STUDIES OF HERBIVORY AND VEGETATION CHANGE IN KAROO SHRUBLANDS

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ABSTRACT

STUDIES OF HERBIVORY AND VEGETATION CHANGE IN KAROO SHRUBLANDS

(Ph.D. thesis Zoology Department, University of Cape Town, Rondebosch. *Supervisor*: Prof. W.R. Siegfried, FitzPatrick Institute, University of Cape Town, *Co-supervisor*: Dr M.C. Rutherford, Stress Ecology Research Programme, National Botanical Institute, Rondebosch)

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The broad objective of these studies was to view present landuse (extensive small stock ranching) in the Karoo against the background of relationships between indigenous plants and animals and to indicate how modification of herbivore regimes might affect this arid environment. Specific objectives were to determine how grazing by domestic livestock brings about vegetation change, why such changes are sometimes irreversible, and whether existing conceptual models of vegetation dynamics adequately explain the impact of domestic livestock on Karoo vegetation.

Three interrelated aspects of plant-animal interactions were considered: the influence of herbivores on the evolution of Karoo plants, food selection by indigenous and introduced herbivores and the effects of herbivory, competition and rainfall on plant reproduction and recruitment. The results of these investigations are presented as 14 papers. The first three papers interpret plant morphology and biogeography to provide information on past spatial and temporal use of the landscape by herbivores, and the next seven provide new information on food selection by invertebrates, indigenous vertebrates and by domestic sheep. Three papers examine the hypothesis that the reproductive output, survival and abundance of some Karoo plant species are influenced by herbivory. The possible consequences of various land management options on diversity and productivity of Karoo rangelands are discussed in the concluding paper.

It was inferred, from biogeographic trends in the relative abundance of plants with thorns or propagules adapted for epizoochoric dispersal, that densities of large mammalian herbivores decreased from the north eastern to the southwestern Karoo. Within the most arid parts of the Karoo, mammalian herbivory appears to have been concentrated along drainage lines and in pans.

All the herbivores studied were selective feeders. Plant chemistry, moisture content, abundance, architecture, longevity and phenology influenced the acceptability of plants to herbivores. Insect herbivores (tephritid flies, harvester ants and cicadas) utilized plant species that were avoided by most vertebrates. The tortoise (*Geochelone pardalis*) selected plants with a high moisture content and appeared to be tolerant of chemicals that are toxic to many vertebrates. Foraging ostriches (*Struthio camelus*) avoided dry and woody material and rarely fed on plants known to be toxic to ruminants. Springbok (*Antidorcas marsupialis*) selectively browsed regrowth shoots and green vegetation in pans. Sheep (*Ovis aries*) ate lignified material but avoided toxic plant species and most succulents.

The relative abundance of seeds produced in experimental plots was related to vegetation composition, age structure and herbivory. Exclosure trials demonstrated that sheep removed a large percentage of flower buds and unripe seeds. Seed production determined the relative abundance of seedlings of selected plant species, but microtopography (soil surface features, litter and plant cover) dictated whether a species with small, water-dispersed or large, wind-dispersed seeds would establish on a given site. Germination was limited both by rainfall and temperature. Clearing experiments indicated that competition from established plants was the major factor limiting seedling survival in arid Karoo shrublands. Seedlings survived better on heavily grazed than on lightly grazed rangeland but seedling assemblages on heavily grazed range were dominated by species unpalatable to sheep.

Prolonged, heavy and selective grazing by large herbivores (whether introduced or indigenous), gradually alters the composition of vegetation by reducing the reproductive potential of preferred species. Removal of herbivores is unlikely to restore vegetation to its former composition because recruitment is limited by established plants. Removal of established plants, in combination with sowing of seed and exclusion of livestock when forage plants are reproducing, may improve the productivity of some Karoo rangelands.

STUDIES OF HERBIVORY AND VEGETATION CHANGE IN KAROO SHRUBLANDS

General Introduction

Livestock ranching has changed the composition of vegetation in arid regions worldwide (Schofield & Bucher 1986; le Houerou 1989; Westoby *et al.* 1989). In response to herbivory by domestic livestock, the density of palatable plants decreases (Noy-Meir 1982; Crawley 1983; Westoby *et al.* 1989; O'Connor 1991) and the relative abundance of well defended (Weaver & Clements 1929; Moore 1989; Taylor & Ralphs 1992) and ephemeral plants increases (Hoffman & Cowling 1990a). The consequence of these changes is a reduction in the carrying capacity of natural rangelands for domestic livestock (Friedel *et al.* 1990, Taylor & Ralphs 1992; Dean & Macdonald in press), which is equivalent to a loss in agricultural production.

The plant species composition of the arid interior (Karoo) of South Africa has reportedly changed over the last 200 years in response to settled pastoralism with domestic small-stock (Shaw 1875; Talbot 1961; Roux & Theron 1987). Referring to resultant losses in agricultural productivity in the Karoo, South Africa, Talbot (1961) wrote:- "The European colonist ... gradually exterminated most of the native fauna and substituted in its place one or more of three kinds of farm animals. ...... Prolonged selective grazing, (and)... frequent overgrazing (by domestic animals) ... have impoverished the plant cover over wide area. Palatable and nutritious plants have become fewer while toxic and unpalatable species have become abundant". These effects were first noted around water points and in the vicinity of *kraals* (stone enclosures) where Karoo shepherds herded their livestock at night (Talbot 1961). Although *kraals* were no longer used after about 1930, when government subsidies facilitated the enclosure of most farms in stock- or jackal-proof fencing (Roux & Opperman 1986), the vegetation in the vicinity of *kraals* continues to be dominated by plant species unpalatable to domestic livestock (pers. obs). Similarly, camp sites cleared by hunter-foragers (San) in the eastern Karoo at least 300 yr B.P., and *kraal* sites used by prehistoric herders (900 - 1200 yr B.P.) are characterized by disturbance indicators including thorny shrubs *Lycium* spp and ephemerals (Sampson 1986).

Effects of overgrazing on vegetation composition (Roux & Theron 1987; Bosch & Gauch 1991;) and on carrying capacity (Downing 1978; Dean & Macdonald in press) have been well documented, but the mechanisms for such changes (Hoffman & Cowling 1987) and the reasons for the failure of vegetation to recover from overgrazing, when rested, have not been investigated

Objectives and rationale

The objective of the studies in this thesis is to determine how grazing by domestic livestock brings about vegetation change, why such changes are sometimes irreversible, and whether existing conceptual models of vegetation dynamics adequately explain the impact of domestic livestock on Karoo vegetation. In order to achieve these objectives, it was necessary to view present landuse in the Karoo (extensive small stock ranching) against the background of past and present herbivory by indigenous animals, as well as to monitor plant population dynamics on grazed and protected rangelands. I believe that an improved understanding, of the effects of domestic livestock on Karoo vegetation, will provide a basis for management decisions relating to the conservation of plant and animal

(250-500 mm yr^{-1}) north-eastern parts of the Karoo receive convectional rainfall in summer, whereas 60% of the rainfall in the arid (20-300 mm p.a.) western districts is derived from cyclonic fronts in winter (Cowling 1986). Rainfall occurs erratically in the intermediate zone running northwards from the southern Cape to the Namib Desert (Cowling 1986; Rutherford & Westfall 1986).

Karoo soils, in common with aridosols in other parts of the world, are generally shallow, alkaline and poor in organic material (Ellis & Lambrechts 1986). The most widespread Karoo soils are sandy clays and loams derived from sedimentary mudstones, but sands derived from dolerite intrusions and aeolian deposits occur in the northwest of the region (Ellis & Lambrechts 1986).

The flora of the southwestern or Succulent Karoo is affiliated with the evergreen Fynbos shrublands of the coastal mountain ranges but is characterized by a high diversity of endemic succulents and asteraceous shrubs (Gibbs Russel 1987; Hilton-Taylor 1987). The vegetation of the northern and eastern Karoo is grassy and grades into grassland and savanna vegetation as rainfall increase (Acocks 1953; Gibbs Russel 1987).

Extensive livestock farming (ranching) on natural rangeland is the major form of landuse in the Karoo (Roux *et al.* 1981) and 94.2% of the surface area of the Karoo is used for this purpose (Department of Agriculture 1985a & b, 1986), the remainder being used for crop production. Only 0.7% of the Karoo is protected in nature reserves (Cowling 1986), but all of these reserves were once livestock ranches. Sheep are the most abundant and widespread livestock (about 10 million), whereas cattle (0.3 million) are restricted to the grassier northern parts of the region and Angora goats (1.1 million), Ostriches *Struthio camelus* (0.2 million) (Department of Agriculture 1985a; Directorate of Agricultural Information 1991) and an indigenous antelope (Springbok) *Antidorcas marsupialis* (Jooste 1983) are ranched in the shrubby areas to the south and east.

The whole region was included in biogeographical studies of plant evolution in the Karoo (Chapters 3 and 4). Studies of food selection by Ostriches and Springbok (Chapters 10 and 11) were based at sites in the northwestern (Namib Desert 22°S, 14°E and Aggeneys 29°S, 19°E) and southern (Prince Albert District 33°S, 22°E) extremes of the region. All other research presented in this thesis was carried out at the Tierberg Karoo Research Centre and on adjacent properties in the Prince Albert District of the southern Karoo. The history, physical environment, flora and fauna of the Research Centre are described in Appendix 1.

Thesis presentation

The chapters of the thesis are grouped into three sections. The first section considers the relative influence of herbivores on the evolution of plants across a climatic gradient in the Karoo. This information was needed to predict differential impact of herbivory by domestic livestock on plant assemblages in winter and summer-rainfall regions of the Karoo. The second section examines food selection by a range of common Karoo herbivores including three species of arthropods, a reptile (*Geochelone pardalis*), a bird (*Struthio camelus*), an indigenous mammal (*Antidorcas marsupialis*) and the domestic sheep (*Ovis aries*). An understanding of the influence of food quality and quantity on food choice by herbivores was needed in order to predict the response of indigenous herbivores to vegetation change.

In the third section, I present the results of observational and experimental studies designed to separate the effects of herbivory on plant reproduction and mortality, from the effects of competition and rainfall on these population parameters. These studies provide insight into the mechanisms of vegetation change in the southern Karoo. The concluding

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PART 1

THE INFLUENCE OF HERBIVORES ON THE EVOLUTION OF KAROO PLANTS

1. INFLUENCE OF HERBIVORES ON EVOLUTION OF KAROO PLANTS

1.1 Lifestyles of plants in four habitats in an arid Karoo shrubland.

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Abstract: *This inter-habitat comparison of plant morphology, dispersal and phenology in succulent Karoo vegetation in South Africa, indicates that selective pressures vary over short distances. Local differences in soil-moisture and nutrient status lead to uneven use of sites by animals. The influence of animals on plants increased from the plains through washes to drainage lines where many species defended themselves against damage by mammals and were zoochorically dispersed. Fugitive plants in nutrient-rich patches (*heuweltjies*) on the plains were adapted for dispersal by mammals, but perennials were autochorous and modified for tolerating drought and high salinity. Plants species occupying wet sites in arid regions should show more animal-associated adaptations than other members of the flora.*

Introduction

Most research on plant-animal interrelationships in South Africa has been carried out in relatively mesic fynbos (Bond & Slingsby 1983; Rebelo 1987; Knight 1988) and savanna (Boughey 1963; Cooper & Owen-Smith 1985; 1986). In these vegetation types, soil-nutrient status has been identified as a major factor influencing both plant morphology (Campbell 1986; Campbell & Werger 1988) and the distribution of grazing mammals (McNaughton 1988).

In arid regions, moisture is probably the most important factor affecting the distributions of plants and animals, both on regional and local scales (Werger 1985). Animals tend to concentrate in and move between mesic sites in arid landscapes, eg. watercourses on Karoo (Acocks 1976) or desert (Louw & Seely 1982) plains in southern Africa, and it can be predicted that plant species limited to such "oases" should have a wider range of animal-asociated adaptations than those common in the surrounding xeric vegetation.

Recent studies in the Karoo (Milton, Siegfried & Dean 1990; Dean, Milton & Siegfried 1990), and elsewhere (Sorensen 1986), support the notion that plant dispersal mechanisms are unevenly distributed between habitats. The present study aims to investigate the hypothesis that the incidence of animal-associated adaptations in plants differs between habitats as a function of moisture or nutrient availability in an arid shrubland.

Study site

The study was carried out at the field site of the Tierberg Karoo Research Centre (33^{0}10'S, 22^{0}17'E) situated on the southern edge of the Karoo (**Plate 1a**). This semi arid inland region supports a short, scrubby vegetation, ranging from succulent, dwarf-shrubland (Succulent Karoo) in the south and west to non-succulent, grassy shrubland (Nama Karoo) in the north and east (Rutherford & Westfall 1986). The vegetation at Tierberg is typical of the southern Karoo.

Taxonomy follows Gibbs Russell *et al.* (1985 and 1987) except that the Mesembryanthemaceae are included under Aizoaceae following Bittrich & Hartmann (1988).

Structural and functional attributes of plant assemblages (see **Tables 1-5**) were compared by allocating every species present in the sample quadrats to a mutually exclusive class for each of the five descriptors defined below. The number and cover of species with given attributes were then expressed as a percentage total species number and plant cover for sample quadrat. Data were averaged for each topographic unit sampled. The structural and functional descriptors were defined as follows:-

leaf longevity: deciduous or evergreen (retaining some leaves at all times);

lifeform: tree, parasite, non-succulent shrub, succulent shrub, forb, grass, geophyte;

leaf size: leafless, leptophyll: $<26\ \text{mm}^2$, nanophyll: $26\text{-}225\ \text{mm}^2$, microphyll: 226-2025;

spinescence classified according to origin of spine (leaf, shoot-tip spines, inflorescence, stem outgrowth);

seed dispersal mechanisms based on fruit morphology and observed occurrence of intact seeds in mammal dung, are

1: anemochorous (fruit winged, plumed or inflated);

2a: active autochorous (fruit opens rapidly in response to desiccation or wetting);

2b: passive autochorus (seeds released as fruits decay), but note that some species placed in this category by Hoffman & Cowling (1987) are considered endozoochorous here;

3a: epizoochorus, on pelage (barbed, adhesive fruit, see Sorensen 1986);

3b: epizoochorus, as nest material (seeds attached to fluffy fruit or peduncle, see Dean *et al.* 1990);

4a: endozoochorus, by birds (hard seeds in fleshy, brightly coloured fruits, see Knight 1988);

4b: endochorous, by mammals (seeds in dull, fleshy fruits or small and hidden among foliage, see Janzen 1984);

5: myrmecochorus (see Bond & Slingsby 1983).

The diversity of lifeforms in each habitat was compared by calculating the Shannon-Weber diversity index (H'):

$H' = (N \ln N - \text{sum}\ (f_i \ln f_i))/N$ (Zar 1984), where N is the sample size and f_i is the number of species in lifeform category i.

Every three to five weeks I recorded the flower, leaf and shoot condition of one individual each of 25 common species on run-off sites (plains and *heuweltjies*) and about 45 species in run-on sites (washes and drainage lines). The observations were made on unmarked individuals, the phenology of which appeared to be consistent with other members of the species within the same habitat. Observations were made 18 times in summer (October to March) and 14 times in winter (April to September) between December 1987 and February 1990. Flowers and leaves were rated as absent, new, mature, or withered. Shoots were classified as growing (flexible at the tip), or not growing. Leaf loss and gain relative to rainfall and the timing of shoot growth in run-on and run-off sites were analysed graphically. Kruskal-Wallis analysis of variance by ranks was used to test the hypothesis that there were no habitat or seasonal differences in the numbers of plants with open flowers, new leaves and extending shoots.

Results

Species composition

Ordination of sample plots formed groups that fitted *a priori* habitat designations (**Figure 1a**). Plant assemblages on *heuweltjies* were least similar to those of drainage lines. The vegetation of the lightly grazed plains at the Tierberg study site was relatively homogeneous, and had little in common with plant

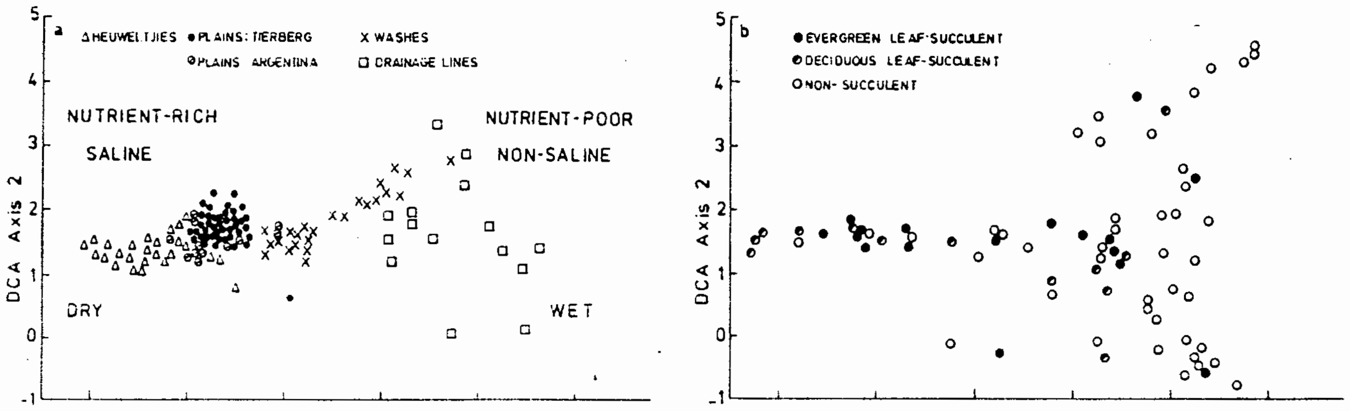
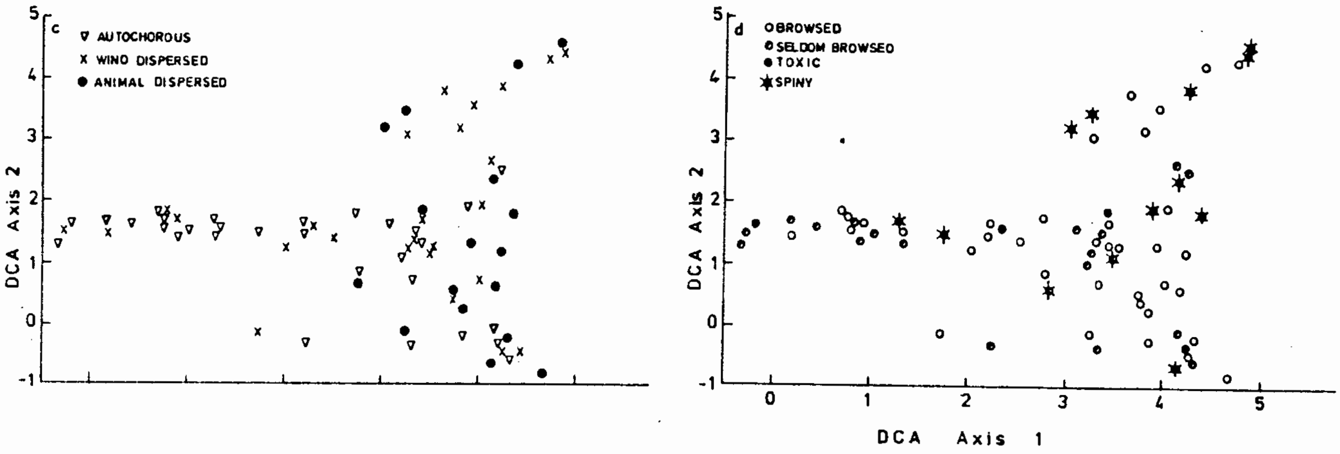


Figure 1. DECORANA ordinations of 73 perennial plant species in 119 sample plots. (**a**) Differences between plots appear to be related to species composition responses to available moisture and soil chemistry. Symbols refer to *a priori* field classification of habitats.

(**b**) Succulence is more prevalent on the *heuweltjie* end of the gradient.



(**c**) Seed dispersal mechanisms: animal-dispersed plant species are clustered at the drainage-line end of the gradient.

(**d**) Plant defences: palatable and spinescent plant species appear to increase towards the drainage lines end of the gradient.

Structural and functional attributes

Ordination of plant species indicated that leaf persistence, succulence (**Figure 1b**), dispersal mechanisms (**Figure 1c**) and defensive strategies (**Figure 1d**) all varied across the gradient from *heuweltjies* to drainage lines.

Leaf longevity

In sharp contrast with the evergreen nature of the surrounding plains' vegetation (**Table 1**), *heuweltjie* plant associations comprised 72 % deciduous or fugitive species. These grew rapidly after good rain, increasing total plant cover by up to 5 %. Annuals, such resprouting forbs as *Lessertia annularis*, and winter-deciduous trees (*Acacia karroo*, *Diospyros lycioides*) accounted for the high proportion of drainage line species with short-lived leaves.

Table 2. Diversity of plant lifeforms of plants in the southern Karoo. The table shows **(a)** contribution of the various lifeforms to the species composition and **(b)** the proportional contributions of the lifeforms to total projected canopy cover for each habitat. Tierberg has a history of moderate grazing by merino sheepand Argentina a history of heavy grazing by dorper sheep.

Habitat	Plains		Heuweltjie	Wash	Drainage
Farm	Tierberg	Argentina	Tierberg	Tierberg	Tierberg
Quadrats sampled	42	12	26	24	15
(a) Species composition					
Total number	39	34	36	65	86
trees > 1.5 m	0	1	2	1	11
parasites	0	0	0	1	5
succulent shrubs	21	18	17	26	23
non-succulent shrubs	10	6	5	24	27
forbs	5	6	9	5	14
grasses	1	1	1	2	4
geophytes	2	1	0	6	2
Growth form diversity[1]	2.85	2.62	5.66	4.35	6.62
(b) Projected canopy cover					
Habitat avg ± sem	18 ± 1	15 ± 1	28 ± 2	20 ± 1	37 ± 4
% trees > 1.5 m	0.0	0.3	4.0	5.4	42.6
% parasites	0.0	0.0	0.0	0.1	0.6
% succulent shrubs	55.6	74.2	78.1	35.0	15.4
% non-succulent shrubs	43.5	23.0	12.3	55.4	34.3
% forbs	0.4	1.9	3.6	2.1	3.2
% grasses	0.1	0.3	0.1	0.4	2.1
% geophytes	0.1	0.3	0.0	0.8	0.1

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[1] Diversity calculated using Shannon index $(N \ln N - \text{sum}(f_i \ln f_i))/N$ (Zar 1984, p.33)

Leaf sizes

Aphyllous and very small-leaved species were most abundant in washes and drainage lines, whereas relatively large-leaved species occurred on *heuweltjies* (**Table 3**). On the plains, most species had nanophyll leaves, but during dry periods many became leptophyllous by shedding their larger leaves.

Spinescence

There were three spinescent plant species on the plains and 13 in drainage lines. The contribution of spinescent species to the total number of species in a habitat increased from the plains through *heuweltjies* and washes to drainage lines (**Table 4**). Spinescent plants made up a greater proportion of the total plant cover in drainage lines than in other habitats. On moderately grazed plains at Tierberg, spinescent plants made up 24.5 % of the total cover, but nearly all of this (24 %) was accounted for by one (or two) spinescent *Ruschia* species. These plants have small spines derived from sterile inflorescence branches. Plant species with woody spines (shoot tips and stem outgrowths) were found mainly in the drainage lines (**Table 4**).

Table 4. Spinescence classified according to origin of spine (leaf, shoot-tip spines, inflorescence, stem outgrowth). Spinescent cover given as a proportion of the total projected canopy cover in each habitat. Tierberg has a history of moderate grazing by merino sheep and Argentina a history of heavy grazing by dorper sheep.

Habitat	Plains		Heuweltjie	Wash	Drainage
Farm	Tierberg	Argentina	Tierberg	Tierberg	Tierberg
Quadrats sampled	42	12	26	24	15
Contribution of spinescent plants to community					
% of total cover	24.5	1.1	7.9	23.7	31.8
% of all species	7.6	8.8	11.1	10.7	15.1
Spine ontogeny (number of species in each category)					
Leaf tip or margin	1	0	0	1	2
Shoot tip	0	0	0	2	2
Inflorescence	1	1	1	2	1
Stem outgrowth	1	2	3	1	8
Total spinescent spp	3	3	4	6	13
Height range (m)	0.2-0.6	0.2-0.6	0.3-1.2	0.2-1.0	0.3-6.0

Seed dispersal mechanisms

Zoochoric species were most abundant in drainage lines where 18 (21 %) of the species are adapted for dispersal by birds and another 13 (15 %) for other types of zoochory (**Table 5**). There were only six zoochoric species on plains. Plants with wind-dispersed seeds were common in all habitats, but proportionally less so on *heuweltjies*, where autochorous and mammal-dispersed species were prevalent.

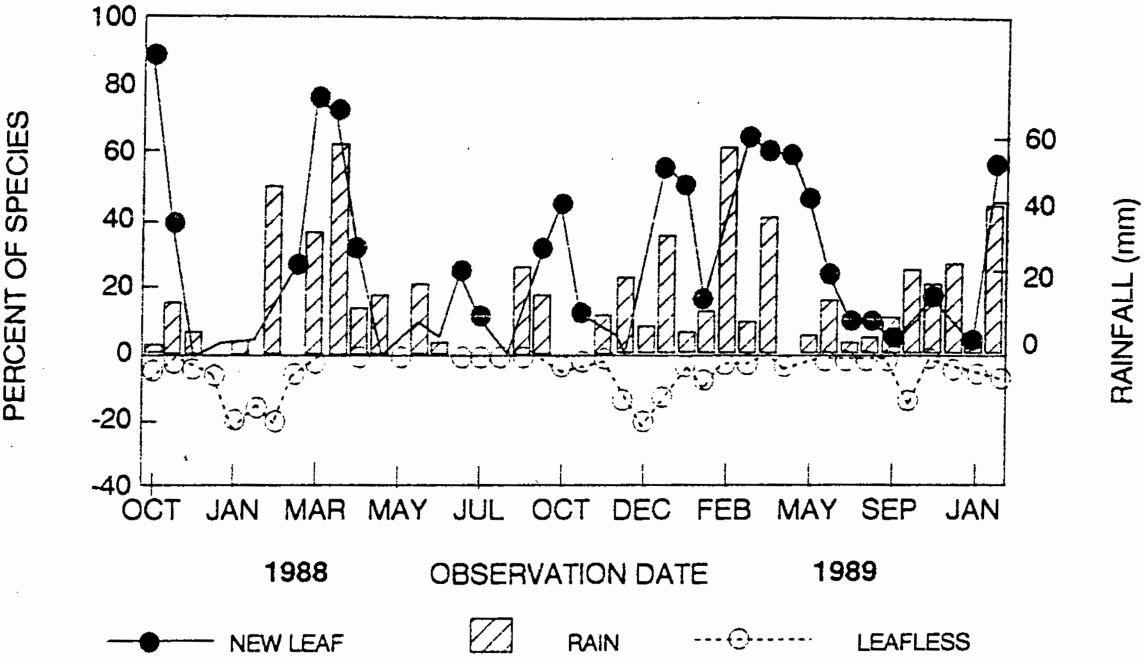

Figure 2. Timing of leaf gain and leaf loss relative to rainfall in the intervening period (Tierberg field site). The percentage of species which have shed all leaves is shown on the negative axis of the graph.

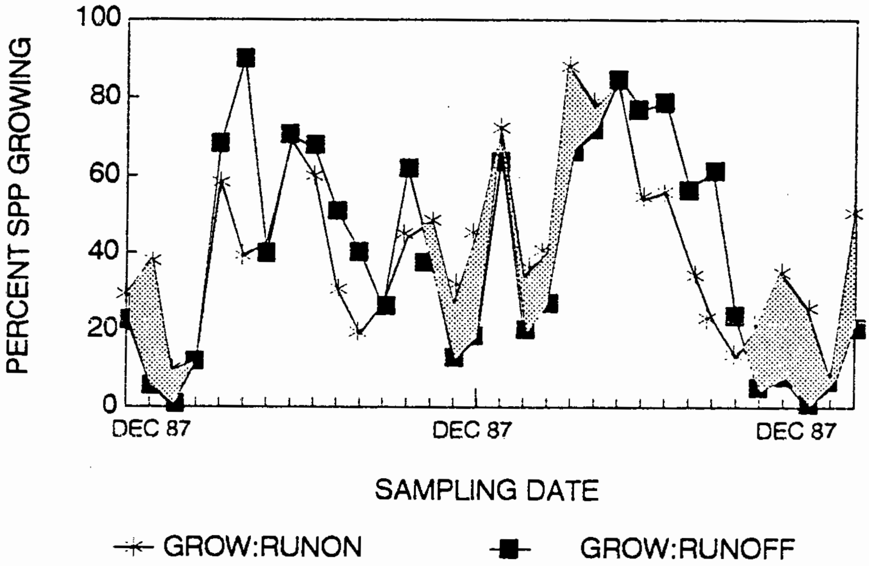

Figure 3. Shoot-growth phenology of plants in run-on (wash and drainage line) and run-off (plains and *heuweltjies*) habitats. Graph overlaps are shaded to highlight differences in timing of growth.

Evolutionary response of plants to the physical environment

Most of the rain falling during heavy summer thunder-showers runs off rapidly from the plains and collects in washes and drainage lines, so that the effective rainfall of run-on habitats is far higher than that of watersheds. This explains why deep-rooted, summer-growing tree and shrub genera (eg *Acacia*, *Diospyros*, *Rhus*, *Grewia*) of tropical or savanna origin (Gibbs Russell 1987) are limited to drainage-lines. In winter, light drizzle soaks into the soil of the plains and there is little run-off to the rivers. Shallow-rooted plains species, mainly members of the Aizoaceae and Asteraceae with centres of diversity in the winter-rainfall region of the south western Cape (Gibbs Russell 1987; Hilton Taylor 1987), grow more sporadically than riverine species, and are especially active in winter.

Differences in the periodicity of growth in run-on and run-off habitats, paralleled differences in phenology of plant communities along an aridity gradient in the eastern Cape (Hoffman 1989). Timing of growth might be related to photosynthetic pathways. Many succulent plants, such as those that dominate the plains (**Plate 1c**) and *heuweltjie* vegetation at Tierberg, are known to have CAM and intermediate photosynthetic pathways (Pierce & Cowling 1984) which minimize water loss (Evenari 1985); non-succulent plants, such as those of the shrubby communities of drainage lines use C_3 and C_4 photosynthetic pathways (Werger 1985). Leaf succulents, by rapidly absorbing and storing water (Milton 1990), apparently make better use of small rain events than non-succulent perennials. The non-succulent species of the plains, such as *Pteronia pallens*, cope with changes in soil moisture status by producing large leaves under moist conditions and smaller ones towards the end of the growth flush. The large leaves are shed first, when the plant becomes moisture stressed. This ability to regulate leaf-surface area but retain some leaves has been documented for plant species in other arid regions (Orshan 1954; Nilsen *et al.* 1986).

The food and faecal accumulations of rodents (du Plessis 1989), termites (Coaton 1958) and other animals which forage and defecate on *heuweltjies* (Milton & Dean 1990) raise salt and nutrient levels of soils in these patches. Soil nutrient status can be reflected in the plants (Day & Detling 1990) and may explain why sheep preferentially graze these sites (Armstrong & Siegfried in press). Succulent, deciduous and fugitive plants characterize *heuweltjies* throughout the western Cape (Olivier 1979; Knight, Rebelo & Siegfried 1989). Saline soils evidently make *heuweltjies* unsuitable, during dry periods, for plants that cannot store water. After rain *heuweltjies* are rapidly colonised by succulent forbs, a plant life form characteristic of saline soils (Box 1981).

As soil salinity, conductivity and nitrogen status decreased from *heuweltjies* through plains to drainage lines, there was a concomitant reduction of cover by succulent species (**Figure 4**). Lloyd (1989), in an ordination of vegetation and soils from Vaalputs in the northern Karoo, found that dwarf succulent shrublands with *Ruschia* spp and *Brownanthus ciliatus* occurred on saline soils. Succulents also dominate saline pans in the non-succulent vegetation of the Kalahari (Leistner 1967). My data partly support Campbell & Werger's (1988) finding that succulence, together with (drought) deciduousness and the presence of annuals, is characteristic of nutrient-rich soils. However, cover by deciduous plants was similar on *heuweltjies* (58 %) and in drainage lines (59 %), and lower (9 - 26 %) on the plains.

Similarly to resource-limited evergreen plants elsewhere (Coley *et al.* 1985), many of the plains plants are known to have carbon-based metabolites such as oxalic acid (*Drosanthemum*, *Mesembryanthemum*), mesembrine (*Psilocaulon*) and other alkaloids (*Pteronia pallens*) which make them toxic or unpalatable to mammals (Kellerman *et al.* 1988). Nutrient-rich patches on the plains (*heuweltjies*) provide nutritious grazing but, only after good rains when palatable, endozoochorically dispersed fugitive plants grow and multiply. During dry periods, there are no green plants on *heuweltjies* except those perennial species of the Aizoaceae which are unpalatable to ruminants.

Plains species which evolved with small selective herbivores (rodents, lagomorphs, small antelope, tortoises) may not be able to survive frequent heavy defoliation. This appears to have occurred on the plains of the farm Argentina, where cover by palatable plant species decreased. The plants which have replaced them are fugitive, unpalatable or disturbance-tolerant species normally associated with *heuweltjies*. Dunging by livestock probably altered the soil chemistry and contributed to this change.

Drainage lines are an important source of food, shelter or nesting material for many species of insects, birds and mammals. Data collected at Tierberg show that during summer droughts there are more green and flowering plants in these run-on sites than on the plains and *heuweltjies*. If the flora of drainage lines, which is similar throughout the Karoo (Acocks 1976), evolved with a greater biomass and diversity of animals than the flora of the surrounding shrublands on the plains, then components of drainage line flora should show relatively more modifications co-existence with animals. These modifications would be expected to include means of protection from damage by trampling and browsing and adaptations for exploiting the mobility of animals to transport seeds to distant but similar habitat patches (**Plate 1d**).

Why are so many drainage-line plants (15 % of species; 32 % cover) spinescent? Chemical defences can be reduced by repeated defoliation (du Toit *et al.* 1990). Moreover chemicals provide no protection from trampling or crushing (Leistner 1967). The effective protection from large mammals offered by certain types of spines (Boughey 1963; Cooper & Owen-Smith 1986) may explain why plants with hard long or hooked spines (*Lycium cinereum*, *L. oxycarpum*, *Acacia karroo*, *Carissa haematocarpa*) are so well represented in drainage-line vegetation. Prickly leaf margins and inflorescence-derived spines of plains plants (eg. spinescent *Ruschia* sp, *Berkheya spinosa*) might reduce browsing by lagomorphs and small antelope, but evidently provide little protection from larger browsing herbivores. These two species appear to have been greatly reduced by Dorper sheep on the farm Argentina, whereas species with woody spines are as abundant on this heavily grazed site as they are on moderately grazed Tierberg.

Since major drainage lines make up less than 3 % of the landscape in this part of the southern Karoo, directed, long-distance dispersal of pollen and seed could be important for the survival of species confined to these drainage lines. Pollination mechanisms were excluded from this study because of the paucity of information on pollinators of Karoo plants. However, genera with tubular flowers (eg. *Lycium*, *Aloe*, *Rhigozum*) which are visited by sunbirds are confined to run-on and *heuweltjie* habitats in the study site. Many of the Aizoaceae and Asteraceae of the plains are visited and possibly pollinated by wasps (Gess & Gess 1989), bees and flies (pers. obs).

Many drainage-line plant species achieve directed dispersal of seeds by producing succulent fruits eaten mainly by a small suite of specialized frugivorous birds which feed and nest in tall vegetation (Skead 1967). Others use nesting birds (Dean *et al.* 1990) or mammals to disperse seeds (Milton *et al.* 1990).

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Appendix 1 ctd....

HABITAT		PLAINS				HEUWEL	WASH	DRAIN
FARM		T	T	T	A	T	T	T
SPECIES GROUP		1.3	1.1	1.2	1.4	2	3	4
PLOTS SAMPLED		19	11	12	12	26	24	15
FAMILY	SPECIES							
Asteraceae	*Felicia filifolia* (Vent.) Burtt Davy	-	-	-	-	-	V	II
Bignoniaceae	*Rhigozum obovatum* Burch.	-	-	-	-	-	II	II
Fabaceae	*Lessertia annularis* Harv.	-	-	-	-	I	II	IV
Asteraceae	*Eriocephalus ericoides* (L.f.) Druce	-	-	-	-	-	II	II
Asteraceae	*Pentzia incana* (Thunb.) Kuntz	-	-	-	-	-	II	III
Asteraceae	*Pteronia glauca* Thunb.	-	-	-	-	-	II	II
Iridaceae	*Moraea speciosa* (L.Bol.) Goldbl.	-	-	-	I	-	II	-
Polygalaceae	*Polygala leptophylla* Burch.	-	-	-	-	-	(II)	I
Zygophyllaceae	*Zygophyllum gilfillanii* N.E.Br.	-	-	-	-	I	II	II
Asteraceae	*Pteronia scariosa* L.f.	-	-	-	-	-	I	-
Asteraceae	*Pteronia sordida* N.E. Br.	-	-	-	-	-	I	I
Viscaceae	*Viscum rotundifolium* L.f.	-	-	-	-	-	I	-
Colchicaceae	*Ornithoglossum viride* (L.f.) Ait.	-	-	-	-	-	I	-
Asphodelaceae	*Aloe variegata* L.	-	-	-	-	-	I	I
Aizoaceae	*Limeum aethiopicum* Burm.	-	-	-	-	-	R	-
Crassulaceae	*Crassula pseudohemisphaerica* Friedr.	-	-	-	-	-	I	-
Asteraceae	*Ericephalus spinescens* Burch.	-	-	-	-	-	I	I
Sterculiaceae	*Hermannia pulverata* Andr.	-	-	-	-	-	I	-
Crassulaceae	*Tylecodon reticulatus* (L.f.) Toelk.	-	-	-	-	-	I	-
Hyacinthaceae	*Albuca* sp	-	-	-	-	-	I	-
Asclepiadiaceae	*Fockea comaru* (E.Mey.) N.E. Br.	-	-	-	-	-	R	-
Aizoaceae	*Tetragonia fruticosa* L.	-	-	-	-	-	I	II
Poaceae	*Schizobasis intricata* (Bak.) Bak.	-	-	-	-	-	(I)	-
Zygophyllaceae	*Zygophyllum retrofractum* Thunb.	I	-	-	-	I	II	II
Aizoaceae	*Trichodiadema bulbosa* (Haw.) Schwantes	-	-	-	-	-	II	-
Crassulaceae	*Crassula muscosa* L.	I	I	I	-	-	II	III
Asteraceae	*Gazania krebsiana* Less.	I	-	I	-	R	II	III
Asparagaceae	*Protasparagus recurvispinus* Oberm.	-	I	-	I	II	III	I
Brassicaceae	*Lepidium africanum* (Burm.f.) DC.	I	-	-	I	II	I	III
Asteraceae	*Berkheya spinosa* (L.f.) Druce	I	-	I	-	-	II	III
Euphorbiaceae	*Euphorbia caterviflora* N.E. Br.	I	-	-	-	R	II	II
Asteraceae	*Leysera tenella* DC.	-	-	-	(I)	-	-	(I)
Asteraceae	*Ursinia nana* DC.	-	-	-	(I)	-	-	(II)
Asclepiadiaceae	*Microloma massonii* (Schultes) Schltr.	R	-	-	-	-	I	I
Portulaccaceae	*Anacampseros telephiastrum* DC.	R	-	-	R	-	R	-
Chenopodiaceae	*Salsola tuberculata* (Moq.) Fenzl	I	I	-	I	-	I	-
Asteraceae	*Pteronia viscosa* Thunb.	-	-	R	-	-	I	I
Poaceae	*Aristida adscensionis* L.	-	-	R	-	-	(I)	I
Fabaceae	*Melolobium candicans* Eckl.& Zeyh.	-	-	-	-	-	I	IV
Asteraceae	*Rosenia humilis* (Less.) Bremer	-	-	-	-	-	I	III
Aizoaceae	*Sphalmanthus bijliae* (N.E.Br.) L.Bol.	-	-	-	-	-	-	IV
Asteraceae	*Felicia muricata* (Thunb.) Nees	-	-	-	-	-	I	III
Santalaceae	*Thesium lineatum* L.f.	-	-	-	-	-	I	III
Aizoaceae	*Delosperma cf. subincanum* Schwant	-	-	-	-	-	I	II
Asteraceae	*Senecio angustifolius* (Thunb.) Willd.	-	-	-	-	-	-	II
Anacardiaceae	*Rhus undulata* Jacq.	-	-	-	-	-	-	II
Solanaceae	*Lycium oxycarpum* Dun.	-	-	-	-	-	-	II

1. INFLUENCE OF HERBIVORES ON EVOLUTION OF KAROO PLANTS

1.2 The distribution of epizoochoric plant species: a clue to the prehistoric use of arid Karoo rangelands by large herbivores

Authors: Milton, S.J., Siegfried, W.R. & Dean, W.R.J.
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Abstract: *Adhesive dispersal mechanisms are rare in the flora of the plains of the arid south-western Karoo, South Africa, and most plants lack the long or hooked thorns normally associated with defence against browsing mammals on nutrient-rich soils. The flora of drainage lines, however, differs from that of the surrounding flats in that many of its species are thorny, bear pods or succulent fruits palatable to mammals, and more species have adhesive propagules. The few adhesive fruits that are found in domestic Merino sheep fleeces in the arid Karoo belong to alien species, annual grasses, and plants of drainage lines. Fleeces from the higher rainfall, grassier eastern and northern parts of the Karoo carry many more adhesive diaspores, especially those of grasses.*

Introduction

Barbed, hooked, spiny or viscous diaspores of plants, as well as spinescent stems or leaves, are presumed to be indicative of co-evolution between floras and herbivorous vertebrate faunas (van der Pijl, 1982; Janzen, 1986). New Zealand, which has no indigenous mammals, has few plant species which are either adapted for epizoochoric dispersal by mammals (data from Flux 1967, interpreted by Carlquist & Pauly, 1985), or armed with thorns (Greenwood & Atkinson, 1977). The genus *Solanum* L. is very prickly in Australia where it has a long history of presumed co-evolution with browsing marsupials, but few *Solanum* species on oceanic islands with limited mammalian fauna are prickly (Symon, 1986). Oceanic island populations of epizoochoric genera such as *Bidens* L. tend to lose their dispersal ability (Carlquist, 1966), either because dispersal is less important for survival on islands than on the mainland, or because the lack of suitable dispersers gives adhesive diaspores no selective advantage over simpler fruits.

