The habitat study concluded that a wide variety of perennial shrubs, leaf succulents and a strong annual component characterize optimal Karoo Korhaan habitats. Because of the opportunistic nature of the species' diet, the habitat represents a mosaic of temporally and spatially discrete resource patches arrayed against a background of more widely distributed resources that allow individuals to forage whilst moving between patches.

Due to the varying phenological responses of different plant species guilds to moisture availability, a generally abundant invertebrate fauna and the dietary opportunism of the Karoo Korhaan, the species' habitat, although patchy in terms of particular events (i.e. flowering and fruiting of certain taxa), represents distribution of widely available, economically defensible, resources inducing a dispersion of competitors and consequent territoriality.

Analysis of the data collected at the four permanent study sites has shown that there is a strong negative correlation between mean annual rainfall and both the mean size and spacing of Karoo Korhaan groups. Thus, as rainfall decreases, groups tend to be larger and more widely dispersed.

The larger Karoo Korhaan group sizes in areas of low rainfall and territory saturation represent an unusual situation as it is reasonable to hypothesize that territorial aggression and therefore exclusion would increase with competition for scarcer resources. The lower rainfall areas have larger groups that defend larger territories. These larger groups represent parental pairs, augmented by sub-adult male offspring. The retention of male offspring may represent a strategy of increasing the defensibility of the territory from intrusion of unrelated conspecifics. This phenomenon

has been illustrated with Pied Wagtails, *Motacilla alba* (Davies & Houston, 1981). The territories of Karoo Korhaans need to be larger in areas of low rainfall due to the reduced availability of resources (see Chapter 3). It may be better to tolerate the presence of the offspring than to have to incur the costs of excluding them (Brown, 1982). Defence of a Karoo Korhaan territory is shared by all members of the group and so a larger group, in areas of poor resource availability, can defend a larger area, as is the case with other species that defend group territories (e.g. Scrub Jays, *Aphelocoma caerulescens*; Woolfenden & FitzPatrick, 1978). The situation in Karoo Korhaans is such that the extra members are, with rare exceptions, sub-adult males. Male bustards are known to exhibit greater delays in sexual maturation than females (Osborne *et al.*, 1984) and therefore do not represent sexual competition to the dominant male. Furthermore, if experience is an important determinant of an individual's ability to obtain and maintain a territory, the parents may benefit, indirectly, from allowing their male offspring to remain in the natal territory by producing more competitive young (Emlen, 1978), rather than excluding them and forcing them into sub-optimal or marginal habitats. Males play a greater role in territorial defence than do females: males always initiated the duet in response to the taped duet, took longer to return to foraging after a dispute and, in the only instance of "fighting" observed during the study, only males were involved. Therefore, although males are significantly larger than females and represent a greater drain on resources than an additional female, they contribute more to the defence of the group territory.

In different geographical areas of the species' range, Karoo Korhaan group size varies according to the rainfall. It is well known that plants in the Karoo are reliant upon erratic rainfall and are affected differentially in terms of growth, reproduction and establishment (Cowling, 1986). The summer rainfall areas which receive their rainfall mainly in spring and summer favour the establishment of perennial grasses. The winter rainfall areas (i.e. Touwsrivier) and the even summer rainfall areas (i.e. Sutherland) receive most of their rainfall in autumn, winter and late spring which favours shrubs (Roux, 1966). Lower rainfall areas have a lower sustained availability of vegetable dietary components than the higher rainfall areas, but when it does rain the rapid response and production of ephemeral plants is well documented (Van Rooyen *et al.*, 1979^b; see also Chapter 3). Thus in such areas, high value foods are available to the Karoo Korhaan for a shorter time than that necessary for the group to exhaust the supply. In such areas it would pay a pair to tolerate the presence of a sub-adult male as defence costs would be low, available foraging time would be high and the additional member would not greatly affect the *per capita* consumption of the group (Pulliam & Millikan, 1982). At other times of the year resources are scarce and the extra individual will aid the parental pair in defending the larger territory necessary to provide adequate resources.

The seven groups of four were all parental pairs with sub-adult males of different ages. This implies, but does not necessarily prove, that the presence of immature males does not affect the breeding success of the pair. In the bustard family, males generally play no part in the raising of the offspring (Osborne *et al.*, 1984) and it is not thought that groups of three or more, even when three

individuals have been observed at the nest (Kemp & Tarboton, 1976), indicates any evidence of cooperative breeding with the subordinates acting as "helpers" in any other way than contributing to territorial defence.

The increased vigilance of a group of more than two is important during territorial defence, as visibility (seeing others and being seen) is a major component of the display. Korhaans are preyed upon by Tawny Eagles *Aquila rapax*, (Butler, 1908; Steyn, 1971), Martial Eagles *Polemaetus bellicosus* (Brown, 1952; R. Davies, pers. comm.), Black Eagles (R. Davies, pers. comm.) and Giant Eagle Owls *Bubo lacteus* (Vernon, 1971) and have been observed scanning the sky for aerial predators (this study). The density of korhaan predators at all the sites was low. Although all sites fall well within the known range of the Martial Eagle (Maclean, 1986), they were only seen in the Ceres area during this study and Black Eagles were infrequent at all sites.

The fate of dispersing females is not known. In this study, by virtue of the method of censusing, only territorial groups were studied. Individuals that do not defend territories do not reply to the tape and therefore were not recorded. Although broadly site faithful, individuals range over many kilometres (Quinton, 1948; pers. obs.). The results of the study also imply that females disperse more readily than males. The benefits of having an extra female in a monogamous, non-cooperative breeding group, who does little to increase the territory holding capacity of the group, are few. It has been shown in other species that females range farther than males. Schultz (1986) found that female Little Bustards (*Tetrax tetrax*) range as far as 30Km from the nesting site and observations of Ludwig's Bustards (*Neotis ludwigii*) during this study showed that the larger groups were male dominated and that single individuals were generally females, implying that males flock together but females remain alone. Bustard females generally mature sooner than the males (Osborne *et al.*, 1984) and males may pair with females and defend territories even when the female is sexually immature.

In low rainfall areas resources are patchy resulting in an increase in competition for such resources that are available. There are also few possibilities for a sub-adult male to establish a territory. In such areas there are obvious benefits to the parental pair in retaining male offspring to contribute to territorial defence and foraging efficiency when resources are patchy and widely spaced. The concomitant benefits for the offspring in helping to maintain an already established territory in an area where the possibility of establishing a territory alone is low, indicates a dual strategy on behalf of both the parental pair-group and the male sub-adult offspring to increase their respective "fitness" in marginal areas.

CHAPTER SEVEN

**IS THE KAROO KORHAAN AN INDICATOR
SPECIES**

INTRODUCTION

In this section I will bring together the conclusions from the habitat, distribution, diet and group size studies and discuss them in the framework of the Karoo Korhaan as a component of the Karoo ecosystem. I will also put them in to the context of the Karoo Biome Project (KBP), of which this project was a part, and discuss the value of the Karoo Korhaan as an indicator of environmental conditions in the Karoo

One of the central priorities of the KBP was to obtain a detailed characterization of the ecosystem in terms of the climate and floristic and structural-functional attributes of communities and how they vary along environmental and disturbance gradients (Cowling, 1986). It was proposed that such an approach would lead to a predictive understanding of the functioning of the Karoo ecosystem and provide the basis for the development of meaningful management guidelines.

Vernon (1986) states that the majority of birds endemic to the Karoo are species of "natural" habitats. He hypothesized that, if their specific habitat preferences were identified, these birds would be useful indicators of regional gradients and temporal changes in those habitats. As a corollary, a priority of the KBP should be the definition of the habitat preferences of endemic species (*op. cit.*).

The indicator species concept has been used extensively in the study of plant communities and the agricultural potential of land. An indicator has come to mean "an organism or ecological community so strictly associated with particular environmental conditions that its presence is indicative of the existence of these conditions" (Morrison, 1986). Birds are conspicuous, mobile and familiar and, as such, have been widely recognised as potentially valuable indicators of environmental conditions (Bock & Webb, 1984). They have been used most successfully in detecting and monitoring the effects of environmental contamination (Carson, 1962; Ratcliffe, 1967; Jenson *et. al.*, 1969; Grue, *et. al.*, 1984) and are often the most conspicuous victims of pollution such as oil spillage.

It has been a general theme in ecology that the distribution and abundance of most terrestrial bird species is determined primarily by vegetation, and that bird communities "echo" the seral succession of plant communities (Shugart & James, 1973). It has been, and still is, common practice to define bird communities by the plant communities they inhabit. However, although certain bird communities tend to reach maximal abundance at certain seral stages, there is a high degree of overlap in numbers and distribution of bird communities between plant communities (Johnston & Odum, 1956). Liversidge (1962) maintains that there is little correlation between bird distributions at the species level and the distribution of vegetation types.

The overlap of bird communities across plant communities, the different degrees of sensitivity to environmental contamination between species and the fact that birds most often respond to the secondary or tertiary effects of a primary cause (i.e factors affecting food supply) all restrict the use of birds as "indicators". To place this in an ecological perspective, the distinction between indicators of

direct (primary) and indirect (secondary or tertiary) change can be compared with Lacks' (1954) concept of ultimate and proximate factors. Ultimate factors are concerned with survival value and proximate factors with behavioural and physiological adaptations (Morrison, 1986). A study of vegetation as regards its effects on bird communities may correlate with proximate abundance but does not measure ultimate factors such as food supply, which are far more complex factors to quantify.

