

Habitat selection by the gerbils *Gerbillurus paeba* and *G. tytonis* in the Namib Desert dunes

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Habitat selection, in relation to plant species diversity, plant biomass, plant cover and substrate compaction was investigated in the pygmy hairy-footed gerbil *Gerbillurus paeba* and the dune hairy-footed gerbil *G. tytonis* at three study areas situated across the Namib Desert dune fields. Plant species diversity and substrate compaction were the major habitat variables implicated in ecological segregation between the congeners. *G. tytonis* preferred habitats with high plant species diversity, avoided compact soils and at the most easterly study site preferred soft shifting sand. *G. paeba* avoided areas with high plant species diversity and preferred habitats with low plant species diversity. In the absence of *G. paeba*, *G. tytonis* selected habitats with a high plant species diversity suggesting that the presence of *G. paeba* did not influence the habitat selection of *G. tytonis*. There is no competitive release and *G. tytonis* does not invade habitats usually occupied by *G. paeba*.

Keywords: desert, dunes, gerbils, *Gerbillurus*, habitat selection, Namib

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Introduction

The habitat preferences of the pygmy hairy-footed gerbil *Gerbillurus paeba* and the dune hairy-footed gerbil *G. tytonis* are unknown. Griffin (1990) captured *G. tytonis* frequently on sandy substrates and *G. paeba* on hard substrates, while Jarvis (pers. comm.) caught *G. tytonis* near dune crests and *G. paeba* at dune bases. *G. paeba* is widely distributed in the arid zones of southern Africa and its general ecology is known (Perrin, Dempster & Downs, in press a), but *G. tytonis* is confined to the dune fields of the Namib Desert, and its ecology is virtually unknown (Perrin, Downs, Dempster & Boyer, in press b).

Non-quantitative studies have shown that *G. paeba* occurs on sandy or alluvial substrates with grass, scrub or scant light woodland (Smithers 1971; Downs & Perrin 1989). In the Kalahari they are common on sand, particularly on dune slopes, but are scarce on calcrete riverbanks and pans where fine soil predominates (Nel & Rautenbach 1975). In north-eastern Botswana they do not occur on consolidated soils, but in Mozambique they occur on the sandy alluvium of the Bube River (Skinner & Smithers 1990). *G. p. coombi* is restricted to sandy areas of the Northern Transvaal (Rautenbach 1982), and in the Eastern Cape *G. p. exilis* uses coastal dunes, preferring dune valleys to dune crests (Ascaray 1986); Christian (1979) reported *G. p. paeba* as occurring only on the eastern edge of the Namib dune field bordering the gravel plains of the Pro-Namib.

The aim of this study was to quantify the habitat preferences of the two species in the central Namib Desert dune fields. It was hypothesised that *G. paeba* and *G. tytonis* may coexist by selecting different habitats (Hughes, Ward & Perrin 1994) and/or different substrates (Nel & Rautenbach 1975; Hughes, Ward & Perrin 1995) and that the presence and density of gerbil populations is influenced by plant biomass and cover (Harris 1984; Thompson 1982; Christian 1980; Kotler & Brown 1988).

Methods

Study area

The Namib varies from extreme desert to semi-desert conditions, with hot to mild temperatures (McGinnies, Goldman & Paycore 1977; Lovegrove 1993). It is a coastal desert extending from southern Angola, through Namibia, to the Olifants River in the Republic of South Africa. The main area of dunes within this region occurs between the Kuiseb River and Luderitz, 400 km to the south (Barnard 1973). There is a marked climatic gradient from east to west (Besler 1972), with the highest amount of rainfall on the eastern edge of the dune field. Most rainfall occurs between January and March, when mean temperatures are highest, while the months June to September are somewhat cooler than the period October to January (Lancaster, Lancaster & Seely 1984). Unlike other deserts, temperature extremes are relatively uncommon.

In the Namib, soil development is nonexistent on the dunes and the bedrock surfaces (Rutherford & Westfall 1986; McGinnies *et al.* 1977; Lovegrove 1993). The soils range from slightly alkaline to slightly acidic and are dominantly reddish-brown. The study sites were located on linear dunes which run north to south and, except at the site Far East, were separated by wide interdune valleys. The Namib has very little vegetation and some plants are leafless, succulent or halophytic (Louw & Seely 1982; Lovegrove 1993). In the inner Namib, a short grass develops in summer (December onwards) depending on rainfall.

