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

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Received 1 October 1991; accepted 9 December 1991

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 naterials 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.

Die mis van bergskilpaaie *Geochelone pardalis* wat in rotsagtige habitatte van die suidelike Karoo versamel is, het ten minste 75 gras-, vetplant- en opslagplantsoorte bevat wat aan 26 families behoort het. Sagte groen plante is blykbaar goed verteer maar takkies, dorings en veselagtige materiaal is nie deur vertering afgebreek nie. Blomme, vrugte en sade het 67% van 356 uitgekende plantdele uitgemaak. Ontkiemingstoetse het aangedui dat bergskilpaaie lewensvatbare sade van Aizoaceae, Chenopodiaceae, Crassulaceae, Cyperaceae, Fabaceae, Poaceae en Scrophulariaceae sou kon versprei.

Adult leopard tortoises *Geochelone pardalis* (Bell) weigh 8 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, Bourn & Swingland 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).

In the present study the diet of the leopard tortoise in the arid Karoo near the south-western limits of its distribution range is described, and its potential for dispersing viable seeds of indigenous and alien plants, is discussed.

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 × 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) 5-min 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 h of field work on plains at Tierberg Research Centre (for site description see Milton, Dean & Kerley in press) and during 50 h spent on surrounding rocky ridges. The study was confined to the Prince Albert District (32–34°S / 22–24°W) 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°C, minima 1–17°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, Reid, van

Rooy & Smook 1985; Gibbs Russell, Welman, Retief, Immelman, Germishuizen, Pienaar, van Wyk & Nicholas 1987 for all groups except the Aizoaceae, where treatment follows Hartmann & Bitrich (1991). These authors recognize five suprageneric groups: the Aizooideae, Sesuvioideae, Tetragonioideae, 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 (*sensu* 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 of the leopard tortoise faecal samples from the southern Karoo were collected on rocky ridges (31) 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 large beetles and a cicada), bone fragments and small stones made up the remaining 1% of faecal contents.

The frequency of plant-life forms in *G. pardalis* faeces differed significantly from the frequency of plant-life forms in the vegetation where the faeces were found (χ^2 = 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,

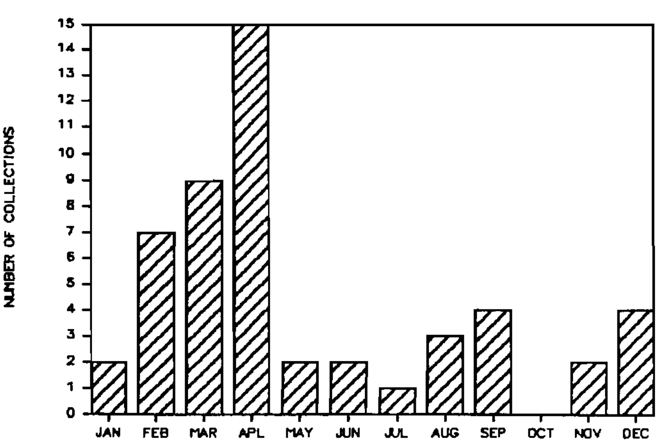

Figure 1 Seasonal distribution of collections of leopard tortoise faeces from the southern Karoo.

Table 1 Items identified from a sample of 51 leopard tortoise (*Geochelone pardalis*) faeces collected in the southern Karoo. Asterisks denote non-indigenous plant species

Genus and species	Total incidence	Flowers and fruit	Number of seeds
Plants			
Poaceae			
Aristida spp.	11	4	2
Cynodon spp.	3	3	0
Digitaria argyrograpta (Nees) Stapf	2	1	0
Enneapogon scaber Lehm.	29	26	10
Enneapogon devauxii Beauv.	10	6	45
Eragrostis obtusa Munro	6	5	57
Fingeruthia africana Lehm.	3	3	0
Unidentified grass leaves	21	7	25
Unidentified grass bases	18	4	0
Hordeum murinum L.	2	1	0
Karoochloa purpurea (L.f.) Con. & Teur.	1	1	5
Lolium sp.	1	1	10
Oropetium capense Stapf	1	1	0
Setaria verticillata (L.) Beauv.	1	1	30
Tragus sp.	1	1	1
Cyperaceae			
Unidentified sedge	2	2	66
Hyacinthaceae			
Albuca sp.	1	1	0
Asphodelaceae			
Haworthia glauca Baker	4	0	0
Haworthia semiviva (V.Poelln.) B.M. Bayer	1	1	0
Santalaceae			
Thesium lineatum L.f.	1	1	2
Polygonaceae			
Polygonum sp.	1	1	3
Chenopodiaceae			
Atriplex lindleyi Moq.*	2	2	1
Atriplex semibaccata Aell.*	2	2	4
Chenopodium sp.	6	6	10
Amaranthaceae			
Amaranthus sp.	2	2	36
Aizoaceae: Aizooideae, Sesuvioideae, Tetragonioideae			
Galenia papulosa (E.& Z.) Sond.	9	9	18
Hypertelis salsoloides (Burch.) Adamson	6	6	27
Limeum aethiopicum Burm.	19	19	328
Tetragonia spicata L.f.	1	1	1
Tetragonia echinata Ait.	5	5	10
Trianthema trinquetra Willd.	1	1	31
Aizoaceae: Mesembryanthemoideae & Ruschioideae			
Ruschia spinosa (L.) H.E.K. Hartm.	3	0	0
Malephora lutea (Haw.) Schwant.	2	2	0
Pleiospilos compactus (Ait.) Schwant.	1	1	30
Skeletium sp.	1	0	0
Phyllobolus sp.	2	2	0
Trichodiadema sp.	3	0	0
Unidentified mesembryanthema	19	13	17
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