In order to evaluate the use of a species such as the Karoo Korhaan as a practical indicator of habitat parameters both the proximal and ultimate factors that influence the ecology of the species must be investigated. Throughout this study climate has been stressed as a driving force affecting the structure and floristics of local plant communities. The effects of climate and moisture availability, both temporally and spatially, ultimately influence the resources available to the Karoo Korhaan.

RESULTS

The analysis of the species' habitat showed that, in some habitat types, Karoo Korhaans were present seasonally. Although the Karoo Korhaan is a territorial species, it appears that within sites on a localized scale the species forms a mosaic of territories which become increasingly plastic as resource availability increases. The group size study showed clearly that the sizes of korhaans groups do not vary seasonally (Table 26) but densities do (Table 28). The habitat study concerned groups in the immediate vicinity of fixed vegetation quadrats whereas the group size study concerned all korhaans in the area regardless of their precise location. This highlights the plastic nature of the species' territories because, although actively maintaining similar sized territories throughout the year, the precise location of these territories is variable. One may conclude that territoriality in this species is more of a spacing mechanism than a protection of a specific site and that the species occupies a fluid mosaic of territories throughout the landscape.

Areas of low resource availability are characterized by high temporal and spatial concentration of resources (mostly annual plants, but also out-breaks of orthopterans and mass emergences of curculionids): this leads to an increase in territory size and a subsequent decrease in Karoo Korhaan densities. In areas where such events are spatially discrete, individuals can be displaced into marginal areas which have abundant resources at certain times and few at others (such as highly disturbed areas dominated in spring by monocultures of ephemeral plants). This fluctuation of bird densities is most marked in highly disturbed areas such as the Tanqua Karoo and the frontiers of karroid encroachment of grasslands.

Information statistics of growth form showed that summer and spring differed most in phenology but not growth form spectra. This identified functionally different responses of taxa with no changes in growth-form dominance and consequently a description of the phenology of growth forms is of more importance than description of growth forms *per se*.

The habitat study also highlighted that the variety of species of certain growth forms is more important than the total cover of the growth form itself (i.e. variety of perennial shrubs, variety of annuals). Although the percentage cover of annuals was a strong correlate of bird abundance, the variety of annuals was negatively correlated with bird distribution suggesting that birds favour the monocultures of annual activity that typify disturbed areas (Werger, 1978; Leistner, 1979).

Growth forms responded to seasonal rainfall differentially in different areas. In Beaufort West the percentage cover of succulent shrubs in autumn was correlated (weakly) with bird presence. In other areas their percentage cover was negatively correlated with bird densities. Therefore at the landscape level Karoo Korhaan favour areas with a small succulent component but at the local level these succulents, when in flower, are important sources of food.

Seasonality of rainfall played a far greater role than the annual means in determining plant community structure and phenology and any description of the plant processes of an area that does not account for variability in the rainfall will ultimately be of little value.

The analysis of diet showed, unequivocally, that the species relies on a wide range of both plant and animal resources that are adapted to a pulse-driven system. Many of the common dietary items were taxa that are known to be abundant in disturbed areas (Brachycerid weevils, termites, annuals and alien fodder species). The dietary study also highlighted the extreme variability in the diet and indicated that the Karoo Korhaan is perhaps influenced more strongly by relative resource abundance than resource quality. It is difficult to determine whether birds respond to the same environmental cues as the flora or whether they are reliant upon the flora (i.e. If the distribution of the Karoo Korhaan is affected by floral responses to environmental parameters or whether both birds and flora are responding directly).

CONCLUSIONS

Group sizes varied from place to place in response to rainfall, which effected the vegetation and hence the availability of resources to Karoo Korhaans. The main dietary preference is for both plants and insects that are adapted to variable moisture availability. The species is reliant on the reserves and responses of lower trophic levels. However, in certain areas, this is compensated for by the wide provision of high value resources as evidenced by the species' preference for areas with a high diversity of species. Therefore in high rainfall, low disturbance areas, the availability of food is such that both territories and group sizes tend to be small (i.e. Sutherland and Touwsrivier). In low or unpredictable rainfall areas or disturbed areas resources tend to be explosive (i.e. annuals, orthopterans, curculionids) and although the diet of the species is broad enough to exploit the full range of resources available, these resources are widely dispersed temporally and clumped spatially. This has led to an increase in both territory size and group size.

In conjunction with the findings of the habitat survey, namely that monocultures of certain annuals and wide variety of perennial shrubs are a determinant of habitat choice, one could conclude that the species is not only a successful inhabitant of areas of disturbance but that it may serve as an indicator of such disturbance.

The caution to be observed here is that the response of the Karoo Korhaan to such habitat parameters is the result of proximate factors and that the causes of these effects or the ultimate factors can only be determined by detailed analysis of the response of various plant communities to factors such as variable rainfall, defoliation and disturbance. The present position is such that knowledge of these processes is not sufficient, that there are few or no data on the life histories and fecundity of any Karoo plants (Hilton-Taylor, 1987). Hence, a predictive understanding of the phenological and demographic responses of plant taxa to climate and grazing is lacking (Hoffman & Cowling, 1987). However the analysis of the phenology of the plant species in the various habitats highlighted the seasonality of such resources and their availability to the Karoo Korhaan. The species and growth form spectra varied in their influence on habitat and resource variability in different areas in response to the specific moisture inputs to those areas.

The conclusions to the various section of this study could in some regards be seen as being contradictory. There is an apparent conflict between group sizes increasing and density decreasing in areas assumed to be of "poor quality". A brief observation of Karoo Korhaans in the Ceres site, for example, may lead the observer to conclude that the generally larger group sizes are indicative of greater breeding success and therefore "good quality" habitat, as normally one would expect density to be an indicator of habitat quality. Densities can, however, be higher in poorer quality habitats. Better quality habitats may maintain socially dominant individuals and the offspring or surplus individuals may congregate in lower quality habitats at higher densities. The Karoo Korhaan generally conforms to the criteria supposed to result in the decoupling of density and habitat quality; being a territorial, generalist species of a patchy, seasonal and temporally unpredictable habitat (Van Horne, 1983). However, density increases only in terms of group size, and overall density at a landscape level decreases.

Generally speaking the Karoo Korhaan can serve as an "indicator species" within the limitations of the concept because of its wide occurrence and ease of censusing.

Changes in the distribution and abundance of the Karoo Korhaan are closely linked to long term changes in vegetation quality. The findings of the habitat studies and those of the diet when considered in conjunction with the group size study illustrate that the distribution of the species is closely linked to the variety of plant taxa and growth forms. Long term gradual changes in the species composition and structure of the vegetation communities of a particular area, due to the processes of selective grazing by small stock or due to climatic changes, will affect the suitability of that area as habitat for the Karoo Korhaan. Monitoring the distribution and abundance of the Karoo Korhaan (through studies such as the southern African Bird Atlas Project) therefore may identify critical, gradual changes in the plant and insect communities of the Karoo.

CHAPTER EIGHT

CONCLUSIONS

The Karoo Korhaan is one of three species that form part of a sub-generic radiation of the Otididae in southern African. The three species endemic to southern Africa (Karoo Korhaan, *Eupodotis vigorsii* the Rüppell's Korhaan, *Eupodotis rueppellii* and the Blue Korhaan, *Eupodotis caerulescens*) are presumed to have evolved from a common ancestor and radiated into karoo, desert steppe and grassland respectively (Snow, 1978; Clancey, 1986). Being a karoo specialist in these terms, the Karoo Korhaan evolved within, or at least became specialised for, an ecosystem driven by climatic unpredictability. The historical fauna of the Karoo, before the effects of European settlers became apparent, inferred by Acocks (1979) on the basis of travellers' records, place names and refuge plant populations, would have had a profoundly different influence on the dynamics of plant communities. It could be hypothesized that the habitat preferences of the Karoo Korhaan, suggested by studies of plant communities and growth-form distributions (Chapters 2 & 3), are a result of the species' evolving within an ecosystem, markedly different from that of the present day, where non-selective grazing promoted species diversity. The ability of the Karoo Korhaan to utilize ephemeral resources may have evolved as a strategy to survive the dry seasons (when most animals, both mammals and birds, moved to more mesic areas). Therefore, what evolved as a means of overcoming lean periods in the past is now a daily survival strategy in some of the more disturbed areas. Arid ecosystems generally are defined as having a primary productivity that is water limited (Noy-Meir, 1973). The moisture regime of such areas is known to have a large random component that results in unpredictability in both timing, duration and magnitude of precipitation events and unpredictability in the likelihood of follow-up rains. The proliferation of tactics of both plants and animals (i.e. drought evaders and drought endurers) indicates that they are well adapted to rainfall variability. Organisms have to adapt to this unpredictability by adopting "pulse reserve" patterns (i.e. annual plants and explosive breeding insects such as curculionids and orthopterans), by exploiting the reserves of other organisms (i.e. seed eaters) or by flexible feeding habits that allow the organism to exploit whatever pulse or reserve is available at any time (Noy-Meir, 1973). The descriptions of Karoo Korhaan habitat illustrated the local heterogeneity of karoo veld. Identifiable plant communities, differing in both species and growth-form composition, were present at all of the study sites. The seasonal changes in community structure and phenological responses to moisture availability highlighted that in certain areas, resources are available to the Karoo Korhaan throughout the year. The diet of the species was found to be broad enough to exploit whatever is available, both animal and vegetable. Annuals and the seeds, fruits and flowers of a wide variety of perennial shrubs were found to be important components of Karoo Korhaan habitats and important in the species' diet. The seasonal study of habitats showed that growth-forms vary in their response to rainfall such that throughout the year there is a broad availability of different resources. Almost nothing is known about the seasonality of the different animal items in the species' diet other than that at certain times Orthoptera, Lepidoptera and Curculionidae emerge in considerable numbers. Certain growth-forms may be essential for these species; such as geophytes for weevils (especially the Brachycerinae) and grasses for orthopterans. Therefore, although certain growth-forms are important components of the diet of the Karoo Korhaan (i.e. annuals, perennial shrubs and leaf succulents), others such as geophytes and grasses may be of limited importance to the

diet of the Karoo Korhaan but may be essential to the diet of other species that are, themselves, important dietary items. The findings of the habitat and diet studies, therefore, highlight not only the broad tolerance of the species but illustrate that the species relies on the pulse-reserve responses of other taxa (*sensu* Noy-Meir, 1973). The quickly responding seeds bank of annuals, the generally rich seed bank of other plants being widely distributed in the soil and in the canopy, and the wealth of insect species result in a temporal mosaic in the availability of diverse resources.