If the incidence of both epizoochory and spinescence in floras is influenced by diversity of herbivorous mammals (Fenner, 1985; Campbell, 1986; Janzen, 1986; Plitmann, 1986), then fewer plant species adapted for dispersal by mammals, and mechanical protection against them, could be expected to occur in South African Karoo, fynbos or forest biomes than in savanna or grassland where the diversity of herbivorous mammals is twice as great (Rautenbach, 1978). Moreover, since species dispersed by adhesion do not attract their dispersers by advertising (Sorenson, 1986), and may even cost them irritation and injury (Chippendall, 1955; Agnew & Flux, 1970), associations of epizoochoric and thorny plants with habitats frequented by mammals in search of food, water or shelter can be expected.

In this report we reveal a relationship between the dispersion of herbivorous mammals and the incidence of epizoochoric plants in the Karoo biome of South Africa, by addressing the following questions:

The sites (co-ordinates and environmental data given in **Appendix** 1) lie between Prince Albert in the arid southwestern Karoo and Cradock in the more mesic northeastern Karoo. Precipitation (Cowling, 1986), carrying capacity for domestic livestock, which is an index of productivity, (Vorster, 1985), altitude, the proportion of the annual rain that falls in summer, and the prevalence of C_4 grasses in the vegetation (Werger, 1985), all increase along this south-west to north-east gradient.

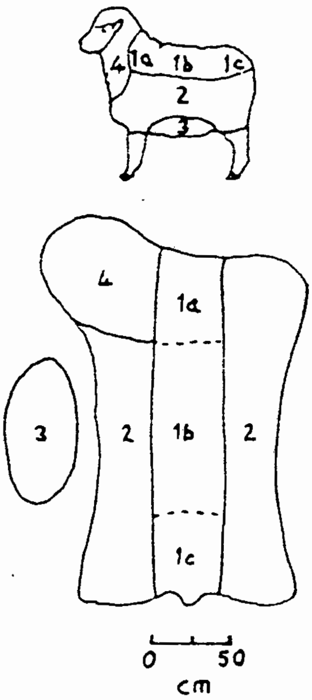

Figure 2. Diagram of a Merino sheep and a sheep fleece showing four zones examined for diaspores. Zone 1: back divided into subsections 1a (shoulders), 1b (mid back), 1c (rump); zone 2: flank; zone 3: belly; zone 4: neck.

Newly shorn fleeces were placed on sorting tables (about 2.2m x 1.7m) in the manner traditionally used to class wool, and were subsampled by placing a wire hoop (132mm diameter) on predetermined zones of a fleece (**Fig.** 2). All diaspores seen in the wool within the hoop were hand picked using fine forceps. Diaspores were later sorted, identified and counted. Seed fragments and seedless fruits were discarded. Seeds extracted from multi-seeded fruits were counted individually.

Habitat comparisons of epizoochory. In order to assess whether the contribution of epizoochoric species to the flora differed with habitat, and whether epizoochory was associated with structural characteristics of the vegetation, we made checklists of all plant species in approximately one hectare of each of three habitats at site A: an alluvial plain, a rocky ridge and a wooded drainage line.

Regional comaprisons of epizoochory: We compared the prevalence of epizoochoric dispersal in southern African biomes by analysing checklists of indigenous angiosperms from 18 sources (**Appendix** 3). Barbs, hooks, spines and viscid glands (**Fig.** 3) on fruits were considered to be adaptations for adhesive dispersal. The number of thorny species (ie plants bearing stem, stipule or leaf thorns but not thorny fruits) was also counted in each checklist. Where a species was not well known to the authors, reference was made to descriptions given in Chippendall (1946, 1955) and Dyer (1976), and to illustrations in guides to the flora of southern Africa. Alien species were deleted from checklists on the basis of their listing by Wells *et al.* (1986).

occurred in more than 10% of the samples, but the most abundant seeds were *Galenia africana* L., *Lycium* sp. and *M. polymorpha*. The Poaceae contributed more species (15) than any other plant family and provided 11 of the 15 kinds of diaspores apparently modified for epizoochoric dispersal. Only two of the five alien species appeared to be adapted for epizoochory, but seeds of alien plants occurred in 32% of the samples at site B. The percentage of samples containing indigenous epizoochorous diaspores ranged from 1% at site A (sampled in August 1987) to 88% at site C (sampled in October 1987).

TABLE 1. Distribution of seeds of indigenous (I) and alien (A) plants in four zones of Merino sheep fleeces from four sites in the Karoo.

	Back		Flank		Belly		Neck	
	I	A	I	A	I	A	I	A
Total species	37	1	20	2	19	2	12	0
Epizoochoric species	8	0	7	1	11	2	4	0
Perennial dicots.	25	0	10	0	5	0	7	0
Annual dicots.	3	1	1	2	3	1	0	0
Grasses	9	0	9	0	11	1	5	0
Total spp	38		22		21		12	
No. quadrats sampled	126		126		129		15	

The highest seed densities and the greatest diversity of species were found in zone 1a of fleeces (ie between the shoulders), known to wool farmers as the "crow's nest" because of the sticks, seeds and other organic debris which collects there. Only 21% of the species found in the back zone (1a,b,c) were adhesive (**Table 1**); bird droppings and fruits of tall shrubs contributing many of the seeds in this zone. Flank and belly zones generally carried lower seed densities, although at site D more seeds were found on the belly than on other parts of the fleece (**Appendix 1**). Epizoochoric seeds of low-growing plants, especially grasses, dominated amongst the diaspores found on the flanks and belly (**Table 1**).

Of the indigenous epizoochoric species, seven grasses had needle-like fruits with backwardly directed trichomes, three grasses had hooked or barbed spikelets, and three dicotyledons had spiny fruits probably transported embedded in skin or hooves (**Fig. 3**). Large spiny burrs were uncommon. Heavy trample burrs were absent.

Habitat comparisons of epizoochory

The incidence of epizoochory and thorniness in graminoids, annual and perennial dicotyledonous plants from each of these habitats is shown in **Table 2**. There was a significant correlation (r = 0.992; P < 0.01) between the numbers of epizoochoric and thorny species in a habitat. Epizoochoric plant species were most common along drainage lines among tall, thorny vegetation, although few epizoochoric species were either tall or thorny. No epizoochoric species was found in the sparse, succulent shrubland of the plain.

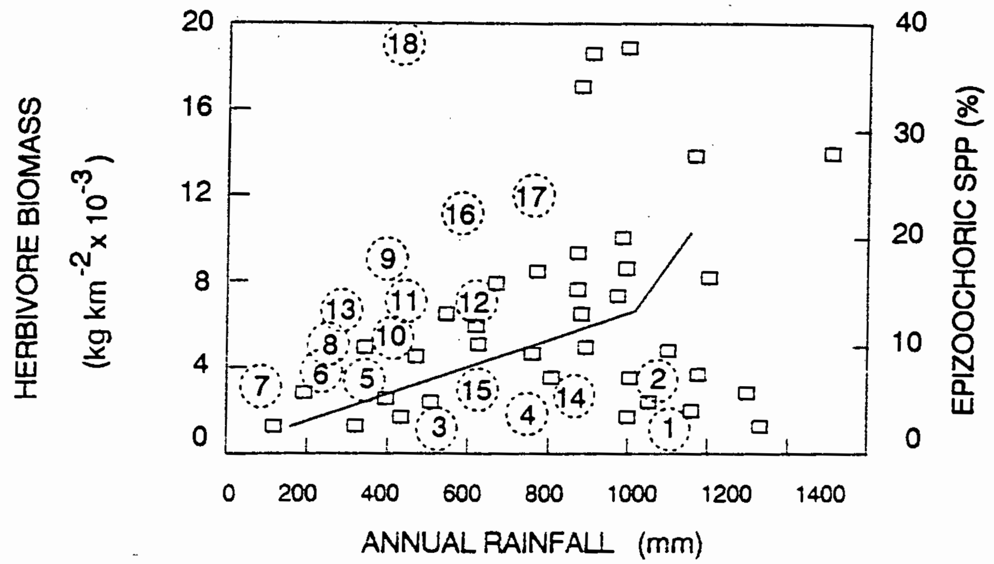

Figure 4. Relationship between the percentage of epizoochoric species in angiosperm floras at 18 sites (numbers in circles refer to sites listed in Appendix 3), and mean annual rainfall in South Africa, and Bell's (1982) data for mammalian biomass in African savannas (squares). The curve of Bell's graph shows the relationship between herbivore biomass and annual rainfall on fertile soils. Biomass points falling to the right of the line are generally on infertile soils. The incidence of epizoochory shows the same trends as herbivore biomass.

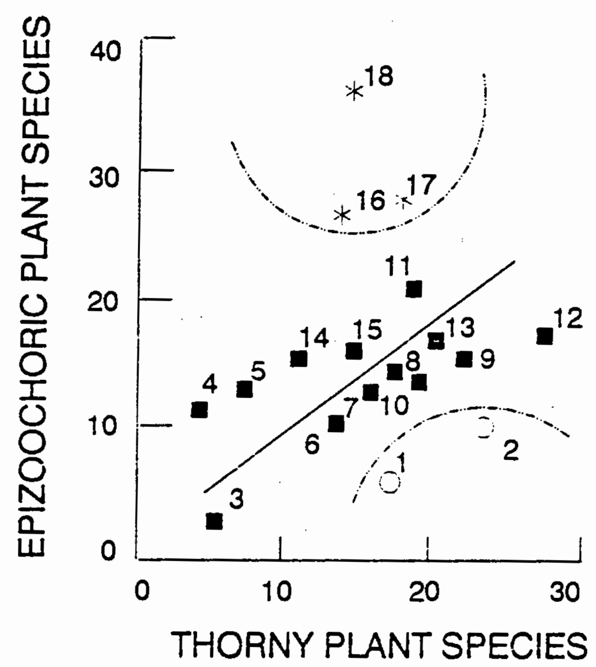

Figure 5. Relationship between the percentages of epizoochoric and thorny species in angiosperm floras at 18 sites (see Appendix 3) in South Africa. Percentage data have been arcsine transformed. Regression line ($y = -0.797 + 1.095x$; $r = 0.822$, $p < 0.001$) excludes grassland (x) and forest (o) data.

Crassulaceae, Euphorbiaceae, Portulacaceae and Zygophyllaceae, are Karoo endemics (Werger, 1985). A long history of aridity, possibly dating from the mid-Tertiary (Lancaster, 1984) may explain the prevalence of drought tolerant, endemic plant species in the Karoo (Hilton-Taylor, 1987). This aridity was interrupted by humid conditions during three periods between 23 000 and 4 000 y BP (Tyson, 1987), when riverine habitats and grazing animals would have expanded their distributions. Charcoal samples from caves near Oudtshoorn and Calitzdorp, show that there has been considerable desiccation in the southern Cape over the last 2 000 to 4 000 years, with *Acacia karroo* Hayne replacing woody evergreen genera such as *Olea* L. and *Dodonaea* Mill. (Deacon & Deacon, 1986). During this period the southern Cape appears, on the basis of palaeoecological and oxygen-isotope speliotherm evidence, to have been cooler, but drier, than at present. As the Karoo became drier, populations of herbivorous mammals would have decreased. Concomitantly, a decrease in mesic plant species, together with a reduction of pressure from mammalian herbivores, may have permitted speciation of the unarmed, anemochorous and antitelechorous Asteraceae and Aizoaceae which now characterize the plains of the summer arid south-western Karoo.

We have provided both original data and information from the literature to indicate that vegetation types with a high proportion of epizoochoric species are (with the exception of grassland) also defended by thorns against excessive damage by mammalian herbivores. Thorny and epizoochoric floras usually occur in regions where a high biomass of herbivorous mammals would be predicted from altitude, precipitation and edaphic data. In very arid areas epizoochoric and thorny species are generally limited to mesic sites in water courses and among rocks on ridges. On this basis, we infer that, during the post-pleistocene period in the south-western Karoo, herbivorous mammals exerted less selective grazing-browsing pressure on plant assemblages of the plains than on those of the water courses and ridges. Plains bushes, with their spineless, finely divided branches, tough aromatic or deciduous leaves, are probably better defended against excessive damage by birds and insects than by mammals. We suggest that large, herbivorous mammals resident in the south-western Karoo during the past 10 000 years tended to be solitary rather than herding species. The presence of small soft burrs (*Tragus*, *Cenchrus ciliaris*) as well as larger diaspores (*Cuspidia cernua* (L.f.) B.L. Burtt, *Setaria verticillata*), and fine, short spines as well as long hard thorns, point to the use of riverine and rocky habitats by both large and small mammals.

In the central and northeastern Karoo, at altitudes between 500 m and 1 500 m a.s.l., annual epizoochoric grasses are abundant on the plains, particularly after spring or summer rain. Perennial epizoochoric grasses such as *Themeda triandra* occur on the rocky hills. The flora of this region, and in particular spring flowering annuals, probably evolved in concert with relatively high levels of mammalian herbivory. Large herbivores which feed in open habitats generally form herds: so we infer that herd animals were present on the plains of the central and north-eastern Karoo periodically. At high altitudes, which preclude woody plants of tropical affiliation, we infer from the dominance of perennial epizoochoric grasses with hard, barbed diaspores (*Merxmuellera* Conert, *Themeda* Forssk., *Heteropogon* Pers., *Cymbopogon* Spreng.), that large mammals with thick skins and/or pelages, and capable of surviving on low-quality forage during the cold winters, were present during the evolution of this flora.

Mammal distributions: present and historical

The last worldwide cold spell, 600 - 400 years ago, appears to have been followed by moister, milder conditions in southern Africa in the C18th and C19th (Tyson, 1987), the period

Conclusion

Epizoochoric dispersal, and thorniness have evolved in plants of productive habitats which support a large diversity and biomass of herbivorous mammals. This suite of plant species, like the mammals, extends its distribution along water courses into less productive arid regions. We infer from the large proportion of endemic Karoo plants lacking epizoochoric diaspores and thorns, and from the low abundance and diversity of adhesive fruits in sheep fleeces in the southwestern Karoo, that the vegetation of this region evolved with little impact from herbivorous large mammals. Whereas low densities of seeds in sheep's wool are economically desirable, they are also indicative of low carrying capacities and sensitivity of vegetation to grazing.

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Appendix 2. List of species represented by diaspores collected from sheep fleeces in the Karoo. Those species considered to be epizoochoric are marked *, and alien species have the superscript $^{+}$.

Species	Total seeds	% presence in samples					
Site		A1	A2	B	C	D	All
Quadrats sampled		90	100	90	26	90	396
POACEAE							
*_Aristida_ L. spp	159	0	5	14	88	7	10.3
*_Bromus murinum_ L. $^{+}$	2	1	0	0	0	0	0.2
*_Cenchrus ciliaris_ L.	20	0	0	0	31	0	2.0
Enneapogon Desv. ex Beauv.	4	2	0	0	1	0	0.7
Fingeruthia africana (Lehm.) Nees	18	1	4	5	8	0	2.7
*_Heteropogon contortus_ (L.) Roem. & Schult.	3	0	0	0	8	2	0.5
*_Hyparrhenia hirta_ (L.) Stapf.	7	0	0	0	8	0	0.5
Rhyncheletrum repens (Willd.) C.E. Hubb.	3	0	0	0	1	0	0.2
*_Setaria verticillata_ (L.) Beauv.	82	1	0	1	11	0	1.3
Polypogon monspeliensis (L.) Desv.	11	0	2	0	0	0	0.5
*_Stipagrostis ciliaris_ L.	4	0	0	0	12	0	0.7
*_S. obtusa_ (Del.) Nees	2	0	0	0	8	0	0.5
*_Themeda triandra_ Forssk.	76	0	0	0	34	32	9.6
*_Tragus_ Haller	7	0	0	2	12	0	1.3
*Unidentified	1	0	0	0	0	1	0.2
CHENOPODIACEAE							
Salsola L.	8	2	0	5	0	0	1.7
Atriplex lindleyi Moq.$^{+}$	1	1	0	0	0	0	0.2
Atriplex muelleri Benth.$^{+}$	31	8	2	7	0	0	4.0
AIZOACEAE							
Aizoanthemum Schwant	8	3	0	0	0	0	0.7
Aridaria N.E.Br.	7	1	0	0	0	0	0.2
Drosanthemum Schwant	1	0	0	1	0	0	0.2
Galenia africana L.	290	20	21	8	0	0	12.4
Psilocaulon N.E.Br.	7	1	0	0	0	0	0.2
Sphalmanthus N.E.Br.	2	1	0	0	0	0	0.2
Tetragonia L.	1	1	0	0	0	0	0.2
Unidentified Ruschioideae	16	3	2	1	0	0	1.5
FABACEAE							
Acacia karroo Hayne	2	2	0	0	0	0	0.5
*_Medicago polymorpha_ L.$^{+}$	264	0	3	9	8	4	4.5
Melolobium candicans (E.Mey) E. & Z.	3	0	0	1	0	0	0.2
ASTERACEAE							
Berkheya Ehrh.	1	0	1	0	0	0	0.2
Chrysocoma ciliata L.	4	0	2	0	0	0	0.5
*_Cuspidia cernua_ (L.f.) B.L. Burtt	45	0	1	16	0	0	4.2
Eriocephalus L.	5	0	0	0	0	3	0.7
Osteospermum calendulaceum L.f.	1	0	0	1	0	0	0.2
Pentzia incana (Thunb.) Kuntze	5	0	2	0	0	3	1.3
Pteronia pallens L.f.	125	40	1	5	0	0	11.6
P. viscosa Thunb.	11	0	6	0	0	0	1.5
Unidentified	15	0	0	0	0	4	1.0

Appendix 3. Incidence of epizoochoric and thorny species in local angiosperm floras at 18 sites in seven biome types in South Africa. Approximate carrying capacity (CC) for domestic small livestock at each site is based on information in Tainton (1981) and Vorster (1985).

Biome & Site Locality	No. of plant species Epiz.	Thorny	Total	Carrying capacity	Source
Forest					
1 Knysna	7	19	398	0.15	Geldenhuys, 1986
2 Drakensberg	1	11	79	0.15	Edwards, 1967
Fynbos					
3 Cape Point	7	21	1058	0.46	Taylor, 1985
4 Stellenbosch	29	12	784	0.46	Duthie, 1930
Fynbos-Karoo ecotone					
5 Nieuwoudville	10	8	280	0.21	Snijman & Perry, 1987
Succulent karoo					
6 Worcester	16	18	392	0.32	Natl.Bot.Gdn., 1987
7 Springbok	39	44	582	0.32	Rosch, 1977
Nama karoo					
8 Prince Albert	16	20	205	0.13	S.J. Milton
9 Great Karoo	12	12	102	0.29	Acocks, 1953
10 Karoo	35	41	490	0.29	Blom, 1980
11 Karoo	19	25	230	0.29	Vorster, 1985
Savanna					
12 Tugela scrub	16	29	156	0.31	Edwards, 1967
13 Kalahari	19	18	189	0.21	Leistner, 1959
14 Waterberg	21	10	328	1.20	Westfall _et al_, 1982
15 W. Transvaal	65	63	1004	1.00	v.d. Meulen, 1979
Grassland					
16 Winberg	15	5	75	1.50	Acocks, 1953
17 Kranskop	9	4	39	1.50	Edwards, 1967
18 Bloemfontein	15	3	42	1.20	Anderson & Roberts,1986

1. INFLUENCE OF HERBIVORES ON EVOLUTION OF KAROO PLANTS

1.3 Plant spinescence in arid southern Africa: does moisture mediate selection by mammals?

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Abstract: *The predictions that spinescence in plants increases with aridity, soil fertility and mammalian herbivory were examined at regional and local scales in southern Africa. Spinescence tended to increase with aridity. Within arid areas, vegetation of moist, nutrient-rich habitats was more spinescent than that of the surrounding dry plains. Spinescence in plants of drainage lines and pans in arid southern Africa occurs in a wide range of genera and appears to have been selected by the impacts of large mammals which concentrate on these moist patches. It is concluded that spinescence may be selected by breakage as well as herbivory, and that in arid areas moisture may be important in mediating mammalian selection of spinescence.*

Introduction

Selection for antiherbivore defences in plants may be related to the life form (apparency) of a plant (Feeny 1976), the fauna with which a plant evolves (Greenwood & Atkinson 1977; Janzen 1986; Symon 1986; Bryant *et al.* 1989; Stafford Smith & Morton 1990), and abiotic factors that determine the rate at which plants grow (Coley 1987).

Slow-growing plants of oligotrophic soils are unpalatable and of low nutritional value to most vertebrate herbivores (Bryant *et al.* 1983; Campbell 1986; Owen-Smith & Cooper 1987; Stafford Smith & Morton 1990). Plant species which grow on nutrient-rich soils in moist, sunny sites deter herbivores with mobile nitrogen-based toxins, or compensate for herbivory with rapid regrowth (Coley 1987). As is the case with plant chemistry, the physical attributes of plants are closely linked with environmental variables (Campbell & Werger 1988). In the Cape Province of South Africa, spinescence is one of the attributes which increases with soil-nutrient status and aridity (Cowling & Campbell 1983). In arid areas of Africa and the Americas, many species of plants, especially water-storing Cactaceae and nitrogen-rich Fabaceae palatable to large mammals, are spinescent (Leopold 1963). Spinescence in these regions is considered to have been selected by mammalian herbivory (Cooper & Owen-Smith 1986; Janzen 1986; Bucher 1987).

The predictions that spinescence increases with aridity, soil fertility and mammalian herbivory, are examined here, firstly on floristic data sets for the whole of southern Africa and secondly, on plant-community data from the most arid parts of this region.

Study sites and methods

Comparison of spinescence in regional floras

Checklists from 38 sites (**Figure 1: Appendix 1**) representing all the biomes of southern Africa (Desert, Savanna, Grassland, Nama-Karoo, Succulent Karoo, Fynbos and Forest) were used as a basis for relating spinescence levels in floras to environmental parameters. For each

Inter-habitat comparisons of spinescence

The contributions of spinescent plants to total vegetation cover and to species richness on upland, plains and bottomland habitats on various soil types were measured along 49 sets of line transects (50-650 m in length). Transect measurements were made at eight sites between 25^0 and 33^0S latitude in the western part of southern Africa (**Figure 2**).

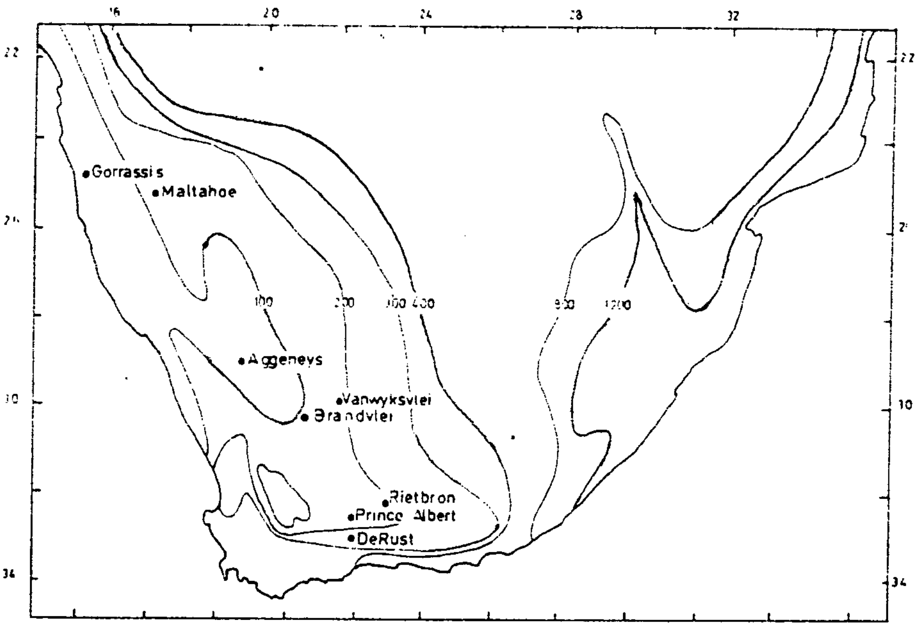

Figure 2. Localities where relative cover and species richness was measured using line transects, plotted on a map showing the mean annual rainfall.

With the exception of the southernmost site (de Rust, rainfall of 330 mm p.a.), all sites were arid with mean annual rainfalls of less than 200 mm p.a. Vegetation data included total canopy cover and relative (arcsine transformed) canopy cover of spinescent, succulent and graminaceous species. All plants encountered were identified to species, and spinescent species are listed in **Appendix 2** together with species known to be toxic to some mammals (Watt & Breyer-Brandwijk 1962; Vahrmeijer 1981). Environmental data were limited to mean annual rainfall (from nearest weather station), coded topographic position (1: hill or dune, 2: plain, 3: drainage, 4: pan), and soil type coded as for the regional comparison.

The frequency of spinescent species in genera encountered on transects was noted (**Appendix** 3), in order to examine the hypothesis that selection for spinescence has taken place *in situ* at the species level.

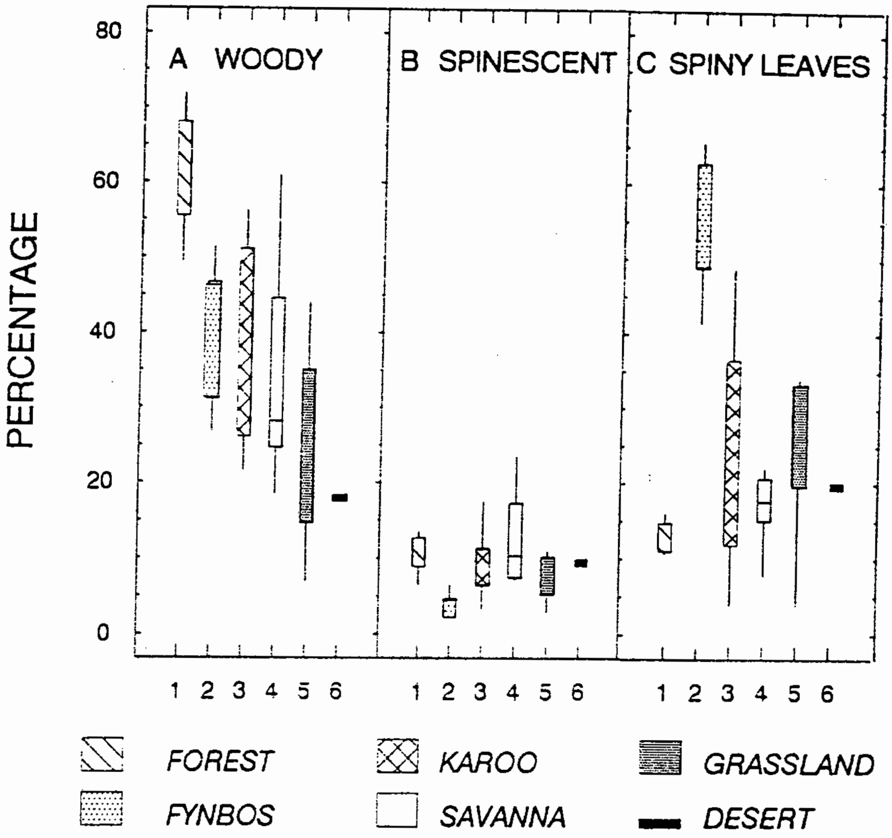

Figure 3. Percentage contributions of (a) woody and (b) spinescent species to spermatophyte floras of southern African biomes, and of (c) spiny-leaved species to the total number of spinescent species. Statistics presented are medians, lower and upper quartiles and ranges for all biomes except the desert biome where only one data source was used (Appendix 1).

Levels of spinescence differed between biomes (one-way ANOVA: df = 6, 31; F = 3.447; P < 0.01). Fynbos had the least spinescent flora (**Figure** 3), but the proportion of spinescent species with leaf-spines was significantly greater in fynbos (52% ± se 9) than in other southern African floras (t = 2.175, df = 36, P < 0.05), (**Figure** 3).

Interhabitat comparison of spinescence

Analysis of plant and environmental variables in arid areas showed that spinescence was positively correlated with run-on drainage and high soil fertility, and negatively correlated with the grassiness of the vegetation (**Table 2**). Total vegetation cover was generally higher in run-on habitats, but hills and plains were more grassy than pans and drainage lines (**Table** 3). Relative canopy cover of spinescent plants was more than twice as great in run-on habitats (42% ± se 3) than in plains and hills (**Table** 3), but did not differ significantly between drainage lines (42% ± se 4) and pans (43% ± se 5).

Table 4. Numbers of spinescent taxa intercepted on line-transect samples of hill, plain, drainage and pan habitats.

	Hill	Plain	Drainage	Pan
Samples	20	10	14	5
Families	6	7	10	9
Genera	9	8	19	12
Species	10	9	28	15
Spp:sample ratio	0.5	0.9	2.0	3.0

Of the 38 spinescent species encountered in run-on habitats, 13 belonged to largely non-spinescent genera (**Appendix** 3). Spines in such genera were derived from leaves, peduncles and shoot tips (**Appendix** 2).

Spinescence was also correlated with soil type. Relative cover values for spinescent plants increased from sand to shale and from shale to silt, whereas grasses showed the opposite trend (**Table 5**). The contribution of spinescent species to total species richness was low on sand, but similar on shale and silt (**Table 5**). Fertile soil was associated with many run-on habitats ($r = 0.337$, df = 49, $P < 0.05$), but also occurred on hills and plains. The combined effects of topography and soil on spininess of vegetation are shown in **Figure** 4.

Table 5. Results of t-tests comparing levels of spinescence and other vegetation attributes in habitats with sandy, shaley and silty soils. Cover values are arcsine transformed percentages of total projected canopy cover. Within rows, means with like symbols do not differ significantly. Probability that "a" = "b", or "b" = "c" is < 0.05, and that "a" = "c" is < 0.01.

	Sand mean ± se	Shale mean ± se	Silt mean ± se
spinescent cover	15 ± 6^a	34 ± 3^b	44 ± 3^c
spinescent species	14 ± 4^a	28 ± 2^c	31 ± 2^c
succulent cover	2 ± 2^a	24 ± 5^c	21 ± 4^c
grass cover	47 ± 7^a	17 ± 3^b	9 ± 3^c
total cover	29 ± 3^a	28 ± 1^a	40 ± 5^b

Mammal distribution and impact

Herbivore distribution across arid landscapes is very uneven and reflects drainage-induced patterns in water and nutrient availability (Walter 1985; Werger 1985; McNaughton 1988; Stafford Smith & Morton 1990). Large mammals are attracted to run-on sites by the availability of surface water (Leistner 1967; Ayeni 1975; Robinson 1976; van Wyk *et al.* 1985a), the presence of green forage in the dry season (Ayeni 1975; Nel 1983; van Wyk *et al.* 1985b), salt deposits (Leistner 1967; Weir 1969; Parris & Child 1973) and, in the larger drainage line, by the shelter from sun, wind, cold and predators afforded by tall woody plants (Acocks 1976; Skead 1980).

By their grazing, trampling and dunging, large mammals can bring about changes in soils and vegetation of habitats they selectively frequent (Lindroth 1989). It has been noted that thickets of spinescent rather than unpalatable or toxic plants develop on alluvial terraces and pans "overgrazed" by domestic livestock (Leistner 1967; Bredenkamp *et al.* 1989; Kooij *et al.* 1990). Thorn thickets are also a feature of waterholes and pans where native herbivores congregate (Boughey 1963; Child *et al.* 1971; Nel 1983).

Spinescent plants are apparently more successful than unpalatable plants in sites highly impacted by large mammals for two reasons. First, soils in run-on habitats of these arid regions are relatively fine textured, nutrient-rich and often saline (Ellis & Lambrechts 1986). Dunging raises soil nitrogen concentrations (Georgiadis & McNaughton 1990) and salinity enhances its uptake by plants (Spencer *et al.* 1988) and availability to mammals (Westoby 1989). Plant species which are normally unpalatable to herbivores, become acceptable and digestible when fertilized with nitrogen (Bryant *et al.* 1987). Under these circumstances, phenolic compounds may provide little protection from herbivory. Secondly, mammalian impact on run-on sites is not confined to herbivory. Alkaloids effectively reduce herbivory on nutrient-rich soils (Coley 1987), but are no protection from large mammals which trample bushes and break branches in their search for forage, water, saltlicks and shelter.

Chemical defences are seldom found in combination with spines (Owen-Smith and Cooper 1987). *Asaemia minuta* (L.f.) Bremer (Asteraceae), an evergreen shrub restricted to, and often forming monospecific stands in, temporary pans in the arid Karoo, is unusual in that it is both spinescent and toxic to ruminants (Vahrmeijer 1981). Some spinescent *Solanum* and *Melolobium* species found in drainage lines in arid southern Africa may also contain toxic alkaloids (Watt & Breyer Brandwijk 1962; Kellerman *et al.* 1988; van Wyk *et al.* 1988). The existence of doubly defended species further supports the contention that in moist habitats in arid areas, spinescence is selected by trampling as well as herbivory.

Origin of spinescent plant species

Riverine plant communities are similar throughout the arid parts of southern Africa (Leistner 1967; Acocks 1976) and appear to be outliers of a more mesic savanna found to the north and east of the region (Acocks 1975). It may therefore be argued that many of the spinescent floristic elements of drainage lines (eg *Acacia*, *Blepharis*, *Carissa*) evolved with the greater biomass and diversity of herbivores present in mesic savannas (Rautenbach 1978; van den Berg 1983); and later expanding their range westwards along river corridors. When spinescence is a fixed generic character it could be considered to be "the ghost of predation past".

No such argument may be applied to the flora of pans, where species belong either to families characteristic of the arid biomes (Chenopodiaceae, Zygophyllaceae, Aizoaceae), or to genera with centres of diversity in winter rainfall and arid regions eg. *Hermannia*, *Osteospermum*, *Aptosimum* and *Lycium* (Gibbs Russell 1987). The western part of southern

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Appendix 2 Spinescent plant species recorded on transect lines. Habitats coded 1: hill, 2: plain, 3: drainage line, 4: pan. Spine types:- I: derived from inflorescence, L: spinescent leaf tip or leaf margin, S: stipules and outgrowths from stem, T: sharp shoot tip. Life form, D: deciduous, E: evergreen, Ch: chamaephyte, NP: nanophanaerophyte, P: phanaerophyte. Information on toxicity from 1 Watt & Breyer-Brandwijk (1963), 2 Vahrmeijer (1981), 3 Kellerman *et al*. (1988) and 4 van Wyk *et al* (1988).

Family	Species	Hab 1234	Height m	Spine type	Life form
Acanthaceae	*Barleria irritans* Nees	1---	0.4	S	D Ch
	Blepharis grossa (Nees) T Anders	--3-	0.2	L	T
	B. mitrata CB Cl	--3-	0.3	L	E Ch
	B. villosa (Nees) CB Cl	1---	0.2	L	E Ch
Aizoaceae	*Eberlanzia* Schwant	-2-4	0.2	I	E Ch
Anacardiaceae	*Rhus longispina* Eckl & Zeyh	--3-	2.5	T	E P
Apocynaceae	*Carissa haematocarpa* (Eckl) A DC	--3-	2.0	S	E NP
Asparagoideae	*Protasparagus aethiopicus* (L) Oberm	--3-	0.6	S	D H
	P. denudatus (Kunth) Oberm	---4	0.6	S	D H
	P. recurvispinus Oberm	-2-4	0.6	S	D H
	P. retrofractus (L) Oberm	--3-	2.5	S	D H
	P. suaveolens (Burch) Oberm	---4	0.5	S	D H
Asteraceae	*Asaemia minuta* (L f) Bremer	---4	0.3	T	D Ch
	Berkheya heterophylla (Thunb) O Hoffm	--3-	1.0	L	T
	Berkheya sp	--34	0.2	L	T
	Eriocephalus spinescens Burch	-23-	0.6	T	E Ch
	Osteospermum armatum T Norl	1---	0.8	I	D Ch
	O. spinescens Thunb	1--4	0.6	I	E Ch
	Othonna pteronioides Harv	---4	0.7	T	D Ch
	Pentzia spinescens Less	1234	0.2	I	E Ch
	Pteronia faciculata L f	1---	0.7	L	E Ch
	Xanthium spinosum L*	--3-	0.7	L	T
Bignoniaceae	*Catophractes alexandri* D Don	---4	1.5	T	D Ch
Fabaceae	*Acacia erioloba* E Mey	--3-	3.5	S	D P
	A. karroo Hayne	--34	3.0	S	D P
	A. mellifera (Vahl) Benth	--3-	2.5	S	D P
	A. reficiens Wawra	--3-	2.0	S	D P
	Indigofera pungens E Mey	-23-	0.3	T	D Ch
	Melolobium candicans (E Mey) Eckl & Zeyh	-23-	0.5	T	D Ch
	Parkinsonia africana L	--3-	3.0	S	D P
	Xerocladia viridiramis (Burch) Taub	--34	1.2	S	D Ch
Geraniaceae	*Sarcocaulon* Sweet	-2--	0.2	S	D Ch
Liliaceae	*Haworthia herrei* V Poelln	1---	0.2	L	E Ch
Malvaceae	*Hibiscus engleri* K Schum	1-3-	0.5	L	T
Poaceae	*Stipagrostis namaquensis* (Nees) de Wint	--3-	1.0	L	E Ch
Scrophulariaceae	*Aptosimum spinescens* (Thunb) Weber	--34	0.3	L	E Ch
Solanaceae	*Lycium cinereum* Thunb	-23-	0.8	S	D Ch
	L. hirsutum Dun	--3-	2.5	S	D Ch

Appendix 3 Distribution of spinescent species in indigenous genera encountered in arid parts of southern Africa sampled in this study. Total numbers of species in southern African genera taken from Gibbs Russel _et al_. (1987). Information on spinescence based on inspection of plant specimens at Bolus Herbarium, University of Cape Town or reference to descriptions in generic revisions.

Genus	**A.** Total sth Afr species	**B.** Spin sth Afr species	A/B	Recorded in present study	
				Run-on sites	Runoff sites
Spinescent genera					
Berkheya	64	64	1.0	2	0
Blepharis	47	47	1.0	2	1
Acacia	45	45	1.0	4	0
Protasparagus	38	38	1.0	5	1
Eberlanzia	26	26	1.0	2*	1
Lycium	15	15	1.0	4	2
Sarcocaulon	15	15	1.0	0	1
Carissa	7	7	1.0	1	0
Melolobium	19	ca 16	0.84	1	1
Monospecific genera					
Asaemia	1	1	1.0	1	0
Catophractes	1	1	1.0	1	0
Parkinsonia	1	1	1.0	1	0
Xerocladia	1	1	1.0	1	0
Non-spinescent genera					
Aptosimum	18	8	0.44	1	0
Solanum	53	ca 10	0.19	2	0
Barleria	58	5	0.08	0	1
Eriocephalus	26	2	0.07	1	1
Osteospermum	77	5	0.06	1	2
Stipagrostis	36	2	0.06	1	0
Rhus	73	4	0.05	1	0
Zygophyllum	42	2	0.05	1	0
Pentzia	34	1	0.03	1	1
Pteronia	74	2	0.03	0	1
Othonna	94	2	0.02	1	0
Hibiscus	57	1	0.02	1	1
Indigofera	231	2	0.01	1	1
Haworthia	186	2	0.01	0	1
Hermannia	158	1	0.01	1	1

Spinescent genera (9)	species	21	7
Monospecific spinescent genera (4)	species	4	0
Non-spinescent genera (15)	species	13	10
Totals: Genera (28)	Species	38	17

* _Eberlanzia_ and a morphologically similar genus (_Ruschia_) are undergoing revision. Species boundaries have yet to be defined.

PART 2

HERBIVORE SELECTIVITY RELATIVE TO RESOURCE ABUNDANCE AND QUALITY

2. HERBIVORE SELECTIVITY RELATIVE TO RESOURCE ABUNDANCE AND QUALITY

2.1 An underground index of rangeland degradation - cicadas in arid southern Africa.

Authors: Milton, S.J. & Dean, W.R.J.
Published 1992: *Oecologia* 91: 288-291

Abstract: *The prediction that density of long-lived, underground herbivores (Cicadidae) is a function of rangeland condition was examined in arid shrublands in the Karoo, South Africa. It was found that the density of adult cicadas was correlated with cover of deep-rooted, perennial plants. Differences in perennial plant cover were independent of soil type and rock cover. On degraded rangelands, where perennial plants had been replaced by ephemerals and short-lived plants, cicada densities were significantly depressed. We concluded that vegetation transformation by domestic livestock is likely to affect invertebrate populations and their vertebrate predators.*

Introduction

Resource quality and quantity are major factors controlling herbivorous invertebrate populations (Mattson 1980) so that the invertebrate populations of rangelands may be expected to vary in response to rangeland management (Hutchinson and King 1980; Seastedt *et al.* 1988; Freckman and Virginia 1989;). Grazing of natural vegetation by domestic livestock may bring about changes in resource availability that range from reduced root:shoot ratios within individual plants (Schuster 1964; Polley and Detling 1989) to modification of vegetation structure and species composition (Harper 1977; Andrew 1988). In arid shrublands, nutrient enrichment and trampling by grazing animals may result in a decrease in plant biomass and an increase in short-lived nitrophilous plant species at the expense of deep-rooted perennials (Andrew 1988).

We examined the hypothesis that in arid Karoo shrublands, the density of long-lived, underground herbivores (Homoptera: Cicadidae) was a function of rangeland condition. The biology of southern African Cicadidae is not well known. Cicada nymphs live below ground feeding on root xylem sap and require a number of years to complete their development (Theron 1985). Final instar nymphs emerge synchronously from the soil, moult, mate, oviposit on plant stems and die within a few weeks. The biomass of the cicada *Quintillia* cf. *conspersa* Karsch, for example (**Plate 2a**), is greater than that of indigenous mammalian herbivores in some localities in the arid southern Karoo (Dean and Milton 1991), and densities of this and other local cicada species, such as *Q.* cf. *vitripennis* Karsch, appear to vary with rangeland condition (Dean and Milton 1992).