Table 1 Continued

Genus and species	Total incidence	Flowers and fruit	Number of seeds
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
Cactabeae			
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
Asteraceae			
Chrysocoma ciliata L.	1	1	1
Cuspidia cernua (L.f.) B.L. Burtt	10	10	14
Eriocephalus sp.	2	2	9
Leysera tenella D.C.	5	4	10
Osteospermum calendulaceum L.f.	1	1	2
Pteronia sp.	4	4	0
Ursinia nana D.C.	2	2	4
Unidentified succulent leaves	21	0	0
Total occurrences	356	238	1289
Animal matter			
Insecta			
Coleoptera: Tenebrionidae (>15 mm)	5		
Homoptera: Cicadidae (>15 mm)	1		
Heteroptera: Pentatomidae (<10 mm)	1		
Hymenoptera: Formicidae (<10 mm)	3		
Inorganic matter			
Bone fragments (8–10 mm)	2		
Stones (4–7 mm diameter)	4		

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

	Faeces		Vegetation			
Life-form	Occurrence	(%)	Cover	(%)	χ^2	p
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

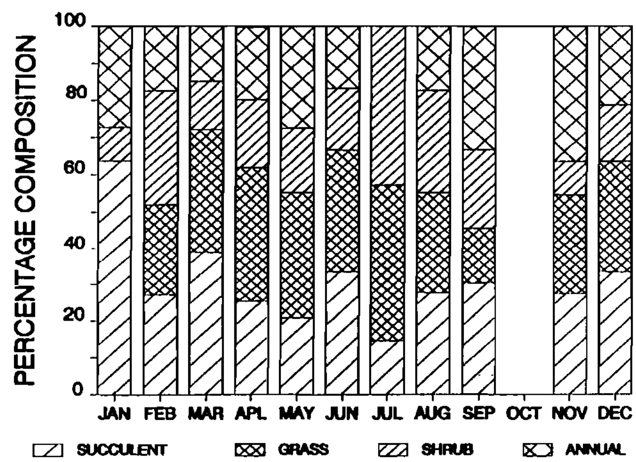

Figure 2 Monthly distribution of succulents, shrubs, grasses and annuals in the leopard tortoise faeces from the southern Karoo.

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: $df = 49$; $r^2 = -0{,}385$; $p < 0{,}01$).

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 × 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.

A total of 1289 seeds were found in 38 of 51 faeces collections sorted under magnification and a mean of 25 seeds/faeces sample ($SD = 38$; range 0–179) was obtained using this method (Table 1). Of these seeds, 36% were Aizoaceae, 19% grasses and sedges and 12% Fabaceae. The most abundant seeds identified were *Limeum aethiopicum* Burm.

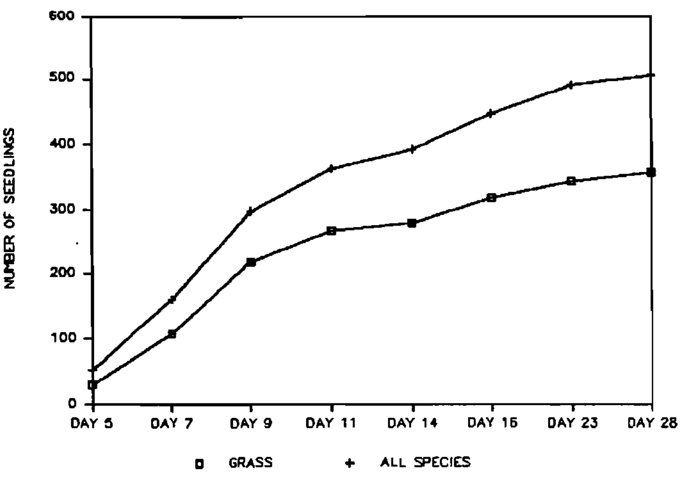

Figure 3 Cumulative germination of grass and forb seeds from faeces of leopard tortoises collected in the southern Karoo.

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

	Sample number												
Plant identity	1	2	3	4	5	6	7	8	9	10	11	12	Total
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
Mesembryanthema	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

(Aizoaceae) a low-growing shrub present in 38% of the samples.