None of the species of bustards in southern Africa (and few elsewhere) has been the focus of an ecological study. Bustards are repeatedly detailed as being overwhelmingly insectivorous, often disregarding all vegetation in the diet (even when accounting for up to ten times the bulk of the more conspicuous animal fraction; Earlé *et. al.*, 1988). A problem arising from investigating an unknown species is the general lack of testable hypotheses prior to the study. Most of the hypotheses addressed in this study arose from anecdotal references in the literature and preliminary field observations. It is inevitable that such a study will pose more questions than it answers. The fact that a species has not been investigated previously is no basis for a scientific study, but the hypotheses tested in this study and the conclusions drawn from them address deficiencies in our understanding of both bustard and karoo ecology. Furthermore they provide a basis for meaningful and testable hypotheses concerning this and the other bustard and karoo bird species.

The overwhelming occurrence of disturbance taxa (both animal and plant) in both the habitat and the diet of Karoo Korhaans reflects the abundance of such items at certain times of the year. The ephemeral nature of such resources necessarily demands flexibility in the diet of species feeding on them.

The alarming rate at which the Karoo is spreading at the expense of grassland and sub-tropical thicket (Acocks, 1975; Jarman & Bosch, 1973; Huntley, 1984) carries with it mixed blessings for the Karoo Korhaan. If Acocks' (1975) predictions for the extent of the Karoo by the year 2050 are realized then the range of the Karoo Korhaan can be predicted to increase north-eastwards and approximately double in extent. However, the advance of the Karoo into the territory of tropical vegetation "is leaving behind it a desert vacuum" (Acocks, 1975). Consequently, although the range of the Karoo Korhaan is increasing due to the karroid invasion of grassland and sub-tropical thicket, the Karoo itself is increasingly subject to desertification. The effects of overgrazing and other anthropogenically induced forms of disturbance the Karoo, with a marked reduction in species variety throughout the biome, will be such that, although increasing in extent, the resulting habitat will be less suitable for the Karoo Korhaan. The findings of the group size study concluded that the generally more disturbed vegetation will have groups of larger than average size defending large territories. Because the territories defended by the larger groups tend to be far larger and spaced farther apart than those of smaller groups an increase in the extent of the Karoo will not necessarily signal an increase in the habitat available to the species and the species will not greatly increase in numbers.

We are becoming increasingly aware of the impact we are having on the resources of our planet. The rapid increases in desertification worldwide have long been a cause for concern but recently awareness has been heightened by the predictions of major global climatic changes due to the build-up of "greenhouse" gases in the outer atmosphere. These predictions of global warming, ozone depletion and increasing desertification have brought about the inception of the International Geosphere Biosphere Programme. Models of the climatic changes likely to occur in the next decade predict an increase in daily rainfall over northern tropical countries of southern Africa, a reduction in rainfall in sub-tropical countries in the summer (Wilson & Mitchell, 1987) and a general degeneration of the winter rainfall areas of the south western arid zone to summer rainfall. A priority of the southern African research community is to establish the extent and effects of climatic change on local ecosystems. This study has highlighted several aspects of the effects of seasonal rainfall on the distribution and responses of the flora of four areas and their concomitant influence on the ecoethology of the Karoo Korhaan. There exist several reviews of the Karoo and its vegetation (Acocks, 1975; Werger, 1978) and the effects of climate on such areas (Roux, 1966; Noy-Meir, 1973; Leistner, 1979; Westoby, 1980; Rutherford & Westfall, 1986) but none link the responses of the vegetation to species at higher trophic levels. Furthermore, there are no long-term data concerning karoo plant dynamics and the development of realistic models of community change by the Karoo research community (integral to the IGBP's aims) will be difficult. It is hoped, therefore, that this study will provide some insights in to the effects that climate can have on a species and its habitat. It is tentatively suggested that this study of aspects of the Karoo Korhaan's eco-ethology give insight to changes in vegetation in the area studied that will be of use in constructing more complex ecosystem models. If the existing models of climatic changes in southern Africa are accurate then one could predict that the Karoo Korhaan will disappear from the more arid winter rainfall regions (such as the Tanqua Karoo) where low rainfall is compensated for by its predictability. Species such as the Karoo Korhaan have a valuable role to play in the modelling of the effects of such climatic changes.

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APPENDIX ONE

INFORMATION STATISTICS TABLES

SPRING INFORMATION STATISTICS

TABLE A1

	TR	C	S	BW
TR		**	**	**
C			**	**
S	**	*		**
BW	**	**	**	

PERCENTAGE COVER
(SPINES)
C>BW>TR>S

PERCENTAGE COVER (TOTAL)

C>BW>TR>S

TABLE A2

	TR	C	S	BW
TR		**		**
C	**			
S				**
BW	**	**	**	

NUMBER OF SPECIES
(ANNUALS)
TR>S>C>BW

PERCENTAGE COVER (ANNUALS)

TR>S>C>BW

TABLE A3

	TR	C	S	BW
TR			**	**
C	**		**	**
S	**	**		**
BW		**		

PERCENTAGE COVER
PERENNIAL GRASS
BW>S>C>TR

PERCENTAGE COVER (DEAD MATERIAL)

C>S>BW>TR

SPRING INFORMATION STATISTICS

TABLE A4

	TR	C	S	BW
TR			**	**
C			**	**
S	**	**		
BW	**	**	**	

NUMBER OF SPECIES
LEAF SUCCULENTS
C>TR>BW=S

PERCENTAGE COVER
LEAF SUCCULENTS

C>TR>BW>S

TABLE A5

	TR	C	S	BW
TR		**		
C			**	**
S		**		
BW		**		

NUMBER OF SPECIES OF
PERENNIAL SHRUBS
S>BW>TR>C

PERCENTAGE COVER STEM SUCCULENTS

C>TR>S>BW

TABLE A6

	TR	C	S	BW
TR				
C				*
S				**
BW	*	**	**	

INDEX OF FRUITING
C>S>TR>BW

INDEX OF FLOWERING

C>S>TR>BW

SUMMER INFORMATION STATISTICS

TABLE A7

	TR	C	S	BW
TR		**	*	**
C			**	
S	*			**
BW	**	**	**	

PERCENTAGE COVER
(SPINES)

C>BW>TR>S

PERCENTAGE COVER (TOTAL)

BW>C>TR>S

TABLE A8

	TR	C	S	BW
TR		**		
C	**		**	**
S	**	**		
BW	**	**	*	

NUMBER OF SPECIES
PERENNIAL SHRUBS

S>BW>TR>C

PERCENTAGE COVER PERENNIAL SHRUBS

S>BW>TR>C

TABLE A9

	TR	C	S	BW
TR				**
C	*			**
S	**	**		**
BW	**	**		

PERCENTAGE COVER
PERENNIAL GRASS

BW>S>C>TR

PERCENTAGE COVER (DEAD MATERIAL)

C>TR>S>BW

SUMMER INFORMATION STATISTICS

TABLE A10

	TR	C	S	BW
TR			**	**
C	**		**	**
S	**	**		
BW	**	**	**	

NUMBER OF SPECIES OF
LEAF SUCCULENT
C>TR>S>BW

PERCENTAGE COVER LEAF SUCCULENTS

C>TR>BW>S

TABLE A11

	TR	C	S	BW
TR			*	
C	*		*	
S	**	**		
BW	**	**		

INDEX OF FRUITING
C>TR>BW>S

PERCENTAGE COVER STEM SUCCULENTS

C>TR>S>BW

AUTUMN INFORMATION STATISTICS

TABLE A12

	TR	C	S	BW
TR		**		**
C			**	**
S	*	**		**
BW	**	**	**	

PERCENTAGE COVER
(SPINES)

C>BW>TR>S

PERCENTAGE COVER (TOTAL)

C>BW>TR>S

TABLE A13

	TR	C	S	BW
TR		*	**	**
C				
S		**		
BW		*		

NUMBER OF SPECIES
(ANNUALS)

TR>C>BW>S

PERCENTAGE COVER (ANNUALS)

C>TR>BW>S

TABLE A14

	TR	C	S	BW
TR		**		*
C	**			
S	*			
BW	**			

NUMBER OF SPECIES
(GEOPHYTES)