Rodents were sampled at three study areas situated across the east-west climatic gradient; at Nara Valley, Bushman's Circle and Far East (Table 1 and Figure 1).

Collection of data

Price (1977) has shown experimentally that capture rate indicates level of habitat use by rodents. Here, habitat preferences were inferred by the presence (capture) of *G. paeba* or *G. tytonis* in trapping grid cells with known habitat

Table 1 A comparison of some of the physical parameters of the three study sites. Meteorological data, from Lancaster *et al.* (1984), were obtained from weather stations near to the study sites or on a similar longitude, or are extrapolated from stations situated on longitudes adjacent to the sites. Extrapolations for Bushman's Circle were not always possible (N/A)

	Nara Valley	Bushman's Circle	Far East
Grid reference	23°37'S, 14°58'E	23°42'S, 15°22'E	23°47'S, 15°48'E
Distance from coast (km)	45	85	130
Elevation at base of dune (m)	420	600	890
Average annual rainfall (mm)	20	50	100
Maximum period without effective rain (years)	7	N/A	2
Average annual fog precipitation (mm)	50	20	0
Average number fog-days/year	40	20	2
Maximum period without fog (days)	60	N/A	700
Average annual maximum temperature (°C)	28.0	29.0	28.5
Average annual temperature (°C)	21.0	21.5	21.5
Average annual minimum temperature (°C)	12.5	14.0	15.0

characteristics.

Plant species diversity, plant biomass, plant cover and substrate compaction (see below), across the dune profile were recorded. Hill's (1973) species diversity index was employed as an indicator of the effective number of plant species present in a community. It accounts for diversity and evenness of species by weighting for proportional abundance. Hill (1973) recognised that there is almost unlimited scope for

mathematical generality in relation to measures of diversity and taxonomic differences, but that simple and well understood indices should be used. He summarised his notion of diversity as being little more than the effective number of species present. This was achieved by defining a diversity number to be the reciprocal of a mean of proportional abundance by employing a notation which graded these numbers according to their propensity to include or to exclude the rarer species in the enumeration (Rényi 1961). Plant biomass was computed from data collected on plant density (number of plants per unit area), mean individual plant diameter, and allometric growth curves for each species (Boyer 1989). Plant crown cover was determined by the intercept method (Greig-Smith 1983); all standing plant material including perennial ephemerals, live or dead, was recorded as cover. Several of the species occurring in the study areas appeared to be perennial ephemerals; e.g. *Stipagrostis ciliata*, *Centropodia glauca*, *S. lutescens*, *Kohautia ramosissima*, *Hermania minimifolia*.

Plant cover was reported as a percentage of the total surface area. Coefficients of variation were presented to indicate the homogeneity of cover of the various species within each area. Percentage cover was arcsine transformed (Zar 1984).

To enable comparisons between sites and between the two substrates i.e. dune and interdune plain at each site, and with other deserts, average plant cover was reported separately.

Substrate compaction was measured as penetrability using a penetrometer (Johnson pers. comm.) and converted to compaction Units (Boyer 1988). Compaction was measured at each trapping station and at the four compass points 2 m away from the sample point, giving 10 data points at each 20-m interval. If a sample point coincided with vegetation the nearest point of bare sand, not occurring beneath the plant canopy, was sampled. Compaction values were averaged within 20-m intervals at depths of 5 cm and 10 cm, and in areas of low compaction, at 15 cm and 20 cm. Owing to mechanical problems with the penetrometer, it was only possible to obtain