Viability trials with 12 trays of faeces yielded a total of 524 seedlings, most of which emerged during the first 10 days. The number of seedlings germinating ranged from 1 to 92 with a mean of 44 (SD = 36) per tray. No germination was observed after 33 days although the faeces were watered for seven weeks. After 48 days the seedlings showed symptoms of nutrient deficiency and few survived long enough to be identified to generic level. Grasses constituted 63% of the seedlings (Figure 3) and the remainder comprised Aizoaceae (9%), Brassicaceae (5%), Chenopodiaceae (3%), Crassulaceae (1%), Cyperaceae (4%), Fabaceae (1%), Scrophulariaceae (8%) and unidentified forbs (6%) (Table 3).

Discussion

The present study confirms reports (Boycott & Bourquin 1988; Branch 1988) that *G. pardalis* has a diverse diet and, although largely vegetarian, nay occasionally eat bone fragments (Branch 1958; 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 south-western 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, Medica & Lyons 1984).

Among the succulents eaten by *G. pardalis* were plants topped with multi-pronged spines (*Euphorbia stellaspina; Ruschia spinosa)* and chemically defended species including *Tylecodon* spp. which contain cardiac glycosides and Mesembryanthemoideae nany of which have high concentrations of oxalic acid, sodium or the alkaloid, mesembrine (Kellerman, Coetzer & Naude 1988). These succulents are generally avoided by sheep, goats and indigenous antelope (Henrici 1947; Davies, Botha & Skinner 1986; pers. obs.) but are eaten by some indigenous rodents. Succulents, including chemically defended species, constitute 50–60% of the diet of the whistling rat *Parotomys brantsii* Smith (du Plessis 1989), a common herbivorous rodent in the southern Karoo. Oxalates can be denatured by micro-organisms in the unusually large caecum of desert rats (McBee 1971) and it is possible that oxalates may be excreted in crystalline form by tortoises and other desert reptiles which excrete uric acid crystals rather than urea (Louw & Seely 1982). Desert herbivores such as tortoises, lizards and rodents which lack sufficient mobility to track standing water have apparently been selected to cope with the physical and chemical defences of succulent plant families including Aizoaceae, Cactaceae, Crassulaceae, and Euphorbiaceae.

Large tortoises such as *Geochelone pardalis* and *G. gigantea*, which take up to three weeks to digest food (Hnatiuk 1978) and have a home range of 1–2 km^2 (van Zyl 1966; Branch 1988), disperse large quantities of seed. The species which appears best adapted for dispersal by large tortoises is *Enneapogon devauxii*, a small annual grass indigenous to arid parts of southern Africa, and North and South America which bears cleistogamous seeds in the base of the tuft (Hitchcock 1950; Chippendall 1955). The Ruschioideae subfamily of the Aizoaceae with their woody capsules, which are swallowed and passed intact by leopard tortoises, also appear to be well suited for tortoise dispersal. Although Mesembryanthema are dispersed mainly by rain drops (Herre 1971), the small seeds are evidently durable and can survive digestion by rodents (Jump 1988).

Many annual and ruderal plants are eaten by *G. pardalis* and the presence of eight non-indigenous plant species in the faeces indicate that leopard tortoises occasionally forage on road verges or in disturbed vegetation near waterpoints used by domestic livestock. Changes in Karoo vegetation caused by heavy grazing by sheep or goats usually result in a decrease in perennial grass and shrub cover and a concomitant increase in the succulent and ephemeral component of the vegetation (Roux & Vorster 1983). Since *G. pardalis* makes little use of woody shrubs and includes many ephemeral plants in its diet, it is unlikely that grazing by small stock could greatly reduce its food source. Barriers such as roads, railway lines and fences could restrict movement of larger tortoises thereby reducing mate choice or access to water. *Geochelone pardalis* is viewed with disfavour by those farmers who not only believe that they compete for grazing with domestic animals (Boycott & Bourquin 1988), but also maintain that tortoises urinate and sometimes drown in drinking troughs, making the water unacceptable to livestock (pers. comm., C.P. Marinkowitz). Some landowners kill tortoises which frequent water points.

It is uncertain why *G. pardalis* is absent from the Central Karoo. Some authors consider that it may have been exterminated by man in the Central Karoo (Greig & Burdett 1976; Boycott & Bourquin 1988), but it seems likely that the distribution of this species is limited by temperature extremes (W.R. Branch *in litt.*), the availability of suitable hibernation and nest sites or food availability. These requirements may also determine local distributions of the species. Sightings of *G. pardalis* confirm faecal distribution data and indicate that in the southern Karoo this tortoise is largely restricted to rocky ridges and is generally absent from the intervening silty plains, except in the green oases that develop around livestock water points. Large *G. pardalis* have little physiological control over their body temperature (Perrin & Campbell 1981), but individuals living on ridges would be able to control their temperatures to some extent by 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.* in press), there would appear to be few temperature refuges for large tortoises.

Acknowledgements

I am grateful to C.P. Marinkowitz, H. Wright and my husband Richard Dean for their observations on tortoise behaviour and for collection of tortoise faeces and thank the many farmers in the Prince Albert and Rietbron areas who gave me permission to work on their land. Critical comments by W. Branch, W.R.J. Dean and an anonymous referee improved this paper. The research was supported by the Foundation for Research Development and by the University of Cape Town.

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