TR>S>C>BW

PERCENTAGE COVER (GEOPHYTES)

TR>S>C>BW

AUTUMN INFORMATION STATISTICS

TABLE A15

	TR	C	S	BW
TR			**	**
C	**		**	**
S	**	**		
BW	**	**	**	

PERCENTAGE COVER LEAF SUCCULENTS

NUMBER OF SPECIES OF
SUCCULENT LEAVES

C>TR>BW>S

C>TR>BW>S

TABLE A16

	TR	C	S	BW
TR		**		*
C	**		**	**
S	**	**		
BW	**	**		

PERCENTAGE COVER PERENNIAL SHRUBS

NUMBER OF SPECIES OF
PERENNIAL SHRUBS

S>BW>TR>C

S>BW>TR>C

TABLE A17

	TR	C	S	BW
TR		*	*	**
C			**	**
S				
BW	*	**	**	

PERCENTAGE COVER PERENNIAL GRASS

PERCENTAGE COVER
OF DEAD MATERIAL

C>TR>S>BW

BW>S>C>TR

TABLE A18

	TR	C	S	BW
TR		*	*	**
C			**	**
S				
BW	*	**	**	

PERCENTAGE COVER STEM SUCCULENTS

INDEX OF FLOWERING

BW>C>TR>S

C>TR>S>BW

WINTER INFORMATION STATISTICS

TABLE A19

	TR	C	S	BW
TR		**	**	**
C			**	**
S	**	**		**
BW			**	

PERCENTAGE COVER
(SPINES)

C>BW>TR>S

PERCENTAGE COVER (TOTAL)

C>TR>BW>S

TABLE A20

	TR	C	S	BW
TR			*	*
C			*	*
S	**	**		
BW	**	**	**	

NUMBER OF SPECIES
(ANNUALS)

C>TR>S>BW

PERCENTAGE COVER (ANNUALS)

C>TR>S>BW

TABLE A21

	TR	C	S	BW
TR				**
C	**			
S				**
BW	**			

NUMBER OF SPECIES OF
GEOPHYTES

TR>S>C>BW

PERCENTAGE COVER (GEOPHYTES)

TR>S>C>BW

WINTER INFORMATION STATISTICS

TABLE A22

	TR	C	S	BW
TR				*
C				*
S				
BW	**	**	**	

NUMBER OF SPECIES
PERENNIAL GRASS
BW>C>S>TR

PERCENTAGE COVER PERENNIAL GRASS

BW>C>S>TR

TABLE A23

	TR	C	S	BW
TR			**	**
C	**		**	**
S	**	**		
BW	**	**	**	

NUMBER OF SPECIES OF
LEAF SUCCULENTS
C>TR>BW>S

PERCENTAGE COVER LEAF SUCCULENTS

C>TR>BW>S

TABLE A24

	TR	C	S	BW
TR		**		
C	**		**	**
S	**	**		
BW	**	**		

NUMBER OF SPECIES
PERENNIAL SHRUBS
S>BW>TR>C

PERCENTAGE COVER PERENNIAL SHRUBS

S>BW>TR>C

TABLE A25

	TR	C	S	BW
TR			**	**
C	*		*	*
S		*		
BW				

INDEX OF FRUITING
S>BW>C>TR

PERCENTAGE COVER (DEAD MATERIAL)

C>S>BW>TR

APPENDIX TWO

**BOX AND WHISKER PLOTS OF THE RESULTS OF
THE DIET ANALYSIS**

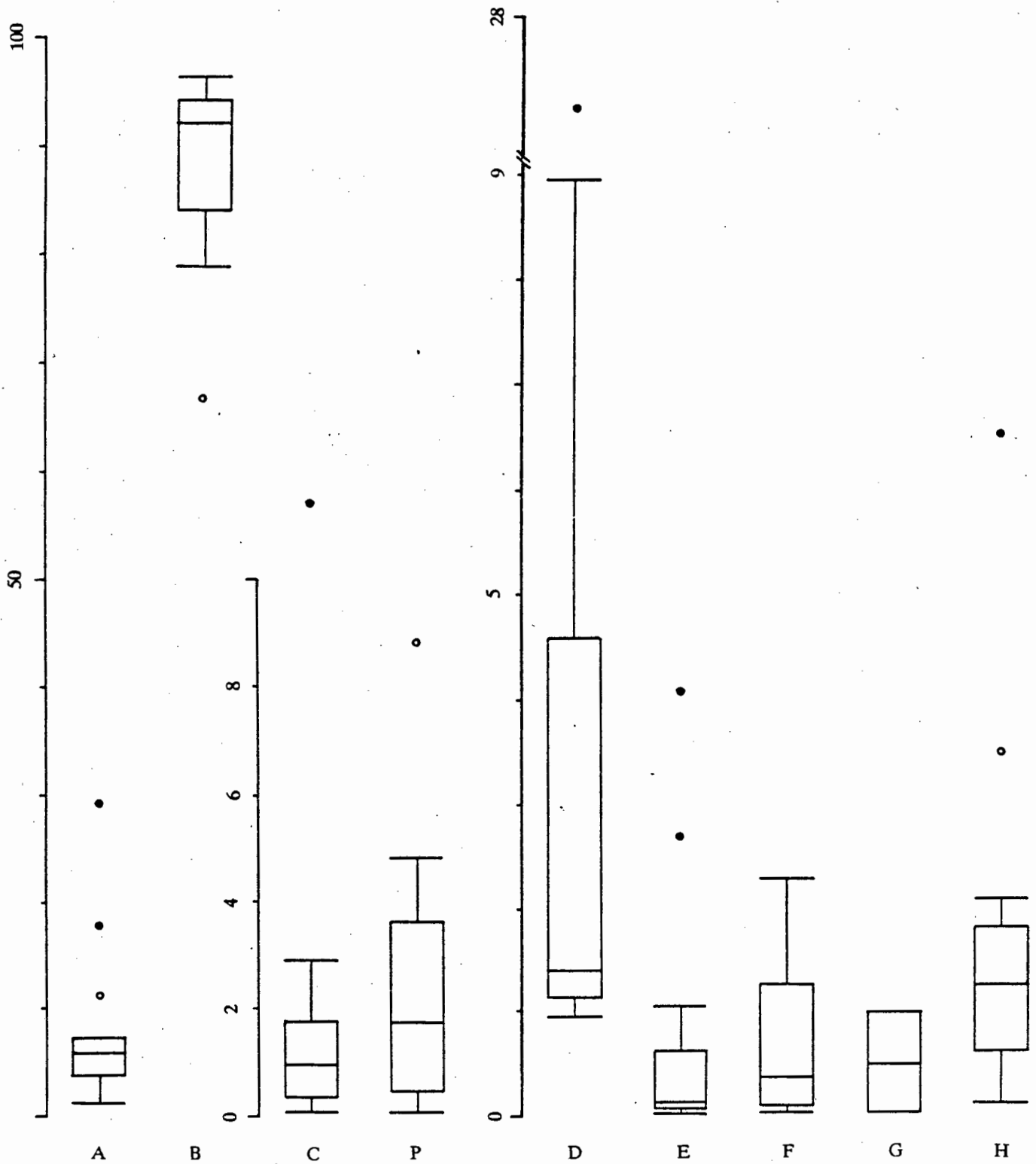


Figure 2.1. Box and whisker plots of the percentage volume of the major classes of food items and the insect orders.

A = Arthropods (Total); B = Vegetation (Total); C = Gastroliths; D = Curculionidae; E = isoptera; F = Formicoidea; G = Buprestidae; H = Indeterminable; P = parasites.
 (open circles denote strays, closed circles denote outliers)