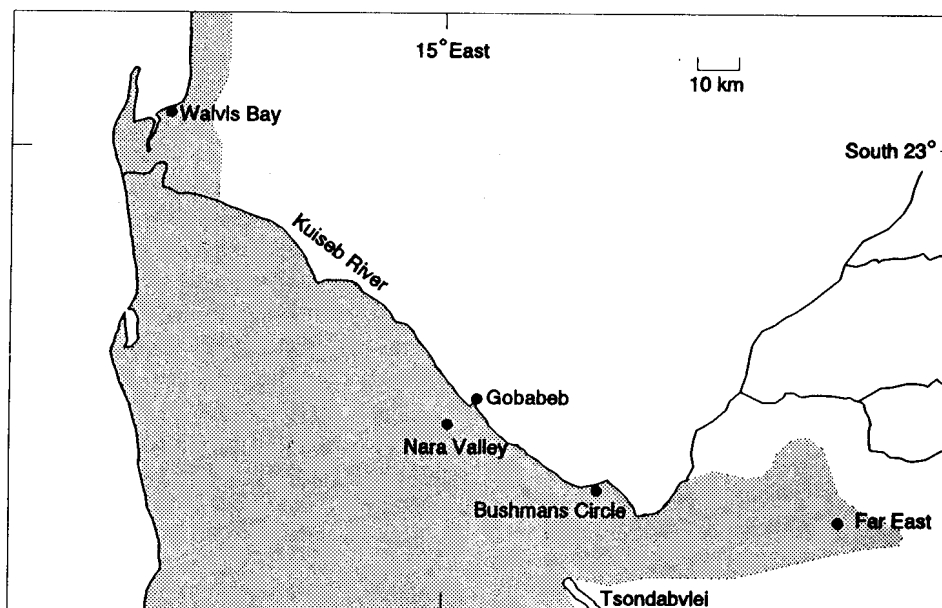


Figure 1 Study sites were situated at Nara Valley, Bushman's Circle and Far East in the Namib Desert dunefields. Shading = dunefields; unshaded = gravel plains.

data for the 5 cm, 10 cm and 15 cm soil depths at Nara Valley, averaged.

Capture rates were obtained from capture-mark-recapture live trapping at the three study sites between February 1984 and August 1985 (Boyer 1988). Single box traps baited with peanut butter and oats were set at each station on a 5 × 30 grid with 20-m spacing for two nights each month at each study area. Traps were checked twice daily yielding four capture opportunities.

Correlation coefficients between the habitat parameters and the use of habitats by *G. tytonis* were calculated separately for each study area. Data from the three study sites were then pooled and used to test for correlations between each of the four measured habitat parameters and the occurrence of *G. tytonis*. Partial correlation coefficients were calculated (Zar 1984) between rodent habitat use and each of the habitat variables, while holding the effect of other variables constant. This was particularly appropriate where habitat variables, such as plant biomass and cover, and to a lesser extent plant species diversity and soil compaction, had some degree of interdependence. *G. paeba* occurred only at Far East and the sample size was too small to allow analysis by partial correlation.

Results

Vegetation was relatively sparse at all sites with plant cover ranging from 1.5% at Nara Valley to over 7% at Far East and Bushman's Circle. The structure of the plant community was simple even in comparison with other deserts. The dune profile comprised western dune base and plinth, dune crest, and eastern dune plinth and base habitats (Figure 2). The highest plant species diversity index (4.83) was recorded at Nara Valley suggesting that the most complex community comprised only five effective species (Figure 2). At Far East plant diversity was similar to that at Bushman's Circle (ranging from 1.00 to 2.56), while at Nara Valley most vegetation zones comprised a few species, with a maximum diversity of 4.83 at the dune base. Most plant species were grasses, and the dune area at Far East was dominated by two grass species, *Cladographis spinosa* and *Stipogrostis ciliata*, while *Hermania minimifolia* was uncommon. Nara Valley had one dominant species *S. sabulicola*, although *Trianthema hereroensis* constituted 25% of the total plant cover. At Bushman's Circle, four plant species were relatively common, *S. sabulicola*, *S. cf. nama-quensis*, *S. lutescens* and *Centropodia glauca*. *S. ciliata* was the dominant plant species on the interdune plains at each study site. Substrate compaction was lowest on the dune crest and highest on the interdune plains at all study areas (Figure 2).

Some green vegetative material was available at all times, with peak periods of growth occurring after the rains for plant species occurring on the lower dune slopes at Far East and Bushman's Circle. The species occurring on the upper dune slopes, and those at Nara Valley, however, showed little seasonality of vegetative production. Total plant production was estimated at 200 kg ha⁻¹ year⁻¹ at Far East and Bushman's Circle, while at Nara Valley it was minimal (Boyer 1988).