Study sites and methods

The study was confined to the Sandrivier Valley in the southern Karoo, Cape Province, South Africa. The valley is situated at 33°10'S and from 22°00'E to 22°30'E and lies between folded shale ridges inland of the Swartberg mountains. The gradient is gentle, descending evenly from 800 m a.s.l. to 600 m a.s.l. over a

Cicada densities on fixed plots

Cicada density on fixed plots was marginally greater at the Tierberg Research Centre in 1991 than in 1989 (n = 12, t = -1.73, P <0.05) but densities did not differ significantly between the two years on the adjacent farm (n = 10, t = -1.03, P > 0.3). The heavily grazed farm appeared to support lower mean densities of cicadas (1989: 5.0 ± SD 1.8 cicadas/25 m^2; 1991: 8.7 ± 11.0) than livestock exclosures (1989: 15.1 ± 9.2; 1991: 23.4 ± 17.9) and a moderately grazed farm (1991: 22.5 ± 9.6).

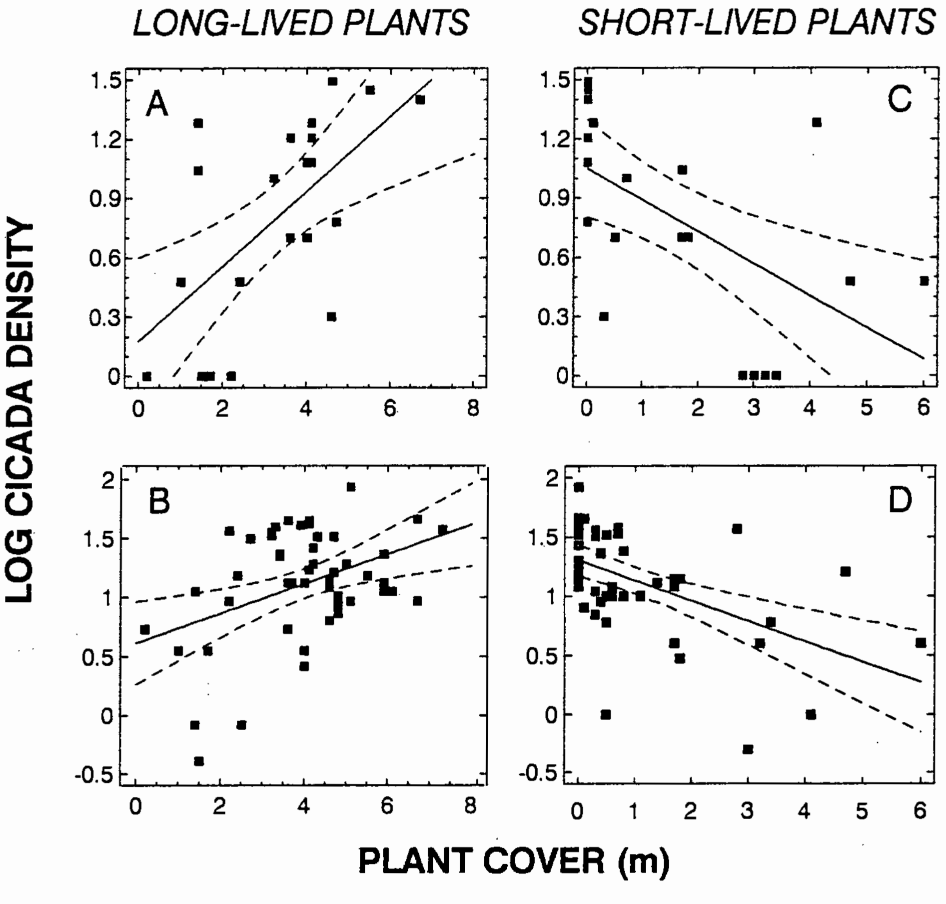

Figure 1. Relationships between density of emerging cicadas and plant canopy cover at Tierberg Karoo Research Centre and on adjoining farms. The four figures show log-transformed cicada density plotted against: **A** long-lived cover in 1989: Y = 0.175 + 0.189X; and **B** 1991: Y = 0.664 = 0.119X; and against **C** short-lived cover in 1989: Y = 1.015 - 0.161X and **D** 1991: Y = 1.302 - 0.171X. All four regressions are significant (*P* <0.01) and *dotted lines* indicate the 95% confidence limits.

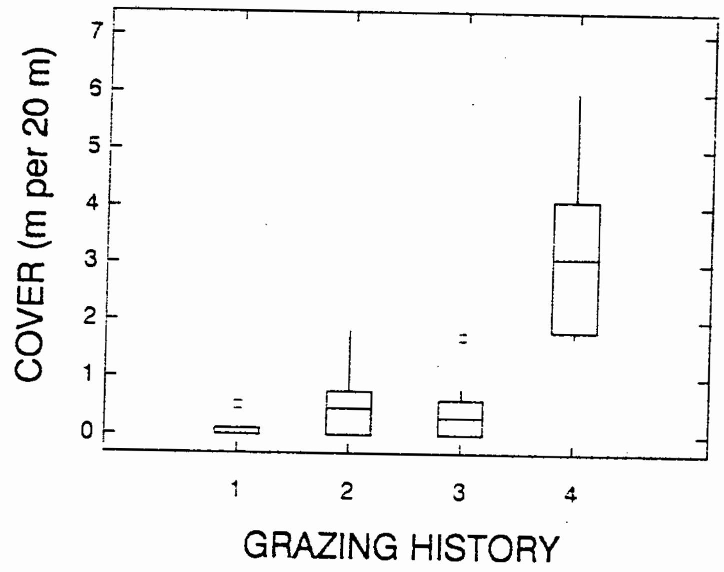

Figure 2. Cover of short-lived plant species in grazing exclosures (1), livestock exclosures (2), on a moderately grazed (3) and a heavily grazed site (4) at the Tierberg Karoo Research Centre, southern Karoo. *Box and whisker plots* show medians, upper and lower quartiles and ranges of cover values for each treatment.

In both 1989 and 1991 (**Fig. 1**), densities of cicadas in fixed plots were positively correlated with cover of long-lived plants (n = 22 and 50 respectively; r = 0.61 and 0.41; P <0.01) and negatively correlated with cover of short-lived plants (n = 22 and 50; r = -0.59 and -0.52; P <0.001). Short-lived plant cover apparently increased as range quality decreased (n = 50, r = -0.705, P <0.001) and was most abundant on the heavily grazed farm (**Fig. 2**).

Inter-site comparisons of Cicada density, 1991

At interspersed sites along the Sandrivier Valley, cicada densities in 1991 were significantly greater (one-way ANOVA df 2,58; F = 12.701; P <0.0001) in good rangeland than in moderate and poor range (**Table 1**) and were greater on silty soil than on sandy or rocky soils (F = 6.564; P <0.01). Cicada densities did not differ significantly between ridges, plains and drainages (F = 0.996; P = 0.375).

multiple regression model, $C = -0.338 - 0.258R + 0.226S + 0.0017A$; $F = 16.57$; $P < 0.001$) where C = log transformed cicada density, R = range condition, S = soil type and A = altitude, explained 44% of the variability in cicada density.

Discussion

Grazing by domestic livestock alters the quality and quantity of food available to below-ground herbivores by increasing nitrogen concentration in plant tissues (Seastedt *et al.* 1988) and decreasing below ground plant biomass (Schuster 1964). The density and biomass of some root feeding invertebrates, including nematodes and Scarabaeid beetle larvae, is generally greater in moderately grazed rangeland than in lightly or heavily grazed rangeland (Hutchinson and King 1980; Roberts and Morton 1985; Seastedt 1985; Andersen 1987; Stanton 1988). This trend has been interpreted as a response to a grazing induced increase in food quality (Seastedt *et al.* 1988).

Cicadas in the southern Karoo did not appear to respond positively to moderate grazing. A possible explanation is that cicadas are xylem feeders (White and Strehl 1978) and therefore do not benefit as greatly from increased nitrogen concentrations as do phloem-feeding nematodes. If they are unable to respond to improved root quality, then in accordance with the model of Seastedt *et al.* (1988), cicada biomass should be determined by root availability and should decrease as grazing intensity increases.

Frequent grazing and accompanying nutrient inputs through dung, together with soil compaction caused by trampling, alter the structure and composition of vegetation (Crawley 1983; Andrew 1988). In overgrazed Karoo shrublands, perennial shrubs with rooting depths of 5-7 m (Scott and van Breda 1939) are replaced by short-lived, shallow-rooted ephemerals and succulents (Hoffman and Cowling 1990). A transition from a perennial to an ephemeral resource base in response to grazing by domestic livestock is likely to affect long-lived, root-feeding insects.

In common with the Apache cicada *Diceroprocta apache* of the North American deserts (Glinski and Ohmart 1984), *Quintillia* cf. *conspersa* nymphs apparently take about three years to develop. Slow-growing cicada nymphs are probably dependent on a perennial food source and this may explain why degraded rangeland, dominated by ephemeral and short-lived plant species, supported fewer cicadas than relatively undisturbed shrublands. Moreover, oviposition by *Q. conspersa* (Dean and Milton 1991) and the unidentified cicada species (pers. obs. SJM) is confined to perennial plants. No egg batches were encountered on ephemerals or short-lived plant species.

Underground herbivore densities differ between plant species (Stanton 1988). Although *Q.* cf. *conspersa* appears to be polyphagous, the distribution of its emergence holes (Dean and Milton 1991) suggests that it avoids non-woody succulents (eg *Augea capensis* and *Malephora lutea*). These plant species are not grazed by domestic livestock and often dominate degraded rangeland. Cicada populations would be expected to decline if the plant species they require for food or oviposition were to be displaced by unacceptable species.

Mortality of eggs and nymphs may have contributed to the observed variability in cicada density. *Quintillia* cf. *conspersa* eggs are inserted into twigs of shrubby Aizoaceae and Asteraceae (Dean and Milton 1991), many of which are palatable to sheep and goats. It is probable that unhatched eggs are consumed with forage by browsing ungulates. Cicada eggs hatch in about 35 days (Dean and Milton 1991) so that on farms where stock camps are utilized rotationally, egg loss to domestic livestock is likely to vary between camps.

In the deserts of the southwestern United States, non-periodic cicadas occur at densities similar to those recorded in lightly grazed shrublands in the Karoo, and are the staple

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2. HERBIVORE SELECTIVITY RELATIVE TO RESOURCE ABUNDANCE AND QUALITY

2.2 Selection of seeds by harvester ants (Messor capensis) in relation to condition of arid rangeland

Authors: Milton, S.J. & Dean, W.R.J.

Published 1992 : *Journal of Arid Environments* **23:**

Abstract: *Food plant selection by herbivorous mammals and by harvester ants* Messor capensis *was compared for three sites differing in past and present management. At all three sites the ants collected an estimated 4.1 million seeds (7.1 kg)/ha/yr which amounted to 13% of the seeds and 25% of the annual seed biomass production of common plants. Seed removal by* M. capensis *did not appear to compound the effects of herbivorous mammals on the reproductive potential of plants, because ants concentrated on the most abundant seeds > 0.3 mg. Ant granaries on degraded rangeland contained more seeds of ruderals and of plant species unpalatable to sheep.*

Introduction

In arid regions, ranching has changed the vegetation so that plant species avoided by domestic livestock have increased at the expense of palatable species (Roux & Vorster, 1983; Bucher, 1987; Friedel *et al*., 1988).

Granivores (consumers of seeds) and general herbivores (consumers of herbage including flowers and unshed seeds) alter the reproductive potential of plants (Hendrix, 1988; Andersen, 1991) and initiate changes in the species composition of vegetation (Harper, 1977; Brown *et al*., 1979). Ants are major post-dispersal seed predators in Australia and arid regions of Africa and the Middle East (Morton, 1982; Marsh, 1987; Kerley, 1991) removing up to one quarter of the annual seed production (Ofer, 1980; Briese, 1982).

Some granivorous ants forage selectively for certain types of seeds (Tevis, 1958; Andersen, 1982) and others forage for the most abundant seeds or at the largest clumps of seeds (Briese, 1982). Depending on how granivorous ants forage, they could compound or buffer the effects of domestic livestock on the plant species composition of arid rangelands.

In this paper we compare the effects of mammalian herbivores and a granivorous ant (*Messor capensis*) on the seed availability of plant species in three arid rangelands with differing histories of range management.

Study area

The study was carried out in an arid shrubland in the Karoo region of the southern Cape Province of South Africa ($33^0$10'S, $22^0$17'E). Rainfall ranges from 50-400 mm p.a. (mean 167 ± SE 7 mm, n = 95 yr) of which 50-60% falls in summer. The study area was situated in the Sandrivier valley and included the Tierberg Karoo Research Centre (Site 1) more fully described in Milton *et al*. (1992) and those portions of the sheep ranches Tierberg (Site 2) and Argentina (Site 3) that adjoin its boundaries. The fine-grained, saline colluvium of this flat-bottomed valley is sparsely vegetated with perennial succulent and non-succulent shrubs about 400 mm in height and grasses and annuals are restricted to sandy watercourses.

A crude estimate of the amount of seed taken annually by *M. capensis* (seeds/ha) was calculated from rates of seed collection (seeds/minute/nest), daily activity (minutes/day), seasonal activity (days/year), seed availability (days/year) and nest density (nests/ha). Offtake was then expressed as a proportion of total seed production.

Seed storage by Messor capensis

The relative abundance of seed species stored in *M. capensis* nest mounds were sampled five times between October 1988 and October 1990. All sampling took place at a minimum distance of 100 m from boundary fences because ants had been observed collecting seeds at distances of up to 40 m from their nests. The first ten mounds encountered along 1000 m transects were sampled using a 48 x 130 mm (235 cm^3) stainless steel corer inserted at an angle of approximately 45^0 into the side of each nest mound. The contents of each soil core were mixed and all seeds were removed from a 15 cm^3 subsample sorted under a dissecting microscope (16 x magnification).

The average number of seeds stored by *M. capensis* at any one time was calculated for each of the three sites as follows:

S = N x V x D where

S = the number of seeds stored by ants (seeds/m^2),

N = mean seed density of ant mounds (seed/cm^3)

V = mean volume of ant mounds (cm^3)

D = mean density of ant mounds (mounds/ha)

Seed weights used in calculations of seed biomass production and off-take are means of samples of 20 seeds per species or, in the case of seeds weighing less than 1 mg, are means for 20 batches of ten seeds.

Preference index

A preference index (PI) for use of plant species by herbivores and ants was calculated as PI = U/A where:

U (use) = the proportional contribution of each species to total records of utilization by herbivores or seed storage by ants and

A = the availability of each plant species expressed as its contribution to total plant cover or total seed density.

Results

Use of plants by sheep and wild mammals

Plant species differed greatly in their abundance and importance to herbivorous mammals (**Table 1**). Utilization of plant species was selective and ranged from 100% of sampled plants for *Osteospermum sinuatum* (DC.) T. Norl. to 0% for *Augea capensis* Thunb., *Malephora lutea* Schwant. and *Pteronia pallens* L.f. Shoot removal from all species was more intensive at Argentina than at other sites (**Figure 1**).

Rangeland composition in relation to management

Paired comparisons (Wilcoxon signed-ranks tests) across three boundary fences (**Table 2**) showed that "palatable" plant species tended to have lower cover values and unpalatable species to have higher cover values on the areas with a history of heavier stocking. These differences were significant (P < 0.01) for *Ruschia spinosa*, *O. sinuatum* and *Galenia fruticosa* which decreased and for *Malephora lutea* which increased on degraded rangeland.

Table 2. Comparisons of canopy cover of common plant species along three pairs of line transects at the Research Centre exclosure (1), Tierberg ranch (2) and Argentina ranch (3). Direction of difference in mean cover value is indicated by signs (+,-) and significance (Wilcoxon matched-pairs, signed-ranks test) by aterisks (* $P < .05$, ** $P < .01$, *** $P < .001$). Plant species are arranged in order of importance for sheep (Table 1).

Pair	A		B		C	
Site	1	2	1	3	2	3
Transect	1.1	2.1	1.2	3.1	2.2	3.2
Samples	10	10	10	10	8	8
G. fruticosa	5.1	3.3 -	4.2	1.0 -**	3.2	2.6 -
O. sinuatum	1.7	2.6 +	3.3	0.4 -**	0.7	0.1 -
R. spinosa	4.9	3.4 -	8.4	0.1 -***	8.8	0.7 -***
D. montaquense	1.3	1.1 -	0.8	0.7 -	2.0	1.9 -
P. empetrifolia	1.6	1.1 -	0.4	0.0 -	0.4	0.0 -
T. spicata	0.1	0.3 +	0.1	0.0 -	0.2	0.0 -
H. lutea	0.6	0.7 +	0.7	0.1 -*	0.2	0.2
R. macroura	0.3	2.6 +*	0.1	1.0 +	0.0	0.6 +
P. pallens	4.2	3.7 -	1.9	5.0 +	5.4	6.7 +
B. ciliatus	0.9	1.1 +	2.2	6.2 +*	0.4	1.0 +
M. lutea	0.2	0.1 -	0.7	5.4 +***	0.3	1.1 +
R. approximata	0.5	0.2 -	0.1	0.0 -	0.6	0.0 -
A. capensis	0.0	0.1 +	0.2	0.3 +	0.0	0.0
Total cover	21.9	20.5 -	24.3	21.3 -	23.1	16.8 -

Seed production in relation to rangeland management

Plant species preferred by sheep tended to produce fewer seeds and avoided species to produce more seeds on land utilized by sheep (**Table 3**). Seed densities for palatable plant species ranged from 2632 seeds/m^2 at the Research site from which sheep were excluded, through 630 seeds/m^2 on moderately utilized rangeland at Tierberg to 268 seeds/m^2 at Argentina with its history of heavy stocking. Inter-site differences in total seed biomass production were less marked as a number of species avoided by sheep produced relatively large seeds.

Collection of seed by Messor capensis

Harvester ants *Messor capensis* collected seed mainly in the summer months (October to March) but spent more time in the late summer maintaining seed stores (**Figure 2**). Maintenance work included soil excavation, trimming of seeds for storage by removing wings and pappus bristles and transporting this debris from storage chambers onto the top of the mound of soil and organic matter which covers *M. capensis* nests.

The ants collected seeds weighing 0.3-28.5 mg (fresh mass) and containing 0.1-4.6 mg of food material (**Table 4**). Polymorphic workers brought seeds to their colonies at an average rate of 4.35 seeds/minute for four hours per day under warm, windless conditions. An average colony collecting seeds at the rate of 4280 seeds/day on 108 days per year (colonies were foraging on 296 out of 1000 observations), would collect 462 240 seeds annually. The density of *M. capensis* colonies (n = 40, mean 8.88, SD 5.2, range 2 to 28 colonies/ha) did not differ significantly (ANOVA $F_{2,37} = 2.3$, $P > 0.10$) between the three sites (**Figure 3**). Seed collection by *M. capensis* was therefore estimated at 411 seeds$\cdot$m$^{-2}\cdot$ yr^{-1} or 13% of the annual seed crop (**Table 5**). In terms of biomass, *M. capensis* removed 7.1 kg$\cdot$ha^{-1}yr^{-1} or 25% of the seed production.

Table 4. Weights (mg ± SE) of seeds commonly collected by harvester ants Messor capensis at study sites in the southern Karoo. Fresh seeds include dispersal appendages (pappus and wings), trimmed seeds stored by ants lack appendages, husked seed weight excludes the testa. Husked masses given in parentheses are estimates based on a husked to trimmed seed ratio of 0.45.

	Fresh seed	Trimmed seed	Husked seed
Osteospermum sinuatum	15.17 ± 0.69	9.10 ± 0.45	4.60 ± 0.16
Augea capensis	28.50 ± 3.75	6.60 ± 0.48	3.00 ± 0.21
Pteronia spp	3.50 ± 0.11	1.90 ± 0.18	1.50 ± 0.17
Galenia fruticosa	0.62 ± 0.05	0.62 ± 0.05	0.26 ± 0.02
Mesembryanthema	0.26 ± 0.02	0.26 ± 0.02	(0.11)
Felicia filifolia	1.00 ± 0.10	0.88 ± 0.05	(0.40)
Atriplex semibaccata	2.90 ± 0.55	2.90 ± 0.55	(1.31)
Tetragonia echinata	3.40 ± 0.40	3.40 ± 0.40	(1.52)
Other species *	0.4 to 6.5	0.4 to 6.5	(0.2 to 2.9)

* Uncommon ephemerals and shrubs restricted to drainages.

Table 5. Seed collection by Messor capensis at the Research Centre exclosure (Site 1) and its impact on the annual post-herbivory seed crops of common plants. Seeds of Pteronia species and Mesembryanthema were not identified to species level.

Plant species	Number/m^2	mg/m^2	% annual crop
Osteospermum sinuatum	11	104	17.3%
Augea capensis	21	138	43.5%
Pteronia spp	162	308	78.7%
Galenia fruticosa	178	110	8.1%
Mesembryanthema	16	4	3.0%
Other species *	23	46	---
Total seed number	411	---	13.4%
Total seed mass	---	710	25.2%

* Seed production not assessed for uncommon ephemerals and shrubs in drainages.

Table 6. Densities of stored seeds in core samples (235 cm^3) from nest mounds of Messor capensis at the Research Centre (Site 1, n = 46), Tierberg Ranch (Site 2, n = 46) and Argentina ranch (Site 3, n = 40).

	Site 1	Site 2	Site 3
Galenia fruticosa	746 ± 294	1013 ± 428	132 ± 94
Pteronia spp	383 ± 122	231 ± 78	460 ± 137
Augea capensis	200 ± 55	93 ± 33	277 ± 76
Osteospermum sinuatum	29 ± 10	28 ± 14	0 ± 0
Mesembryamthema	1 ± 1	2 ± 1	5 ± 2
Felicia filifolia	88 ± 47	15 ± 12	0 ± 0
Atriplex semibaccata	0 ± 0	0 ± 0	2 ± 1
Tetragonia echinata	1 ± 2	3 ± 2	6 ± 3
Other species *	4 ± 2	3 ± 2	4 ± 2
Total seeds/core	1452 ± 345	1388 ± 424	886 ± 220
Husked mass mg/core	1647 ± 420	1173 ± 384	1591 ± 396
Trimmed mass mg/core	2863 ± 671	1965 ± 569	2821 ± 720

* Uncommon ephemerals and shrubs restricted to drainages.

Factors influencing the diet of Messor capensis

Although harvester ants removed a similar fraction of the total seed production from all three sites, their impacts on the seed populations of individual plant species appeared to differ between sites (**Tables 5 & 6**). Seeds of *Osteospermum sinuatum* and *Galenia fruticosa* occurred at significantly lower densities (for both species: Kruskal-Wallis ANOVA, df = 2, H = 13, $P < 0.01$) in ant mounds at Argentina than on other sites. On the other hand, seeds of an annual forb (*Tetragonia echinata*) and an introduced perennial forb (*Atriplex semibaccata*) were more abundant at Argentina than elsewhere (df = 2, H = 9.6 and 9.4 respectively, $P < 0.01$).

The abundance of a seed type in *M. capensis* granaries was not significantly correlated (df = 19) with seed size (r = 0.181) or availablity in terms of density (seeds/m^2) (r = 0.422) or biomass/unit area (r = 0.344). Nevertheless, plant species that produced large numbers of seeds tended to dominate granaries and if mesembryanthema seeds (< 0.3 mg) were excluded from the analysis, the positive relationship between seed availability and seed in granaries was significant (df = 16, r = 0.57, $P < 0.05$).

Plant species preferences of sheep and harvester ants

The shrub *Galenia fruticosa* was an important component in the diet of both mammalian herbivores and harvester ants *M. capensis* at all sites (**Tables 1 and 6**). However sheep showed a strong preference for *Osteospermum sinuatum* even at Argentina where this species was uncommon (**Figure 4a**). Harvester ants showed a preference for *Augea capensis* and *Pteronia* spp (**Figure 4b**) which made up 39% and 36% of the husk-free mass of their food stores.

harvester ant *Messor capensis* possibly provide an indication of the future composition of Karoo rangelands relative to livestock management.

Seeds of Mesembryantha were smaller (< 0.3 mg) than those of any other perennial plants in the study area and were common in food caches of smaller ants (*Monomorium* spp and *Pheidole* spp) although rarely collected by *Messor capensis*. This avoidance of a potentially abundant food source may be related to seed size or to seed availability. Other large-bodied harvester ants forage preferentially on seeds of plant species which simultaneously shed large quantities of seeds (Whitford, 1978). Mesembryanthema seeds are retained in hygroscopic capsules which open and release some seed during a number of different rainfall events, whereas seeds of the woody shrubs that dominated the granaries of *M. capensis* released their entire seed crops during summer (January-February) when ant activity peaked.

In the Karoo, as in other arid regions of the southern hemisphere, ants remove more seeds than do birds or rodents (Kerley, 1991). *Messor capensis* at our study sites took about 13% (7 kg/ha) of the annual seed production. Comparable levels of seed removal by harvester ants have been reported from Senegal where *M. galla* harvests 4-5 kg/ha (Gillon *et al.*, 1984), Israel where *Messor ebonius* and *M. semirufus* took 20% of the production of a wheat crop (Ofer, 1980) and Australia, where harvester ants took 20-24% of the annual seed production of rangelands (Briese, 1982). The large harvester ants (*Pogonomyrmex* and *Veromessor* spp) of North American apparently have less impact on seed production, taking only 1-2% of the total seed crop (Tevis, 1958) and up to 32% of the seed production of preferred species (Whitford, 1978).

Like many harvester ant species in North America (Brown *et al.*, 1979), Australia (Briese, 1982) and Namibia (Marsh, 1987), *M. capensis* concentrated on the most abundant of the larger seeds available. At our Karoo study site, *M. capensis* took a greater proportion of the seed bank of species producing abundant seed than of species producing meagre seed crops. The plant species preferred by ants (*Augea capensis* and *Pteronia pallens*) were unpalatable to sheep and to most other mammalian herbivores.

If foraging by *M. capensis* is generally density dependant, these ants would tend to buffer the effects of domestic livestock by concentrating on seeds of species which increase on degraded rangeland. Removal of *M. capensis* from degraded rangeland is therefore unlikely to increase seed banks of forage plants or to improve the plant species composition of Karoo rangelands.

Although *M. capensis* is a granivore, some of the stored seeds escape destruction. While stored in cells of ant heaps, seeds are protected from temperature extremes and sunlight as well as being concealed from avian and rodent granivores. A high proportion (40-60%) of seeds in ant granaries are viable and some of these seeds are returned to the seed bank (W.R.J.D. unpublished data) by predators of ants (Antbears *Orycteropus afer* and Bateared foxes *Otocyon megalotis*) which periodically excavate *M. capensis* mounds in search of alates.

Conclusion

Harvester ants may be useful indicators of rangeland condition as their seed caches reflect seed availability. Their activities are unlikely to lead to rangeland deterioration because they do not show a preference for plant species which are palatable to domestic livestock. The caches contained viable seeds some of which are returned to the seedbank.

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3. EFFECTS OF HERBIVORY AND OTHER FACTORS ON PLANT REPRODUCTION, GROWTH AND DEMOGRAPHY

2.3 Effects of Rain, Sheep and Tephritid Flies on Seed Production of two Arid Karoo Shrubs in South Africa.

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Abstract: *(1) The density of* Pteronia pallens *(Asteraceae), a shrub toxic to sheep, increases in Karoo rangeland at the expense of a congeneric palatable shrub* (Pteronia empetrifolia). *The effects of rainfall, herbivory by sheep and tephritid fly damage on seed production of these shrubs were compared over a four year period.*

(2) Flowering and seed set varied between sites and years, increasing in response to moisture (both species) and nutrient availability (P. pallens).

(3) The percentage of capitulae damaged by Desmella anceps *(Diptera: Tephritidae) larvae differed between the* Pteronia *species, but was greater in both shrub species in dry years when flowers were scarce.*

(4) Browsing of P. empetrifolia *by sheep during flower development reduced flowering by 80-90% and caused a 40% decrease in the number of seeds set per capitulum.* Pteronia pallens *was not browsed and flowering and seed set did not differ between a sheep camp and an exclosure in any year.*

(5) In high rainfall years, arid rangeland shrubs produce large crops of viable seeds. If palatable shrubs such as P. empetrifolia *were protected from domestic livestock during flower development in such years, their populations might stabilize.*

Introduction

Herbivores feeding on foliage and flower buds may reduce production of viable seed (Hendrix 1988). In selectively grazed natural rangelands preferred forage species suffer repeated reproductive failure and often are gradually replaced by less palatable plants (Westoby 1980; O'Connor 1991). The impact of herbivores on plant reproductive success could be compounded if, by preventing "mast" seeding in good years, it increased the proportion of seeds lost to granivores.

Seed predators are seldom able to exploit mast-fruiting plant species efficiently (Janzen 1976). In unpredictable environments reproductive output of plants may fluctuate widely in response to resource availability (Lee 1988). As in the case of mast fruiting, annual variation in seed production may prevent close tracking of seed by granivores so that in good years, a larger proportion of a seed crop may escape predation (Solbreck & Sillen-Tullberg 1986; Borowicz & Juliano 1986).

The present study examines the hypothesis that the proportion of the seed crop lost to a predispersal insect predator increases in years or localities where fruit production is scarce.

Materials and methods

Study site

The study was carried out at the Tierberg Karoo Research Centre (more fully described in Milton, Dean & Kerley 1992) and on the adjacent the sheep ranch "Tierberg" which lie at the southern edge of the Great Karoo ($33^0$10'S, $22^0$17'E, 800 m a.s.l.). The region is arid with variable and unseasonal rainfall (mean 167 mm p.a.; range 50-400 mm over 92 years). Annual rainfall (January to December) at the Research Centre during the study period was as follows 1987: 147 mm, 1988: 268 mm, 1989: 248 mm, 1990: 183 mm, 1991: 165 mm. Absolute temperatures range from -5 ^{0}C (winter minimum) to 43 ^{0}C (summer maximum). The landscape is fairly flat with wide plains and occasional low ridges of shale. The plains are crossed by many small dry washes and dotted with mounds known as "*heuweltjies*". These are patches of relatively nutrient-rich soil (about 175 m^2 in area) that overlie nests of the termite *Microhodotermes viator* (Milton & Dean 1990). Soils are silty and have a high base status but little organic matter.

The sparse vegetation (canopy cover 15-25%) comprise succulent mesembryanthema and non-succulent shrubs up to 600 mm in height. The dominant non-succulent shrubs (all Asteraceae) include *Pteronia empetrifolia* DC (**Plate 3a & b**), *P. pallens* L.f. (**Plate 3c**) and *Osteospermum sinuatum* (DC.) T. Norl.

Study species: Plants

The *Pteronia* species are both evergreen microphylls but differ in their value as fodder for domestic livestock: sheep browse *P. empetrifolia* shoots and flowers (**Plate 3b**), but avoid *P. pallens* which contains a liver toxin (Kellerman, Coetzer & Naude 1988). Flower buds of both *Pteronia* species develop in winter (July-August) and anthesis occurs in spring (September-October). The bristly achenes (15-30 per capitula) are held on the plants until late summer (February). *Pteronia pallens* grows on plains, in small washes and on the edges of *heuweltjies* but *P. empetrifolia* occurs only on plains (Milton *et al.* 1992).

Study species: Tephritid flies

The fly *Desmella anceps* (Loew) (Diptera: Tephritidae) was a predispersal granivore on both *Pteronia* species on the study site. Dissections of *Pteronia* capitula revealed that larvae of *D. anceps* were present in *P. empetrifolia* and *P. pallens* capitula between October and January each year (1988-1992). No other tephritid species were collected from capitula of these *Pteronia* species, and *D. anceps* was not found in the winged achenes of *O. sinuatum* growing in the same area.

Adult *Desmella anceps* flies were observed laying eggs on newly opened *Pteronia* flowers. Up to eight larvae occurred simultaneously in a single capitula but each larva appeared to require only one fertile seed in order to complete its development. A single *D. anceps* pupa completely filled a *Pteronia* achene, which was destroyed, whether or not the *D. anceps* pupa was subsequently parasitized by a Chalcidoid wasp (*Eurytoma* sp.: Hymenoptera: Eurytomidae; *Antistrophoplex* sp.: Hymenoptera: Torymidae).

Experimental design

The effects of mammalian herbivores on seed production were assessed by excluding sheep from a 100 ha area of a 6000 ha plain from June 1987 until the conclusion of the experiment. Management of sheep grazing on the remainder of the plain remained unchanged, *ie*., grazed by 2000 Merino sheep between March and August and rested from September to February. Prior to establishment of the experimental exclosure, both sites had been managed as a single stock camp. For this reason the size class distributions of the two *Pteronia* species in the exclosure and on adjacent grazed land were similar (**Figure 1**).

Germination tests on 120 filled and 120 empty achenes of each species indicated that none of the empty achenes was viable but that viability of filled achenes was 51% for *P. empetrifolia* and 55% for *P. pallens*.

Tephritid damage

The proportion of *Pteronia* capitula containing tephritid larvae was assessed by examining ten capitula from each of ten randomly selected shrubs. This sampling was carried out in the field between November 1987 and December 1991. Wilcox paired signs tests were used to compare arcsine transformed percentage occupation by tephritids using the following paired data sets: *P. empetrifolia* grazed or protected (n = 11) and *P. pallens*: on or off *heuweltjies* (n = 4), grazed or protected (n = 8), watered or not watered (n = 12). Differences in numbers of Tephritid larvae per capitula in response to watering and nutrients were compared using the Chi-squared statistic.

Results

Flowering response to resource availability and herbivory

Flowering varied with timing and quantity of rainfall. *Pteronia empetrifolia* produced fewer flowers in 1991 following a dry winter than in the previous three years. *P. pallens* flowered most abundantly at both sites in 1989 (**Table 1**).

Table 1 Flowering response to rainfall and herbivory. Table shows mean (S.D.) number of capitula per plant (>20 mm b.d). Numbers of bushes sampled were: *Pteronia empetrifolia* protected site (n = 39), grazed site (n = 43); *Pteronia pallens* protected site (n = 69), grazed site (n = 68).

Year	Annual rainfall		Capitula per plant		t-statistic
	mm	season	Protected	Grazed	(treatment)
Pteronia empetrifolia					
1988	286	autumn	145 (95)	13 (15)	9.167 ***
1989	246	autumn	117 (59)	19 (22)	10.761 ***
1990	193	autumn	147 (88)	103 (75)	2.607 **
1991	165	spring	5 (7)	1 (1)	3.698 ***
ANOVA F (years)			33.63 ***	58.87 ***	
Pteronia pallens					
1988	286	autumn	22 (41)	31 (40)	-1.263 ns
1989	246	autumn	39 (46)	47 (43)	-1.030 ns
1990	193	autumn	16 (22)	32 (35)	-3.055 **
1991	165	spring	13 (16)	20 (27)	-1.799 *
ANOVA F (years)			7.82 ***	6.25 ***	

* P <0.05, ** P <0.01 and *** P <0.001

The number of capitula (a) per non-grazed plant was correlated with basal diameter (b) for both species (*P. empetrifolia*: a = 3.4, b = 17.2, df = 180, r = 0.81; *P. pallens*: a = 1.9, b = 3.9, df = 301, r = 0.29). Protected *P. empetrifolia* produced more flowers for a given stem diameter than did *P. pallens*. Slopes of regression lines differed between the exclosure and the sheep camp for both *P. empetrifolia* (t = 138.2, P <0.0001) and *P. pallens* (t = 5.8, P <0.001). Flowering of *P. empetrifolia* plants >20 mm in basal diameter was significantly less in the sheep camp than in the exclosure in all four years (**Table 1**) but the difference was less marked in 1990 when the sheep were removed from the camp in June, three instead of the

Table 2 Achenes numbers in Pteronia empetrifolia and P. pallens capitula for plants growing in an exclosure or in a sheep camp at Tierberg in three consecutive years. Mean and standard deviation (S.D.) is given for total achenes and filled achenes (intact plus parasitized). Sample sizes varied from 50-100 capitula per site for each year. Significances for effects of treatments (chi-square) and years (ANOVA F) are as follows: * P <0.05, ** P <0.01 and *** P <0.001.

Year	Exclosure		Sheep camp		Chi-square
	Total	Filled	Total	Filled	(treatment)
Pteronia empetrifolia					
1989	15.0 (2.4)	6.5 (3.0)	14.9 (2.6)	4.2 (3.7)	24.8 ***
1990	15.8 (2.8)	4.3 (3.1)	16.7 (2.6)	4.8 (3.6)	6.4 *
1991	16.9 (2.9)	2.5 (2.4)	15.6 (2.9)	1.2 (1.5)	16.3 ***
F (year)	9.3 **	35.5 ***	9.3 **	17.9 ***	
Pteronia pallens					
1989	20.5 (2.3)	11.0 (3.8)	21.6 (3.2)	10.3 (5.4)	2.9 ns
1990	22.7 (4.0)	3.6 (3.6)	18.5 (2.2)	7.1 (2.6)	0.2 ns
1991	20.5 (2.3)	2.9 (1.9)	19.2 (2.4)	2.6 (2.7)	0.2 ns
F (year)	12.5 ***	112.1 ***	12.2 ***	44.9 ***	

Seed-fill in *P. pallens* did not differ consistently between habitats. In 1990, seed fill was marginally greater (ANOVA $F_{(2,\ 177)}$ = 2.9, P = 0.057) on *heuweltjies* (5.2 S.D. 3.5 seeds/capitula) than on plains (3.9 S.D. 3.7) or on a rocky ridge (2.7 S.D. 3.4) but in 1991 the trend was reversed (*heuweltjies* 1.8 S.D. 1.7, plains 2.7 S.D. 2.4, ridge 1.3 S.D. 1.4; $F_{(2,\ 213)}$ = 9.3, P <0.001). The affects of water addition on seed-fill were sampled in 1990 and 1991. Watering increased the proportion of filled seeds in both years (1990: t = -5.61, df = 88, P <0.001; 1991: t = -4.66, df = 103, P <0.001).

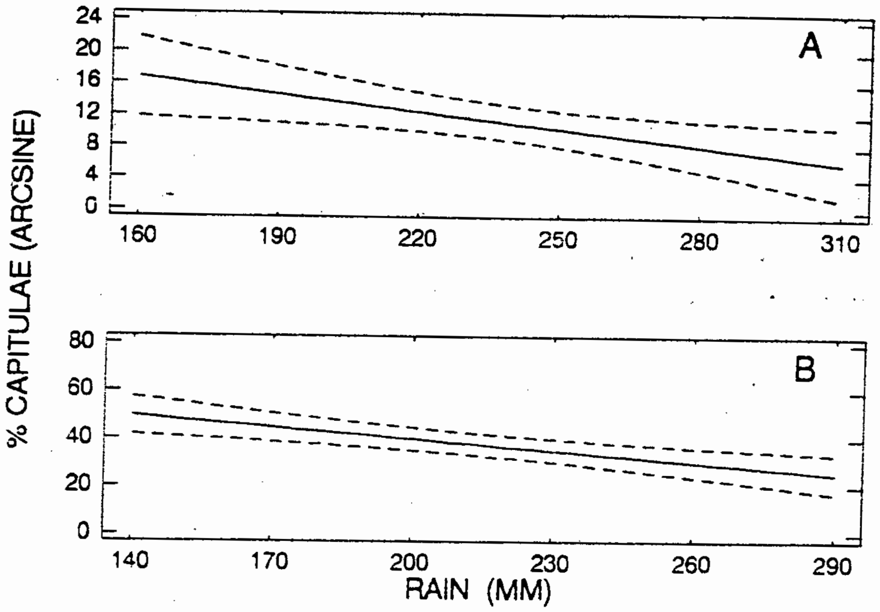

Figure 3. Relationship between annual rainfall and arcsine transformed percentages of capitula containing *Desmella anceps* larvae or pupae. **a)** *Pteronia empetrifolia* r = -0.506, df = 20, P <0.05; **b)** *P. pallens* r = -0.538, df = 38, P <0.001.

Discussion

The carrying capacity of the world's natural rangelands for domestic livestock appears to be decreasing as preferred fodder plants are replaced by less palatable or toxic species (Westoby 1980; Andrew 1988; O'Connor 1991). This trend has long been recognized in the Karoo shrublands and desert grasslands of South Africa (Acocks 1955; Roux and Vorster 1983).

If, as proposed by Liljelund, Årgren, & Fagerström (1988), the relative abundance of a plant species in a given area is a function of longevity and annual seed production, then any factor reducing seed production will eventually reduce the local abundance of that species.

The present study indicated that water availability during the growing season limited flowering and seed production of both *Pteronia* species. In low rainfall years when few seeds were produced, predispersal seed losses to tephritid larvae were relatively large. Similarly, in Sweden when pod production of the milkweed *Vincetoxicum hirundinaria* was limited by drought, the proportion of the fruit crop attacked by tephritids was greatest (Solbreck & Sillen-Tullberg 1986). Both the milkweed and *Pteronia pallens* produced more fruits in dry, than in wet years, when growing on nutrient-rich soils.

Mammalian herbivory, although seldom lethal to plants, often reduces the plants' reproductive output (Hendrix 1988). Browsing by sheep was a major factor limiting seed production of the palatable shrub *Pteronia empetrifolia*. In the absence of sheep, *P. empetrifolia* produced more flowers per bush than did the toxic shrub *P. pallens*. However, on a winter-grazed range this situation was reversed. When sheep grazed *P. empetrifolia*

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2. HERBIVORE SELECTIVITY RELATIVE TO RESOURCE ABUNDANCE AND QUALITY

2.4 Insects from the asteraceous shrubs Osteospermum sinuatum and Pteronia pallens in the southern Karoo

Author: Milton, S.J.
Submitted Oct 1992: *African Entomology*

Abstract: *A wide variety of polyphageous, chewing insects utilized the broad-leaved shrub* Osteospermum sinuatum *which is palatable to mammalian herbivores. The range of insects collected on an evergreen shrub* Pteronia pallens *that is toxic to mammalian herbivores was small by comparison, and was dominated by sucking insects.*

Evergreen plants have long-lived leaves which are exposed to herbivory throughout the year. By comparison with deciduous and fugitive plant species, evergreens are chemically well defended against generalist herbivores (Coley 1987). Chemically defended plants, including ferns (Hendrix 1980; Ottosson & Anderson 1983) and *Elytropappus rhinocerotis* Less., a microphyllous shrub of the winter rainfall region of the southwestern Cape (Theron 1984), support a disproportionately large ratio of sucking to chewing insect species. Sucking insects can utilize such plants because their mouthparts penetrate selected cells or vessels, thereby avoiding protective coatings and resin ducts (Weis & Berenbaum 1989). I predicted that a deciduous Karoo shrub, palatable to domestic livestock, would support more chewing insect species than a sympatric evergreen shrub known to be toxic to ruminants.