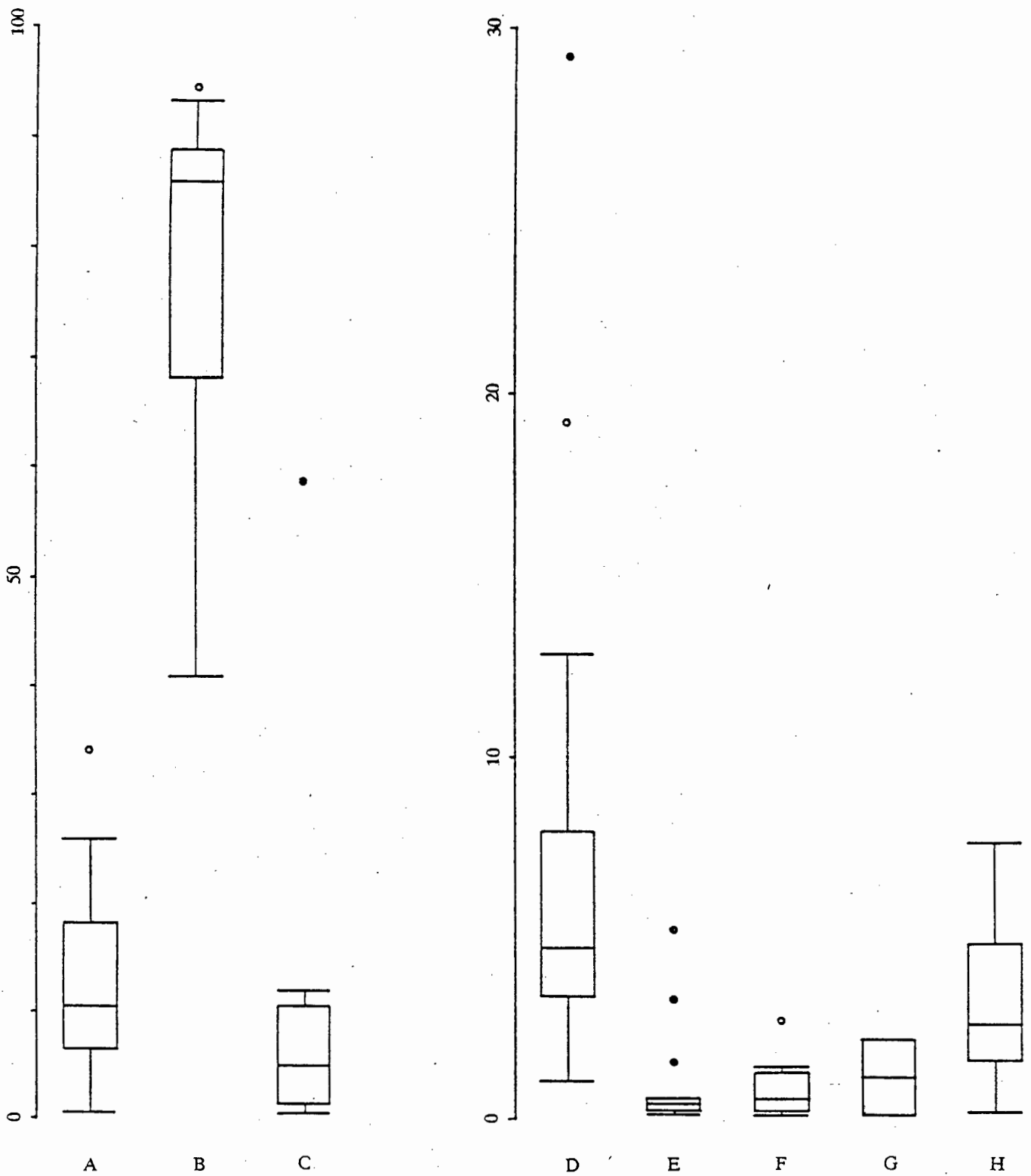


Figure 2.2. Box and whisker plots of the percentage mass of the major classes of food items and the insect orders.

A = Arthropods (Total); B = Vegetation (Total); C = Gastroliths; D = Curculionidae; E = Isoptera; F = Formicoidea; G = Buprestidae; H = Indeterminable.

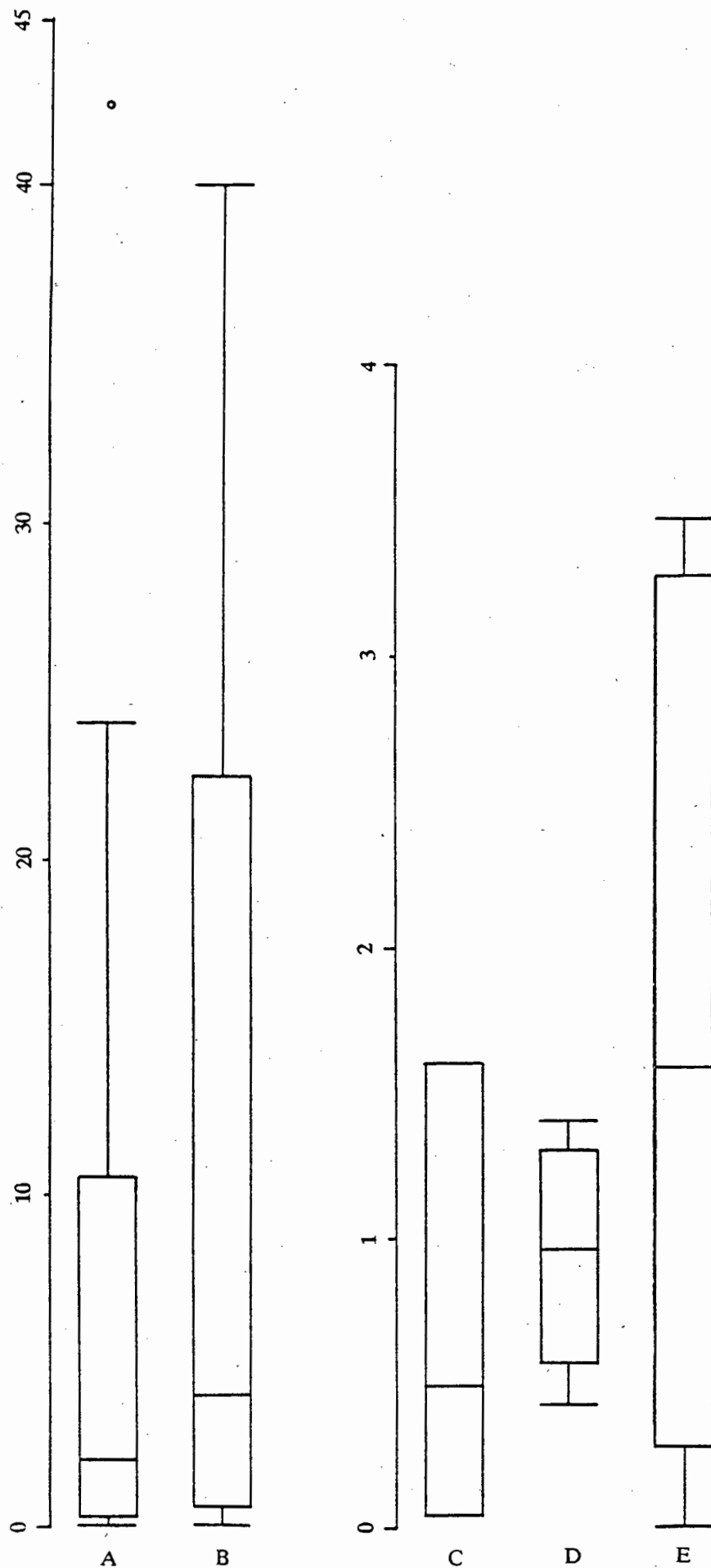


Figure 2.3. Box and whisker plots of the percentage volume of plant families. A = Solanaceae; B = Asteraceae; C = Brassicaceae; D = Euphorbiaceae; E = Mesembryanthemaceae.

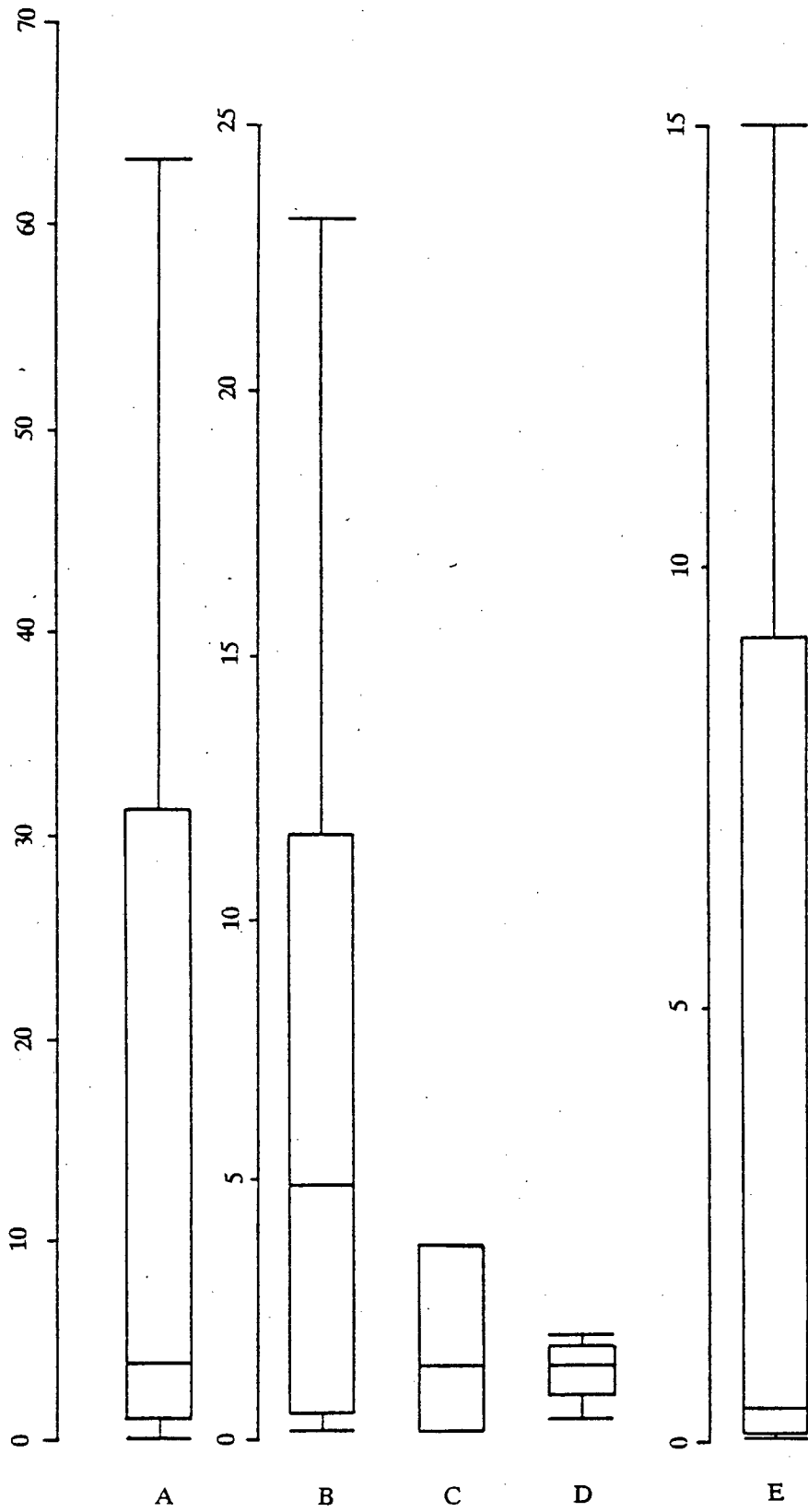


Figure 2.4. Box and whisker plots of the percentage mass of plant families. A = Solanaceae; B = Asteraceae; C = Brassicaceae; D = Euphorbiaceae; E = Mesembryanthemaceae.

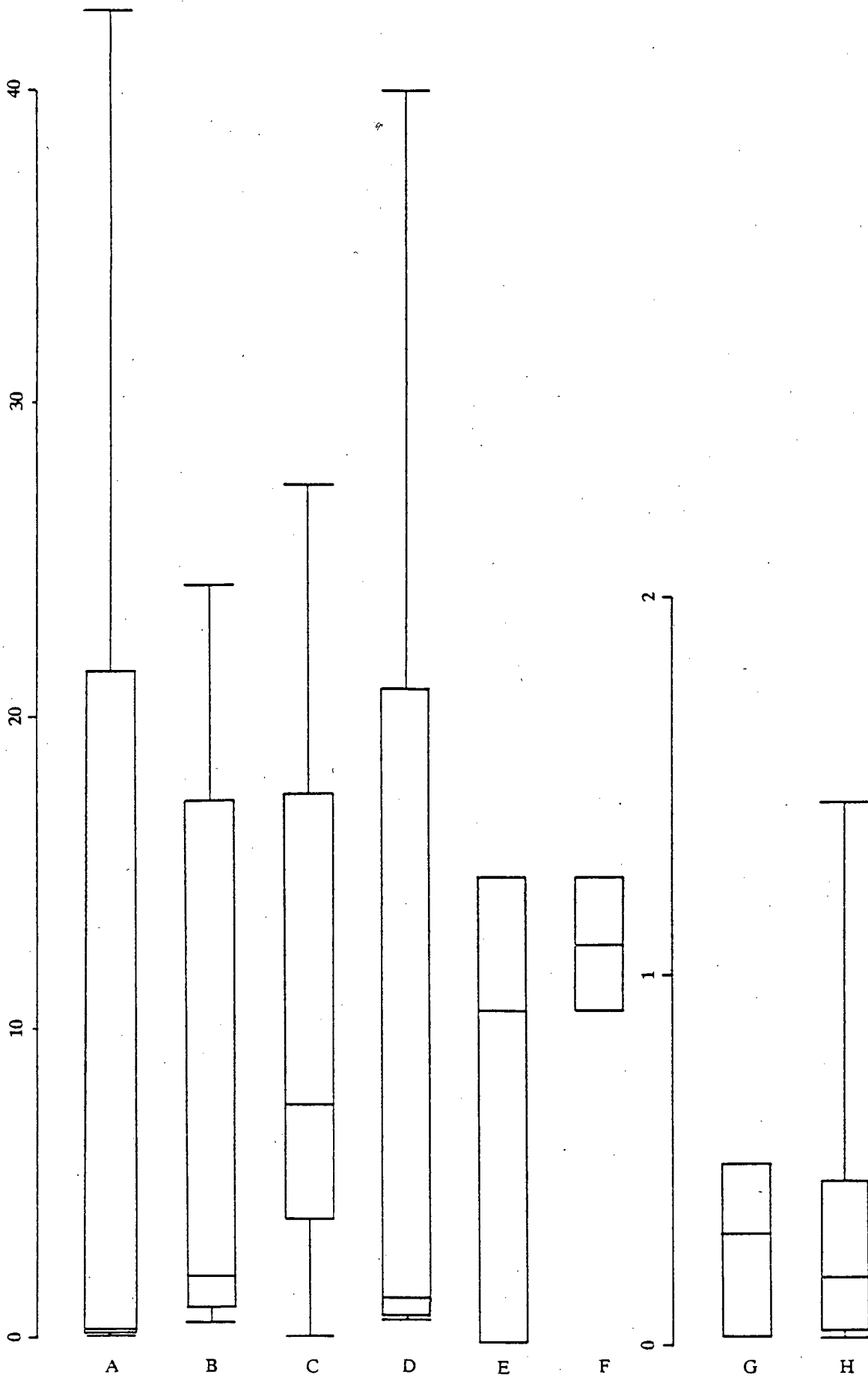


Figure 2.5. Box and whisker plots of the percentage volume of plant species. A = *Solanum* sp.; B = *Lycium* sp.; C = *Atriplex* sp.; D = *Ursinia* sp.; E = *Rosenia* sp.; F = *Sonchus* sp.; G = *Cuspidia* sp.; H = *Osteospermum* sp.

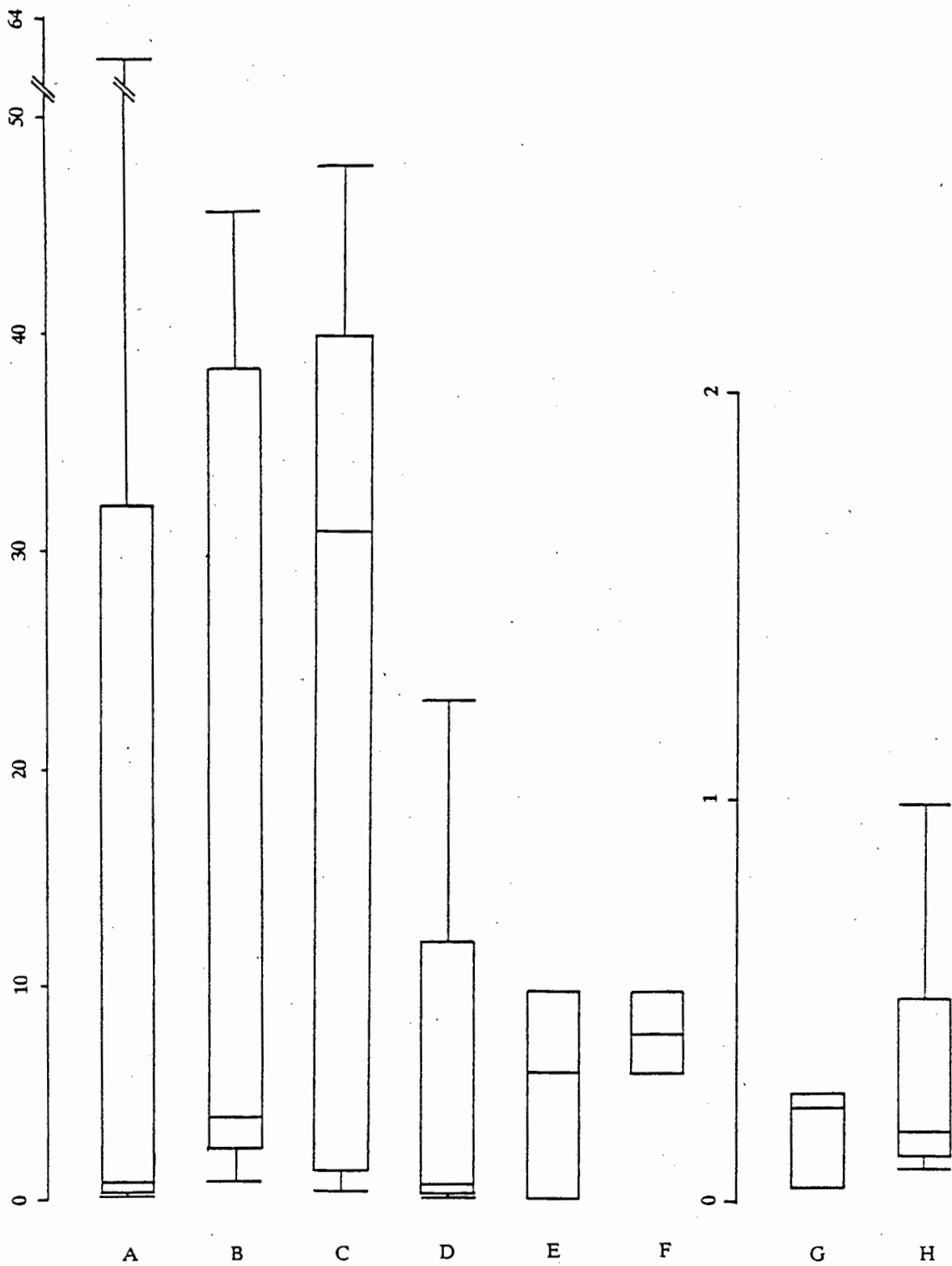


Figure 2.6. Box and whisker plots of the percentage mass of plant species. A = *Solanum* sp.; B = *Lycium* sp.; C = *Atriplex* sp.; D = *Ursinia* sp.; E = *Rosenia* sp.; F = *Sonchus* sp.; G = *Cuspidia* sp.; H = *Osteospermum* sp.