Osteospermum sinuatum (DC.) T. Norl. and *Pteronia pallens* L.f. are common in the succulent dwarf shrublands of the southern Karoo. Both shrub species are 200-700 mm in height, long-lived, woody and non-succulent. However they differ in phenology and in palatability to herbivorous vertebrates. Insects were collected opportunistically on these shrubs between 1988 and 1992 at the Tierberg Karoo Research Centre (TKRC) which lies at 33°10'S, 27°17'E and 800 m a.s.l. and has a mean annual rainfall of 168 (SD 68) mm. Mean densities of *O. sinuatum* and *P. pallens* at TKRC were 6500 and 3000 plants ha^{-1} respectively (Milton & Dean 1990).

Osteospermum sinuatum is a broad-leaved, facultatively drought-deciduous species that grows and flowers when conditions are adequately moist, but sheds all its foliage during dry spells (Milton in press). This nutritious species (**Table 1**) is palatable to hares (Kerley 1990), indigenous ruminants and sheep (Van Breda & Barnard 1991; Milton & Dean 1992). *Pteronia pallens*, a narrow-leaved, evergreen shrub, grows in the relatively mesic winters and flowers in spring. The leaves, shoots and capitula of *P. pallens* have a resinous coating, contain a high concentration of ether-extractable substances (**Table 1**) and are toxic to domestic livestock (Kellerman *et al.* 1988). Despite its high protein and energy content, *P. pallens* is not eaten by ostriches (pers. obs), antelope or sheep (Milton & Dean 1992).

Of the 27 phytophageous insects collected on *O. sinuatum* (**Table 2**), 14 species had larvae

Table 2. Phytophagous insects collected on Osteospermum sinuatum at Tierberg (33°10'S, 27°17'E) in the Prince Albert district of the southern Karoo in winter and spring months from 1987-1992. Immat. refers to nymphs and larvae, Lf = leaf, Fl = flower, Sd = seed.

Phytophage	Freq.	Stages collected		Plant part			
		Immat.	Adult	Lf	Stem	Fl	Sd
Orthoptera							
Pyrgomorphidae							
unidentified sp	*	+	.	+	.	.	.
Tettigoniidae							
unidentified sp	*	+	.	+	.	.	.
Hemiptera							
Lygaeidae							
Spilostethus rivularis Germar	**	+	+	.	.	.	+
Melanostethus marginatus Thunb	*	.	+	.	+	.	.
Nysius sp	*	.	+	.	+	.	.
Pentatomidae							
Andocides vittaticeps Stal.	*	.	+	.	.	.	+
Agnoscelis puberula Stal.	**	.	+	.	+	.	.
Cicadellidae							
Bloemia sp	*	+	+	.	+	.	.
Lacciferidae							
Tachardina sp	**	+	+	.	+	.	.
Coccidae							
unidentified black scale	*	+	+	+	.	.	.
Pseudococcidae[1]							
unidentified sp	**	+	.	+	.	.	.
Coleoptera							
Chrysomelidae							
Chrysomelinae							
Chrysolina sp	***	+	+	+	+	.	.
Clytrina sp	*	.	+	.	.	+	.
Cassidinae							
Cassida sp	**	+	+	+	.	.	.
Eumolipinae							
Macrocoma sp	*	.	+	+	.	.	.
Curculionidae							
Lixinae							
Larinus sp	*	.	+	.	+	.	.
Scarabaeidae							
Hopliini							
Lepisia sp	*	.	+	.	.	+	.
Bupestidae							
unidentified sp	**	.	+	.	+	.	.
Diptera							
Tephritidae							
Tylapsis crocea	*	+	+	.	+	.	.
Stylia granulata (Munro)	***	+	+	.	.	+	+

Table 2 continued over page

Table 3. Phytophagous insects collected on Pteronia pallens at Tierberg (33^{0}10'S, 27^{0}17'E) in the Prince Albert district of the southern Karoo in winter and spring months from 1987-1992.

Phytophage	Freq.	Stages collected		Plant part			
		Immat.	Adult	Lf	Stem	Fl	Sd
Hemiptera							
Pentatomidae							
Veterna natalensis	**	+	+	.	+	.	.
Miridae							
unidentified sp	*	+	.	.	.	+	.
Cicadellidae							
Bloemia heiroglyphica Naude	**	+	+	.	+	+	.
Issidae							
unidentified sp	*	+	.	.	+	.	.
Coccidea							
unidentified sp	**	+	+	+	+	.	.
Pseudococcidae							
unidentified scale	***	+	.	+	.	.	.
Coleoptera							
Rhizophagidae							
Phyconomus sp	*	.	+	.	.	.	+
Curculionidae							
Rhytirrhinus sp	**	.	+	+	+	.	.
Dermestidae							
Attagenus juncundus Peringuey	*	.	+	.	+	.	.
Diptera							
Tephritidae							
Desmella anceps Loew.	***	+	+	.	.	+	+
Lepidoptera							
cf. Psychidae	**	+	.	.	.	+	.

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2. HERBIVORE SELECTIVITY RELATIVE TO RESOURCE ABUNDANCE AND QUALITY

2.5 Plants eaten and dispersed by leopard tortoises Geochelone pardalis (Reptilia: Chelonii) in the southern Karoo.

Author: Milton, S.J. 1992

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Abstract: *Leopard tortoise* Geochelone pardalis *faeces collected in rocky habitats in the southern Karoo contained at least 75 species of grasses, succulents and forbs belonging to 26 plant families. Soft, green plants were broken down by digestion but twigs, thorns and fibrous materials were not digested. Flowers, fruits and seeds made up 67% of 356 identified plant fragments. Germination trials demonstrated that leopard tortoises could disperse viable seeds of Aizoaceae, Chenopodiaceae, Crassulaceae, Cyperaceae, Fabaceae, Poaceae and Scrophulariaceae.*

Introduction

Adult leopard tortoises *Geochelone pardalis* (Bell) weigh eight to 12 kg (maximum 43 kg) and are the largest of the 12 species of tortoises found in southern Africa (Greig & Burdett 1976; Branch 1988). Their faeces resemble those of the Aldabran giant tortoise *Geochelone gigantea* (Schweigger) in that they contain plant fragments which appear little altered by digestion. The digestion of the Aldabran giant tortoise is slow and inefficient (Coe *et al.* 1979) and its faeces contain large numbers of viable seeds (Hnatiuk 1978).

Leopard tortoises occur throughout the savanna regions of Africa from the Sudan to the Southern Cape, but are rare in high altitude grasslands, fynbos and in the arid western and central Cape (Greig & Burdett 1976; Boycott & Bourquin 1988). They are considered to have a wider dietary range than other African tortoises (Greig & Burdett 1976), feeding on grasses, forbs, succulents and fruits (Boycott & Bourquin 1988; Branch 1988) and are omnivorous in captivity (Rose 1962).

The present study describes the diet of the leopard tortoise in the arid Karoo (**Plate 4a**) near the southwestern limits of its distribution range and discusses its potential for dispersing viable seeds of indigenous and alien plants.

Study site and methods

Faeces of *G. pardalis* can be distinguished from those of small sympatric tortoises *Psammobates tentorius tentorius* (Bell) and *Chersina angulata* (Schweigger) by their large size (20-25 mm x 100-150 mm). All adult *Geochelone pardalis* faeces encountered during the course of monthly botanical surveys were collected. From November 1988 to August 1991 (excluding October 1989) five-minute searches for tortoise faeces were made at each of 40 sites which included six rocky ridges, 12 stony plains, 19 non-stony plains and three sites adjacent to permanent water sources. Searches were also made during an estimated 600 hours of field work on plains at Tierberg Research Centre (for site description see Milton *et al.* 1992) and during 50 hours spent on surrounding rocky ridges. The study was confined to the Prince Albert District (32^0S-34^0S, 22^0W-24^0W) at the southern edge of the Great Karoo. This northern fringe of the Cape fold-belt, described by Acocks (1951) as

Karroid Broken Veld, comprises low Dwyka tillite ridges and extensive shale plains with a sparse vegetation of low shrubs, succulents and ephemeral grasses and forbs. Temperatures are extreme (mean monthly maxima 16-33^{0}C, minima 1-17^{0}C) and rainfall scanty and unpredictable (mean annual rainfall 176 mm, range 50-400 mm).

Faeces were dissected under magnification and leaves, stems, fruits and seeds were identified by comparison with reference material. The proportion (by volume) of grass was estimated visually for each sample. The number of species of tall and dwarf shrubs, succulents, grasses and annual plants present in a faecal sample were recorded for each collection. Dissected faeces were air dried and stored for germination trials.

In March 1991, 12 nursery trays lined with newspaper were half filled with shredded faeces, three samples being combined in each tray. Trays containing tortoise faeces and two control trays filled with sawdust were covered with fine wire mesh to exclude seed predators and wind-blown seeds. All samples were watered daily and germinating seedlings were counted.

The relative abundance of plant life-forms in tortoise habitat was estimated by measuring the canopy cover of tall shrubs (>300 mm), low shrubs, succulents, grasses, forbs and geophytes along a 50 m line transect at each of 12 sites where faeces were collected. The Chi-square statistic was used to compare the occurrence of these six plant life-forms in the vegetation and in the faeces of *G. pardalis*. The hypothesis that the incidence of annuals, grasses, shrubs and succulents in the diet differed between the warm (October to March) and cool (April to September) seasons of the year was tested using the Mann-Whitney U test.

Plant nomenclature follows Gibbs Russell *et al.* (1985, 1987) for all groups except the Aizoaceae, where treatment follows Hartmann & Bittrich (1991). These authors recognize five suprageneric groups: the Aizooideae, Sesuvioideae, Tertagonioideae, Aptenioideae and Ruschioideae. The first three groups include a wide range of non-succulent and semi-succulent forbs and shrubs and the latter two groups together comprise the Mesembryanthemaceae (*senu* Gibbs Russell *et al.* 1987), all of which are succulent.

Results

Faeces were found throughout the year but were apparently most abundant in late summer (**Figure 1**). Most (31) of the leopard tortoise faecal samples from the southern Karoo were collected on rocky ridges (**Plate 4b**) but faeces were also found on stony plains (14) and near windmills, vleis and drainages (6). No *G. pardalis* faeces were found in non-grassy, succulent shrubland on non-stony colluvium or alluvium despite the fact that the search effort was concentrated in this type of habitat. The vegetation where *G. pardalis* faeces were found was sparse (mean canopy cover 25.7%, range 19-34%) and shrubby with scattered succulents, grasses and forbs.

Hand sorting of 51 faecal samples yielded a total of 74 recognizable plant species including 24 succulents (Aizoaceae, Cactaceae, Crassulaceae, Euphorbiaceae, Zygophyllaceae), 22 forbs, 13 grasses and 13 shrubs, a geophyte and a sedge (**Table 1**). Grass contributed 71% (SD 32%) and dicotyledonous plants 28% to faecal volume. Insect remains (including exoskeletons of

Table 1 ctd...

Genus and species	Total incidence	Flowers & fruit	Number of seeds
Portulacaceae			
Portulacaria afra Jacq.	1	0	0
Illecebraceae			
Dianthus sp.	1	0	0
Papaveraceae			
Argemone mexicana L. *	1	1	67
Brassicaceae			
Heliophila sp.	2	2	6
Lepidium spp.	8	8	60
Crassulaceae			
Adromischus spp.	4	1	0
Crassula muscosa L.	7	0	0
Crassula subaphylla (E. & Z.) Harv.	5	3	100
Tylecodon reticulatus (L.f.) Toelk.	1	1	0
Tylecodon ventricosus (Burm.f.) Toelk.	1	0	0
Tylecodon wallichi (Harv.) Toelk.	4	0	0
Fabaceae			
Acacia karroo Hayne	3	0	0
Indigofera pungens E.Mey.	5	5	0
Lessertia annularis Burch.	1	1	25
Lotononis sp.	16	16	118
Medicago polymorpha L.	5	5	7
Zygophyllaceae			
Augea capensis Thunb.	1	0	0
Tribulus terrestris L.	3	3	35
Zygophyllum sp.	2	1	0
Euphorbiaceae			
Chamaesyche inequilatera (Sond.) Sojak	4	4	1
Euphorbia sp.	1	1	9
Euphorbia stellaspina Haw.	3	0	0
Anacardiaceae			
Rhus sp.	1	0	0
Malvaceae			
Malva parviflora L. *	2	2	6
Sterculiaceae			
Hermannia spp.	10	3	12
Cactaceae			
Opuntia ficus-indica (L.) Mill. *	1	0	0
Solanaceae			
Datura sp. *	1	1	0
Scrophulariaceae			
Aptosimum indivisum Burch.	8	7	24
Nemesia sp.	2	2	8
Zaluzianskya sp.	1	1	0
Selaginaceae			
Walafrida sp.	1	1	2
Acanthaceae			
Blepharis sp.	3	3	0

large beetles and a cicada), bone fragments and small stones made up the remaining 1% of faecal contents.

The frequency of plant life-forms types in *G. pardalis* faeces differed significantly from the frequency of life-forms in the vegetation where the faeces were found (Chi-square = 178, df = 5, $P < 0.001$). Whereas shrubs dominated the vegetation, grasses and forbs were the most frequent items in the diet (**Table 2**).

The proportion of shrub, succulent, grass and annual forb species in faeces varied seasonally (**Figure 2**). Grasses were more prevalent in the diet during the cool season (n = 27, 24; Z = 2.204; P = 0.027) and succulents appeared to increase during the warm season (n = 27, 24; Z = -1.545; P = 0.122). There was a negative relationship between the incidence of grasses and succulents in the diet (Spearman Rank Correlation: df = 49; $r_s = -0.385$; $P < 0.01$).

Flowers and fruits made up 67% of all 356 plant items identified in faeces. A number of small annual grasses (notably *Enneapogon devauxii* Beauv.) had been uprooted and swallowed whole, but many woody stems in the faeces appeared to have been bitten rather than torn from plants. Large pieces (60 x 20 mm) of tough plants (such as *Haworthia glauca* Bak.) had been swallowed and apparently little altered by digestion. Multi-pronged spines (*Euphorbia stellaspina* Haw., *Ruschia spinosa* (L.) H.E.K. Hartm.) and prickly leaves (*Blepharis* sp., *Cuspidia cernua* (L.f.) B.L. Burtt) were frequently found in faeces of large tortoises.

Table 2 Frequencies (%) of plant life-forms in faeces of adult *Geochelone pardalis* and in the vegetation where the faeces were collected. Incidence of a life-form in faeces was calculated as SUM(n_1..n_{51}) where n was number of species of the life-form found in each of 51 faecal collections. Abundance of life-forms in vegetation was calculated as SUM(c_1...c_{12}) where c was arc-sine transformed plant canopy cover for 12 sites where *G. pardalis* faeces were collected.

Life-form	Faeces		Vegetation		Chi-square	P
	Occurrence	(%)	Cover	(%)		
Tall shrub	5	(1)	157	(21)	56	< 0.001
Dwarf shrub	52	(15)	235	(31)	20	< 0.001
Succulent	91	(26)	162	(21)	2	NS
Grass	109	(30)	95	(12)	35	< 0.001
Forb	98	(27)	92	(12)	28	< 0.001
Geophyte	1	(1)	24	(3)	9	< 0.05

Table 3 Seedlings emerging from Geochelone pardalis faeces kept watered in nursery trays for 48 days.

Plant identity	Sample number												Total
	1	2	3	4	5	6	7	8	9	10	11	12	
Poaceae													
unidentified	22	7	73	43	3	67	4	-	22	91	-	-	332
Cyperaceae													
unidentified	-	3	-	3	1	-	-	-	13	-	-	-	20
Chenopodiaceae													
Atriplex spp.	6	-	10	-	-	-	-	-	1	-	-	-	17
Aizoaceae													
Galenia sp.	9	-	-	-	1	-	-	2	-	-	-	-	12
Pleiospilos sp.	-	-	-	-	-	-	-	-	-	-	-	9	9
Trichodiadema sp	-	-	-	-	-	7	-	-	-	-	-	-	7
Mesembryanthemas	5	-	-	1	2	-	3	1	2	-	3	1	18
Brassicaceae													
Lepidium sp.	14	1	-	-	-	-	1	9	-	-	-	-	25
Crassulaceae													
Crassula sp.	-	-	-	5	-	-	3	-	-	-	-	-	8
Fabaceae													
Lotononis sp.	-	-	-	1	1	-	-	-	-	-	-	-	2
Scrophulariaceae													
Veronica sp.	-	-	-	-	-	-	-	-	42	-	-	-	42
Unidentified forbs	2	3	-	-	-	20	-	1	5	1	-	-	32
Seedlings/tray	58	13	83	53	8	94	11	13	85	92	3	10	524

Discussion

The present study confirms reports (Boycott & Bourquin 1988; Branch 1988) that *G. pardalis* has a diverse diet and, although largely vegetarian, may occasionally eat bone fragments (Branch 1988; Esler 1991) and large insects. The tortoises appeared to have foraged selectively for grasses and forbs and avoided woody shrubs. Grasses constituted most of the faecal volume but succulents and forbs, which were fragmented during digestion, may have been under-represented by faecal analysis. In the arid southwestern part of its range investigated, *G. pardalis* included a wide variety of succulents in its diet and this component appeared to increase in the summer months. The negative relationship between the incidence of grasses and succulents in the diet suggests that the tortoises switch to succulents when green grass is unavailable. Succulents likewise constituted >30% of the diet of the Californian desert tortoise (*Scaptochelys agassizii*) and increased to 86% during drought (Turner *et al.* 1984).

Among the succulents eaten by *G. pardalis* were plants topped with multi-pronged spines (eg. *Euphorbia stellaspina* and *Ruschia spinosa*) and chemically defended species including *Tylecodon* spp and other Crassulaceae that contain cardiac glycosides and moving from shady to sunny or from windward to leeward aspects of the ridge. In the succulent, dwarf shrublands of the valley bottoms (Milton *et al.* 1992), there would appear to be few temperature refuges for large tortoises.

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2. HERBIVORE SELECTIVITY RELATIVE TO RESOURCE ABUNDANCE AND QUALITY

2.6 Food selection by ostriches on wildlands and ranches in southern Africa

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Abstract: *Observations of food selection by ostriches* Struthio camelus *were made in southern African savanna, desert, arid shrubland and fynbos (macchia) vegetation. Gizzards contained well graded, hard stones mostly 3-15 mm in diameter. Ostriches fed on green annual grasses and forbs when these were available. At other times they plucked leaves, flowers and fruits from succulents and woody plants. Dead or woody material and animal matter (other than bone) was virtually absent from the diet. Ostriches selected for fiber and against phenolics in forbs, for protein in graminoids, for fiber and against calcium in succulents and for sodium and against ether-extractable substances in woody plants. Ostriches did not feed on plant species known to be toxic to mammalian herbivores. Foraging on feed with energy densities between 8 and 9 MJ/kg dry mass and a protein content of 12%, ostriches need to consume 5.7-7.7 kg fresh mass daily. The mobility and selectivity, which enables ostriches to obtain adequate, high quality forage in arid environments, makes them destructive to rangeland when confined by fences and stocked at unnaturally high densities.*

Introduction

The commercial ostrich industry has grown exponentially in South Africa since the mid 1980's in response to the growing demand for ostrich leather and low cholesterol meat. An ostrich farming industry has also been developed in Australia (Swart 1990), northern Africa, Israel, Canada and the United States of America (Crawford 1991, Ellis 1991). In South Africa, ostriches *Struthio camelus* are reared for slaughter on lucerne pastures, but breeding animals are kept on natural rangeland (Smit 1963, Siegfried *et al.* submitted). Despite a wealth of literature on the behaviour and physiology of ostriches (R.K. Brooke unpublished bibliography of ostrich literature), their natural diet has been little studied and there is no empirical basis for calculating the carrying capacity of natural vegetation for ostriches (Siegfried *et al.* submitted).

Ostriches are popularly believed to eat anything, but are in fact almost entirely herbivorous (Bertram 1985). They forage in patches of green vegetation in arid environments (Williams *et al.* in press), and feed on a wide range of plant species (Smit 1963, Robinson and Seely 1975, Kok 1980, Keffen 1984, Williams *et al.* in press, W.R. Siegfried and G.G. Bradley unpublished data). The factors that determine their choice of food have not previously been investigated. The present study deals with food and gizzard-stone selection by ostriches foraging at various densities on natural rangelands in southern Africa. We discuss the implications of our findings for the management of ostriches in rangelands and in conserved areas.

Methods

Analysis of Stomach Contents

The contents of 20 ostrich stomachs were analysed, including 12 from Namibia, 3 from Botswana and 5 from the southern Karoo. The Namibian sample included one adult apparently killed by a leopard in April 1990, 6 adults and 4 subadults shot in May 1990 and one adult found dead in October 1990. One subadult and two adults were shot in Botswana in April 1991. Stomach samples from the Karoo were collected from one subadult and 4 adult birds that had died accidentally after being chased onto fences. The stomachs of freshly dead birds were excised and the components weighed in the field. Where facilities were available, subsamples of the food in the proventriculus were oven dried and the moisture content was calculated.

Stomach and gizzard contents were stirred in water to extract gravel which was air dried and weighed. Stones from Botswana and Karoo ostriches were sorted by color and type (white quartz, ochre to brown sand- and mudstone, red to grey granite) and size class (5 mm class intervals) and each category was weighed to assess its contribution to the total stone content of the stomach. Subsamples of organic matter from the stomachs (about 25% by volume) were sorted to species (or genus) level, dried at 70^{0}C and weighed in order to calculate their contributions to the diet on a dry mass basis. Dried samples were then sorted to separate roots from shoots, and these two components were weighed.

Observations of Ostriches and Vegetation

Where stomach samples could not be obtained (CGHNR and four Karoo ranches), food selection by ostriches was observed with the aid of a Kowa 20-6 zoom telescope. The focal animal method (Altmann 1974) was used to collect feeding data throughout daylight hours at CGHNR. The duration of feeding on each species was recorded during 1034 hours of observation. In the Karoo, a scan sampling method (Altmann 1974) was used to record the number of times that ostriches fed on available plant species. All ostriches within 100 m of single observer were continually scanned during 1-2 hr observation periods and 207 feeding records were collected.

Plant availability was quantified at ostrich observation sites in the Karoo by recording the identities of the first 100 plants observed through the telescope at a distance of approximately 50 m from the observer. This method underestimated the relative abundance of plants <0.1 m in height (unpublished data, S.J. Milton) and was used only for comparison with telescopically collected feeding records. Ground surveys (four 0.1 m wide and 50 m long belt transects per site) were used to sample all sites for which stomach contents were available. Direct observations of feeding were supplemented by rating plants observed through the telescope and on belt transects as partially defoliated or undamaged (253 feeding records from 1074 plants). The parts of plants selected by the ostriches were classified as flowers and unripe fruits, seeds and dry fruits, leaves/shoots and entire plants including roots. The information is presented diagrammatically for each of the four vegetation types.

Physical Attributes of Plants

Physical attributes of plants taken and avoided by ostriches were described in terms of growth form (forb, grass, succulent, shrub, tree), leaf duration (deciduous, evergreen) and spinescence (none, stem spines, leaf or fruit spines). Chi-square contingency analysis was used to compare physical attributes of plants eaten by ostriches with those apparently avoided by ostriches. Plant growth-form composition for each site was quantified for Karoo sites using telescope and line-transect survey data, and for other regions was based on published vegetation surveys (Taylor 1969, Field 1977, Williams *et al.* in press).

Results

Stomach Contents

When filled to capacity, stomachs (proventriculus plus ventriculus) of adult ostriches contained 4.5-5.5 kg fresh weight. The weight of stones in the ventriculus varied with the size of the bird (subadults: x 444 g, SD 130 g, adults: x 646 g, SD 266), and averaged 0.83% of body weight (**Table 1**). The mean dry weight of organic matter in the stomachs of subadults was 375 g (SD 113 g) and of adults was 608 g (SD 286 g). The ventriculi contained 30% (SD 11%) of this organic matter. The ratio of organic matter in the ventriculus to stones was 1:1.0 on a fresh mass basis and 1:3.5 on a dry mass basis. Green plants constituted 99% of all organic material in the sample of 19 stomachs. The stomach of the bird found dead in the Namib during the dry period contained only the dormant bases (roots and leaf stubble) of perennial *Stipagrostis* spp. grass tussocks. Resin (1/20 stomachs), large seeds (*Acacia, Zea mays*, 10/20), small (1-3 mm) insects evidently ingested with plants (ants, aphids, flies (5/20), preened feather fragments (1/20), ostrich shell (1/20), antelope faecal pellets (3/20) and mammal bones and teeth (5/20) made up the remaining 1% of the organic matter in the stomachs.

Selection of Gizzard Stones

Gizzard stones were well graded (about 3-15 mm diameter, 0.5-1.2 g). Ostriches ingested relatively little sand with their food and swallowed few stones >20 mm diameter (**Fig. 1**). Gizzards of Botswana ostriches contained 49% sandstone, 34% granite and 17% quartz. Hard white quartz predominated in gizzards of Karoo birds reared on soft black shale (**Fig. 2**).

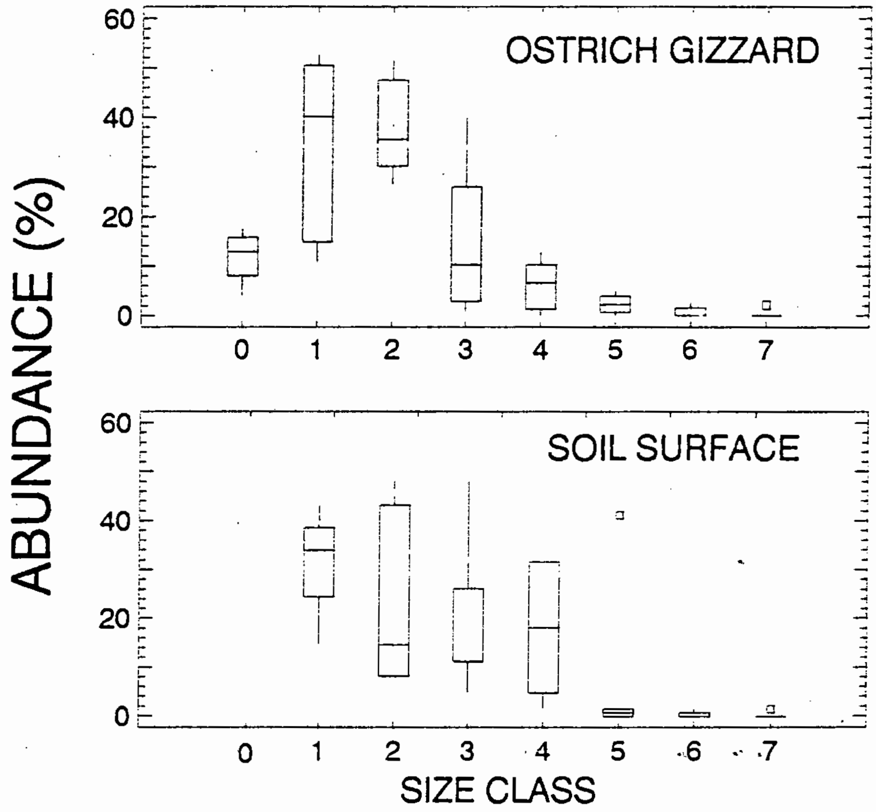

Fig. 1. Size-class distributions of stones in ostrich gizzards and on the soil surface in the Prince Albert District of the Karoo, Cape Province, South Africa.

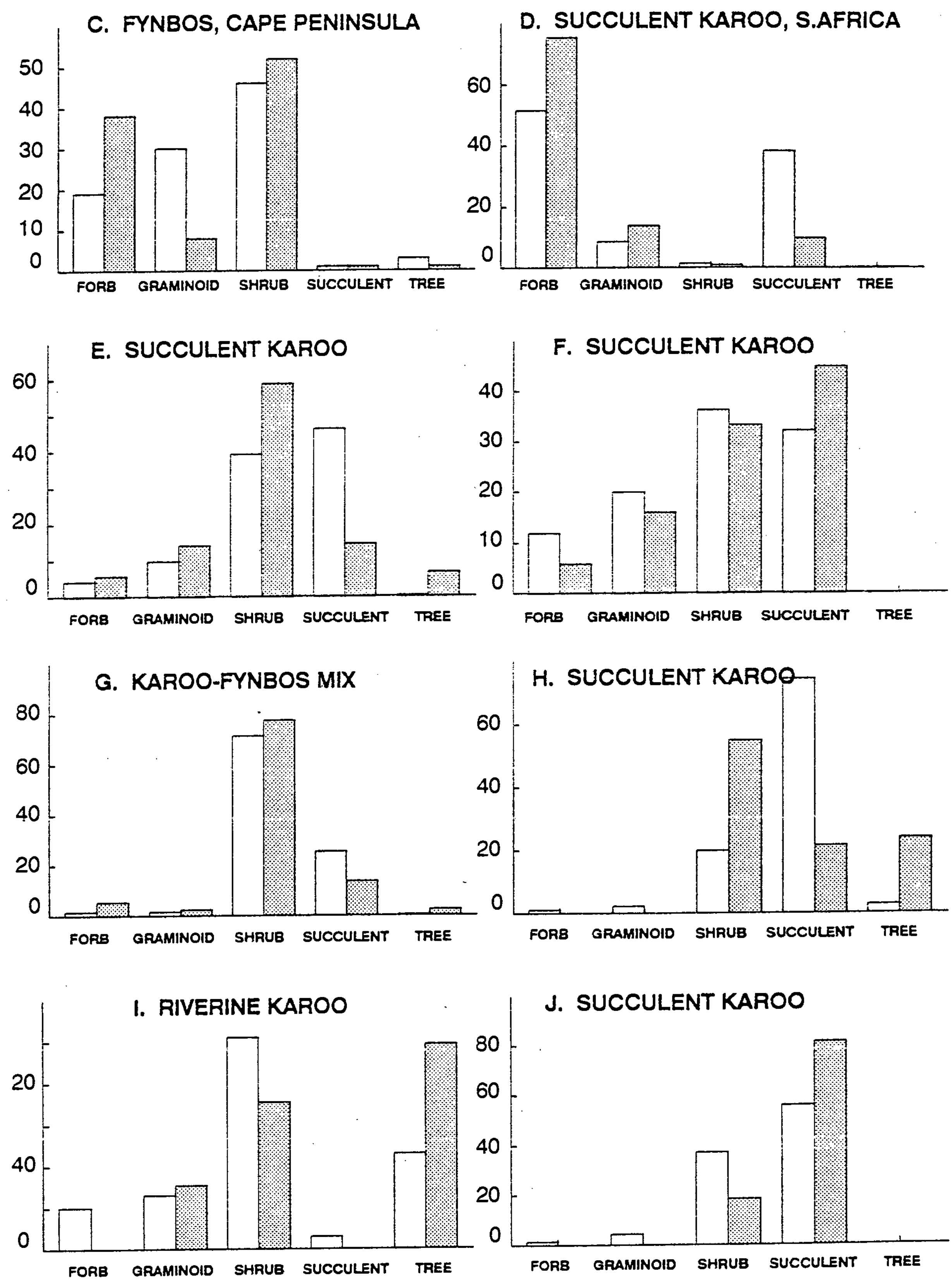

Fig. 3. Relative abundance of plant growth-forms in vegetation (☐) and in ostrich diets (▨) at sites where ostriches are stocked at <5 ostriches/km^2 (**C, D**), 5-99 ostriches/km^2 (**E, F, G**) and 100-300 ostriches/km^2 (**H, I, J**).

Table 1 Fresh and oven-dry masses (g) of stomach contents of ostriches in southern Africa. Total fresh mass (FM) of stomach contents includes stones. Water content calculated by subtraction. A = adult, j = subadult bird.

Place	Sex	Age	Body wt	Stomach contents (g)				
			kg	Total FM	Water	Stone	Bone	Food DM
Namib	F	A	---	2800	----	---	0	----
Namib	M	A	---	3500	2988	---	0	417
Namib	M	A	94	4600	3568	670	0	362
Namib	F	A	73	1620	792	415	0	413
Namib	F	j	51	2260	1535	295	6	430
Namib	F	j	53	1900	1143	407	0	350
Namib	F	j	50	2890	1860	499	4	531
Namib	M	j	50	2000	1284	382	0	334
Namib	M	A	86	3450	2349	645	0	456
Namib	F	A	90	2680	1564	661	0	455
Karoo	F	A	--	3000	----	---	0	---
Karoo	F	A	--	----	----	329	0	---
Karoo	F	A	--	2581	1036	692	0	344
Karoo	F	A	--	4800	3458	607	1	735
Karoo	M	A	--	2785	1710	302	40	733
Botsw	-	j	45	1100	232	638	0	230
Botsw	F	A	114	4500	2389	1042	0	1069
Botsw	M	A	109	5500	3299	1099	0	1102

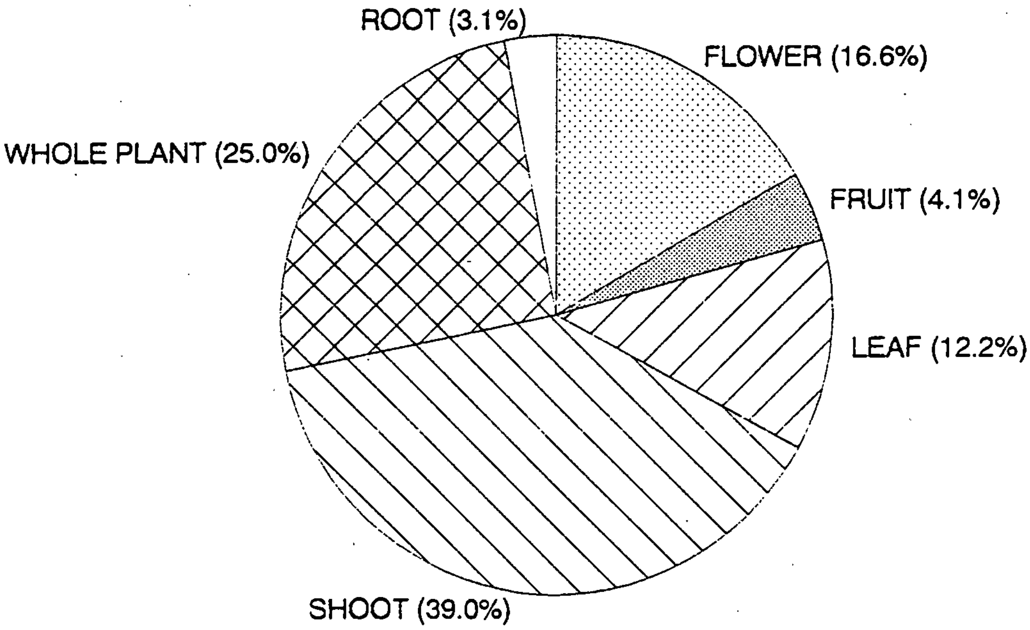

Fig. 5. Relative frequency of various plant parts in diets of ostriches foraging in natural vegetation in southern Africa.

Table 2. Physical attributes of plants taken or avoided by ostriches. The number (%) of plant species that were recorded in ostrich habitats were subjectively allocated to growth form, leaf duration and spinescence classes. Contingency tables (X^2 statistic) were used to compare the distributions of plant attributes for species taken or not taken by ostriches.

Attribute	Taken		Not taken			
	No.	%	No.	%	X^2	P
Number of records	162	(100)	169	(100)		
Growth form					6.40	0.21
Forb	45	(28)	29	(17)		
Grass	16	(10)	17	(10)		
Succulent	34	(21)	49	(29)		
Woody	67	(41)	74	(44)		
Leaf duration					7.65	<0.01
Deciduous	106	(65)	82	(48)		
Evergreen	56	(35)	87	(52)		
Spinescence					0.11	0.94
None	136	(84)	144	(85)		
Stem spines	17	(10)	16	(10)		
Leaf or fruit prickles	9	(6)	9	(5)		

ns = P > 0.1, ** < 0.01

Table 3. Chemical composition (expressed in g/kg oven dry mass) of plant species included or excluded from diets of ostriches foraging in semi-arid and winter-rainfall regions of southern Africa. Wilcoxon unpaired rank tests were used to test the null hypotheses.

Component	Included in diet			Excluded from diet			
	n	x	SD	n	x	SD	P
Water % fresh mass	43	69.7	22.3	11	68.8	15.7	0.64
Crude fiber	79	243.4	96.3	27	231.4	110.4	0.70
Crude protein	93	119.2	53.1	32	99.5	47.7	0.10
N-free extract	79	447.1	95.1	27	472.3	84.3	0.17
Ether extract	89	34.6	26.1	23	56.2	44.0	0.03
Metabolic energy[1]	79	9.9	1.6	27	10.5	1.9	0.06
Ash	87	164.2	99.6	32	144.9	123.9	0.17
Silica	12	25.4	15.4	--	-----	-----	----
Sodium	82	22.3	31.5	31	12.7	33.7	0.01
Potassium	53	13.4	9.0	21	9.5	5.9	0.16
Phosphate	81	1.7	0.8	31	1.4	0.7	0.17
Calcium	81	13.3	11.6	31	12.1	9.2	0.78
Tannin: hyrdolizable	18	8.6	11.5	4	9.4	8.5	0.83
Tannins: condensed	10	0.5	0.1	8	0.9	0.5	0.10
Phenolics	13	11.5	6.1	6	19.5	3.6	0.01
Oxalates	19	155.9	82.8	4	150.0	180.2	0.52
Palatability[2]	47	1.5	0.7	18	0.5	0.7	<0.001

[1] Metabolic energy (MJ/kg oven dry mass) was calculated as the sum of each organic component (g/kg) multiplied by its physiological fuel value (MJ/g) as given in Ministry of Agriculture (1975). ME = 0.005 CF + 0.012 CP + 0.014 NFE + 0.031 EE

[2] Palatability ratings of plant species for sheep (see text for sources)

Preference indices for the entire data base (n = 97 for major constituents) were correlated positively with sodium and negatively with EE, condensed tannin, phenolics and metabolizable energy content. However correlates differed among plant growth forms (**Table 4**). Ostriches preferred those species of forbs which had high fiber contents, grasses which had relatively high protein contents, succulents which had low calcium and high fiber contents and woody plants which had relatively high sodium concentrations. Preference for high fiber or sodium contents may be equivalent to avoidance of EE or tannins and phenolics with which they were negatively correlated (**Table 5**). Ostriches also avoided other toxins not assayed in the present study (**Appendix 6**). There was a difference (X^2 = 1.1, P < 0.01) in the proportion of toxic plants between ostrich food- and non-food species. Substances (mostly alkaloids) known to be poisonous to sheep, cattle or horses occurred in 8/159 plant species that had ostrich preference ratings >0.1 and in 24/166 species with ostrich preference ratings <0.1.

Table 5. Rank correlations (r_s) among crude fiber, sodium and water content and allelochemicals in some common plant species from arid and semi-arid southern Africa.

	n	CF	Na	Water
Na	97	-0.50		
		***		
Water	97	-0.69	+0.58	
		***	***	
CP	97	-0.71	+0.39	+0.31
		***	***	*
NFE	97	+0.34	-0.55	-0.42
		***	***	***
ASH	97	-0.70	+0.68	+0.59
		***	***	***
EE	97	-0.35	+0.05	-0.13
		***	NS	NS
ME	97	+0.16	-0.55	-0.29
		NS	***	NS
P	97	-0.59	+0.39	+0.14
		***	NS	NS
Ca	97	-0.52	+0.17	+0.13
		***	NS	NS
Tannin H	23	+0.10	-0.61	-0.35
		NS	***	NS
Tannin C	18	-0.02	-0.18	+0.14
		NS	NS	NS
Phenol	18	-0.04	-0.55	-0.08
		NS	***	NS
Oxalate	23	-0.16	+0.43	+0.41
		NS	***	*

with their heads held about 300 mm above the soil surface. They are able to select flowers from amongst foliage and to detect small, prostrate forbs (eg *Trianthema triquetra*, *Lotononis pungens*, *Lasiopogon* spp.) that have low visual apparency. Because they cannot bite through woody branches, ostriches pluck and pull at food plants. These mechanical limitations restrict their choice of food to easily broken shoots, leaves and fruits or plants small enough to be swallowed whole. Ostriches seldom browse leaves from shrubs at seasons when forbs and green grasses are available (Kok 1980). Stem and leaf spines did not prevent ostrich herbivory. Ostriches swallowed prickly leaves and inflorescences and were able to pluck leaves, pods and flowers from amongst thorns. Nevertheless, whereas ostriches browsed moderately thorny forms of *Ruschia spinosa* (Mesembryanthemaceae) they seldom utilized highly spinescent forms of this species (S.J.M. pers. obs.). Ostriches selected for high fiber rather than high protein content in most types of food. We suggest that this preference may be related to the inverse relation between fiber and chemical deterrents to herbivores in woody plants and to the correlation between fiber and energy content in forbs and succulents.

Plant species containing high concentrations of ether-extractable substances, phenolic compounds, tannins and possibly sodium and calcium oxalate were seldom eaten by ostriches. Although they are sometimes found to be ineffective defences against mammalian herbivory (Cooper and Owen-Smith 1985), some hydrolyzable tannins reduce protein digestion as effectively as condensed tannins (Hagerman *et al.* 1992). Both hydrolyzable tannins (gallotannins) and condensed tannins appeared to deter feeding by ostriches. The birds also avoided certain plant species known to be toxic to ruminants. *Dimorphotheca cuneata*, *Euriops latifolius*, *Geigeria* spp., *Pteronia pallens*, (all Asteraceae), *Euphorbia mauritanica* (Euphorbiaceae), *Nicotiana glauca* and some *Solanum* spp. (Solanaceae), *Tylecodon* spp. and other Crassulaceae were not eaten by ostriches even when these plants were abundant in the habitat.

Ostriches observed in enclosures that they had occupied for many months would move among toxic plants making no attempt to feed on them, and it was assumed that they identified these species by sight. Taste or smell appeared to play a role in detection of palatability, since foraging ostriches occasionally dropped plucked plant material. A number of the plants avoided by ostriches, including *Salvia clandestina*, *Acrotome fleckii* (both Lamiaceae), *Osteospermum calendulaceum*, *Pegolettia senegalensis* (both Asteraceae) and *Sutera tomentosa* (Scrophulariaceae), were glandular and strong-smelling but not known to contain any toxin. Although chemoreception is poorly developed in birds, a number of species have been shown to respond to plant volatiles (Mason & Adams 1989) and some phenolic compounds are effective as avian repellents (Jakubas *et al.* 1992).

Succulents constituted 5-20% of the diets of ostriches in parts of the Karoo where succulent plants dominated the vegetation. The birds showed no preference for succulents when foraging in this vegetation type and they avoided succulents with sodium concentrations exceeding 9% and selected species with relatively low concentrations of calcium and oxalate (Appendix 6). However, preference for halophytic succulents may depend on the availability of sodium in the environment. Ostriches selectively foraged for saline *Trianthema triquetra* in the Namib where most plants contained <1% sodium (Appendix 6). Succulent members of the Mesembryanthemaceae (Smit 1963), Cactaceae (Smit 1963), Euphorbiaceae (Skadhauge *et al.* 1984), Liliaceae (Keffen 1984), Portulacaeae (Keffen 1984) and Zygophyllaceae (Robinson and Seely 1975, Kok 1980) are known to be eaten by ostriches throughout their range. Ostriches foraging at low densities in natural vegetation are reportedly independent of

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APPENDIX 1. Food items from stomachs of 11 ostriches collected in desert grasslands in Namibia in May 1990. Plant parts eaten are coded as follows flowers (F), leaves (L), seeds (S) and whole plants including roots (W). Types of plants distinguished were forbs (1), graminoids (2), shrubs (3), succulents (4) and trees (5). Number refers to the number of stomachs containing each item and % mass refers to the percentage contribution of the items to the total oven-dry organic content of stomach samples. Plant families are listed in alphabetical order and nomenclature follows Gibbs Russell *et al.* (1985, 1987 and 1990).

Food items	Type	Part	Number	% mass
Plant material				
Acanthaceae				
Blepharis spp.	3	W	11	3.90%
Monechma arenaria	3	L	10	20.93%
Petalidium setosum	3	L	10	1.26%
Aizoaceae				
Trianthema triquetra	4	W	11	5.46%
Asteraceae				
Dicoma capensis	1	L	11	5.57%
Hirpicium gazanioides	1	W	5	2.34%
Capparaceae				
Cleome angustifolia	1	W	10	1.44%
Fabaceae				
Indigofera spp.	1	W	9	3.80%
Poaceae				
Enneapogon devauxii	2	W	3	1.33%
Eragrostis spp.	2	L	8	2.81%
Schmidtia kalahariensis	2	W	9	20.61%
Stipagrostis spp.	2	W	8	4.03%
Zygophyllaceae				
Tribulus spp.	1	W	10	1.83%
Unidentified plant fragments			9	22.95%
Other plant material				
Wood and moribund grass			3	0.07%
Animal material				
Insects (Diptera, Hemiptera, Formicidae)			3	<0.01%
Antelope faeces			3	<0.01%
Bone fragments			3	<0.01%

Species contributing <1% of dry matter in ostrich stomach samples from the Namib in May 1990:

Aizoaceae: *Giseckia pharnaceoides*, *Hypertelis salsoloides*, *Limeum aqute-carinatum*, Amaranthaceae: *Sericorema sericea*, Asteraceae: *Cuspidia cernua*, *Helichrysum candolleanum*, *Osteospermum crassifolium*, Chenopodiaceae: *Salsola tuberculata*, Euphorbiaceae: *Chamaesyche glanduligera*, Fabaceae: *Acacia erioloba*, *Crotalaria spartioides*, *Lotononis platycarpa*, *Otoptera burchellii*, *Parkinsonia africana*, Geraniaceae: *Monsonia umbellata*, Molluginaceae: *Mollugo cerriana*, Ophioglossaceae: *Ophioglossum polyphyllum*, Poaceae: *Aristida adscensionis*, *Tragus berteronianus*, Urticaceae: *Forsskaolea candida*.

APPENDIX 3. Food items observed to be taken by ostriches on ranches in the succulent dwarf-shrublands of the southern Karoo, South Africa, or present in stomachs of five ostriches collected in this region in March 1990, June 1990, 1992, July 1992, October 1991. Nomenclature and coding as in Appendix 1. Observations are the number of times that an item was observed to be taken by ostriches and % mass refers to the percentage contribution of the items to the total oven-dry organic content of stomach samples.

Plant families and species	Type	Part	Obs.	% mass
Plant material				
Aizoaceae				
Drosanthemum hispidum	4	W	3	6.4
Drosanthemum montaguense	4	L F	2	2.8
Galenia africana	3	L F	6	0.5
Galenia fruticosa	3	L F	2	1.1
Malephora lutea	4	L F	17	0.1
Tetragonia echinata	1	W	3	6.0
Asteraceae				
Eriocephalus sp.	3	L	3	0.1
Gazania krebsiana	1	L F	6	2.0
Gazania lichtensteinii	1	W	2	8.7
Lasiopogon glomerulata	1	W	2	11.5
Leyssera tenella	1	W	3	6.8
Pteronia sordida	3	F	6	0.0
Ursinia nana	1	W	3	3.3
Lepidium spp.	1	W	3	0.9
Chenopodiaceae				
Atriplex lindleyi	1	W	9	5.2
Atriplex semibaccata	1	L F	1	2.4
Salsola sericata	3	L	55	0.0
Salsola sp.	3	L	7	0.0
Fabaceae				
Acacia karroo	5	L F S	29	2.5
Acacia karroo	5	resin	1	14.3
Lotononis sp	1	W	2	2.8
Malvaceae				
Malva parviflora	1	W	1	2.1
Papaveraceae				
Argemone mexicana	1	L F	2	3.8
Poaceae				
Fingeruthia africana	2	L F	4	0.2
Karoochloa tenella	2	W	4	3.0
Schismus barbatus	2	W	1	4.0
Stipagrostis ciliata	2	L F	3	0.0
Stipagrostis obtusa	2	L F	16	0.0
Unidentified grasses	2	L	5	0.0
Solanaceae				
Lycium spp.	3	L F	23	1.1
Supplements (lucerne, maize)			14	4.0
Animal material				
Mammal bone			2	1.5

APPENDIX 4. Plant species observed to be consumed by ostriches foraging in coastal macchia and fynbos (heathland) in the Cape of Good Hope Nature Reserve, Cape Province, South Africa between January 1985 and July 1986. Nomenclature and coding as in Appendix 1. Observations are the number of times than a species was observed to be taken by ostriches. Data taken from an unpublished manuscript (G.G. Bradley 1987) with permission of Percy FitzPatrick Institute of African Ornithology, University of Cape Town.

Plant families and species	Type	Part	Obs.	% obs.
Asteraceae				
Anaxeton lavae	3	F	117	3.5
Arctotis acaulis	1	L F	81	2.4
Berkheya barbata	3	F	57	1.7
Haplocarpa lanata	3	L F	149	4.4
Ifloga ambigua	3	L F	625	28.1
Othonna pinnata	1	L F	77	2.3
Plecostachys serpyllifolia	1	F	35	1.0
Senecio arenarius	1	F	35	1.0
Senecio hastatus	1	L F	38	1.1
Campanulaceae				
Monopsis lutea	1	L F	40	1.2
Chenopodiaceae				
Exomis microphylla	3	L F	304	9.0
Ericaceae				
Erica plukenetii	3	F	115	3.4
Haemdoraceae				
Empodium plicatum	2	F	164	4.8
Liliaceae				
Trachyandra ciliata	2	F	35	1.0
Trachyandra revoluta	2		35	1.0
Oxalidaceae				
Oxalis spp.	1	W	472	14.0
Plantaginaceae				
Plantago carnosa	1	F	276	8.1
Rhamnaceae				
Phylica imberbis	3	F	186	5.5
Selaginaceae				
Selago corymbosa	1	F	43	1.3

APPENDIX 5. Nutrients and energy values of ostrich stomach contents and plants collected in the southern Karoo in July and March 1992 respectively. Plant species arranged in order of ostrich preference index. For analysis techniques see methods. Abbreviations are CF: crude fiber, CP: crude protein, NFE: nitrogen-free extract, EE: ether extract, ME: metabolic energy content (MJ/kg) on a dry mass (DM) and fresh mass (FM) basis.

Plant species	Water % FM	CF g/kg	CP g/kg	NFE g/kg	Ash g/kg	ME[1] DM	Pref. index
Ostrich stomach	71	127	134	367	339	8.37	----
Gazania krebsiana	88	125	159	315	374	7.80	5.06
Drosanthemum montaguense	86	184	112	381	281	8.90	3.40
Salsola aphylla	70	145	134	414	286	8.76	3.10
Aridaria noctiflora	90	207	105	454	204	9.58	2.70
Drosanthemum hispidum	93	138	140	368	298	9.26	2.60
Delospermum subincanum	89	165	69	482	246	9.55	2.25
Psilocaulon utile	89	94	167	410	291	9.37	2.00
Galenia fruticosa	76	196	107	430	245	8.92	1.90
Tetragonia echinata	90	140	172	376	278	9.09	1.40
Kochia salsoloides	75	153	241	375	215	9.39	1.40
Galenia africana	70	182	141	504	137	10.75	1.10
Ruschia spinosa	79	116	78	628	146	11.30	0.98
Galenia papulosa	76	121	163	350	323	8.79	0.76
Osteospermum sinuatum	68	152	188	333	288	8.87	0.68
Sphalmanthus brevifolius	90	128	126	397	292	9.46	0.55
Malephora lutea	94	57	121	369	429	7.68	0.23
Brownanthus ciliatus	89	88	175	381	315	9.15	0.10
Drosanthemum uniflorum	90	92	138	408	321	9.08	0.18
Sphalmanthus tetragonus	93	94	113	337	408	8.02	0.05
Augea capensis	91	45	114	291	517	6.68	0.00
Hereroa latipetala	79	52	163	556	193	11.10	0.00
Pteronia empetrifolia	61	208	136	422	149	11.20	0.00
Pteronia pallens	73	119	163	405	226	10.92	0.00

2. HERBIVORE SELECTIVITY RELATIVE TO RESOURCE ABUNDANCE AND QUALITY

2.7 Preferential utilization of pans by springbok (Antidorcas marsupialis marsupialis).

Authors: Milton S.J., Dean W.R.J. & Marincowitz C.P.

Published 1992: *Journal of the Grassland Society of southern Africa* 9(3), 114-118

Abstract: *Forage utilization in pans and surrounding habitats was compared at one karroid shrubland site and two desert grassland sites and was found to be greater in pans than on adjacent plains and dunes. Springbok used pan areas for various social interactions and there was noticeably more springbok dung in pans. Pan soils had a higher Ca, K, Na and P concentrations and plants remained green for longer in pans than in surrounding areas. The high quality of food in pans together with the suitability of pans as display sites may explain the preferential use of pan areas by springbok.*

Introduction

Springbok (*Antidorcas marsupialis*) are the most common game animal farmed in combination with wool sheep in the Karoo (Jooste 1983). Although both springbok and sheep are mixed feeders, Davies *et al.* (1986) and Fairall *et al.* (1990) found a large degree of diet separation between these species in the Karoo. Although springbok have been found to use rangeland more evenly than Merino sheep during drought (Davies & Skinner 1986), springbok confined to farms and game reserves reportedly select denuded, poorly-drained areas. In arid and semi-arid transitional grasslands, springbok are associated with short, non-grassy vegetation (Leistner 1967; Bigalke 1972; Novellie 1990). In this paper we document selective utilization of dry pans by springbok and provide some explanation for this behaviour.

Procedure

Observations were made in and around three pans (temporarily flooded depressions) in areas lying between the 100-200 mm isohyets and having non-seasonal and unpredictable rainfall. Pan 1, one of six similar pans on the southern Karoo farm Kleinsleutelfontein ($33^0$10'S,$22^0$26'E), was a poorly vegetated, silty area (80 m x 120 m) in a slight depression on a shale plain. The farm lies inland of the Swartberg Mountains in the Karroid Broken Veld (Acocks, 1975) and is stocked with sheep (5 ha/sheep rotated over the farm on a 25% rest basis) and springbok (continuously grazed at 1/3 of the grazing capacity for sheep ie one springbok per three sheep). Pans 2 and 3 were at Brabees ($29^0$17'S, $18^0$52'E), a privately owned reserve (72 000 ha) in False Desert Grassveld (Acocks 1975) on red sands in the north-western Cape. The reserve was stocked with approximately 300 springbok and 30 gemsbok (*Oryx gazella*). Pan 2 was a hard clay depression (50 m x 60 m) on gravel plains and Pan 3 was a calcrete pan (350 m x 170 m) surrounded by dunes.

Plant utilization data for both the southern and northern Cape sites were collected in February 1990 when all the pans were dry (rainfall for period 1st September 1989 to 20th February 1990 was respectively 45 mm and 13 mm). All plants present in 30 randomly

Table 2 Phenology of plants in February 1990 at Pan 3 and on surrounding dunes

Phenological state	Pan 3	Dune 3
Total plants observed	76	159
Flowers	21	0
Green leaves	64	9

Eleven plant species were recorded at Pan 3, eight in the pan and four on surrounding dunes (**Appendix** 1). Phenology of plants in pans generally appeared to differ from plants in adjacent areas. At Pan 3, more plants bore flowers (Chi square = 46.8, P <0.001) and green leaves (Chi square = 148.3, P <0.001) in the pan than on the surrounding dunes (**Table** 2).

Table 3 Mean (SD) nutrient levels in soil samples from a pan and adjacent shale plain at Kleinsleutelfontein (1) and from shale plains on Klipgat farm (1a) in the southern Karoo and from pans, plains and dunes in the north-western Cape. Concentrations of all elements expressed in parts per million, conductivity given in micro seconds/cm. No SD is given where n = 1

Southern Karoo shrublands

	Pan 1	Plain 1	Plain 1a	t statistic	
Sample size	2	2	2		
P	115 (71)	67 (16)	44 (20)	3.9	P<0.01
K	859 (12)	418 (129)	481 (210)	3.7	P<0.05
Na	287 (119)	66 (9)	112 (16)	3.5	P<0.05
Ca	2007 (13)	1246 (463)	972 (171)	3.6	P<0.05
Mg	397 (37)	251 (134)	322 (17)	1.6	NS
Conductivity	780 (523)	255 (78)	343 (152)	1.9	NS
pH	8.7 (0.4)	8.5 (0.1)	7.7 (0.3)	1.5	NS

North-western Cape grasslands

	Pans 2	Plains	Dunes
Sample size	3	6	3
P	13 (1)	80 (48)	14 (2)
K	215 (117)	166 (60)	66 (7)
Na	41 (19)	36 (17)	22 (10)
Ca	530 (14)	---	98 (-)
Mg	298 (190)	---	39 (-)
pH	7.8 (0.4)	---	7.7 (-)
Conductivity	210 (28)	---	50 (-)

West in the central Karoo, plant species associated with pans were common in the diets of springbok (Fairall *et al.* 1990). Springbok forage selectively for leaves with high moisture and protein contents (Bigalke 1972) and differ from sheep in that they avoid lignified material (Davies *et al.* 1986).

Table 4. Utilization of plants in and around pans by mammalian herbivores. Shared species are those occurring both in and around a pan

	Observations		% Utilization		Chi-square	
	Pan	Surround	Pan	Surround	statistic	
Pan 1 (Springbok and sheep)						
Shared species	154	164	79	19	115.7	***
Non-shared species	128	35	31	46	1.9	NS
Total plants	282	199	58	24	54.4	***
Pan 2 (Springbok and gemsbok)						
Shared species	85	51	42	25	3.2	NS
Non-shared species	1	0	100	0	---	--
Total plants	86	51	43	25	3.5	NS
Pan 3 (Springbok and gemsbok)						
Shared species	14	149	86	1	105.5	***
Non-shared species	62	10	63	42	2.6	NS
Total plants	76	159	67	3	112.3	***

*** $\underline{P} \leq 0.001$

Our study indicated that the palatability of widespread plant species for springbok (and possibly also for sheep) was greater in pans than in surrounding areas. Their preference for plants in pans may possibly be attributed to the effects of soil chemistry and drainage on forage quality. Places where water collects and evaporates in arid regions tend to be rich in calcium, magnesium, potassium and sodium salts (Richards 1954; Weir 1969). Shortages of these minerals can limit herbivore reproduction (Freeland & Choquenot 1990). Plants with high concentrations of sodium (McNaughton 1988) and plants growing on sodic soil patches (Bailey & Scholes, in press) are generally more palatable to herbivores than plants on non-sodic soils. The succulent shrub *Psilocaulon utile* which was severely browsed in pans at Kleinsleutelfontein but rarely utilized when growing on plains illustrates this change in palatability. Moreover in pans, as in other places where water collects, plants remain green for longer periods after rain (Milton 1990).

Large dung patches frequented by male springbok, occurred in all three pans studied. It is possible that pans and other nutrient-rich or sodic soil patches are selected by male antelope as lek sites because they form part of the females' preferred habitat (Jarman 1974) or because females are attracted to the high quality of forage in these areas (McNaughton 1988). The selection of sparsely vegetated lek sites may also make the displays of advertising springbok rams more conspicuous to females and competing males (Smithers 1983).

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Appendix 1 ctd...

Species	Pans		Surrounding area	
	Total	Utilized	Total	Utilized
Protasparagus recurvispinus	6	6	3	0
Psilocaulon utile	8	6	6	0
Pteronia pallens	1	0	0	0
Pteronia sordida	0	0	1	0
Pteronia viscosa	1	1	5	1
Rosenia humilis	0	0	5	2
Ruschia sp	0	0	2	2
Ruschia spinosa	4	4	23	5
Salsola tuberculata	0	0	1	0
Salvia verbenaca	2	2	1	0
Sisymbrium burchellii	13	11	0	0
Sphalmanthus brevifolius	0	0	4	0
Sphalmanthus nitidus	0	0	2	1
Sphalmanthus tetragonus	4	1	0	0
Stipagrostis obtusa	0	0	3	0
Thesium lineatum	0	0	1	1
Tragus berteronianus	3	0	0	0
Tribulus terrestris	24	14	0	0
Zygophyllum gilfillani	0	0	3	3
Zygophyllum retrofractum	5	4	0	0
unidentified geophytes	1	0	1	0
Totals	282	163	199	47
Pan 2 (Springbok and gemsbok)				
Hypertelis salsoloides	3	0	10	7
Peliostomum album	3	3	4	4
Salsola tuberculata	1	1	0	0
Stipagrostis brevifolius	1	1	25	2
Stipagrostis ciliatus	43	29	1	0
Stipagrostis obtusa	35	3	11	0
Totals	86	37	51	13
Pan 3 (Springbok and gemsbok)				
Aristida congesta	5	3	0	0
Centropodia glauca	0	0	8	2
Galenia sarcophylla	2	2	0	0
Lycium sp	2	0	0	0
Monechma incanum	0	0	1	1
Osteospermum muricatum	19	19	0	0
Rhigozum trichotomum	0	0	1	0
Schmidtia kalahariense	12	12	0	0
Stipagrostis brevifolius	1	1	0	0
Stipagrostis ciliatus	14	12	149	2
Stipagrostis obtusa	21	2	0	0
Totals	76	51	159	5

PART 3

EFFECTS OF HERBIVORY AND OTHER FACTORS ON PLANT REPRODUCTION, GROWTH AND DEMOGRAPHY

3. EFFECTS OF HERBIVORY AND OTHER FACTORS ON PLANT REPRODUCTION, GROWTH AND DEMOGRAPHY

3.1 Effects of rainfall, competition and grazing on flowering of Osteospermum sinuatum (Asteraceae) in arid Karoo rangeland.

Author: Milton, S.J.

Published 1992: *Journal of the Grassland Society of Southern Africa* 9(4),

Abstract: *The shrub* Osteospermum sinuatum, *an important fodder plant in Karoo rangelands, flowered after heavy rain in autumn, winter and spring. The number of flowers produced per bush was positively correlated with basal stem diameter and rainfall in the 12 weeks before anthesis. Flowering increased when neighbouring plants were removed. Grazing during flowering and seed set, by sheep stocked at recommended rates, reduced potential seed set by as much as 90%. Birds, hares and small antelope consumed 10-50% of the flowers. Size class distributions indicated that little recent recruitment had taken place on a ranch where palatable plants were scarce and where* O. sinuatum *flower production was severly depressed by grazing sheep.*

Introduction

Grasses that are obligate reseeders, but produce few seeds and lack persistent seed banks, are considered to be susceptible to local extinction where herbivores severely reduce seed production (O'Connor 1991). There is some evidence that shrubs, such as *Osteospermum sinuatum* (DC) T. Norl., which share these life-history attributes are equally susceptible to being exterminated by heavy grazing.

Osteospermum sinuatum (**Plate 5a**), commonly called *"bietou"*, is a dwarf, drought-deciduous (**Plate 5b**) shrub that produces few, large, winged seeds (**Plate 5c**) and has a wide distribution in the drier parts of the Karoo (Norlindh 1943). It is preferentially grazed by domestic livestock and wild mammals (Van Breda & Barnard 1991; Milton & Dean in press), probably because of its high protein content and low concentrations of secondary compounds (Louw *et al.* 1967, 1968).

This valuable fodder plant is believed to be disappearing from heavily grazed rangeland (Acocks 1955; Joubert & Van Breda 1976) despite its ability to recover rapidly after grazing (Van der Heyden 1992). The failure of *O. sinuatum* to maintain its populations under heavy grazing may be the result of destruction of flowers and unripe fruit by domestic livestock (Milton & Dean 1990). The present paper reports on the relative effects of rainfall, grazing (**Plate 5d**) and interspecific competition on flowering of *O. sinuatum*.

Study sites

The study was carried out at the Tierberg Karoo Research Centre (TKRC) $33^0$10'S, $22^0$17'E and on the sheep farms that adjoin its boundaries, namely Tierberg (T) to the north and Argentina (A) to the west. This arid area (more fully described in Milton *et al.* 1992) lies in the Sandrivier Valley on the southern edge of the Great Karoo. The colluvial soils are stony and alkaline. Vegetation, comprising perennial succulent and non-succulent shrubs 0.2-0.4 m in height, covers 15-25% of the soil surface. Perennial grasses are restricted to drainage

Despite the pseudoreplicated sampling design (see Hurlbert 1984), inferential statistics have been used to test for significant treatment effects. For each sampling date, the mean number of flowers per plant was calculated for plots containing five or more plants with basal stem diameters >5 mm; plots with fewer plants were removed from the data set. For Series 1 plots, mean flower-crop data (normalized by log-transformation) were adjusted using covariance analysis to remove effects of plot position and plant basal diameter. One-way analysis of variance (ANOVA) was used thereafter. Tukey (Zar 1984) tests were used to compare means of grazing treatments.

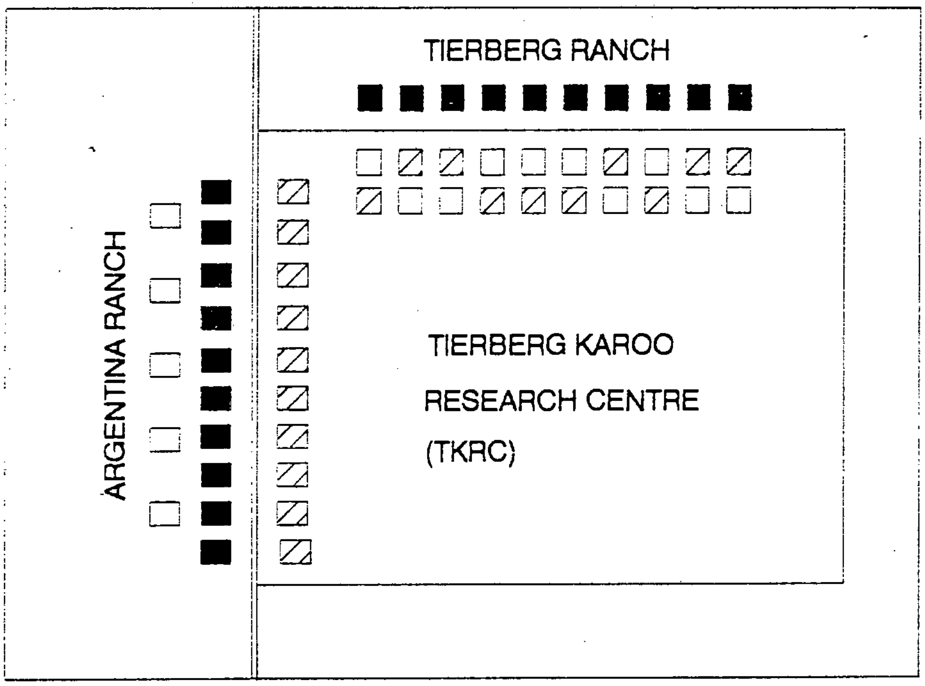

Figure 1 Diagram showing layout of experimental plots at Tierberg Karoo Research Centre, Tierberg ranch and Argentina ranch. Control plots plain, wildlife plots hatched and sheep plots shaded.

Non-parametric statistics were used to compare treatments in Series 2 plots where variances of normalized data were heteroscedastic (Zar 1984). Kruskal-Wallis ANOVA tests (alpha = 0.01) were followed by pairwise Wilcoxon rank testing of means.

In order to assess the effect of protection from sheep on flower crops of plants for which pre-protection flowering data were available, four randomly selected permanent plots on Tierberg ranch were protected from sheep in the fourth year of the experiment (June 1991). Mean flower crops of plants in selected and non-selected plots were compared for five sampling periods prior to protection and for two sampling periods after protection, using Mann-Whitney rank tests (Zar 1984).

Florivory

In order to assess the effects of florivory on seed production, the fates of individually marked *O. sinuatum* flower buds were recorded in September of 1990 and of 1991. Five buds were marked on each of 10 plants in wildlife exclosures, in sheep exclosures and on Tierberg sheep farm. After two and four weeks the

Densities of reproductively mature *O. sinuatum* plants (>5 mm b.d.) did not vary significantly between sites (TKRC range 32-50 plants/100m^2, Tierberg 39, Argentina 22; X^2 = 3, P <0.1), but densities of smaller plants were lower at Argentina than at other sites (TKRC range 24-75 plants/100m^2, Tierberg 26, Argentina 3; X^2 43, P <0.001)

Flowering and basal diameter

Plants with basal stem diameters <3 mm produced no flowers. Flowering was positively correlated with basal diameter during all five flowering events (r ranged from 0.33 to 0.62, df = 118, P <0.001). The slope of the regression line was steep (y = -8.9 + 28.0x) and highly significant (r = 0.61, df = 75, P <0.001) for plants <13 mm b.d. Flower crops of larger plants did not increase significantly (r = 0.29, df = 40, P = 0.058) with increased basal diameter (y = 16.3 + 9.9x)

Flowering and rainfall

The mean number of flowers per plant differed between flowering events in both grazed and control plots (**Table 1**). During the study, ten flowering events occurred, four in winter, three in spring and three in autumn (**Figure 3**). Flowers were born apically on new shoots and opened four to six weeks after relatively heavy rain. The mean number of flowers per plant in control plots was closely correlated with rainfall in the 12 weeks preceding anthesis (r = 0.89, P <0.01; **Figure 4**) but unrelated to rain that occurred during the four-week period when flowers were developing (r = 0.07, P >0.1).

Flowering and herbivory

There were significantly fewer flowers per bush in Series 1 plots grazed by wild mammals and sheep than in control plots during four of seven flowering events (**Table 1**). Flowering differed little between treatments when sheep were absent from the camp. Grazing by wildlife alone had less effect on flower crops than grazing by sheep and wildlife.

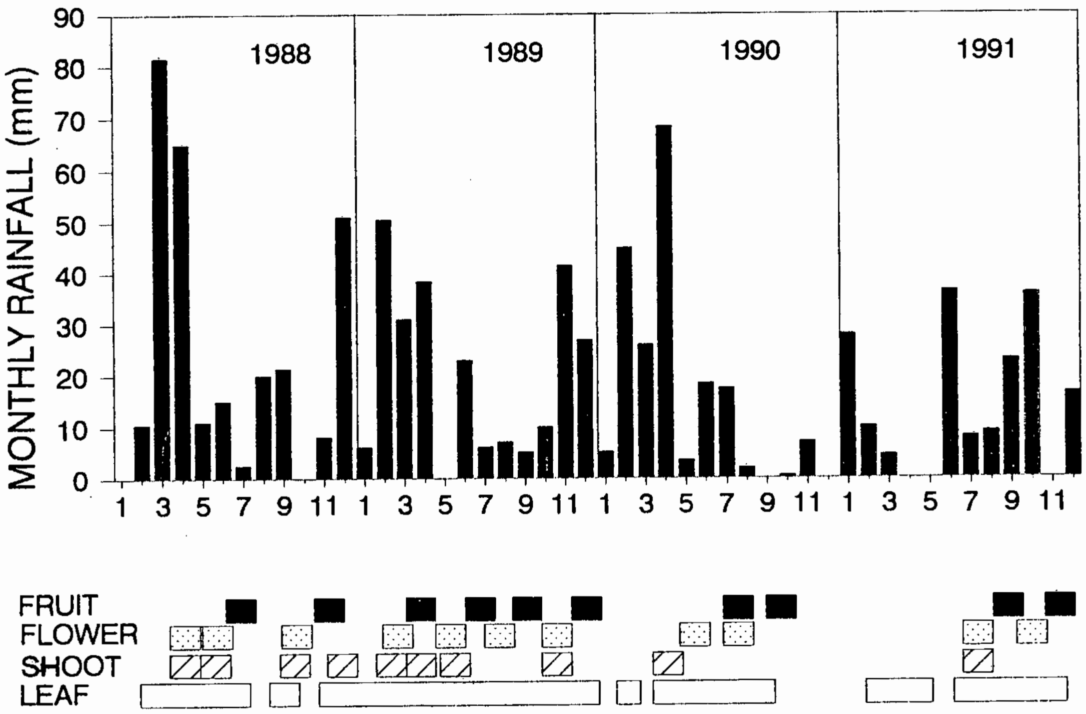

Figure 3 Monthly rainfall and phenology of *Osteospermum sinuatum* at the Tierberg Karoo Research Centre from January 1988 to December 1991.

Table 1. Flower production of <u>Osteospermum sinuatum</u> plants (>5 mm b.d.) under three grazing treatments. Means (± SD) are based on 50-90 plants/treatment. Rotation refers to the presence (in) or absence (out) of sheep in the six weeks prior to flowering. In Series 1, Significance[1] refers to results of ANOVA tests performed on log-transformed mean flower crops in 10 plots; in Series 2, significance refers to Kruskal-Wallis ANOVA tests on untransformed data followed by pairwise Wilcoxon rank testing of means.

Date	Control	Wild mammals	Sheep	Rotation	Signif.
<u>Series 1: TKRC and moderately grazed farm</u>					
88/11	14 (27)^{a}	10 (19)^{a}	15 (58)^{a}	out	NS
89/09	7 (12)^{a}	3 (4)^{a}	<1 (1)^{b}	in	***
89/12	14 (16)^{a}	12 (18)^{ab}	6 (10)^{b}	out	*
90/06	26 (31)^{a}	13 (17)^{b}	11 (16)^{b}	in	**
90/11	3 (20)^{a}	<1 (2)^{a}	<1 (2)^{a}	out	NS
91/09	23 (26)^{a}	12 (19)^{a}	3 (5)^{b}	in	***
91/11	16 (13)^{a}	17 (19)^{a}	12 (8)^{a}	out	NS
<u>Series 2: TKRC and heavily grazed farm</u>					
89/04	-------	1 (4)^{a}	<1 (1)^{a}	in	NS
89/12	------	7 (12)^{a}	1 (3)^{a}	in	NS
90/06	14 (12)^{a}	18 (26)^{a}	1 (2)^{b}	in	**
91/09	15 (13)^{a}	9 (10)^{a}	2 (1)^{b}	in	**

Significance * P <0.05, ** P <0.01, *** P <0.001

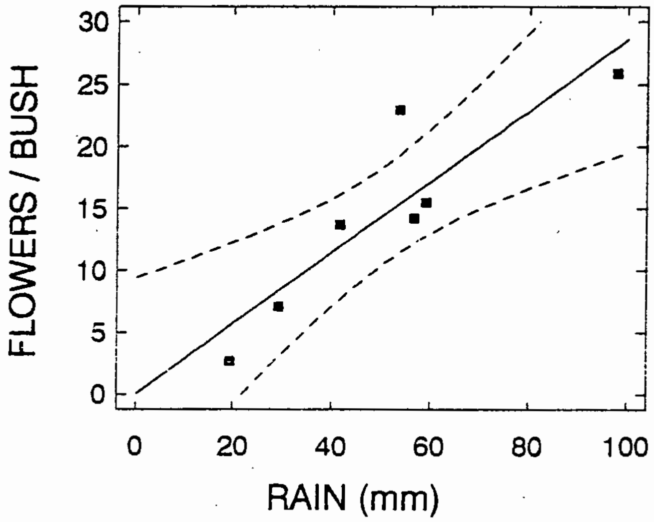

Figure 4 Regression line illustrating the relation between rainfall in the 12 weeks preceding anthesis and mean number of flowers per plant for *Osteospermum sinuatum* >0.5 mm b.d. at Tierberg Karoo Research Centre.

Competition

Osteospermum sinuatum plants in, or adjacent to, cleared plots produced more flowers than plants in undisturbed vegetation ($P < 0.001$), both when protected from and when exposed to grazing by wild mammals (**Table 4**). The effect of reduced competition on flowering appeared to be unrelated to the size of the plants because canopy width did not differ significantly between plants subjected to and freed from competition.

Table 4 Flowering of Osteospermum sinuatum in cleared plots, adjacent to cleared plots and in undisturbed vegetation in the presence and absence of indigenous mammalian herbivores. P refers to significance of Tukey multiple range tests following ANOVA

	Cleared	Adjacent	Undisturbed	
	Mean (SD)	Mean (SD)	Mean (SD)	P
Sample size	40	20	130	
Grazed	25.6 (23.3)^{a}	23.9 (24.4)^{a}	8.6 (15.3)^{b}	<0.001
Protected	41.5 (34.8)^{a}	38.9 (32.2)^{a}	16.1 (23.2)^{b}	<0.001

Discussion

Osteospermum sinuatum appears to be a resilient and tolerant of grazing. Plants on two sheep ranches produced "normal" flower crops in response to the first rainfall that followed protection from grazing. Defoliation stimulates the rate of CO_2 absorption in this species (Van der Westhuizen *et al.* 1981) and non-structural carbohydrate reserves are rapidly replenished after grazing (Van der Heyden 1992). The relationship between flowering and carbohydrate reserves has not, however, been investigated.

The phenology of *O. sinuatum* is flexible *ie.* it appears to be independent of day length. Although no flowering occurred during mid summer, effective rainfall in autumn, winter or spring stimulated growth and flowering. Booyens (1972) reported that *O. sinuatum* produced more flowers when grown at 17^{0}C than at 27^{0}C. An opportunistic flowering response to rainfall has been reported for several deciduous Karoo shrubs, eg. *Lycium cinereum* and *Pentzia incana* (Hoffman 1989).

Osteospermum sinuatum flowered more prolifically in the absence of all plant neighbours. Removal or reduction of neighbouring plants presumably increased local availability of water and nutrients, resources that may possibly limit flowering in *O. sinuatum*. When growing in clay or in the organically enriched soils of harvester ant nests, *O. sinuatum* produced more flowers than when growing in sand (Booyens 1972) or away from ant nests (Dean & Yeaton in press). Although reduction of competition by vegetation thinning may improve seeding and establishment of *O. sinuatum* (Joubert & Van Breda 1976), this practice could expose seedlings to frost damage. More than 90% of exposed two-year old *O. sinuatum* plants in field trials, at Middelburg in the eastern Karoo, died during the frosty winter

O. sinuatum was in full flower (Boobyer 1989; pers. obs).

The seed production estimates in **Table 5** are optimistic. They do not allow for reduced viability caused by predispersal predators such as larvae of tephritid flies (*Stylia granulata* present in 58/1228 achenes), lepidoptera (*Loxostege frustalis* and *Heliothis armigera*), pentatomid bugs (*Spilostethus rivularis*) and chrysomelid beetles; nor are losses to post-dispersal predators, such as seed-eating birds and harvester ants *Messor capensis* (which take about 5 % of the seed, Milton & Dean in press) considered here.

Rapid regrowth and opportunistic flowering should ensure seed production but where sheep stocking rates are high relative to fodder availability or where inadequate time is allowed for regrowth and seeding, even grazing tolerant species may fail to reproduce. Seed availability probably determines future vegetation composition (Liljelund *et al.* 1988). Repeated failure of palatable plants to set seed is therefore likely to lead to changes in vegetation composition such as those outlined by Roux & Vorster (1983) and O'Connor (1991) with a concomitant reduction in carrying capacity for domestic livestock.

Conclusion

The low numbers of young *O. sinuatum* plants at Argentina ranch indicate that this species is unable to maintain its population there. One of the reasons for this may be that the annual seed output of 20000 seeds/ha (2 seeds/m^2) appears inadequate to maintain a healthy population of 3000-5000 mature plants/ha. Small adjustments to stocking rate are unlikely to improve the reproductive output of this species, especially in areas where there is little alternative fodder. Although thinning of non-fodder species might improve seed set in *O. sinuatum* this would be costly and expose soil to erosion. Resting of veld for 12-16 weeks after good rain would appear to be the best way of improving the reproductive output of this valuable fodder plant.

Acknowledgements

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3. EFFECTS OF HERBIVORY AND OTHER FACTORS ON PLANT REPRODUCTION, GROWTH AND DEMOGRAPHY

3.2 Emergence and survival of seedlings in arid Karoo shrubland

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Submitted: July 1992: *Journal of Applied Ecology*

Abstract:

1. *The influence of seed availability, weather, microsite, vegetation clearing and grazing on emergence and survival of seedlings was investigated in arid (<200 mm p.a.) Karoo shrubland. Emergence and survival of seedlings from natural seed banks were recorded in undisturbed vegetation for 38 months. Using small-scale field experiments involving clearing and seeding, I examined hypotheses relating seedling composition to seed availability and, seedling survival to resource abundance and herbivory.*
2. *In undisturbed vegetation 20-800 seedlings* m^{-2} *emerged in the austral autumn when conditions were relatively cool and humid. Densities of emerging seedlings were greater in microsites influenced by grazing, insects, litter and shade than in undisturbed or exposed sites. The species composition of seedling assemblages resembled that of the surrounding vegetation. Survival varied from 5% in 1989 and 1990 to 25% in 1991 and appeared to be limited by the quantity of rain in winter and spring.*
3. *Vegetation clearing increased the amplitude of soil moisture oscillations at 50 mm below the soil surface, but reduced the rate of soil-moisture depletion at 150 mm below the surface.*
4. *Time of emergence of planted seeds was similar in all treatments, but survival of perennial species and growth of both annual and perennial species were better on cleared sites than in undisturbed vegetation. Seeds of a common annual* Tetragonia echinata *(Aizoaceae) showed innate dormancy but those of three perennial shrubs* Pteronia empetrifolia, P. pallens *and Osteospermum sinuatum (all Asteraceae) did not.*
5. *The species composition of perennial seedlings in cleared vegetation was influenced by the original plant cover and the presence of plant debris on the soil surface. Seedling survival and size increased with distance from undisturbed vegetation. Grazing by domesticated sheep and wild animals reduced the size but not the survival of perennial seedlings palatable to mammalian herbivores. Annual plants were larger and more abundant in clearings than in undisturbed shrubland.*

Introduction

Perennial forage plants selectively grazed by domestic livestock are gradually replaced by other perennials less acceptable to mammalian herbivores (Westoby 1980; O'Connor 1991). There is some evidence that rangeland change in Karoo shrublands follows this pattern (Roux & Theron 1987; Hoffman & Cowling 1990). Although changes in the relative abundance of perennial plant species are brought about by grazing, they can seldom be reversed by withdrawing livestock (Westoby *et al.* 1986).

Stocking rates in arid parts of South Africa have decreased by about 50% since the mid

March 1991, by cutting at ground level. Dead plants were left *in situ*.

Seedling emergence and survival

Seedling densities were recorded at monthly intervals from March 1989 to May 1992 by counting all seedlings in 130 wire hoops (160 mm diameter) pinned to the soil surface and dispersed over an area of approximately 30 ha. The hoops were allocated to grazing and disturbance treatments as follows: 20 completly protected from mammalian herbivores at TKRC, 50 exposed to wildlife stocked at very low densities at TKRC, 20 exposed to sheep on a moderately grazed Tierberg ranch, 20 exposed to sheep on degraded Argentina ranch 20 on ant nests and 20 on *heuweltjies* exposed to wildlife at TKRC. Within each treatment, the rings were randomly positioned and the presence or absence of litter or cover by living plants was recorded for each ring. Seedlings were identified to species or genus within a week after emergence. Densities of reproductively mature plants were estimated by counts of plants in 10 plots (5 X 5 m) at each of the three sites.

Spearman rank correlations were used to relate the timing and abundance of seedling emergence to rainfall, temperature and humidity and to compare species composition of parent and seedling assemblages. Non-parametric analysis of variance (Kruskal Wallis) and two sample tests (Wilcoxon unpaired ranks) were used to test the hypothesis that neither year, grazing nor microsite had any effect on the density of germinating seedlings. Contingency tables were used to compare seedling survival in different years and sites.