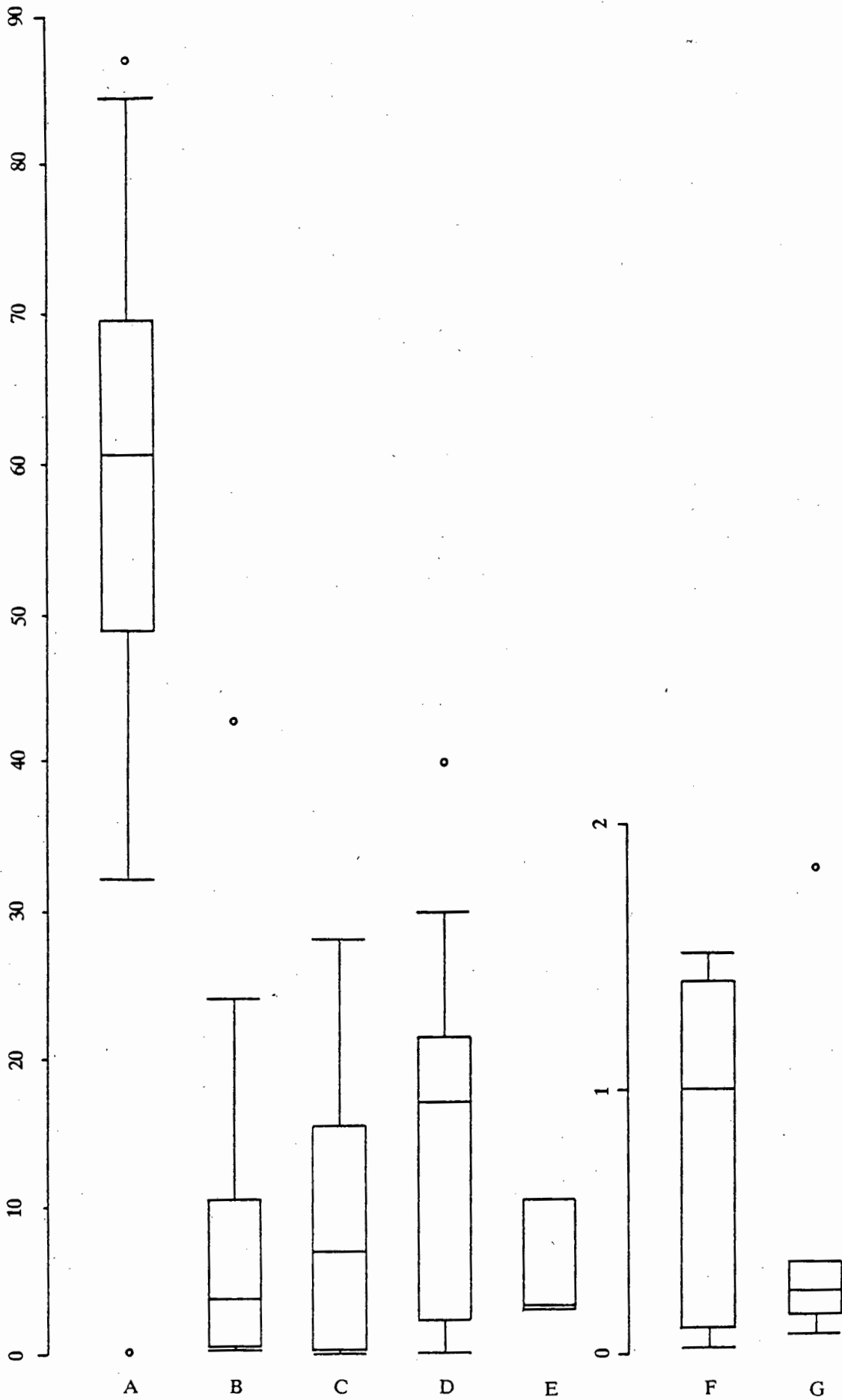


Figure 2.7. Box and whisker plots of the percentage volume of plant categories. A = Misc. veg.; B = Fruits; C = Seeds; D = Flowers; E = Leaves; F = Pods; G = Galls.

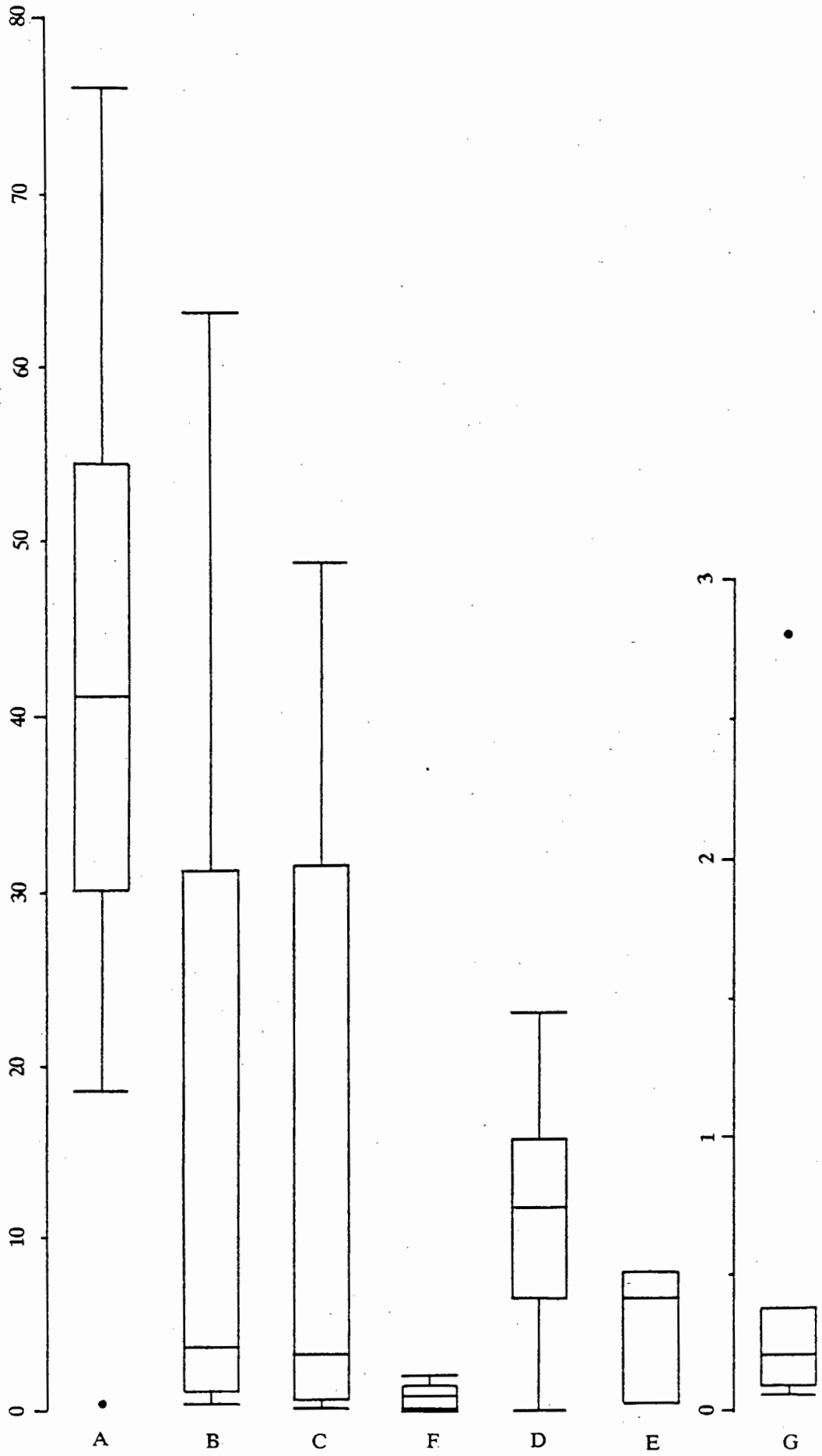


Figure 2.8. Box and whisker plots of the percentage mass of plant categories. A = Misc veg.; B = Fruits; C = Seeds; D = Flowers; E = Leaves; F = Pods; G = Galls.

APPENDIX THREE

DENIZENS OF THE DESERT

BOKMAKIERIE (1987) 40:47-50.

It is remarkable that, for a family that boasts the heaviest flying species of bird (the Kori Bustard weighing in at around 15 kg) and some of the more spectacular mating displays of any species of bird, so little is actually known about any of the 22 species of bustard. What has become very clear over the past decade is that not one of the species has been unaffected by the activities of man.

The bustard family is ancient and closely related to the Cranes and Rails; although there is much confusion surrounding their actual classification. They differ from other families, in that they do not have a preen gland and lack a hind toe. A preen gland is unnecessary in the hot, dry environments they inhabit and they tend their plumage with a friable, powder down. The lack of a hind toe is an adaptation to their cursorial nature. Although bustards are strong fliers and some of the species in the drier places often fly great distances, following the infrequent rains in search of food, they generally prefer to walk away from danger and can do so at remarkable speed. These adaptations to open, dry habitats coupled with the fact that only four species breed wholly outside of the African continent, all point to the drier regions of Africa being their place of origin. The southern African region possesses ten species of which five occur nowhere else. The bustard family does, however, extend throughout Europe, Asia, the Middle East and there is one species (similar to the Kori) in Australia. The fossil record shows that historically the bustard family has never occurred in the Americas.

It is those species that range throughout the densely populated areas of Europe and Asia that have been hardest hit in the all too familiar competition with humans for unspoilt, open grasslands. Three of the four species that do not occur in Africa, are amongst the rarest of all birds.