Sowing experiments

In order to establish whether seedling numbers could be increased by seed addition, seeds of common plant species were hand sown into undisturbed and cleared vegetation exposed to and protected from wild animals and sheep. In March 1990, 10 seeds of each of the palatable shrubs *Osteospermum sinuatum* (DC.) T. Norl. and *Pteronia cf. empetrifolia* DC., the toxic shrub *P. pallens* L.f. and the winter-growing, annual forb *Tetragonia echinata* Ait. were planted 10 mm deep in four parallel rows 150 mm apart. This experimental layout was used in six treatments as follows: vegetation cleared, 10 replicates with and 10 without grazing by wild animals; vegetation not cleared, with 10 replicates in exclosures, 20 grazed by wild animals at TKRC, 10 grazed by sheep at Tierberg and 10 grazed by sheep at Argentina. A total of 2800 seeds was planted in these 70 trials. Preliminary germination trials indicated that the at least 50% of the shrub seeds were viable. None of the seeds of the annual germinated in preliminary trials conducted in March. Observations of germination and survival of seedlings emerging from the planted seeds were made once monthly. It was assumed that seedlings emerging in demarcated rows originated from sown seed, because seeds of the plant species selected for this experiment normally occur at low densities (<1 m^{-2}) in the upper 50 mm of the soil in the study area (Dean & Yeaton in press).

A further trial, using only *O. sinuatum* seeds, was initiated in April 1991. Approximately 100 seeds (1 g) were planted in and adjacent to each of the 13 split plots that had been cleared of vegetation in 1989.

The first sowing produced so few recruits that statistical analysis was unwarranted. Wilcoxon paired rank tests were used to compare the heights of seedlings in the second trial.

Clearing experiments

Ten interspersed pairs of plots (5 X 3 m) exposed to or protected from wild animals were cleared of all plants at TKRC in July 1989 (**Plate 6a & b**). This was achieved by demarcating 5 X 6 m plots so that half of each plot fell on the inside and half on the outside of each of ten 13 m diameter exclosures laid out at 100 m intervals across the northern part of

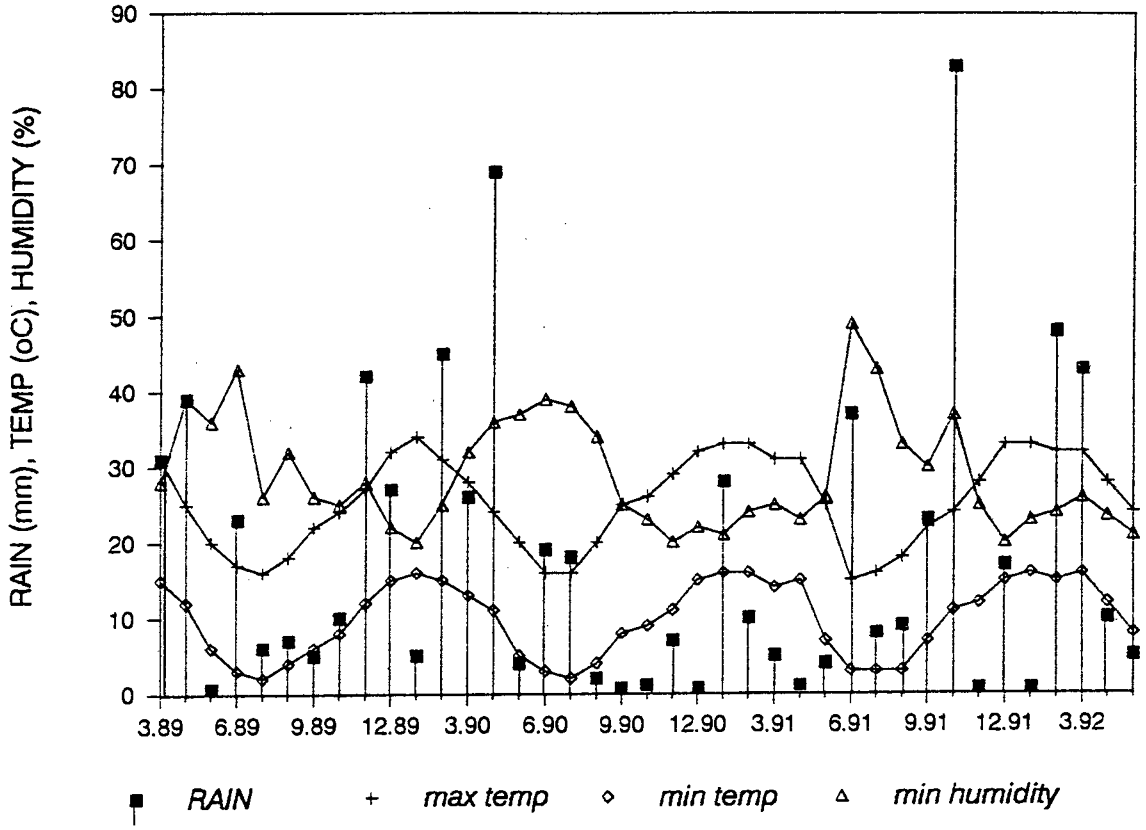

Figure 1. Total monthly rainfall (mm) and monthly means of mean daily minimum and maximum temperature and minimum humidity.

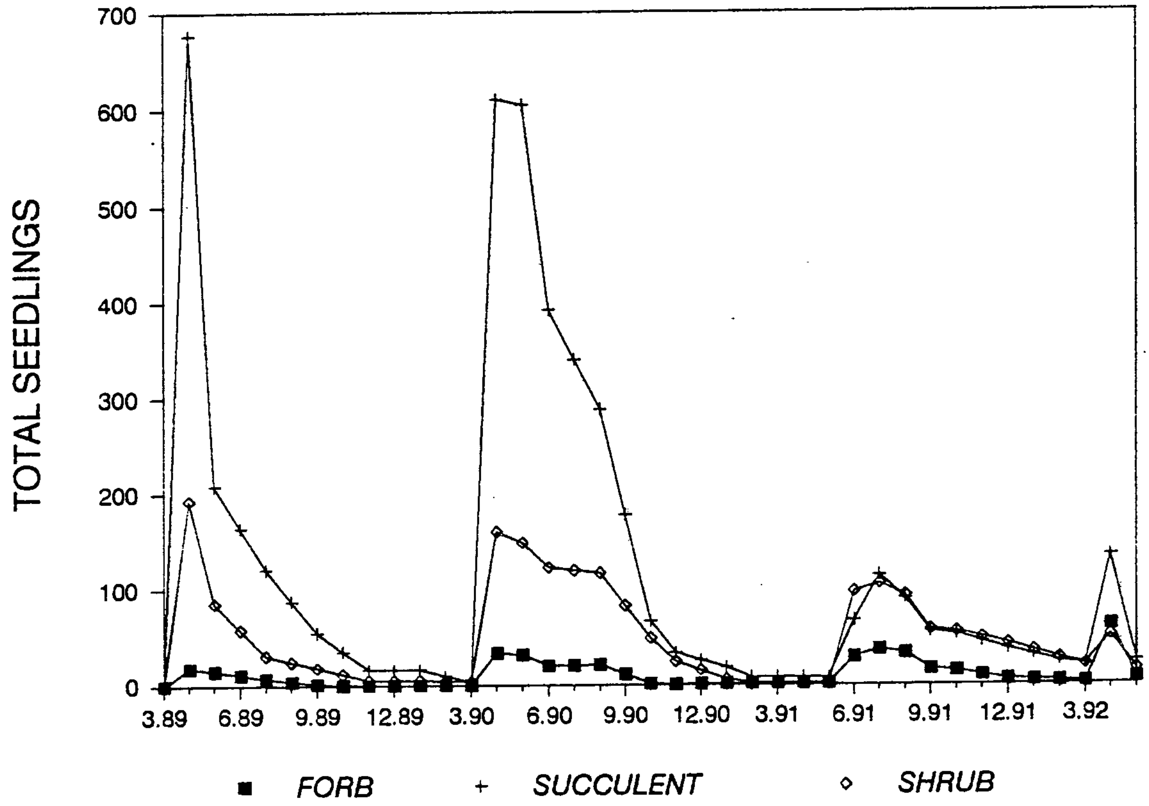

Figure 2. Total numbers of forb, succulent and shrub seedlings recorded in 130 plots (150 mm diameter) between March 1989 and May 1992.

Table 2. Densities of seedlings, parent plants and seeds for six types of plants at TKRC (Site 1), Tierberg ranch (Site 2) and Argentina ranch (Site 3). Densities are expressed as mean (± SD) numbers m^{-2}. Seed production estimates are taken from Milton & Dean (1990).

Site	Plant type	Seedlings	Parents	Seeds
1	Mesembyanthema	149 (219)	1.74 (0.58)	532
2	Mesembyanthema	77 (72)	1.60 (0.40)	566
3	Mesembyanthema	350 (215)	1.62 (0.32)	963
1	*Galenia fruticosa*	43 (51)	0.60 (0.12)	2208
2	*Galenia fruticosa*	26 (25)	0.45 (0.08)	273
3	*Galenia fruticosa*	22 (36)	0.15 (0.04)	146
1	*Pteronia pallens*	12 (26)	0.30 (0.07)	60
2	*Pteronia pallens*	3 (8)	0.30 (0.07)	84
3	*Pteronia pallens*	70 (162)	0.68 (0.36)	143
1	*Osteospermum sinuatum*	1 (4)	0.65 (0.04)	66
2	*Osteospermum sinuatum*	0 (0)	0.66 (0.04)	112
3	*Osteospermum sinuatum*	0 (0)	0.25 (0.05)	3
1	*Augea capensis*	1 (3)	0.01 (0.01)	38
2	*Augea capensis*	0 (0)	0.01 (0.01)	66
3	*Augea capensis*	6 (13)	0.10 (0.04)	192
1	*Tetragonia spicata*	1 (5)	0.10 (0.20)	1
2	*Tetragonia spicata*	4 (8)	0.10 (0.12)	1
3	*Tetragonia spicata*	0 (0)	0.01 (0.90)	0

Table 3. Life-form distribution among emerging seedlings TKRC (protected from sheep for 4 years), Tierberg ranch (history of moderately grazing), Argentina (history of heavy grazing) and on termitaria at TKRC (soil disturbed and nutrient enriched). Body of table shows total seedling numbers (and percentages of total for all life-forms).

Site	Forbs	Succulents	Shrubs
TKRC plains	31 (3%)	653 (71%)	237 (26%)
Tierberg plains	8 (4%)	127 (71%)	45 (25%)
Argentina plains	54 (7%)	559 (74%)	18 (19%)
TKRC termitaria	63 (21%)	242 (78%)	34 (11%)

survival at Argentina than at the other two sites in 1989 (Chi-square = 8.39, df = 2, $P < 0.05$), lower at TKRC in 1990 ($X^2 = 11.25$, df = 2 , $P < 0.01$) and there was no significant difference between sites in 1991. Insects, grazing and litter did not significantly influence seedling survival.

Effects of clearing on soil-moisture fluctuations

Vegetation clearing increased the amplitude of soil-moisture oscillations at 50 mm below the soil surface (**Figure 3a**) but reduced the rate of soil-moisture depletion at 150 mm below the surface (**Figure 3b**).

Sowing experiments

Timing of emergence of planted seeds was similar in all treatments. In autumn 1990, 5-14% *O. sinuatum*, 2-7% *Pteronia* and 2-10% *T. echinata* seeds germinated. In autumn 1991, a further 10-35% of the seeds of the annual *T. echinata* germinated but no further emergence of the perennial species was observed (**Figure 4a-c**). Emergence of seedlings in June 1990 was greater on cleared plots (3.9 ± SD 8.6%) than on undisturbed plots (7.0 ± SD 9.5%), but did not differ between sites or grazing treatments. Most of the seedlings died during their first summer. Recruitment of perennials occurred only in cleared plots where a total of 9 *O. sinuatum*, one *P. empetrifolia* and two *P. pallens* seedlings survived for 22 months, and one *O. sinuatum* seedling flowered.

Grazing and clearing treatments influenced the size (H = 20.7, P <0.001) more than the number (H = 7.3, P = 0.06) of *O. sinuatum* seedlings in the second sowing experiment. Plants in cleared plots protected from grazing were larger than in other sites (**Figure 5a**). Similarly, the mean number of seeds produced by *T. echinata* plants in October 1991 (**Figure 5b**) was greatest in cleared, non-grazed treatments (H = 13.06, P <0.01).

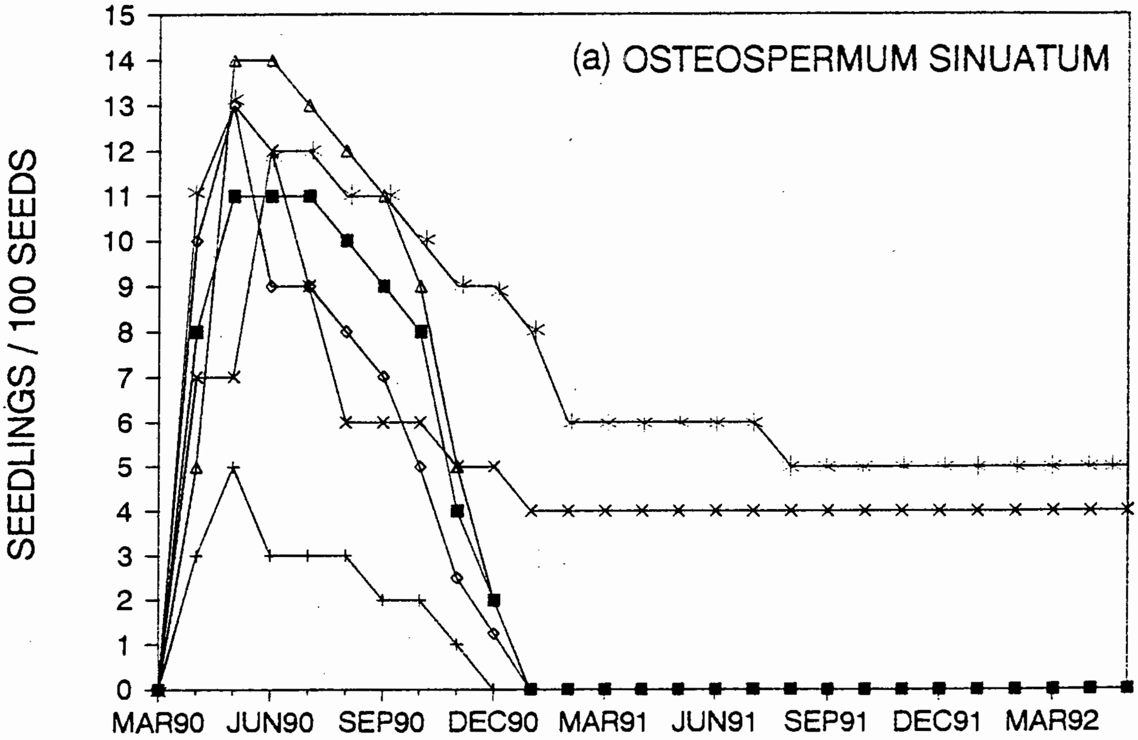

Figure 4a. Germination and survival of sown seeds in undisturbed vegetation protected from grazing mammals (square), grazed by wild mammals (+), grazed by sheep at Tierberg ranch (diamond) and by sheep at Argentina ranch (triangle), and in cleared plots protected from and exposed to wild mammals (x and *). *Osteospermum sinuatum*, a deciduous, broad-leaved shrub, with large, winged seeds.

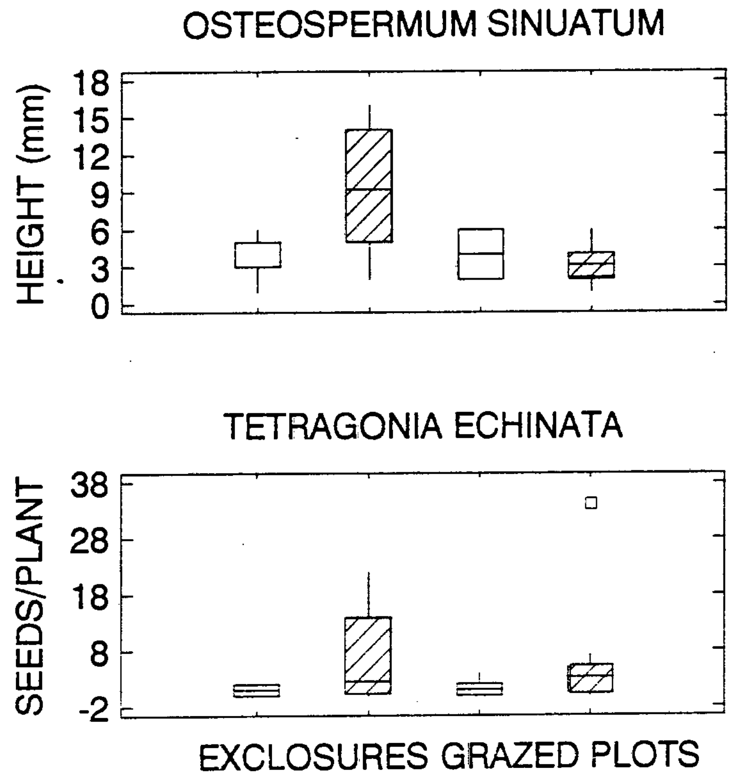

Figure 5. Box and whisker diagrams showing median, quartiles and ranges in (A) heights of one year old shrub (*Osteospermum sinuatum*) seedlings, and (B) numbers of seeds produced by an annual (*Tetragonia echinata*) in undisturbed (plain) and cleared (hatched) plots in exclosures protected from grazing or exposed to grazing by sheep and wild mammals.

Natural regeneration on cleared plots

The species composition of the seedlings that emerged and survived in cleared vegetation (**Appendix** 1) was influenced by the composition of the original vegetation at both TKRC and Argentina (**Table 4**). However large-seeded species comprised only 9 and 11% of seedling populations compared with 29 and 35% of the cover in pre-clearing vegetation (2 x 2 contingency tables, Argentina: $X^2 = 20.7$, $P < 0.001$; TKRC: $X^2 = 78.5$, $P < 0.001$). Litter on the soil surface did not affect total seedling density (bare ground: 5 $^+$ SD 4 annuals and 19 ± 8 perennials m^{-2}, littered ground: 5 ± 3 annuals and 17 ± 7 perennials m^{-2}), but species with large, winged or bristly propagules comprised 7% (196/2865) of all seedlings on littered ground compared with 4% (186/5058) on bare ground ($X^2 = 34$, $P < 0.001$). Seedlings of species normally confined to *heuweltjies* tended to increase in abundance as the distance between cleared plots and *heuweltjies* decreased (*Augea capensis* $r_s = -0.27$, *Malephora lutea* $r_s = -0.37$, *Psilocaulon utile* $r_s = -0.57$).

Table 4. Spearman rank correlations between the species composition of perennial seedlings that emerged and survived in cleared vegetation and the cover and above-ground biomass composition of the original vegetation. At Argentina ranch, a total of 20 species occurred in 6 plots and at TKRC, 25 species occurred in 20 plots. All correlation coefficients were significant (P <0.001).

Site	Year	n	Cover (m)	Fresh mass (kg)
Argentina	1991	120	0.714	0.719
Argentina	1992	120	0.649	0.633
TKRC	1991	520	0.552	0.578
TKRC	1992	520	0.563	0.597

Table 5. Numbers of seedlings of annuals and palatable (Per1) and unpalatable (Per2) perennial plant species on 15 m^2 split plots protected from mammalian herbivores or exposed to sheep (S) or wildlife (W) grazing.

Plot	1991						1992			
	Protected			Grazed			Protected		Grazed	
	Ann	Per1	Per2	Ann	Per1	Per2	Per1	Per2	Per1	Per2
S 1	45	49	202	33	69	155	61	165	71	152
S 2	130	58	135	46	46	90	54	57	52	64
S 3	97	78	68	85	107	119	83	63	98	86
W 1	49	169	6	20	303	80	348	13	463	79
W 2	233	173	19	85	135	23	260	24	262	32
W 3	67	131	3	35	95	2	260	3	260	4
W 4	100	166	62	107	158	64	226	71	209	77
W 5	120	167	52	62	519	81	269	51	653	113
W 6	67	164	45	29	317	13	338	56	467	20
W 7	11	251	18	79	422	24	400	25	532	25
W 8	90	265	72	123	194	87	320	87	269	97
W 9	44	276	10	36	229	9	389	18	410	16
W10	109	275	35	62	290	35	316	45	384	32

There was no significant difference in the number of annuals in the grazed and protected halves of split plots (Argentina 3 pairs: T = 1.15, P >0.1, TKRC 10 pairs: T = 0.95, P >0.1), nor in the numbers of palatable and unpalatable perennial seedlings either in 1991 or 1992 (Argentina 3 pairs: T <1, P >0.1; TKRC 10 pairs: T <2 P >0.1) (**Table 5**). On the other hand, the size-class distribution of seedlings of palatable plant species was significantly affected by grazing (**Table 6**), and large seedlings of palatable species were more abundant in protected than grazed plots.

Table 7. Mean numbers (m^{-2}) of annual plants and perennial seedlings in undisturbed vegetation (Zone 0) and in cleared vegetation at 1, 2 and 3 metres (Zones 1-3 respectively) from undisturbed vegetation. Significance refers to results of Kruskal-Wallis analysis of variance tests[1].

Site	Year	Zone 0	Zone 1	Zone 2	Zone 3	Signif.
Argentina samples		12	54	30	6	
Annual	91	$2^a \pm 2$	$4^a \pm 5$	$4^a \pm 4$	$10^a \pm 8$	0.14
Perennial	91	$10^a \pm 10$	$13^a \pm 8$	$12^a \pm 9$	$15^a \pm 5$	0.24
Perennial	92	$4^a \pm 4$	$11^b \pm 8$	$11^b \pm 8$	$17^b \pm 10$	<0.01
TKRC samples		40	180	100	20	
Annual	91	$1^a \pm 1$	$4^b \pm 5$	$5^b \pm 7$	$10^c \pm 12$	<0.001
Perennial	91	$2^a \pm 3$	$14^b \pm 12$	$23^c \pm 16$	$27^c \pm 17$	<0.001
Perennial	92	$2^a \pm 5$	$24^b \pm 14$	$28^b \pm 16$	$31^b \pm 15$	<0.001

[1] Means of zones with similar superscripts do not differ at P <0.05 when compared within rows

Table 8. Spearman rank correlations between the total number of perennial seedlings that emerged and survived in 1 m^2 cleared subplots and the number of annual plants and coppice shoots in these subplots in 1991 at TKRC and Argentina ranch. The significance of the correlation coefficients is indicated with asterisks.

Site	Year	Type	n	Annuals	Coppices
Argentina	1991	Annual	102	-----	0.098 NS
Argentina	1991	Perenn	102	0.321 **	-0.048 NS
Argentina	1992	Perenn	102	0.354 ***	-0.127 NS
TKRC	1991	Annual	340	-----	-0.237 ***
TKRC	1992	Perennial	340	0.221 ***	-0.409 ***
TKRC	1992	Perennial	340	0.169 ***	-0.403 **

*** P <0.001, ** P <0.01, * P <0.05, NS = P >0.05

Discussion

Germination seasonality

Emergence of annual and perennial seedlings occurred in autumn or early winter in each of the four years of study. Southern Karoo shrubs did not appear to have the flexibility of *Acacia victoriae* and *Cassia* spp. in arid southeastern Australia (Grice & Westoby 1987; Eldridge & Westoby 1991), which germinated at any season in response to rain. In the southern Karoo, where summer humidity is low and soil surface temperatures reach 64^0C, selection has evidently favoured species with germination inhibited by high temperatures. This conclusion is supported by Henrici (1939) who tested 16 Karoo shrub species and found that their germination was more rapid at 20^0C than at 30^0C.

annuals has been shown to increase mortality of seedlings of perennial plants under arid conditions (van Epps & McKell 1983) but in the present study annuals had no detectable effect on survival of perennial perennials.

In arid regions, water has often been identified as the limiting resource (Ehleringer 1984; MacMahon 1987; Harrington 1991). Von Maltitz (1990) found that soil-moisture content increased from undisturbed savanna vegetation into cleared plots, but beyond 1.0 m from the plot edge, remained stable with increasing distance from vegetation. Karoo shrubs similarly influence soil-moisture, so that as in Savanna (Von Maltitz 1990), only disturbances with a minimum radius of 2 m would contain areas unaffected by roots of surrounding plants.

Although rare in established vegetation, seedling recruitment in established vegetation can occur in small disturbances made by animals (Gross 1987). Local examples include alteration of soil properties by ants and termites (Dean & Yeaton in press) and the uprooting of plants by mammals foraging for subterranean insects (aardvark *Orycteropus afer* and bat-eared fox *Otocyon megalotis*) or roots (porcupines *Hystrix austroafricana*) (Dean & Milton 1991). Disease or drought induced mortality of established plants offer additional opportunities for seedling recruitment.

Many studies (reviewed by Sih *et al.* 1985) reported that in terrestrial ecosystems predation determined population size. In the present study, grazing did not affect seedling survival, but selectively reduced the growth of forage species. It has been hypothesized that herbivory might either reduce interspecific competition or weight its outcome (Sih *et al.* 1985). The reduced density and size of woody forage species at Argentina may account for the survival of higher densities of seedlings at this site than on more moderately grazed rangeland. Herbivory might also favor unpalatable species under these circumstances by decreasing the ability of grazed plants to reproduce (Milton & Dean 1990) and to obtain resources (Louda *et al.* 1990), including competition-free establishment sites.

In moist environments, small seedlings are more susceptible to mollusc predation than seedlings of large-seeded plants (Fenner 1985). In the Karoo, there was evidence (bite marks, tracks, dung) that rodents and birds fed on cotyledons of newly emerged *O. sinuatum* (7-10 mm at emergence), whereas seedlings of small-seeded species (1-3 mm at emergence) were frequently found dead after dry periods and showed no evidence of predation.

Implications for reseeding of rangeland

Seed availability and competition from established plants may be more important than the current grazing regime determining the future composition of degraded rangeland. Removal of livestock may increase seeding by forage plants (Milton & Dean 1990) but is unlikely to lead to rapid (within decades) improvement of rangeland in places where forage plants have become rare and unpalatable perennials common (Westoby 1980; O'Connor 1991). My small-scale trials indicated that seed addition could potentially increase forage plant abundance but is unlikely to succeed without some reduction of established plants and temporary protection from grazing.

Large-scale trials are needed to evaluate the economic feasibility of increasing the abundance of forage plants in Karoo rangeland. When planning such trials, artificial means of reducing plant density should be approached with caution because runoff and sediment loss are inversely correlated with vegetation cover (Snyman & Fouche 1991). The possibility of carrying out reseeding programmes after natural disturbances, such as severe droughts (Danckwerts & Stuart-Hill 1988), have thinned perennial plant populations, merits field investigation.

Acknowledgements

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Appendix 1. Densities of seedlings in cleared plots in exclosures or grazed by sheep at Argentina ranch and by wild animals at Tierberg Karoo Research Centre (TKRC). Plant longevities are A: annual, B: biennial and P: perennial. Seed dispersal types are **w**: seeds with wings or pappus, **h**: seeds released from hygroscopic capsules by rain and **e**: seeds in soft or indehiscent fruits dispersed by animals. Uncoded species have no obvious means of dispersal. Families and species are alphabetically arranged. Nomenclature follows Gibbs Russell et al. (1987). Maximum diameters of propagules (seed and appendages) are 1: <1 mm, 2: 1-3 mm, 3: 3-5 mm, 4 >5 mm.

Species	Longevity, seed size & dispersal	Argentina		TKRC	
		Excl	Grazed	Excl	Grazed
Aizoaceae					
Aridaria noctiflora	P h 1	0.0	0.0	0.2	0.1
Brownanthus ciliatus	P h 1	61.7	54.7	12.3	18.5
Drosanthemum hispidum	P h 1	4.3	13.7	0.3	1.4
Drosanthemum montaguense	P h 1	5.7	5.3	6.9	13.5
Galenia fruticosa	P 1	33.7	41.7	181.0	239.1
Galenia papulosa	A e 1	0.7	1.0	0.0	0.0
Hereroa latipetala	P h 1	0.0	0.3	1.4	1.8
Malephora lutea	P h 1	23.3	40.7	3.3	4.3
Mesembryanthemum crystallinum	A h 1	0.3	2.0	0.7	0.5
Psilocaulon utile	P h 1	0.0	0.0	0.4	5.9
Rhinephyllum macradenium	P h 1	43.3	16.0	1.7	0.2
Ruschia approximata	P h 1	0.0	0.0	6.6	5.7
Ruschia spinosa	P h 1	1.7	0.0	7.8	7.0
Sphalmanthus brevifolius	P h 2	2.3	4.3	0.4	0.0
Tetragonia echinata	A e 2	11.3	10.3	4.2	5.4
Tetragonia spicata	P w 4	0.7	0.3	5.0	2.1
Trianthema triquetra	A e 1	0.0	0.7	0.0	0.0
Asteraceae					
Berkheya spinosa	P w 2	0.3	0.0	0.0	0.1
Chrysocoma ciliata	P w 2	1.0	0.0	0.7	1.0
Gazania lichtensteinii	A w 2	0.0	0.7	0.0	0.5
Ifloga polycnemoides	A w 1	0.0	0.0	0.0	0.2
Lasiopogon glomerulatum	A w 1	7.3	2.7	10.9	14.8
Lasiospermum brachyglossum	A w 1	0.3	0.0	0.0	0.0
Leyssera tenella	A w 2	24.0	22.0	63.6	33.4
Osteospermum sinuatum	P w 4	0.3	0.3	1.8	1.1
Pentzia suffruticosa	A 2	0.0	0.0	0.4	0.0
Pteronia empetrifolia	P w 3	0.0	0.0	0.3	1.4
Pteronia pallens	P w 3	2.7	4.0	2.4	3.2
Senecio angustifolius	A w 3	1.3	0.0	0.2	0.4
Ursinia nana	A w 3	22.3	4.3	4.8	3.1
Brassicaceae					
Lepidium spp	A e 2	18.7	5.7	0.0	0.0
Chenopodiaceae					
Atriplex lindleyi	B w 4	9.7	10.7	0.3	0.3
Atriplex semibaccata	P e 3	1.7	0.3	0.0	0.0
Salsola tuberculata	P w 3	0.0	0.0	0.1	0.0
Fabaceae					
Lessertia annularis	B w 3	0.7	0.3	0.0	0.0
Lotononis pungens	B e 2	3.0	1.0	3.8	3.0

Appendix 1 ctd...

3 EFFECTS OF HERBIVORY AND OTHER FACTORS ON PLANT REPRODUCTION, GROWTH AND DEMOGRAPHY

3.3 Growth, flowering and recruitment of shrubs in grazed and in protected rangeland in the arid Karoo, South Africa

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In press 1993: *Vegetatio*

Abstract: *A three-year study involving 1300 marked shrubs of three species differing in palatability to sheep provided evidence that changes in the demographic structure of shrub populations in arid rangelands are a function of seed availability. Sheep reduced canopy size and flowering of their preferred forage species but had no effect on survivorship of seedlings or established plants during the study. Although annual turnover in all populations was low (< 6%), abundant recent recruitment of non-forage species was observed on degraded rangeland. Natality of all three species was positively correlated with flower abundance. Mortality was correlated with natality because seedlings had a low probability of surviving their first year. Recruitment of both forage and non-forage species appeared to be inhibited by competition and seedlings seldom survived near adult plants of the same growth form.*

Nomenclature: follows Gibbs Russell, G.E., Welman, W.G., Retief, E., Immelman, K.L., Germishuizen, G., Pienaar, B.J., van Wyk, M. & Nicholas, A. 1987. List of species of southern African plants. Mem. Bot. Surv. S. Afr. 56: 1-270.

Introduction

Selective and excessive herbivory by domestic livestock is believed to have brought about changes in the botanical composition of southern African rangelands (Acocks 1955, Downing 1978, Roux & Vorster 1983). These changes, although poorly documented, are thought to have taken place between 1850 and 1950, the period of rapid agricultural expansion by European settlers (Downing 1978). Similar changes are reported to have followed European colonization and the development of market-orientated stock farming in Australia (Friedel, Foran & Stafford Smith 1990) and South America (Schofield & Bucher 1986).

The mechanisms of grazing-induced vegetation change in shrublands do not always follow the classical model of change from perennial to annual vegetation (Westoby, Walker & Noy-Meir 1989). In Karoo shrublands sheep graze selectively, reducing seed production of some shrub species while leaving others intact (Milton & Dean 1990). If recruitment is proportional to seed availability (Louda 1982), factors that reduce the reproductive success of forage plants should lead to a decrease in their populations (O'Connor 1991). Shrub species unacceptable to sheep should become more abundant in selectively grazed rangelands if their lifetime seed production exceeded that of forage species (Liljelund, Årgren & Fagerström 1988).

My study of recruitment, growth and survival of three shrub species differing in palatability to sheep provides evidence in support of the hypothesis that recruitment of the pseudoreplicated sampling design (see Hurlbert 1984), inferential statistics have been used to test for significant treatment effects. Non parametric tests were used for all statistical comparisons, because the data were not normally distributed (Zar 1984). Kruskal Wallis ANOVAs were used to test for significant treatment effects on flower production and increments in basal stem diameter, height and canopy area. Association of study species with other plants as well as natality and mortality rates and medians of stem to canopy ratios were compared using contingency tables. Spearman rank correlations were used test for a relationship between basal diameter and increment.

Results

Size class distributions

The distribution of stem basal diameters of *O. sinuatum* fitted an exponential curve at TKRC and Tierberg ranch and a large proportion of the population fell within the smaller size classes, but at Argentina the population distribution was not significantly different from a normal curve ($X^2 = 4$, df = 5, $P > 0.5$). *Pteronia empetrifolia* and *P. pallens* populations were normally distributed at TKRC and Tierberg ranch. At Argentina ranch, *P. empetrifolia* was too rare to sample and *P. pallens* populations had non-normal distribution skewed to the smaller size classes (Figure 1).

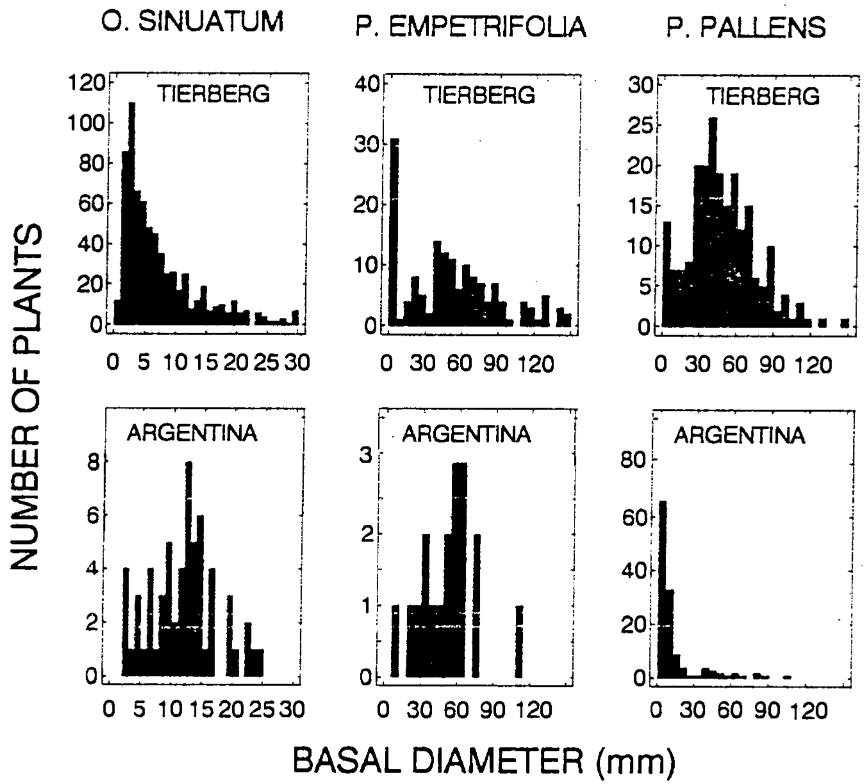

Figure 1. Size class distributions of *Osteospermum sinuatum*, *Pteronia empetrifolia* and *P. pallens* at Argentina and Tierberg ranches.

were associated significantly more often with mat-forming succulents than was predicted from the relative abundance of these growth forms in the vegetation (**Table 2**). However, *P. empetrifolia* did not show this tendency. All three of the study species occurred less frequently with conspecifics than predicted from their relative abundance in the vegetation (P <0.01).

Table 2. The proportion of mat-forming succulents present in the vegetation and associated with three species of shrubs. Real values were used in Chi-square tests for differences in relative abundance. Significant differences are indicated as follows: NS = not significant, ** P <0.1, *** P <0.001.

Site	Proportion of mat-forming plant species			
	Vegetation	O.sinuatum	P.empetrif.	P.pallens
TKRC north	0.36	0.57***	0.36 NS	0.61***
Tierberg	0.39	0.53**	0.32 NS	0.75**
TKRC west	0.29	0.62***	----	0.70***
Argentina	0.45	0.84***	----	0.72***

Table 3. Turnover and change in populations of marked shrubs between November 1988 and December 1991 under various grazing treatments. Annual turnover calculated as: 1/6 x (gain + loss)/initial 1988 population.

Site	Treatment	1988	Gain	Loss	Annual turnover	Nett 3yr change
Osteospermum sinuatum						
TKRC north	Control	154	25	29	6%	-2.5%
TKRC north	Wildlife	140	27	18	5%	+6.4%
TKRC west	Wildlife	317	13	12	1%	+0.3
Tierberg	Sheep	162	13	7	2%	+3.7
Argentina	Sheep	64	4	5	2%	-1.5
Pteronia empetrifolia						
TKRC north	Control	57	6	1	2%	+8.7
TKRC north	Wildlife	52	11	8	6%	+4.7
TKRC west	Wildlife	8	0	0	0%	0.0
Tierberg	Sheep	51	6	3	3%	+5.8
Argentina	Sheep	2	0	0	0%	0.0
Pteronia pallens						
TKRC north	Control	69	3	3	0%	0.0
TKRC north	Wildlife	75	2	2	0%	0.0
TKRC west	Wildlife	52	7	4	4%	+5.7
Tierberg	Sheep	75	3	3	1%	0.0
Argentina	Sheep	164	21	9	3%	+7.3

Table 4. Spearman rank correlations between basal stem diameters of plants measured in 1988 and increments in basal diameters and canopy areas over three years. Significance indicated as in Table 2.

Site	Treatment	Plants	Basal diam.		Canopy area	
Osteospermum sinuatum						
TKRC north	Control	136	-0.011	NS	+0.089	NS
TKRC north	Wildlife	130	-0.288	**	-0.272	**
TKRC west	Wildlife	300	+0.038	NS	+0.171	**
Tierberg	Sheep	147	-0.231	**	-0.515	***
Argentina	Sheep	60	-0.422	**	-0.321	*
Pteronia empetrifolia						
TKRC north	Control	59	-0.336	*	-0.686	***
TKRC north	Wildlife	49	+0.099	NS	-0.596	***
TKRC west	Wildlife	5	+0.500	NS	-0.900	*
Tierberg	Sheep	46	-0.271	NS	-0.558	***
Pteronia pallens						
TKRC north	Control	68	-0.494	***	-0.562	***
TKRC north	Wildlife	61	-0.530	***	-0.542	***
TKRC west	Wildlife	24	+0.015	NS	-0.701	***
Tierberg	Sheep	62	-0.581	***	-0.529	***
Argentina	Sheep	131	+0.163	NS	-0.031	NS

Table 5. Variation in mean basal diameter and canopy growth of shrubs >10 mm b.d. under various grazing treatments.

Treatment	n	Basal diameter (mm)		Canopy area (m x 10^4)	
		1988	% change	1988	% change
Osteospermum sinuatum					
Control	82	191 (104)	+ 9.6	865 (869)	+128.2
Wildlife	112	208 (141)	- 4.5	956 (772)	+ 11.8
Sheep (T)	56	212 (104)	- 6.3	731 (564)	- 24.8
Sheep (A)	43	149 (39)	- 1.0	163 (103)	- 22.6
Pteronia empetrifolia					
Control	47	769 (538)	- 11.3	1071 (687)	- 6.4
Wildlife	40	716 (326)	+ 10.2	1281 (719)	- 12.4
Sheep: (T)	41	650 (380)	+ 9.6	698 (532)	- 8.6
Pteronia pallens					
Control	79	478 (197)	- 5.4	1998 (1159)	- 7.2
Wildlife	73	530 (249)	- 29.2	2712 (1970)	+ 1.9
Sheep (T)	61	586 (278)	- 15.9	2114 (1221)	- 7.6
Sheep (A)	59	383 (272)	- 21.8	2207 (2526)	+ 25.5

producing abundant seed would have a greater chance of exploiting unusual climatic events or reaching these rare, competition-free establishment sites than progeny of plants which have had their reproductive potential reduced by herbivory.

Population structural comparisons (Figure 1) supported the hypothesis that the non-forage species *P. pallens* recruited more frequently on heavily grazed rangeland than selectively grazed forage species *O. sinuatum* and *P. empetrifolia*. On moderately grazed Tierberg, young *O. sinuatum* plants were abundant, whereas size class distributions of *O. sinuatum* populations at Argentina provided little evidence for recent recruitment. Seed production differences were apparently not the only factors determining this recruitment pattern. Size class distributions (Figure 1) indicate that neither of the *Pteronia* species have recruited well on Tierberg ranch in recent years despite their apparently adequate reproductive output. Evergreen, sclerophyllous shrub populations at this site had evidently reached saturation. Inter and intraspecific competition among *Pteronia* plants, (see Yeaton & Esler 1990), appeared to be limiting their further recruitment but having little effect on establishment of broad-leaved, drought-deciduous *O. sinuatum*. The abundant recruitment of *P. pallens* at Argentina ranch may be a function of both seed availability and of reduced competition from *P. empetrifolia* and other palatable evergreen shrubs at this overgrazed site.

Population structure in Karoo shrubs may influence the productivity of rangeland because young plants grow more rapidly than old plants (**Figure 3a-d**). Tierberg ranch and TKRC were characterized by a forage plant (*O. sinuatum*) population skewed towards young plants and by an old and unproductive population of the toxic shrub *P. pallens* (**Figures 3a and 3c**). The opposite trend was evident at Argentina ranch where the *O. sinuatum* population was small and old and the *P. pallens* population was large and productive (**Figures 3b and 3d**).

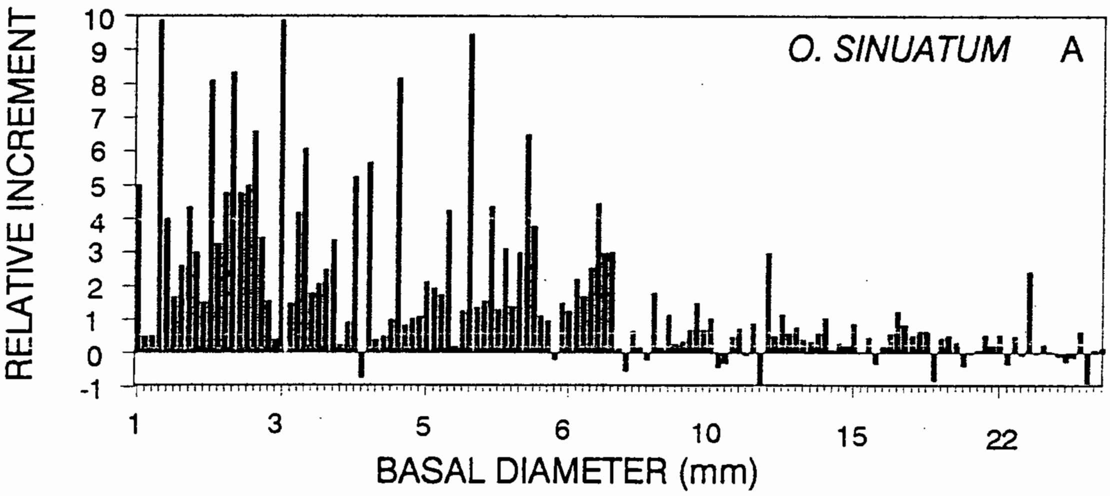

Figure 3. Relative canopy increments of populations of *Osteospermum sinuatum* at A Tierberg ranch. *(ctd over pg.)*

Conservative grazing systems such as that practised at Tierberg ranch for the 40 years prior to this study, are not popular in semi-arid regions of South Africa (Dūval & Scholtz 1992). Although this system has maintained a healthy population of the forage plant *O. sinuatum* at Tierberg, 65% of farmers interviewed by Dūval & Scholtz (1992) felt that moderate stocking combined with long periods of rest was costly and impractical. Improvement of degraded rangeland is seldom viewed as a means of increasing profitability and is not economically feasible in unproductive rangeland (Danckwerts & Marais 1989). In fact, it is unlikely that a change, such as the replacement of long-lived palatable shrubs by equally long-lived unpalatable shrubs in natural rangeland, could be reversed merely by withdrawing livestock (Westoby *et al.* 1989).

In contrast to various other studies of the effects of large mammals on recruitment of forage plants (Crisp 1978, Eldridge *et al.* 1990; O'Connor 1991; Owens & Norton 1992), the present study provides no evidence for increased mortality of seedlings or established plants in plots grazed and trampled by sheep. The preferred forage species *O. sinuatum* is tolerant of defoliation (Van der Heyden 1992) and heavily grazed plants (approximately one fifth their potential height) regained normal proportions when protected for a single growing season. Withdrawal of livestock from camps during flowering of resilient species such as this, may therefore result in more recruitment than would reduced stock density or grazing frequency. Not only does recruitment maintain the population, but it would appear (Figure 3) that vegetation comprising a high proportion of young, but sexually mature, forage plants may be more productive than rangeland dominated by old plants.

Conclusion

Changes in plant species composition of Karoo rangelands over the past century appear to be brought about by shifts in the demographic structure of populations of key plant species. Such shifts are most likely to occur when good rains follow drought-induced mortality of established plants. Grazing by sheep determines the relative abundance of a new generation of seedlings by selectively reducing the sizes and reproductive success of preferred forage plants while giving non-forage species a competitive and reproductive and advantage.

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PART 4

SYNTHESIS: HERBIVORY AND VEGETATION CHANGE

4. SYNTHESIS: HERBIVORY AND VEGETATION CHANGE

4.1 A model of herbivory and vegetation change in succulent Karoo shrublands

Author: Milton, S.J.

Abstract: *The research presented in this thesis has led to an improved understanding of the mechanisms of vegetation change in the Karoo in response to herbivory by domestic livestock. Based on this information, a conceptual model of vegetation dynamics in Karoo shrublands is proposed. The model shows how populations of long-lived shrubs, differing in their acceptability as forage, are perpetuated under various levels of herbivory and how selective herbivory affects interactions among plant species and between plant and animals.*

Introduction

In this concluding chapter, I evaluate the ability of existing models of vegetation dynamics to explain how herbivory by domestic livestock changes Karoo vegetation, and why the vegetation may not always return to its original composition when livestock are withdrawn. On the basis of information presented in this thesis, I provide a new conceptual model of the dynamics of Karoo vegetation and discuss its relevance for the conservation of biotic diversity and of agricultural productivity in the Karoo.

Herbivores and the evolution of Karoo plants

In the first section of the thesis, I considered the possible influence of herbivores on the evolution of plants across a climatic gradient in the Karoo. This was achieved by assuming that zoochory and spinescence evolved in response to herbivory, and then inferring the past distributions of large herbivores from the spatial distributions of these plant attributes. I found: (a) that mammal-adapted attributes of plant species from the southern Karoo were most abundant among species that occurred in relatively moist habitats (**Chapter 1.1**), (**b**) that epizoochoric propagules in wool of domestic sheep were more abundant towards the mesic summer-rainfall extreme, than in the arid, winter rainfall extreme of a rainfall gradient across the Karoo (**Chapter 1.2**), and, (**c**) spinescence of plant assemblages in southern Africa was correlated with carrying capacity for large mammalian herbivores, with topography and with soil nutrient status (**Chapter 1.3**).

Food selection by Karoo herbivores

In the second part of the thesis, I examined food selection by a range of common Karoo herbivores, including three species of arthropods, a reptile (*Geochelone pardalis*, Leopard tortoise), a bird (*Struthio camelus*, Ostrich), an indigenous mammal (*Antidorcas marsupialis*, Springbok) and the domestic sheep (*Ovis aries*). An understanding of the influence of food quality and quantity on food choice by herbivores was needed in order to understand how indigenous herbivores might differ from sheep in their selection of food, and how these herbivores might respond to vegetation change. Food selection studies involved either direct not represented in the vegetation every year, appear to rely on soil-stored seed for their continued existence. Dormancy was present in seeds of a winter-growing annual sown together with the shrub seeds (**Chapter 3.2**;).

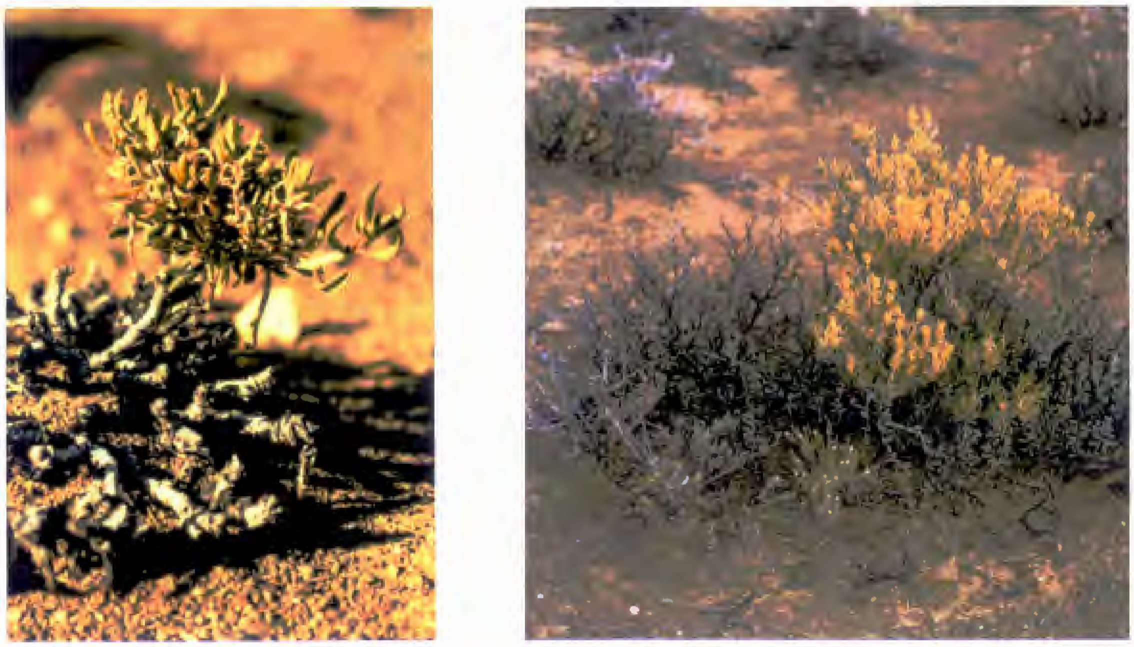
These findings support Grubb's (1988) prediction that, in semi-deserts, recruitment of long-lived shrub species should be dependent on weather conditions and loosely coupled with disturbance, whereas recruitment of short-lived species would be coupled with both disturbance and weather conditions. Thus ephemerals would rely on soil-stored seeds for producing a new generation when conditions were favorable (ie. following unusually large rain events or large-scale mortality of perennial plants). Populations of shrubs and other long-lived plants would be maintained by survival of drought-tolerant, mature plants. Replacement of senescent individuals or of the adult population following catastrophic mortality, would depend on fairly regular (annual) seed production and on "banks" of quasi-dormant seedlings (Noble 1986) for perpetuation. In arid regions, as in forests (Noble 1986), it appears that seedlings competing with established plants survive for many years, but fail to grow (ie. become quasi-dormant), until competition is reduced following the deaths of neighbouring plants.

Both weather and disturbance influenced the germination and recruitment of perennial plants in the southern Karoo. All species germinated in autumn, and little germination was recorded at other seasons (**Chapter 3.2**). Large germination events were related to seed availability, (a function of rain in the previous winter and spring), and seed germination, (a function of the quantity of autumn rain). Recruitment decreased with increased competition for water, and was therefore improved by circumstances that reduced the competitive ability of neighbouring plants (**Chapter 3.2**).

Small-scale recruitment (maintenance of populations) occurred continuously, whereas large scale recruitment events appeared to be sporadic. Continual recruitment occurred in small disturbances created by animals, such as aardvarks, foxes, termites, and harvester ants, that uproot plants, dig holes and redistribute nutrients and seeds (**Appendix 4**; Dean & Milton 1991a; Dean & Yeaton 1992a & b). Pits dug by mammals trap humus and water which, in an arid environment, may improve the survival probability of seedlings that germinate in them (Gutterman 1987; Dean & Milton 1991a; Dean & Yeaton 1992a & b) Large-scale, sporadic recruitment follows disturbances that kill or reduce the sizes of many established plants (**Chapter 3.2**). Examples of large disturbances common in Karoo shrublands are long droughts (Danckwerts & Stuart-Hill 1988), severe hail storms (Milton & Collins 1989) and intensive trampling and grazing (discussed in **Chapters 2.1 & 2.6**; Bosch & Gauch 1991). Small and large-scale disturbances, together with topographic and edaphic factors (**Chapter 1.1**), result in considerable spatial heterogeneity in the composition, structure and demography of Karoo shrublands.

Pattern in Karoo vegetation is also influenced by the size, shape and dispersal ability of the seeds of component species. Seeds of succulents (Mesembryanthemaceae) are released from hygroscopic capsules during rain showers (Ihlenfeldt 1975; pers. obs.). These seeds are small enough to be trapped by fine soil particles (viz. Chambers *et al* 1991) so that their seedlings occur most abundantly in inter-shrub gaps (**Chapter 3.2**). Winged or bristled seeds (Liliaceae, Asteraceae, Aizoaceae) are tumbled over the soil surface by wind until trapped by multi-stemmed succulents or shrubs (**Plate 7a**; **Chapter 3.2**; Hoffman & Cowling 1987) or in pits dug by foraging mammals (Dean & Milton 1991a;). The large-seeded

PLATE 7



a) Seedling of *Tetragonia spicata* L.f. (Aizoaceae), a species with large, winged fruits, emerging from beneath the remains of a dead succulent.

b) Shrub-clump comprising a mixture of species and life-forms.

c) Continuous grazing by ostriches, (400 birds in 300 ha for 9 months in 1992), reduced perennial vegetation and increased annual succulents on a farm to the southeast of Prince Albert.

d) Simplified plant assemblages, dominated by toxic (*Euphorbia mauritanica*, *Pteronia pallens*) and spinescent (*Lycium* spp) on overgrazed land near Prince Albert in 1992.

Herbivory and vegetation change in the Karoo

Models of vegetation change

Changes in vegetation composition are caused by factors that alter the birth and death rates of component plant species (Harper 1977; Huntly 1991).

Conceptual models of vegetation change in arid regions will be reviewed briefly in this section, and their value, as a framework for understanding the dynamics of southern Karoo shrublands, will be considered. The models can be grouped in three categories as follows:

1) oscillations (Roux 1966; Novellie & Strydom 1987; Hoffman *et al.* 1990), pulses (Westoby 1980; Hoffman 1989) or cycles (McAuliffe 1988; Yeaton & Esler 1990) driven by climatic or biotic factors;

2) directional change (succession) which may either be reversible or irreversible (Weaver & Clements 1929; Roux & Vorster 1983; Bosch & Gauch 1991) and is driven by grazing management effects on vegetation and soil; and

3) stochastic transitions among a range of states (reviewed by Westoby *et al.* 1989; George *et al.* 1992), driven by interactions between grazing management and environmental events such as fire, drought or above average rainfall.

Oscillations, cycles and pulses

As demonstrated by contrasts in vegetation across farm boundaries (Roux 1972; Hoffman & Cowling 1990; **Appendix 1 Plates 1b & 7c**), effects of grazing management sometimes override changes caused by climatic oscillations. For example, above-average summer rainfall tends to increase the ratio of grass to shrub cover in the eastern Karoo (Roux 1966; Novellie & Strydom 1987; Hoffman *et al.* 1990). However, where there is heavy grazing during the growing and flowering season of grasses, shrubs can continue to dominate the vegetation even when climatic conditions favour grass (Roux 1972).

Cyclic succession of the type discussed by (McAuliffe 1988; Yeaton & Esler 1990; Montaña 1992) may be modified by herbivory which changes either the relative abundance of the component species or the availability of germination sites (see **Figure 1**). Pulsed germination or recruitment events have been recorded in a number of arid regions (Noy-Meir 1973; Grice & Westoby 1987; Eldridge & Westoby 1991), but the plant species that germinate in greatest numbers during such events will depend on the availability of seed which, as demonstrated in **Chapter 3.2**, may be influenced by herbivory.

Succession and directional change

Successional models assume that grazing and drought change vegetation to an earlier seral stage (Bosch & Booysen 1992). South African rangeland scientists suggest that climax species are more palatable to domestic livestock than plants lower down the successional sequence (Tainton 1981; Bosch & Gauch 1991). Elsewhere, it is thought that late successional plant species are usually well defended against herbivory (Janzen 1986; Bryant 1987). It would appear that palatability of plants to domestic livestock is not necessarily correlated with their successional position. For this reason, successional models which assume such a relationship, are flawed.

The corollary of this type of model is that succession will return the vegetation to a state dominated by "palatable, climax" species when livestock are withdrawn. There is, as yet, no evidence for succession to "better" vegetation after livestock removal in the Karoo. In Namaqualand, 15 yr of protection from grazing resulted in a slight increase in total plant cover, and most of the additional cover comprised unpalatable plant species (Le Roux, unpublished data cited in Novellie 1988). The apparent inadequacy of the successional model

States and transitions represented in Figure 2

Catalogue of states
1. *Mixed species of palatable and unpalatable shrubs of similar in age. Recruitment of seedlings in small scale disturbances. Large-seeded plants have an advantage.*
2. *Mixture of palatable and unpalatable shrubs of all ages. Recruitment frequent and proportional to adult abundance. Opportunities for small- and large-seeded spp to establish.*
3. *Unpalatable shrubs of all ages. Palatable shrubs old heavily browsed: do not set seed. Opportunities for small- and large-seeded spp to establish.*
4 *Unpalatable shrubs mostly old but with some recruitment in small disturbances. Palatable species are rare or lost from system.*
5. *Seedling recruitment beneath and amongst shrubs killed by drought. Seedling composition proportional to pre-drought species abundance. Small-seeded spp have an initial advantage.*
6 *Seedling recruitment beneath and amongst shrubs killed by drought. Seedling composition proportional to pre-drought spp abundance. Small-seeded species have initial advantage. Palatable species are rare or absent.*
7. *Perennials lost through trampling and erosion. Ephemerals present after rain.*

Catalogue of transitions
T 1 Rotational grazing, rests at seed set
T 2 Withdrawal of all domestic livestock
T 3 Continuous grazing at or above recommended rates
T 4 Selective clearing, and sowing of palatable spp
T 5 Severe drought followed by rain and germination
T 6 Sow seeds of palatable species
T 7 Intensive or prolonged grazing and trampling
T 8 Stock withdrawal and environmental amelioration (tilling, mulching) and sowing

change from State 4 to State 2 is unlikely to succeed without some reduction of established plants and temporary protection from grazing. Clearing may be unnecessary where either grazing or drought has reduced above-ground perennial biomass below the normal range (Rutherford & Westfall 1986; **Appendix 2**) for the region (in State 6 of the model. Reduction of living biomass can improve seedling recruitment (**Chapter 3.2**) because it decreases the competition for water.

If it is assumed that a loss of perennial plant cover results in a loss of symbiotic organisms and a change in microclimate (MacMahon 1987) a transition involving the replacement of an ephemeral plant assemblage (State 7) by perennials (States 5 & 6) is likely to require a greater energy input than other transition. Actions required to facilitate such a transition may include erosion control, mulching and reseeding (T8).

Feasibility of Karoo rangeland rehabilitation

A decrease in the amount of forage produced per unit rainfall clearly has serious economic implications for southern Africa (Moore 1989; Dean & Macdonald in press). Unless degraded rangelands can be rehabilitated in a cost-effective way, continued ranching in parts of southern Africa which are dominated by unpalatable, woody plants or have severely reduced secondary productivity, is a drain on the country's resources. Ranching of such areas can be sustained only by subsidies (Danckwerts & Marais 1989).

The reversibility of changes in rangeland composition and productivity may be depend on the magnitude of the changes, and on the biological role of the components (ie. secondary producers, primary producers or physical processes) affected by the changes. Milton, Dean, du Plessis & Siegfried (submitted), in a review of rangeland degradation in the Karoo, concluded that grazing induced changes in this rangeland ecosystem process occurred in three steps. They suggested moreover, that for each step descended, degradation became more difficult and costly to reverse. The steps involved:

i) changes in the reproductive output and population structure of secondary producers, which can be reversed by managing secondary producers (domestic livestock);

ii) the loss of palatable plant species and their replacement by unpalatable species, which could be reversed by management of primary producers (eg. bush clearing and re-seeding);

iii) reduction of perennial plant cover and primary productivity, soil denudation and reduced infiltration. Reversal of this step would require management of the physical environment (mulching, erosion barriers, soil ripping), as well as management of the primary producers.

It is probable that it does not pay farmers to address the problem of rangeland degradation even at an early stage, because moderate stocking generates less income than heavy stocking (Danckwerts & King 1984; Düvel & Scholtz 1992). The reduced profitability of ranching in vegetation that has been changed to an unproductive state (Danckwerts & Marais 1989), together with a prognosis of slow recovery, makes rehabilitation by de-stocking, resowing and bushcutting prohibitively expensive for private landowners.

Where adequate funds are available, clearing of established, unpalatable plants, in combination with seeding of palatable species, could potentially increase the carrying capacity of overgrazed Karoo rangeland. However, for a number of reasons, artificial means of reducing plant density should be approached with caution. Firstly, runoff and sediment loss are inversely correlated with vegetation cover (Snyman & Fouché 1991) and could be accelerated by clearing. Secondly, the effects of established plants on the soil microclimate, soil biota (eg. mycorrhiza and decomposers) and microclimate (eg. wind-speed, soil surface temperature) have not been investigated in the Karoo. Finally, the costs involved in such relationship between vegetation structure and bird assemblages was known, the model could predict whether or not it would be feasible to modify the vegetation so as to conserve particular species of birds.

In its present form the model has limited application for management of conservation areas. Many Karoo nature reserves were originally farms that were too overgrazed to attract other buyers. Most conserved areas also incorporate old ploughed lands and other patches of altered vegetation. The feasibility of applying active management to restore such modified ecosystems remains to be investigated. Although it has been shown that invertebrate assemblages on old fields in the Karoo vary with vegetation structure (Dean & Milton in press), too little is known at present to construct a state-and-transition model for these organisms. There is evidence that grazing-induced changes in the relative abundances of the food plants of invertebrates may either increase (eg. Karoo caterpillar *Loxostege frustalis*, Annecke & Moran 1977) or reduce (eg. cicada) densities of various species of invertebrates **Chapter 2.1**). Accidental ingestion of insect eggs by grazing sheep can also reduce populations of susceptible species eg. *L. frustalis* (Donaldson 1986). Changes in invertebrate populations, whether indirectly or directly caused by grazing management, are likely to affect their insect, avian, reptilian and mammalian predators.

Until there is adequate information to predict changes in faunal assemblages, a model of vegetation dynamics may have to serve as the framework for managing conservation areas, as well as rangelands, in the Karoo. It is therefore essential that such a model be robust and well supported by empirical data. The state-and-transition model presented in this chapter, although crude, represents an advance on current understanding of the processes that determine the composition of vegetation in the succulent shrublands of the Karoo.

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Appendix 1

Tierberg Karoo Research Centre: history, physical environment, flora and fauna.

Milton, S.J., Dean, W.R.J. & Kerley, G.I.H. 1992.
Transactions of the Royal Society of South Africa **48**, 15-46.

TIERBERG KAROO RESEARCH CENTRE: HISTORY, PHYSICAL ENVIRONMENT, FLORA AND FAUNA

By

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SUMMARY

The Tierberg Karoo Research Centre near Prince Albert in the southern Karoo is intended for long-term ecological monitoring and manipulative studies. This paper summarizes information on the management history, geology, soils, climate and vegetation and includes preliminary checklists of 189 vascular plant species, 25 ant, 90 bird, 18 reptile and 18 mammal species known to occur on the 1 km^2 study site. In comparison with arid shrublands in North America, Australia, Israel and elsewhere in southern Africa, grasses and annual forbs are scarce, succulents abundant and there are few alien taxa.

INTRODUCTION

The Karoo is large (652 339 km^2), occupying 31.4% of southern Africa south of 22°S (Rutherford & Westfall 1986), but its biota are so poorly known that even some of the most common plants and insects have yet to be identified. Nevertheless, management decisions which alter drainage, hydrology, ground cover, plant and animal communities in the Karoo are made continually by conservation authorities, managers of nature reserves, ranchers, road engineers, and mining concerns. All but 1.08% of the Karoo is privately owned (Rutherford & Westfall 1986) and used for extensive ranching and intensive, small-scale production of fodder. The conserved areas are fenced and so small that intensive management, including the provision of water points, culling (Novellie 1988) and the introduction of breeding stock, is necessary.

There is a real need in the Karoo for basic research on climate, soils, vegetation changes and plant and animal population dynamics (Cowling 1986), but the region tends to be overlooked by city-based research organizations. The FRD*-funded, Tierberg Karoo Research Centre was set up in January 1987 to stimulate interest in Karoo ecology, and to give local and overseas scientists the opportunity of staying in the field while conducting their research.

As an introduction to users of the Centre, this paper describes the geology, soil, climate, vegetation and vertebrate fauna of the field site, and includes preliminary checklists of vascular plants, birds, reptiles and mammals. Publications dealing in more detail with some of these subjects are referred to in the text.

SITUATION, GEOLOGY, SOIL

The Tierberg Karoo Research Centre (hereafter referred to as the 'study site') is situated on the southern edge of the Great Karoo (33°10'S, 22°17'E) inland and 20 km north of the Swartberg mountain range (Fig. 1). The 100 ha study site lies at 800 m

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above sea level in the 5 km wide and 80 km long valley of the Sandrivier, which flows east along a syncline in folded Ecca shale beds (Visser 1986) for approximately 60 km, before joining the Gamka river. The underlying Ecca shales, Dwyka tillite and Witteberg quartzite emerge as the Doringkloof (1 291 m) and Droëkloofberge (1 340 m), lying to the south, and smaller ridges, including Tierberg ridge (1 200 m), to the north. The Whitehill formation, a conspicuous bed of white-weathering carbonaceous shale with chert, known as the 'White Band', occurs at the base of the Ecca bed near its contact with the Dwyka tillite formation (Toerien & Roby's 1979 geological map; Visser 1986). This band can be seen on the slopes of the ridges to the north and south of the study site and on ridges as far west as Matjiesfontein.

The palaeontology of the sedimentary formations of this part of the Karoo has been well documented (Loock 1967; Oelofsen 1981; Oosthuizen 1981; Rubidge & Oelofsen 1981; Oelofsen & Loock 1987) and is not covered in this paper.

The Sand River valley is filled with a deposit of unstratified colluvium to a depth of at least 2 m. Rocks (shale, tillite, quartzitic sandstone and dolerite) ranging in size from 50 mm to 1 200 mm in diameter occur in the colluvium and are also scattered on the soil surface. Although the study site was selected for its flatness and the homogeneity of its vegetation, it is not completely level, but slopes gently (2 : 100) to the south. It is drained by six small washes which join a single drainage line running SSW roughly through the centre of the 100 ha exclosure. Surface water is present in the area only during heavy rainstorms, when runoff is rapid and muddy rivers incise the washes and the drainage line.

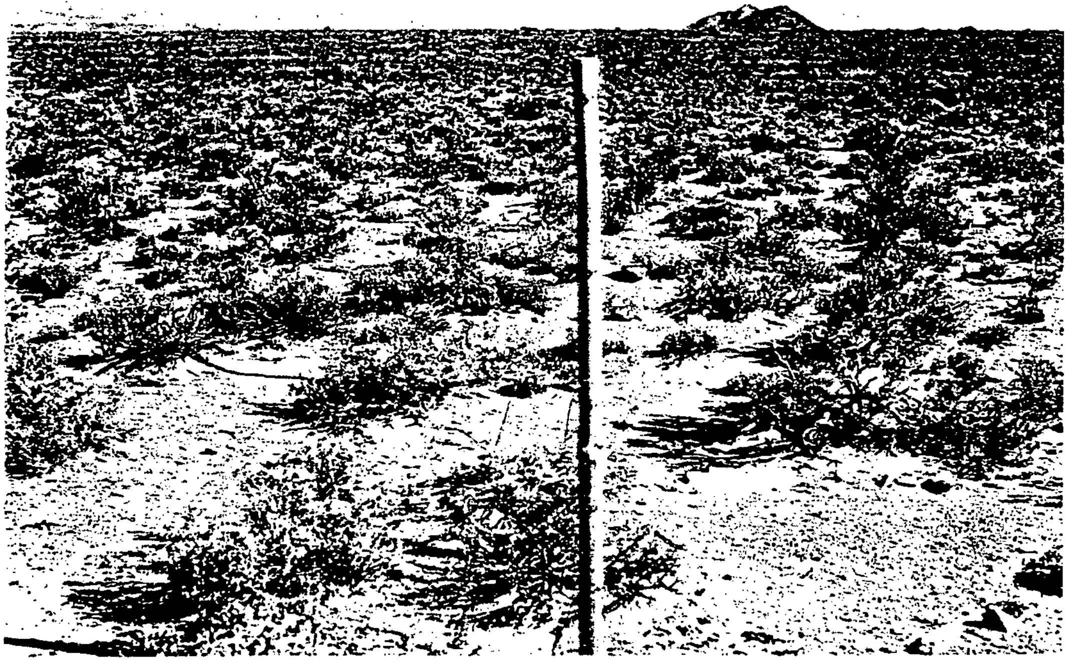

Fig. 2. Northern boundary of study site, looking west towards Prince Albert. Note large gaps between perennial shrubs and lack of grasses and forbs.

(Ellis & Lambrechts 1986). The nutrient status of the A horizon varies greatly between habitats (Table 2), but the soils are generally alkaline with a low nitrogen but relatively high phosphorus and potassium status when compared with norms for A horizons (Ellis & Lambrechts 1986). Organic matter, nutrients and salts are concentrated on the *heuweltjies*, which may also have a higher moisture status (Midgley & Musil 1990). Patches of dark-brown loam, apparently with a low pH and low extractable phosphorus but high magnesium content, occur on slight rises usually associated with quartzitic sandstone rocks and boulders (*Pteronia empetrifolia* community). Soils in and along drainage lines are sandy with low conductivity, little organic matter and low sodium and magnesium levels (Table 2).

Table 2

Chemical and physical properties of soils from the Tierberg Karoo Research Centre study site. 1: organic matter loss by ignition; 2: pH determined in water 1:1; 3: phorphorus by ISfei method (Hunter 1975); 4: exchangeable cations of potassium and sodium mg/kg dry soil. Each sample comprised 10 cores 5 cm diameter and 5 cm deep. Analyses were performed at the Grootfontein Research Institute, Middelburg, Cape.

Site	Date	%OM	cond us/cm	pH	N mg/kg	P mg/kg	K mg/kg	Na mg/kg	Ca mg/kg	Mg mg/kg	Texture Sa Cl Lm
Method		1		2		3	4	4			
Heuweltjie											
1 many rats	6/87	—	3500	8.5	3831	65.5	1640	1665	848	2059	57 36 3
2 many rats	6/87	—	5020	8.5	3327	80.8	1580	2303	841	1895	53 38 12
3 many rats	6/88	18.20	7300	8.3	2816	75.1	1060	2262	7517	1577	Sa Lm
4 few rats	6/88	12.01	5500	8.5	2155	113.7	1080	1569	7048	1044	Sa Cl Lm
5 no rats	6/87	—	2850	8.5	2005	117.0	998	931	6544	961	65 27 14
6 no rats	6/88	9.84	2700	8.2	1518	69.1	509	458	6576	711	Cl Lm
Pteronia pallens flats											
1 random	6/87	—	1220	7.8	727	57.5	267	116	2954	401	77 19 7
2 interbush gap	6/87	—	1800	7.1	519	37.6	237	130	1547	509	73 21 7
3 under bush	6/87	—	400	8.5	742	69.8	382	89	2750	210	93 5 5
Pteronia empetrifolia flats											
1 random	6/87	—	2380	6.1	462	24.4	260	180	1361	884	74 24 7
Random flats											
1	6/88	6.13	2500	7.7	623	54.8	279	239	2730	551	Sa Cl Lm
2	6/88	6.17	2500	7.8	589	52.2	285	199	2593	472	Cl Lm
3	6/88	6.56	3200	7.2	622	31.3	257	233	2531	618	Cl Lm
Drainage line											
1 river bank	6/87	—	510	8.6	577	100.3	350	201	2277	214	80 10 8
2 river bed	6/88	4.36	250	8.7	530	71.5	230	67	2607	233	Sa Lm

CLIMATE

An automatic weather station was established on the study site in August 1987. A summary of the temperature, humidity, and rainfall data is presented in Appendix 1. Rainfall records have been kept at the gaol in Prince Albert (26 km east of the study site) since 1878 and the average annual rainfall of 92 complete data sets is 167 ± s.e. 7 mm. An analysis of these data (Fig. 5) shows that heavy rains are most likely to fall between February and May, and that month-long droughts most often occur between

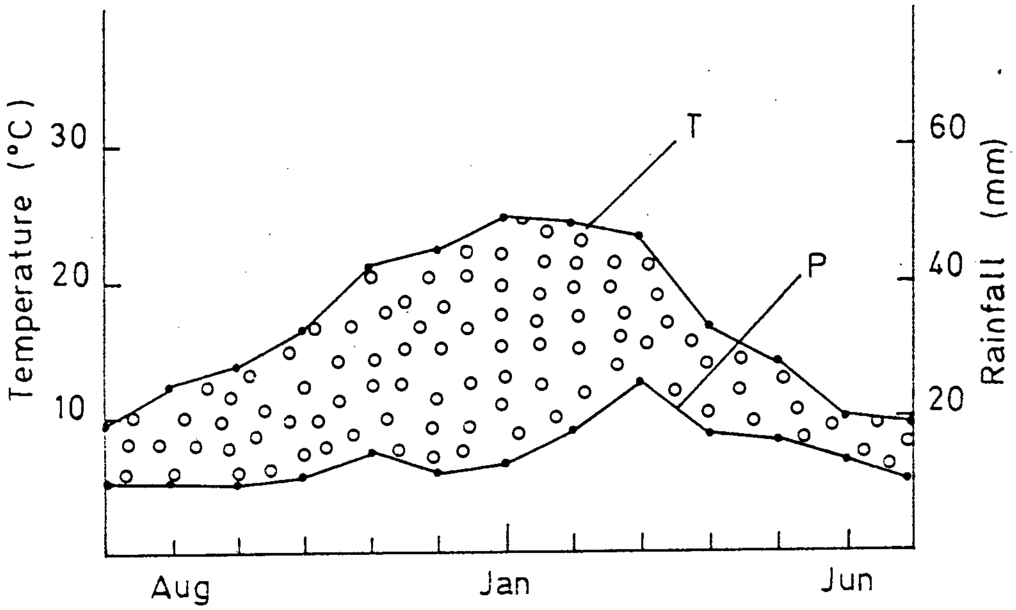

Fig. 6. Walter Leith climate diagram based on temperature data from the Tierberg study site (September 1987 to January 1990) and on 92 years (1978 to 1987) of rainfall data from the gaol at Prince Albert. P = mean monthly rainfall in mm; T = mean monthly temperature in °C. The climate is arid (stippled) through the year.

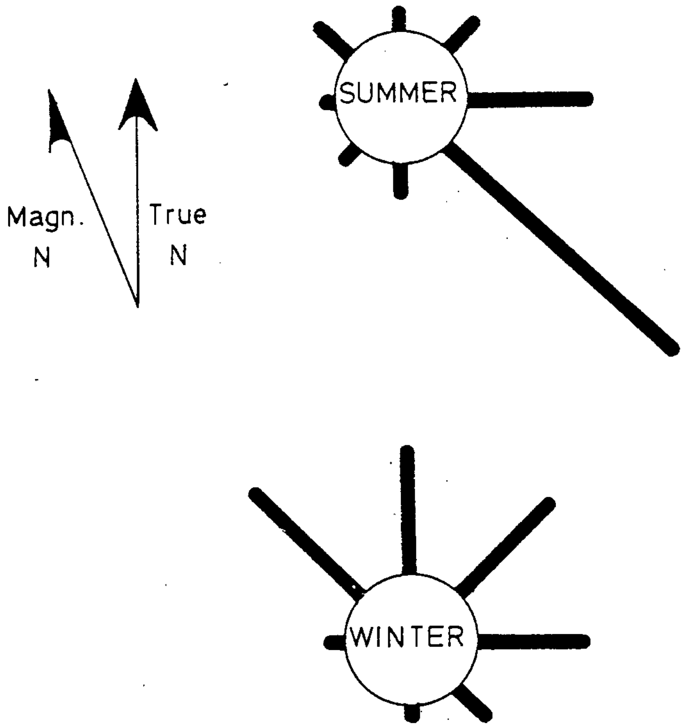

Fig. 7. Wind roses showing wind direction on the study site in summer (October to February) and winter (April to September). Data from on-site logger covers the months May 1989 to June 1990.

ernment. The conflicts between settlers and Khoi-Khoi, which occurred between 1787 and 1793 in the Prince Albert area (Cape Town Archives: I/GR/12/1 cited in H. Bokelmann unpubl.) apparently revolved around hunting or theft of the settlers' domestic livestock.

The shift from free-ranging wild ungulates to contained domestic livestock almost certainly changed both the fauna and flora of the area. Weathered pieces of ostrich eggshell found on *heuweltjies* in the study site, as well as the numerous eggshell fragments excavated from deposits in a nearby rock shelter (Avery & Avery unpubl.), indicate that wild ostriches were resident in the area before European settlement. As yet there is no archaeological record for the Prince Albert district, but on-going excavations of a rock shelter at Tierberg should provide information on the palaeoenvironment of the area.

Contrasts in vegetation texture along farm boundaries are visible on a 1974 air photograph, but not on one taken in 1939. This evidence, together with present day differences in the relative abundance of plant species across farm boundaries, testifies to the fact that Karoo vegetation can be altered within 30 years by grazing management.

The farm Tierberg has been grazed by Merino wethers (castrated male sheep) at a rate of 6 ha SAU^{-1} (SAU = small animal unit, equivalent to one wether) for the past 35 to 40 years. This stocking rate is advocated for the steppe to desert transitional zone of the Prince Albert Division by the Department of Agriculture and Water Supply (Anon. 1981; Vorster 1986). Tierberg is divided into four large camps ranging in size from about 2 000 ha to 5 000 ha and grazed rotationally with periods of stay of two to six months. Periods of stay are based on general climate and vegetation conditions, so that livestock is consolidated in favourable times allowing the remaining camps to rest. In drier times the animals are spread over most of the farm (C. Hobson, pers. comm.).

Domestic livestock have been excluded from the study site since June 1987, but the five-strand fence allows free movement of all wild mammals, and we estimate that the density of indigenous herbivores is equivalent to about 20 ha SAU^{-1}. The farm Argentina was heavily grazed by sheep, goats and domestic ostriches (stocking rate equivalent to 2.7 ha SAU^{-1}) between 1913 and 1960. Although the farm is now stocked at a more moderate rate (6 to 7 ha SAU^{-1}) and rotationally grazed by Dorper sheep, the preferred grazing plants still occur at low density.

VEGETATION

Geographically, the Tierberg site falls within the Koup Karoo (see Hilton-Taylor 1987). In terms of Acocks' (1975) veld types the flora, with its high proportion of succulent species and low abundance of grasses, most closely resembles the Little Karoo form of Karroid Broken veld (veld type 26b).

The four types of habitat mapped (Fig. 8) are visible on air photographs of the study site: plains, *heuweltjies*, washes or minor drainage lines, and major drainage lines. Soil moisture probably explains the structural differences between the vegetation of runoff sites (plains) and runon sites (minor and drainage lines). Soil chemistry and

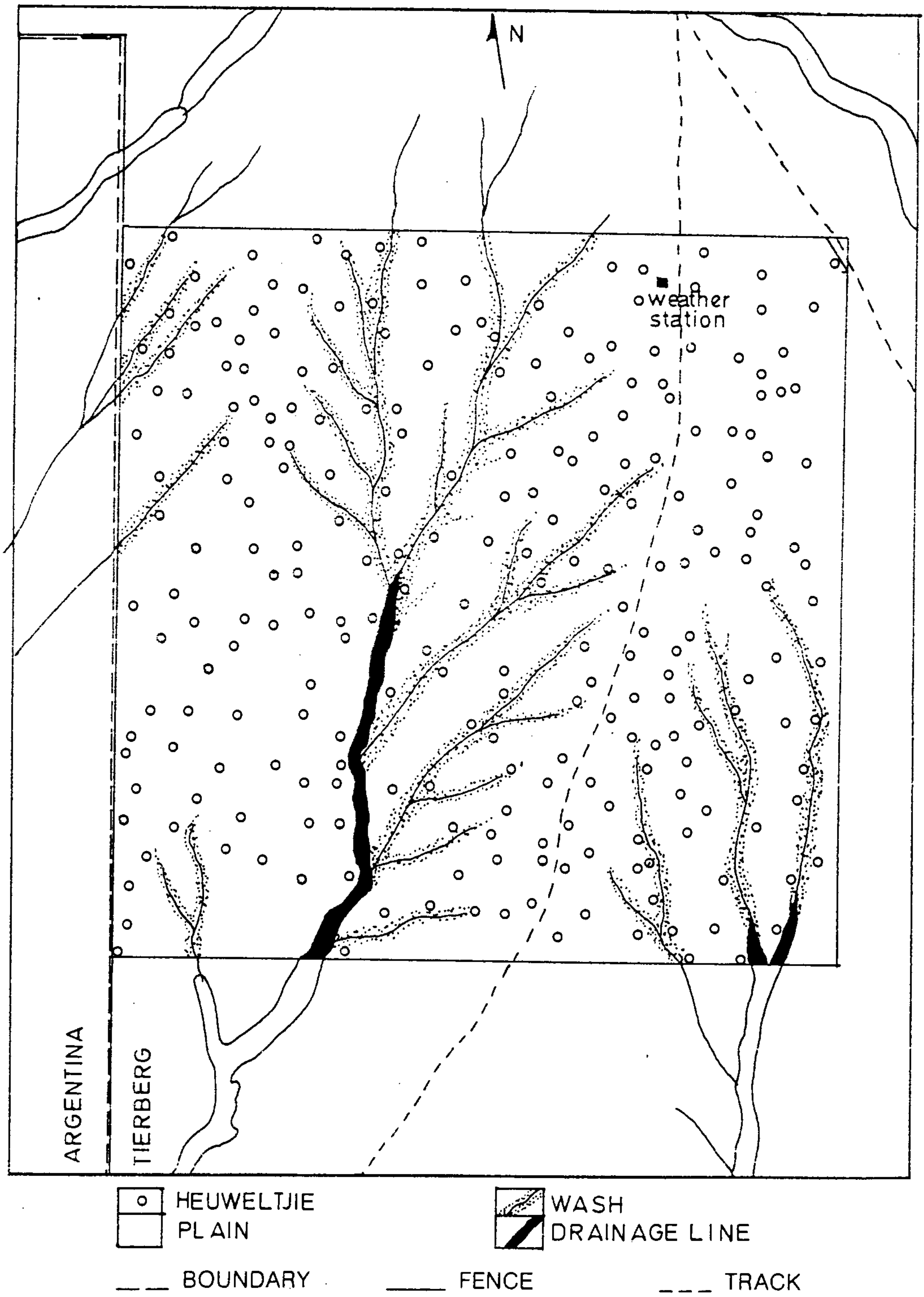

Fig. 8. Map of study site showing farm boundaries, drainage lines and four habitat types discussed in the text.