WANDERERS OF THE PLAINS

The larger bustards are very impressive birds and have always fascinated the inhabitants of the open grasslands, savannas and steppes where they were once abundant. Cave paintings dating from over 4000 years BC. have been found in southern Spain and rock engravings of the majestic Kori can be seen in the northern Cape Province. Early people must have marvelled at these large wanderers of the plains which they would have rarely been able to approach sufficiently, to hunt. Other than taking their eggs and killing the occasional individual, it is unlikely that early people had any effect upon the bustard populations. In fact, the clear felling of many of the forested areas of Europe for pastoral agriculture would have benefited the bustards. That was until humans began making greater demands upon their natural habitats, converting much of the permanent grasslands of Europe and Asia to intensive cultivation. The destruction of suitable habitat by agricultural intensification, the use of pesticides and to a varying extent the greater sophistication and mobility of hunters, have all severely reduced their natural populations. The Great Bustard, once common throughout Europe and Asia, became extinct in many portions of its range by the middle of the last century. Only some 26,500 individuals are thought to be left. The Great Indian Bustard, a species very similar to our Kori, was once recorded in its thousands throughout the extensive grasslands of India and is now reduced by

hunting and habitat loss to a mere 750 individuals in 1.7% of its former range. The Lesser and Bengal Floricans, small and graceful bustards, inhabiting the Indian sub-continent, have both been reduced to numbers of less than a hundred, in small, isolated pockets of protected grassland.

In the early seventies, such conservation bodies as the Tourism and Wildlife Society of India (TWSI), the International Council for Bird Preservation (ICBP) and the International Union for the Conservation of Nature and Natural Resources (IUCN) highlighted the hitherto unknown virtual extinction of the three Indian species. Since then, valuable advances have been made and efforts to halt the decline of these species have set the field for the safe-guarding of all of the world's species. However, it was not the demise of these species that made conservationists first aware of the desperate plight of several members of the bustard family. One species has undergone a far more intensive process of active extermination at the hands of humans; the Houbara.

THE SPORT OF PRINCES

Falconry arose over 2,000 years ago amongst the Arab people, providing an effective means of supplementing the diet with fresh meat when engaged in long treks through the desert. The favoured hunting birds were large migratory falcons such as the female Saker falcon. The most highly prized quarry was the Houbara bustard. The Houbara not only provided the falconer with fresh meat, but also gave good sport by engaging the pursuing falcon in retaliatory combat; albeit fruitless, the Houbara seldom triumphing. This level of hunting placed no great stress on the populations of either species. The race of Houbara found in Iraq, Jordan, Oman, Saudi Arabia and Israel was quite plentiful and supplemented by winter migrants from the Kazakhstan steppes of the Soviet Union and the falcons were released every year to return to their breeding grounds. That was so until the 1950's, when the revenue from oil made the Arab sheiks extremely wealthy. A falconer's status is judged by the type, number and success of his hunting birds. This led to a drastic increase in the trade of falcons and, with the employment of four-wheel drive vehicles, the drastic decrease in the number of Houbara and other quarry in even the most remote places. The increase in pressure was so marked as to virtually eradicate the resident Houbara population and severely reduce the numbers of the migrant population. The scarcity of the resident population caused the falconers to travel further afield in search of their quarry, even to Pakistan, where they arrived in large numbers, with fleets of vehicles and erected large tented camps in the desert. Annual "bags" of 3,000 Houbaras, with few restrictions on the falconers and little adherence to what restrictions did exist, led, in the space of a decade, to a 75% reduction in the Houbara population at the breeding sites in the Soviet Union. The implementation of stricter legislation in response to international concern, controlled the areas open to falconers and limited the annual bag. This caused many of the parties to turn to north African countries such as Morocco, Algeria, Chad, Niger and Sudan; areas where the populations of Houbara are resident and therefore vulnerable to all year round persecution and countries whose governments may be less sympathetic to the needs of the Houbara or to the pleas of world conservation bodies.

SOUTHERN AFRICA - A BUSTARD REFUGE

In southern Africa the level of threat to the ten species that occur here is probably less than in any other region. The availability and possible recent expansion of suitable arid and semi-arid habitats with low human population growth where pastoral agriculture rather than intensive cultivation is the predominant practice is beneficial to the more arid land species. The Karoo Korhaan (an endemic to the karroid interior of southern Africa) and possibly Rüppells Korhaan appear to have been the least affected by mans activities. Of all the bustard species they may even have benefited, as research into the former species has shown that they favour slightly degraded veld.

In South Africa we tend to divide the bustards into two groups, the "bustards" or "Pou" and the smaller "korhaans". This is an arbitrary distinction based on size. The three species of larger bustards (the Kori or "gompou", the Stanleys Bustard or "veldpou" and the Ludwigs Bustard or "ludwigse pou") have all undergone serious declines in population over the past century and as such are all listed as vulnerable in the most recent revision of the South African Red Data Book for birds by R.K.Brooke (1984). Although all the bustards and korhaans are afforded strict legal protection by the four provinces and have been since the beginning of the century, the larger species have been reduced by hunting to a certain extent.

LOCUST BIRDS

The importance of all the species as "locust birds", feeding voraciously on the hoppers of locusts, and therefore the benefit they give farmers, has not stopped them being shot. The korhaan species have by virtue of their cryptic plumage and retiring nature been hunted to a far less extent. The korhaans are all sedentary and do not undergo the long distant movements of the larger species. This has aided their survival. Farmers seem far more reluctant to hunt such faithful and useful residents of their land than they do the more sporadic, occasional visitors. However, the same processes of agricultural intensification that have threatened the survival of bustards elsewhere in the world, are increasingly apparent in the region and certain of the inhabitants of regions of higher rainfall are suffering at the hand of such habitat destruction. The Blue Korhaan is an endemic of the high altitude grasslands of the Orange Free State, the southern Transvaal, Lesotho and western Natal. The Blue Korhaan has the most restricted range of any of the species and although all the indications are that it is not undergoing any serious decline and appears to tolerate some degree of agricultural intensification, it must always remain a cause for concern as the need for agricultural land increases. The only species of korhaan considered to have seriously declined is the Black-bellied korhaan. Ironically, this species (the largest of the korhaans) has been a popular bird for hunters and was the only species of bustard not given full protection in Rhodesia in the 1950's. The remaining species of korhaan, the Red-crested, the White-bellied and the Black korhaan are all potentially vulnerable to the intensification of agricultural practice but are not considered to be endangered at the present time.

SOUTHERN AFRICA AND THE BUSTARD TRADE

The insatiable appetite of the Arabian falconers has recently begun to affect the populations of southern Africa. The lack of local bustards has resulted in the importation of many species of bustards from areas such as Botswana, Somalia and East Africa. These species, including the Black, White-bellied, Black-bellied and Red-crested korhaans and the Kori Bustard are imported by the Arab falconers for training falcons, captive breeding and pets. The ICBP (with its special Bustard Working Group) and the British government got unanimous support from the signatories of CITES (the Convention on International Trade in Endangered Species of Wild Fauna and Flora) for their recommendation to have international trade in all species of bustards regulated.

BUSTARD RESEARCH IN SOUTH AFRICA

Since the 1970's with the inception of the ICBP Bustard Working Group, world interest in the bustard family has increased and several detailed studies, generally of the rarer species, have been carried out. In 1986 the Percy FitzPatrick Institute for African Ornithology (PFIAO) began a study of the southern African species, focusing at first on the Karoo Korhaan. A study of the habitat requirements and distribution of the species has led to an insight into how different plant communities and therefore, grazing management schemes can affect the abundance of such species. It is the larger, rarer species that warrant the most attention, however. Their status and even distributions are poorly understood. They are the only bustards in southern Africa to undergo widescale movements and as such are difficult birds to follow. The PFIAO, with support from the Endangered Wildlife Trust, initiated research into the large bustards in 1987 and it is hoped, that in the future, the use of radio telemetry and even satellite tracking may increase our understanding of these fascinating birds.

ROYAL GAME

In the early days of this century bustards were known as "Royal game", in many areas of South Africa, because, by virtue of their rarity, only royalty should be allowed to hunt them. With the ever increasing need for land, many people feel that conservation is a scarcely affordable luxury and that if we want to protect our natural heritage it must be "cost effective". This has led to the commercialization under strict control, of game hunting in many parts of Africa. It has been suggested that bustards and korhaans too could be a valuable resource if utilized carefully.

It is true that, many people would be attracted by the proposal of hunting these large birds. Some, most notably the Arab sheikhs, would be prepared to pay handsomely for the privilege. People feel that bustards could be bred and restocked to carefully account for the loss through commercial hunting.

If anything has been learnt from the lessons of the declining species in Europe, north Africa, the Middle East and Asia it must be that bustards are very intolerant of hunting pressures. Schemes to

reintroduce rare bustard species into portions of their range where they have become extinct, supported by captive breeding programmes have all been fraught with failure. Only one such programme, in western Australia, has had an appreciable success. Bustards are slow breeders, taking three or more years to reach sexual maturity and then laying, in most cases, only a single egg. Even if a scheme to breed bustards in South Africa succeeded where all others have failed, it is difficult to imagine, with such low breeding rates, how any potential "pheasantry" of bustards could be commercially viable or ecologically acceptable.

It would be nice to think that with the increasing threat to their natural habitats throughout Africa and the rest of the world that South Africa will continue to stand out as being an area where the future of bustards has a degree of security.

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