Washes

Washes or minor drainage lines cover 16,6% of the study site, and are species-rich communities which include plant species found in all other habitats. Canopy cover in washes averaged 20% but was very variable (7 to 30%), depending on the amount of soil eroded during recent rain. The vegetation of washes is taller (up to 60 to 200 cm) and less succulent than the plains shrubland, with non-succulent shrubs making up 55% of the total cover. The tree-like shrub *Rhigozum obovatum*, smaller, asteraceous shrubs (*Berkheya*, *Felicia*, *Pentzia* and *Eriocephalus*), as well as various Fabaceae, differentiate washes from plains communities. Most of the plants found in washes are wind-dispersed, but a variety of other dispersal mechanisms are represented.

Major drainage lines

Major drainage lines cover only 2,5% of the study site but are an essential source of food, shelter or nesting material for many of the bird and mammal species. Drainage line vegetation is denser, with an average canopy cover of 37% (range 23 to 78%), and taller (up to 4 m) than that of the other habitats, and the six tree species found in the study site are restricted to this habitat type. Succulents are of little importance as contributors to either species diversity (23% of species) or cover (15% of cover).

Many of the plants in drainage lines are bird (21%) or mammal (13%) dispersed. Mammals, including bat-eared foxes and kudu, disperse seeds of *Diospyros* spp in their faeces. Other soft-fruited trees, shrubs, and hemiparasites are dispersed mainly by birds, and include *Protasparagus* spp, *Carissa haematocarpa*, *Rhus* spp, *Euclea undulata*, *Lycium* spp, *Viscum* spp, *Moquinella rubra* and *Septulina glauca*. Some of the plant species which are dispersed mainly by the birds which use them as nesting material (Dean, Milton & Siegfried 1990), or on the pelage of mammals (Milton, Siegfried & Dean, 1990), are limited to drainage lines on the study site.

Plant checklist

The provisional checklist of vascular plants of the 1 km^2 Tierberg study site (Appendix 2) contains 189 taxa, including five non-indigenous species. Symbols denoting the abundance and habitats of these species refer exclusively to this site, although some species may occur in other habitats elsewhere. The list will need to be updated periodically to include rare and fugitive species (particularly geophytes) and to correct names of taxa (*Lycium*, *Pteronia*, *Eriospermum*, and many of the Aizoaceae) which are currently undergoing revision.

INVERTEBRATE FAUNA

Harvester ants *Messor capensis* and harvester termites *Microhodotermes viator* are probably the most abundant insects on the site. Colony densities of harvester ants, calculated from counts of nest mounds, are 7,3 h^{-1}. Harvester termite colonies are in excess of 2,2 ha^{-1} (*heuweltjies* density) as many small (1 to 2 m diameter) soil dumps indicating termite 'hives' are interspersed with more conspicuous mounds. Each ant passerines (larks, chats, warblers) and frugivorous mousebirds, dependent largely on trees and shrubs in drainage lines for fruit. Granivorous species tend to be summer visitors to the area. There are a few resident or locally nomadic granivorous canaries and buntings present throughout the year. The density of species on the site varies seasonally, with an influx of sandgrouse and finchlarks increasing the biomass in summer, and local migrants such as Ludwig's bustard increasing the biomass in winter. Preliminary estimates of avian biomass on the site suggest an average of <50 g ha^{-1}. Both the diversity and density of resident birds on the site are low compared with published estimates of density in other Karoo shrublands. For example, Winterbottom (1946) recorded an avian biomass of 334,9 g ha^{-1} in grassy dwarf shrubland at Victoria West, and a biomass of 158,9 g ha^{-1} in succulent dwarf shrubland at Klaarstroom (1968). Both of these estimates were computed from species density data. Vernon (1986) gave further information on bird population densities, breeding times and food guilds in the southern Karoo.

Reptiles

No herpetological research has been done at Tierberg, so the provisional checklist (Appendix 5) is based on observations made during the course of other surveys. No amphibians have been recorded in the study site, but saurids are abundant and snakes and tortoises fairly common.

Mammals

Research on mammals on the study site has been limited to the small mammals (rodents and elephant shrews). Whistling rats (*P. brantsii*) are the most conspicuous species because of their prominent burrow systems on the *heuweltjies*. This species is trap-shy and densities (2,6 rats ha^{-1}) have been derived from an estimate of two to six rats per occupied *heuweltjie*. Whistling rats are herbivorous, with succulents forming more than 50% of their diet (Du Plessis 1989). Localized browsing by whistling rats on and around *heuweltjies* contributes to the observed 'patchiness' of the vegetation (Palmer 1987) and their digging activities probably assist in maintaining *heuweltjies* as disturbed, nutrient-rich sites (Milton & Dean 1990).

The closely related bush Karoo rats *Otomys unisulcatus*, which do not burrow but construct domed nests of sticks and twigs, occur at low densities on the study site (*ca* 1 nest 50 ha^{-1}). This species selects areas of relatively denser (> 30%) and taller (> 1 m) plant cover (Du Plessis & Kerley 1991) and is consequently limited to washes and drainage lines.

Hairy-footed gerbils, *Gerbillurus paeba*, are the dominant small mammals on the study site. The population of this species varies seasonally and annually (2–30 mice ha^{-1}), probably as a function of rainfall (Kerley 1990a). Gerbils tend to be omnivorous, feeding on insects, foliage and seeds (Kerley 1989; 1990a), but at the study site they consume relatively little seed (Kerley 1990a). The diet of the round-eared elephant shrew *Macroscelides proboscideus* (1–5 shrews ha^{-1}) comprises insects and foliage (Kerley 1989; 1990a). Short-tailed gerbils *Desmodillus auricularis* are rare on the study site (Kerley 1990a).

Only five alien species were recorded among 88 families (340 species) of plants and animals for which detailed lists were compiled (Table 3). All the alien taxa were plants, and included four chenopods introduced to the Karoo as fodder plants, and two international herbaceous weeds. Most of the alien plants found in the Karoo occur along perennial rivers or near artificial water sources such as man-made impoundments and windmill tanks. There is no surface water in the study site and the alien species are limited to the major drainage line and to disturbed, organically enriched soils of *heuweltjies*.

Table 3

Summary of numbers of families and species of vascular plants, ants, birds, reptiles and mammals known to occur on the 1 km^2 Tierberg Karoo Research Centre study site. Numbers in brackets refer to species which have been observed within 5 km of the site but not recorded inside its boundaries. For species lists see Appendices 2 to 6.

	Families			Species		
	Native	Alien	Total	Native	Alien	Total
Vascular plants	36	2	36	184	5	189
Ants	1	0	1	25	0	25
Birds	33	0	33	90	0	90
Reptiles	7 (8)	0	7 (8)	17 (18)	0	18 (19)
Mammals	11	0	11	18 (21)	0	18 (21)
Total	88 (89)	2	88 (89)	335 (339)	5	340 (344)

The alien Argentine ant, *Iridomyrmex humilis*, has not been recorded from the study site, nor have we any records of its occurrence within a 5 km radius of the site. No alien bird species have been recorded from the study site, but European starlings, *Sturnus vulgaris*, and house sparrows, *Passer domesticus*, occur about 6 km to the northeast at the Tierberg farmhouse.

We suggest that aridity, absence of surface water, of major man-made disturbances such as roads, dwellings or cultivation, and a history of moderate grazing have preserved the flora and fauna native to this area.

CONCLUSION

This description of the physical environment, history, vascular flora and vertebrate fauna of the Tierberg Karoo Research Centre study site reveals gaps in the present knowledge of the area. Despite high reptile diversity, especially among the saurids (W. Branch pers. comm.), we know of no reptile population censuses in this part of the Karoo. Herbivorous mammal populations may be responding to predator reduction in sheep and goat farming areas, and increases in herbivore populations could alter vegetation, yet mammal census data are too scanty for these hypotheses to be tested. Collections and checklists of non-vascular plants and invertebrates have yet to be made for the study site. Such basic information is a prerequisite for future ecological studies in the area.

Appendix 2

Checklist of vascular plants on Tierberg study site. Frequency ratings indicate the status of each species in the study site: R = rare, O = occasional, C = common, A = abundant; E = ephemeral and not seen every year; * denotes non-indigenous species. Taxonomy of Molluginaceae and Aizoaceae follows Bittrich & Hartman (1988) and that of all other families follows Gibbs Russell *et al.* 1985, 1987. Habitats are: P = plain, H = *heuweltjie*, W = wash, D = drainage line.

Family	Species and author	Habitat	Abundance
Poaceae	_Cenchrus ciliaris_ L.	W.D	R
	Stipagrostis namaquensis (Nees) de Winter	D	O
	S. obtusa (Del.) Nees	W	R
	Aristida adscensionis L.	H.W.D	O
	A. congesta Roem. & Schult.	H.W.D	O
	A. diffusa Trin. subsp. _diffusa_	W	R
	Enneapogon devauxii Beauv.	D	R
	E. scaber Lehm.	H.W.D	O
	Fingerhuthia africana (Lehm.) Nees	H.W	R
	Schizmus barbatus (Loefl. ex L.) Theil.	D	E
Liliaceae	_Ornithoglossum viride_ (L.f.) Ait.	W	O
	Schizobasis intricata (Bak.) Bak.	P	O
	Eriospermum capense (L.) Salter	P	O
	Eriospermum sp	P	O
	Aloe claviflora Burch.	H	R
	A. variegata L.	P	O
	Haworthia semiviva (V.Poelln.) M.B.Bayer	W	R
	H. viscosa (L.) Haw.	W	R
	Albuca spiralis L.f.	P.W	O
	Albuca (SJD 970)	P	C
	Drimia anomala (Bak.) Benth.	P	C
	Ornithogalum unifolium Retz.	P	C
	Urginea virens Schltr.	P	O
	Lachenalia cf. _rosea_ Andr. (SJD 969)	D	O
	Protasparagus recurvispinus Oberm.	P.W.H	C
	P. retrofractus (L.) Oberm.	D	O
	P. suaveolens (Burch.) Oberm.	D	O
Iridaceae	_Moraea speciosa_ (L.Bol.) Goldbl.	W	C
	Tritonia tugwelliae L.Bol	W.D	O
Loranthaceae	_Moquinella rubra_ (Spreng.f.) Balle.	D	O
	Septulina glauca (Thunb.) Tieghem	D	O
Viscaceae	_Viscum capense_ L.f.	W.D	C
	V. continuum E.Mey ex Spraque	D	O
	V. rotundifolium L.f.	H.W.D	C
Santalaceae	_Thesium lineatum_ L.f.	H.W.D	C
Chenopodiaceae	_Chenopodium mucronatum_ Thunb.	H.D	O
	*_Atriplex lindleyi_ subsp. _inflata_ (L.Muell.) P.G.Wilson	H.D	C
	*_A. muelleri_ Benth.	D	O
	*_A. semibaccata_ R.Br.	H.D	O

Appendix 2 (cont.)

Family	Species	Habitat	Abundance
	Ruschia spinosa Hartm. & Stüber (*E.* cf. *vulnerans* (L.Bol.) L.Bol.	P	A
	Trichodiadema cf. *bulbosa* (Haw.) Schwantes	W	O
Portulacaceae			
	Anacampseros telephiastrum DC.	P	R
Brassicaceae			
	Lepidium africanum (Burm.f.) DC.	H,W	C
	L. desertorum Eckl. & Zeyh.	H	E
	Heliophila seselifolia Burch. ex DC.	D	R
	Sisimbrium burchellii DC. var. *burchellii*	H	R
Capparaceae			
	Cadaba aphylla (Thunb.) Willd.	D	R
Crassulaceae			
	Cotyledon papillaris L.f.	W	R
	Tylecodon reticulatus (L.f.) Toelk.	W	O
	T. wallichi (Harv.) Toelk.	W	R
	Crassula deltoidea Thunb.	P	O
	C. muscosa L.	P,W	C
	C. nudicaulis L. var. *platyphylla* (Harv.) Toelk.	P,W	R
	C. pseudohemisphaerica Friedr.	W	O
	C. subaphylla (Eckl. & Zeyh.) Harv.	P,W	A
	C. tetragona subsp. *acutifolia* (Lam.) Toelk.	W	O
	Adromiscus triflorus (L.f.) Beyer	P	O
Fabaceae			
	Acacia karroo Hayne	D	O
	Lotononis cf. *versicolor* (E.Mey) Benth.	P,W,H	C
	Melolobium candicans (E.Mey) Eckl. & Zeyh.	D	C
	Sutherlandia frutescens R.Br.	W	R
	Lessertia annularis Harv.	H,W	C
Geranicaeae			
	Sarcocaulon sp.	D	R
	Pelargonium karooicum Compton & Barnes	W	O
	P. minimum (Cav.) Willd.	D	E
Oxalidaceae			
	Oxalis obtusa Jacq.	W	C
Zygophyllaceae			
	Zygophyllum gilfillanii N.E.Br.	H,W	C
	Z. retrofractum Thunb.	H,W	C
	Augea capensis Thunb.	H,D	A
Polygalaceae			
	Polygala leptophylla Burch.	W	O
Euphorbiaceae			
	Chamaesyce inequlatera (Sond.) Sojak	H,W	E
	Euphorbia caterviflora N.E.Br.	P,W,H	C
	E. braunsi N.E.Br.	W	R
Anacardiaceae			
	Rhus longispina Eckl & Zeyh.	D	R
	R. undulata Jacq.	D	C
Celastraceae			
	Maytenus polyacantha (Sond.) Marais	D	O

Appendix 2 (cont.)

Family	Species	Habitat	Abundance
	Pteronia paniculata Thunb.	W	R
	P. viscosa Thunb.	W	O
	Amellus microglossus DC.	H	E
	Felicia filifolia (Vent.) Burtt Davy	W	C
	F. macrorrhiza (Thunb.) DC.	P	R
	F. muricata (Thunb.) Nees	D	C
	Chrysocoma ciliata L.	P,W,D	C
	Ifloga polycnemoides Fenzl.	D	E
	Lasiopogon glomerulatus (Harv.) Hilliard	H,D	E
	Helichrysum albertense Hilliard	H,D	E
	H. pumilis (O.Hoffm.) Hilliard & Burtt	D	R
	H. rosum (Berg.) var. *rosum*	P,W	O
	Rosenia humilis (Less.) Bremer	W,D	C
	Leysera tenella DC.	D	E
	Pegolettia baccaridifolia Less.	W	R
	Eriocephalus ericoides (L.f.) Druce	W,D	C
	E. spinescens Burch.	W,D	C
	Lasiospermum brachyglossum DC.	D	E
	Pentzia incana (Thunb.) Kuntz	W,D	C
	P. pilulifera (L.f.) Fourc.	H,D	E
	Senecio angustifolius (Thunb.) Willd.	H,D	C
	S. longiflorus (DC.) Sch.Bip.	W	R
	S. radicans (L.f.) Sch.Bip.	W	O
	Othonna protecta Dinter	P	O
	Garulem bipinnatum (Thunb.) Less.	D	R
	Osteospermum calendulaceum L.f.	H	O
	O. pinnatum (Thunb.) T.Norl.	H	E
	O. sinuatum (DC.) T.Norl.	P,H,W	A
	Ursinia nana DC.	P,D	O
	Arctotis venusta T.Norl.	D	E
	Gazania krebsiana Less.	P,W	C
	G. lichtensteinii Less.	H,D	O
	Berkheya spinosa (L.f.) Druce	P,W,D	C
	Cuspidia cernua ssp. *annua* (L.f.) B.L.Burtt	D	R
	Dicoma capensis Less.	H	R
	**Sonchus oleraceus* L.	D	R

Appendix 4

Checklist of birds recorded on the Tierberg study site. Mass is given in grams, and the data are taken from Maclean (1985) and unpublished notes by WRJD. The masses of Redwinged and Palewinged Starlings are from unpublished notes by A. Craig, and the mass of the Black Crow is an estimate.
Status: R = resident, V = visitor, M = migrant.
Abundance or frequency of occurrence are: R = rare, O = occasional, F = frequent, C = common.

Family	Species	Mass	Status	Abundance
Anatidae				
	South African Shelduck *Tadorna cana*	1100	R	R
Sagittaridae				
	Secretary Bird *Sagittarius serpentarius*	3941	V	R
Accipitridae				
	Black Eagle *Aquila verreauxi*	4069	V	O
	Booted Eagle *Hieraaetus pennatus*	975	V	O
	Martial Eagle *Polemaetus bellicosus*	3965	V	O
	Redbr. Sparrowhawk *Accipiter rufiventris*	185	V	R
	Pale Chanting Goshawk *Melierax canorus*	747	R	C
Falconidae				
	Lanner Falcon *Falco biarmicus*	600	V	R
	Rock Kestrel *F. tinnunculus*	192	V	O
	Greater Kestrel *F. rupicoloides*	260	V	O
Phasianidae				
	Greywing Francolin *Francolinus africanus*	400	V	O
	Common quail *Coturnix coturnix*	100	V	F
Otididae				
	Kori Bustard *Otis kori*	13500	V	O
	Ludwig's Bustard *Neotis ludwigii*	6000	M,V	F
	Karoo Korhaan *Eupodotis vigorsii*	1500	R	C
	Black Korhaan *E. afra*	700	V	R
Charadriidae				
	Crowned Plover *Vanellus coronatus*	167	V	R
Glareolidae				
	Doublebanded Courser *Rhinoptilus africanus*	90	R	F
Pteroclidae				
	Namaqua Sandgrouse *Pterocles namaqua*	150	M,V	F
Columbidae				
	Rock Pigeon *Columba guinea*	347	V	O
	Turtle Dove *Streptopelia capicola*	150	R	C
	Laughing Dove *S. senegalensis*	100	V	R
	Namaqua Dove *Oena capensis*	40	V	O
Cuculidae				
	Diederik Cuckoo *Chrysococcyx caprius*	35	M,V	O
Strigidae				
	Spotted Eagle Owl *Bubo africanus*	700	R	F
Apodidae				
	European Swift *Apus apus*	43	M,V	R
	Black Swift *A. barbatus*	42	V	R
	Whiterumped Swift *A. caffer*	24	M,V	R
	Little Swift *A. affinis*	26	V	R
	Alpine Swift *A. melba*	77	V	R

Appendix 4 (cont.)

Family	Species	Mass	Status	Abundance
Muscicapidae				
	Chat Flycatcher *Melaenornis infuscatus*	37	V	F
	Fiscal Flycatcher *Sigelus silens*	26	R	F
	Pririt Batis *Batis pririt*	10	R	F
	Fairy Flycatcher *Stenostira scita*	6	M,V	F
Motacillidae				
	Richard's Pipit *Anthus novaeseelandiae*	24	V	O
	Plainbacked Pipit *A. leucrophyrs*	24	V	R
Laniidae				
	Fiscal Shrike *Lanius collaris*	41	R	F
Malaconotidae				
	Southern Tchagra *Tchagra tchagra*	45	R	F
	Bokmakierie *Telophorus zeylonus*	65	R	C
Sturnidae				
	Redwinged Starling *Onychognathus morio*	140	V	F
	Palewinged Starling *O. nabouroup*	113	V	F
Nectariniidae				
	Malachite Sunbird *Nectarinia famosa*	17	R	F
	Lesser Doublecollared Sunbird *N. chalybea*	8	R	C
	Dusky Sunbird *N. fusca*	10	V	F
Zosteropidae				
	Cape White-eye *Zosterops pallidus*	11	R	F
Ploceidae				
	Cape Sparrow *Passer melanurus*	29	R	C
	Masked Weaver *Ploceus velatus*	27	V	F
Fringillidae				
	Blackheaded Canary *Serinus alario*	12	R	F
	Yellow Canary *S. flaviventris*	17	R	C
	Whitethroated Canary *S. albogularis*	27	R	C
	Cape Bunting *Emberiza capensis*	21	R	C
	Larklike Bunting *E. impetuani*	15	V	F

Appendix 6

Checklist of mammals found on the Tierberg Karoo Research Centre study site, compiled from captures, sightings and observations of activities (tracks scats). Nomenclature follows Meester *et al.* (1986). Mass from Karoo material where available* (Kerley 1990a), otherwise from Smithers (1983), and is in kg except where marked. Status refers to field records: C = common, O = occasional, R = rare and R* = recorded in similar habitat within 5 km of the study site, but not within the site. C^1, O^1, R^1 = see text for estimates of density.

Common name and species	Mass (kg)	Abundance
Ceropithecidae		
Chacma baboon *Papio ursinus*	14–43	O
Hyanidae		
Aardwolf *Proteles cristatus*	7.7–10.0	R
Felicae		
African wildcat *Felis lybica*	2.4–6.4	R*
Caracal *Felis caracal*	8.6–20.0	R
Canidae		
Bat-eared fox *Otocyon megalotis*	3.2–5.4	C
Cape fox *Vulpes chama*	2.3–3.3	R
Black-backed jackal *Canis mesomelas*	5.5–10.0	R*
Mustelidae		
Striped polecat *Ictonyx striatus*	0.6–1.5	R
Small grey mongoose *Galerella pulverulenta*	0.5–1.2	O
Orycteropodidae		
Antbear *Orycteropus afer*	40–65	C
Bovidae		
Kudu *Tragelaphus strepsiceros*	120–258	R
Common Duiker *Sylvicapra grimmia*	15.3–25.4	C
Steenbok *Raphicerus campestris*	8.9–13.2 -	C
Muridae		
Bush Karoo rat *Otomys unisulcatus**	98.7 ± 29.5 g	O^1
Brants's whistling rat *Parotomus brantsii**	105.3 ± 26.0 g	C^1
Hairy-footed gerbil *Gerbillurus paeba**	24.6 ± 3.7 g	C^1
Short-tailed gerbil *Desmodillus auricularis**	30.7 g	R
Striped mouse *Rhabdomys pumilio**	47.5 ± 8.5 g	R*
Hystricidae		
Porcupine *Hystrix africaeaustralis*	10.0–18.2	O
Leporidae		
Cape hare *Lepus capensis*	1.7–2.5	C
Macroscelididae		
Round-eared elephant shrew *Macroscelides proboscideus**	38.2 ± 3.7 g	O^1

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Appendix 2

Above-ground biomass and plant cover in a succulent shrubland in the southern Karoo.

Milton, S.J. 1990.
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Short Communication

Above-ground biomass and plant cover in a succulent shrubland in the southern Karoo, South Africa

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The above-ground, air-dry mass of vegetation in a succulent Karoo shrubland inland of the Swartberg mountains (33°S 22°E) in the southern Cape averaged 3.27 metric tons ha^{-1}, of which 6% was necromass. Linear regression equations relating fresh and dry above-ground biomass to projected canopy cover are presented. Above-ground biomass of succulent Karoo shrublands is comparable with other karroid vegetation types but less than mature vegetation in the adjacent Fynbos shrublands. Plant cover and biomass values for parts of the Mojave Desert (36°S 117°W), North America, are similar to the succulent Karoo shrubland, but the two vegetation types differ in the relative contributions of succulent and non-succulent plants, and in the average sizes and spacing of plants.

Die bogrondse droëmassa van plantegroei in 'n Karoo-sukkulentstruikveld op die binnelandse kant van die Suid-kaapse Swartbergreeks (33°S 22°O), het 'n gemiddelde waarde van 3.27 metrieke ton ha^{-1}, waarvan 6% nekromassa is. Die verhouding tussen vars- en droëbogrondse massa en kroonuitgestrektheidsbedekking is lineêr. Bogrondse fitomassa van Karoo-sukkulentstruikveld is soortgelyk aan ander Karooveldtipes maar laer as aangrensende volwasse Fynbos-struikveld. Plantbedekking en fitomassa van dele van die Mojave Woestyn (36°S 117°W), Noord-Amerika, kan vergelyk word met Karoo-sukkulentstruikveld, maar hierdie veldsoorte verskil in die relatiewe hoeveelheid vetplante, in die gemiddelde groottes van plante en hul plantspasiëring.

Above-ground plant biomass has been sampled in all the South African biomes (Rutherford & Westfall 1986), but few standing crop or biomass accumulation measurements have been made in the Succulent Karoo (Werger 1985). The cover and biomass figures presented here for the Tierberg Karoo Research Centre field site, serve as a baseline for plant recolonization and biomass accumulation studies being carried out at this site.

The Tierberg Karoo Research Centre (33°10′S, 22°17′E) near Prince Albert, is situated in a fold valley on the southern edge of the Great Karoo (more fully described in Milton *et al.* in press). The weakly structured, sandy-loams are alkaline and typical of soils of low-lying positions in arid regions (Ellis & Lambrechts 1986). The average annual rainfall for 92 years at Prince Albert (25 km to the west) is (mean ± *SE*) 167 ± 7 mm. Venter *et al.* (1986) place Prince Albert in a between-seasons rainfall zone, with 50–60% of the annual total rain falling in summer. Temperatures are extreme with daily maxima exceeding 30°C between December and March and daily minima below freezing for about 10 days annually (Venter *et al.* 1986). The prevailing westerly wind probably increases the desiccating effects of the summer heat.

Twenty plots (each 5 m × 2.5 m) were laid out at 100-m intervals along two 1-km transect lines running east to west across plains in the northern quarter of the study site. Sampling was carried out between 25 June and 11 July 1989. The moisture status of the vegetation appeared normal for the time of the year, and rainfall in the 3-month period preceding sampling was as follows: April 39 mm, May 0 mm, June 20 mm. Plant cover was estimated by measuring intercepts of all plant species along four 5-m line transects per plot. All plants were then cut at ground level, sorted into species and weighed in the field. Subsamples of 14 succulent and 11 non-succulent plant species and of dead wood were frozen for 6 weeks to stop metabolic processes and to burst cells, then air dried to constant weight at room temperature for 6 months. The samples were reweighed in January (ambient temperature 3°C, humidity 20%) to obtain an estimate of water content (Table 1). Cover-biomass regressions and estimates of the standing biomass of the plains shrubland (Table 2) were calculated from these data. The mean difference between the estimated moisture contents of air-dried and oven-dried (24 h at 70°C) shrub samples was 6.8% (± *SE* 1.4, $n = 8$).

Moisture contents ranged from 25 to 73% in non-succulent species and from 42 to 87% in succulent species. The above-ground parts of short-lived and shoot-deciduous species contained more moisture than the stems and leaves of long-lived, evergreen shrubs (Table 1). This trend held for both succulent and non-succulent species. Succulents absorb water rapidly becoming turgid within 24 hours of rain (pers. obs.) and they 'tie up' some 2 660 litres of water per hectare (fresh mass of succulents averages 4 011 kg ha^{-1} of which 66.3% is water). These features presumably enable them to compete successfully with annual forbs and non-succulent shrubs in arid areas which receive a number of small rainfall events rather than predictable heavy rains.

The total above-ground (dry) biomass of plains vegetation at Tierberg, 3.27 metric tons ha^{-1} (Table 2), was within the range (0.5 to 7.6 metric tons ha^{-1}) reported for the Succulent and Nama Karoo Biomes (Rutherford 1978; Rutherford & Westfall 1986), but well below the 6 to 25 t ha^{-1} of shrublands in the nearby Fynbos Biome (Rutherford & Westfall 1986). Projected canopy cover averaged (mean ± *SE*) 25.6 ± 1.4% (range 17 to 31%) for the succulent shrubland at Tierberg. Although this is low by comparison with cover values in grassy False Upper Karoo at Middelburg (71% and 76% on north- and south-facing slopes respectively), biomass values are similar: 2.54 t ha^{-1} on north-facing and 4.29 t ha^{-1} on south-facing slopes (Roux 1988). Differences in productivity and turnover in these two vegetation types are expected to be great, because Middelburg receives 365 mm rain annually, over twice as much as Prince Albert.

There were significant ($P < 0.01$, $df = 18$) correlations between total projected canopy cover and total fresh and dry above-ground biomass in 12.5-m^2 sample plots in plains vegetation at Tierberg. The following regression equations can be use to convert canopy cover values of plains differ little in latitude, altitude, topography or total rainfall, should be very similar. Vegetation at Mercury, Nevada (36°S 117°W; 1 060 m a.s.l.) in the Mojave desert, North America, a climatically similar site with a non-seasonal rainfall of 100 to 200 mm p.a., and alkaline soils (McMahon & Wagner 1985), resembles the southern Karoo shrubland in terms of biomass and cover. Above-ground biomass of perennial vegetation in the North American asteraceous shrublands is 2.96 to 5.58 t ha^{-1} and vegetation cover ranges from 22 to 38% (Hunter & Medica 1989). Despite the similarites between the Karoo and North American sites, the relative contributions of the various lifeforms to total biomass differed. Succulents comprised 41% of the biomass at the Karoo site but were rare at sites sampled in the Mojave Desert. On the other hand, ephemerals at times added about 200 kg ha^{-1} to the above-ground biomass in the Mojave but were rare at the southern Karoo site at all seasons regardless of rainfall (pers. obs.). A detailed study of the physical and chemical properties of soils may provide some clue to differences in the relative abundance of these lifeforms, as well as to differences in the sizes and spacing of plants. Plants are smaller in the southern Karoo site (maximum height 58 cm, mean height (±*SE*) is 15 ±1 cm, mean diameter (±*SE*) is 23 ±1 cm than in the Mojave where some shrubs exceed 110 cm in height and diameters average 32 cm (±*SE* 2 cm). Shrub density at Tierberg ranges from 3 to 7 shrubs m^{-2}, compared with densities of 1 to 4 shrubs m^{-2} at the Nevada site (Hunter & Medica 1989).

Studies of above-ground biomass alone may give a biased picture of interactions between plants and of the resources available to herbivores. Scott & van Breda's (1939) pioneering studies of roots of Karoo plants suggest that below-ground phytomass and root 'cover' may well be greater than that of the shoots. Root biomass and production studies would enable us to interpret trends observed in above-ground biomass of Karoo vegetation.

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Appendix 3

Seed production in rangelands of the southern Karoo.

Milton, S.J. & Dean, W.R.J. 1990

South African Journal of Science 86, 231-233.

Seed production in rangelands of the southern Karoo

Suzanne J. Milton and W.R.J. Dean

It has been suggested that seed set in certain Karoo plants is lowered as a result of grazing by domestic livestock and that this leads to changes in species composition of Karoo shrublands.[1] In other arid regions, granivorous insects, birds or rodents remove a large portion of the annual seed production and can change the relative abundance of plant species.[2] The impact of granivores on seed-banks in the Karoo is not yet known and there are no base-line data on seed production in the Karoo against which the relative effects of indigenous granivores and domestic livestock may be measured. Data on seed production of some common Karoo species planted at Grootfontein Agricultural College, Middelburg,[3] unfortunately cannot be converted to seed mass per square metre or kilograms per hectare, or extrapolated for natural veld.

Here we quantify the production of filled seeds for 15 of the most common perennial plant species at the Tierberg Karoo Research Centre and on adjacent grazing land. We present our data as seed numbers per plant as well as seed mass per unit area, so that they will provide a basis for comparative studies of granivory. Our seed production estimates from three different grazing regimes give some indication of the effects of grazing on seed production.

Study site

Seed production was estimated on the farm Tierberg (3322AB) and an adjoining farm, Argentina, in the Prince Albert district, southern Karoo. This area receives an average of 170 mm of rain annually, which falls mainly in autumn and spring. Absolute temperatures range from −5°C (winter minimum) to 43°C (summer maximum). The study area lies on a colluvial plain between low fold-mountains. The plains are dotted with *heuweltjies*, which are disturbed patches of relatively nutrient-rich soil,[4] approximately 175 m^2 in area, occurring at a mean density of 2.2 ha^{-1} on the plains at Tierberg.[5] Vegetation of the plains comprises scattered perennial succulent and non-succulent shrubs generally 40 cm in height. *Heuweltjies* have a dense cover of succulent biennials and shrubs. Grasses and annuals are not an integral part of this plains community although they occur sporadically along water courses.

Methods

All perennial plant species of the plains were counted in 30 plots (25 m^2), 10 of which were on a moderately grazed farm (6.0 ha per sheep, or 8 kg ha^{-1}), 10 in an exclosure lightly grazed (1.4 kg ha^{-1}, unpublished census data, W.R.J.D.) by wild herbivores for the past three years, but previously part of the moderately grazed rangeland, and 10 on an adjoining farm with a history of heavy grazing by sheep, goats and ostriches between 1913 and 1960 (2.7 ha per small animal unit, or 18 kg ha^{-1}). The 12 most common species on the plains, including three Asteraceous shrubs, one non-succulent member of the Aizoaceae (*Galenia fruticosa*), seven succulent, shrubby species of the Mesembryanthemaceae and a succulent biennial (*Augea capensis*) belonging to the Zygophyllaceae, were used to estimate seed production. These species made up over 90% of the total canopy cover on all three sites. An additional three species, limited mainly to *heuweltjies*, were also included in the calculations. The estimate of total seed production excluded 11 relatively uncommon Mesembryanthemaceae (0.17 – 0.26 m^{-2}), succulent undershrubs and annual forbs, which occurred at low and variable densities (0.02 – 0.08 m^{-2}).

Seed production of the study species was estimated by counting fruits (capitulae, capsules or inflorescences) on samples of 10 – 200 plants encountered along line transects. Fifty capitulae of each *Pteronia* species, 60 *G. fruticosa* capitulae and 10 ripe fruits of each of the other species were dissected to obtain a mean number of filled seeds per fruit. Seeds containing endophageous insects were not counted as filled seeds.

The densities of five species common on *heuweltjies* were estimated by counting plants on a sample of 21 *heuweltjies*, seven from each grazing regime. Density per *heuweltjie* was converted to density per unit area of plains by multiplying by 2.2 ha^{-1} (the mean density of *heuweltjies* per hectare visible on an aerial photograph of the study area). The production of filled seeds per unit area was calculated as for the plains' species.

Seed weights shown in Table 3 are means of samples of 20 seeds per species, or, in the case of seeds weighing less than 1 mg, 200 seeds weighed in batches of ten. The weights include the seed testa, dry viscous (*Augea capensis*) or pappilate (*G. fruticosa*) seed covering or, in Asteraceae, the achene with wings or pappus removed.

Results

We estimate that perennial shrubs shed about 3000 seeds per square metre annually on the lightly grazed area where sheep were excluded (Table 2). About half as many shrub seeds were produced in shrubland grazed by sheep (Table 2). *Galenia fruticosa* contributed 72%, Mesembryanthemaceae 17%, and seeds of shrubs unpalatable to sheep (*P. pallens*, *A. capensis*) 4% of all seeds produced in lightly grazed veld. On moderately grazed veld, where plant species composition and density are almost identical (Table 2), grazing appears to have increased the seed production of *O. sinuatum*, but reduced the seed production of *P. empetrifolia* and *G. fruticosa*. On the third site, a history of heavy grazing appears to have been responsible for reducing the numbers of plants that are palatable to sheep. Here, *G. fruticosa* contributes only 10% to the total number of seeds produced. *Osteospermum sinuatum* and *P. empetrifolia* are much reduced in size (Table 1) and produce less than 3 seeds per square metre, but seeds of unpalatable species make up 23% of the total seed production.

The total mass of seeds produced varied little between lightly grazed (33.8 kg

Table 1. Mean canopy volumes (s.e.m. shown in parentheses) of common shrubs on sites lightly, moderately and heavily grazed by mammalian herbivores. Canopy volume was calculated as $c(d_1/2.d_2/2)h$ where d_1 and d_2 are canopy diameters in two directions and h is plant height measured from ground level. The asterisk denotes a plant species palatable to sheep.

Species	n	Volume (cc $\times 10^{-3}$)
Light grazing		
**Galenia fruticosa*	50	23.7 (2.8)
**Osteospermum sinuatum*	174	10.1 (2.0)
**Pteronia empetrifolia*	55	29.9 (4.0)
Pteronia pallens	76	104.0 (11.1)
Moderate grazing		
**Galenia fruticosa*	51	16.2 (1.9)
**Osteospermum sinuatum*	164	9.1 (1.2)
**Pteronia empetrifolia*	53	18.2 (2.7)
Pteronia pallens	76	98.8 (8.4)
Heavy grazing		
**Galenia fruticosa*	51	11.5 (2.0)
**Osteospermum sinuatum*	65	1.6 (0.3)
**Pteronia empetrifolia*	2	7.3 (4.1)
Pteronia pallens	172	54.1 (18.3)

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Table 2. Continued.

Species	Plants m^{-2}	Fruits/plant	Seeds/fruit	Seeds m^{-2}
Heavy grazing (*heuweltjies*)				
Augea capensis	0.008 (0.002)	274 (41)	10 (1)	44
Malephora lutea	0.014 (0.001)	17 (1)	22 (8)	5
Psilocaulon utile	0.004 (0.0004)	178 (3)	5 (1)	4
Drosanthemum hispidum	0.002 (0.0004)	49 (3)	8 (1)	0.8
Sphalmanthus spp.	0.001 (0.0001)	42 (8)	13 (3)	0.5
Total (*heuweltjies*)	0.029			54
Total (plains + *heuweltjies*)	2.82			1453

changes in vegetation can be brought about indirectly by the effects of grazing on seed production. Moderate grazing can increase seed production in species which flower two or three times per year on new growth (*Osteospermum sinuatum*) but reduce seed production in species in which flowers develop once a year over many months (*Galenia fruticosa*, *Pteronia* spp.).

Continuous heavy grazing greatly reduces seed production of all plant species preferred by the grazing animal. Grazers reduce seed production of their preferred food plants both by removing flowers and unripe fruit and by keeping the plants small. We suggest that plant species composition will change in heavily grazed veld, where unpalatable shrub species produce more seeds than palatable species. Such changes in the relative abundance of shrub species will take many years, only becoming evident when seedling establishment fails to compensate for deaths of old plants.

Many mammals, birds and insects in arid regions are granivorous, and factors such as rainfall and grazing, which influence the relative abundance of seeds shed, are also likely to modify animal communities by causing immigration and emigration of granivores,[6,10,14] affecting breeding success and population sizes,[15] and influencing the outcomes of competitive interactions between granivore guilds.[15-19]

Until other estimates of seed production in semi-arid or arid shrublands have been published, we have no means of evaluating our results. Further research on seed production is needed before we can assess the interactions between domestic livestock, granivorous animals and vegetation composition, or understand the relationship between soil seed banks and annual seed production.

Table 3. Estimated seed production (kg ha^{-1}) at Tierberg Karoo Research Centre, Prince Albert, under three grazing treatments, assuming two flowering events for *Osteospermum sinuatum* and *Augea capensis*.

Species	Seeds m^{-2}	mg/seed	kg ha^{-1}
Light grazing			
Galenia fruticosa	2208	0.62 (0.02)	13.7
Pteronia empetrifolia	146	3.7 (0.1)	5.4
Osteospermum sinuatum	66	9.1 (0.4)	6.0
Mesembryanthemaceae	533	0.5 (0.06)	2.7
Augea capensis	48	8.3 (0.3)	4.0
Pteronia pallens	60	3.3 (0.2)	2.0
Total	3053		33.8
Moderate grazing			
Galenia fruticosa	273	0.62 (0.02)	1.7
Pteronia empetrifolia	14	3.7 (0.1)	0.5
Osteospermum sinuatum	112	9.1 (0.4)	10.2
Mesembryanthenaceae	567	0.5 (0.06)	2.8
Augea capensis	66	8.3 (0.3)	5.5
Pteronia pallens	84	3.3 (0.2)	2.8
Total	1078		23.5
Heavy grazing			
Galenia fruticosa	146	0.62 (0.02)	0.9
Pteronia empetrifolia	1	3.7 (0.1)	0.04
Osteospermum sinuatum	3	9.1 (0.4)	0.3
Mesembryanthemaceae	969	0.5 (0.06)	4.8
Augea capensis	192	8.3 (0.3)	15.9
Pteronia pallens	143	3.3 (0.2)	4.7
Total	1443		26.6

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Appendix 4

Mima-like mounds in the southwestern Cape: are the origins so mysterious?

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Mima-like mounds in the southern and western Cape: are the origins so mysterious?

The origin of *heuweltjies*, or Mima–like mounds, in the southern and western Cape Province, has been debated since 1910.[1] These circular, evenly spaced and nutrient-rich patches of soil occur between 29° and 34°S and 17° and 22°W (ref. 1). Their origins and persistence are of interest to ecologists and agriculturalists, because they cause heterogeneity in soil fertility and increase plant and animal species richness.

Of the various hypotheses advanced to explain their origin, Lovegrove and Siegfried[1] consider that the one which ascribes *heuweltjies* to an ongoing, zoogenic process involving termites and molerats, is the most realistic. Their conclusion is based on a study of *heuweltjie* spacing throughout the distribution range of the mounds,[2] and analysis of stone sizes on and off *heuweltjies* at Robertson and Clanwilliam.[2] Lovegrove and Siegfried[3] show that all *heuweltjies* fall within the distribution ranges of the small harvester termite *Microhodotermes viator* and the molerat *Cryptomys hottentotus*. In this paper, we suggest that the generation and maintenance of *heuweltjies* can involve a wide variety of other animals.

In studies on the biology and chemical control of termites, Coaton[4,5] showed that *M. viator* constructs only one 'hive' or breeding chamber per colony. Each of the 28 *heuweltjie* mounds Coaton excavated in the Rietbron area south of Beaufort West contained a *M. viator* nest,[5] as did *heuweltjies* excavated by Merryweather[6] in the Wellington–Malmesbury area. The aggressive interactions between termite workers collected from neighbouring mounds showed that they belonged to different colonies.[4] In the same paper Coaton described the termites' behaviour as follows: 'From its nest the colony of *M. viator* drives outwardly radiating passages through the soil which terminate in a series of foraging holes. The waste soil is deposited in conical dumps less than two inches high. Over the sites of the hive cavities the soil is eliminated in larger dumps.' In having only one hive per colony, *M. viator* differs from the larger harvester termite *Hodotermes mossambicus*.[5] This tropical termite occurs from the north-eastern limits of *M. viator*'s distribution throughout the arid grass and bushveld zones of Africa to Ethiopia. The degree of mounding that occurs over *M. viator* nests is apparently related to the age of the colony,[5] to the clay content of the soil and the likelihood of freshly excavated soil being washed away by rain.[4]

It seems clear that *M. viator* is the principal agent in the formation of *heuweltjies*. But it is less clear that molerats are prime movers in the formation of these mounds throughout their distribution in the southern and southwestern Cape.[1] The inclusion of a particular mammal species in the *heuweltjie* model is conceptually limiting and restricted to a particular area. As an alternative, we suggest that a number of animals are important in disturbing and fertilizing the soils of these mounds.