Using the data summarised in Table 2, partial correlation coefficients were computed (Table 3). *G. tytonis* (n = 158) selected habitats (and zones) with a high plant species diver-

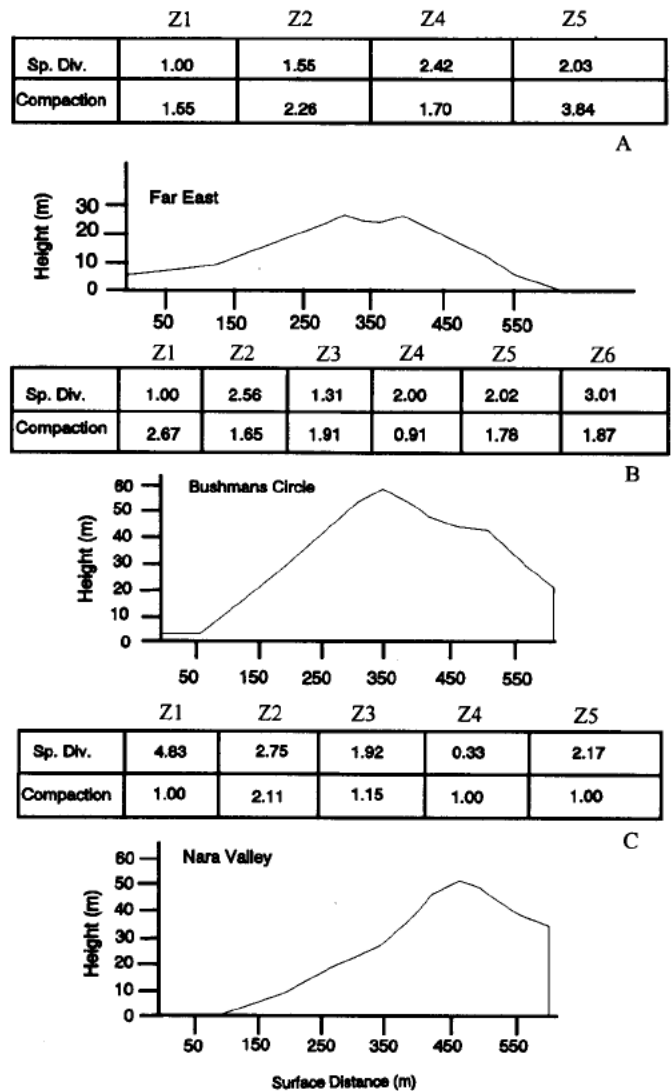


Figure 2 Dune profiles, substrate penetrability (compaction), and plant species diversity (Sp. Div.) for the habitat zones at the three study areas (A) Far East, (B) Bushman's Circle, (C) Nara Valley.

sity ($p = 0.006$) and low sand compaction ($p = 0.005$). However, plant biomass and plant cover, influenced habitat selection of *G. tytonis* only at Bushman's Circle.

With respect to individual populations, that of *G. paeba* (n = 48) at Far East was only marginally negatively correlated with plant species diversity (Table 4) and was not significantly correlated with any other habitat parameters. At Far East, habitat selection by *G. tytonis* (n = 38) tended to favour areas of high plant species diversity but was significantly associated with a soft substratum (Table 4). At Bushman's Circle, *G. tytonis* (n = 73) showed a significant selection for high plant species diversity, and plant biomass (Table 4). The occurrence of *G. tytonis* at Nara Valley was also significantly affected by plant biomass, and marginally by plant species diversity (Table 4). At Bushman's Circle and Nara Valley, plant biomass was significantly correlated with plant cover ($r = 0.98, p = 0.002$). Habitat selection was evident in *G. tytonis*, which is a habitat specialist, but not in *G. paeba*, which is a habitat generalist.

When the densities of the two species in all zones across

Table 2 Capture rates of *G. paeba* and *G. tytonis* and quantification of habitat parameters

Study area	Zone	Capture rate %		Plant species diversity <i>n</i> = 120	Plant biomass kg/ha <i>n</i> = 120	Plant cover m ² /ha <i>n</i> = 120	Substrate compactness MPa <i>n</i> = 10 per site
		<i>G. paeba</i> <i>n</i> = 46	<i>G. tytonis</i> <i>n</i> = 158				
Far East	Z1*	9.0	1.4	1.00	1.800	12.21	2.40
	Z3	7.1	12.2	1.55	2.147	19.62	1.13
	Z4	3.8	15.6	2.42	1.021	12.00	0.86
	Z5	4.8	9.6	2.03	1.047	10.78	1.78
Bushman's Circle	Z1		9.2	1.00	0.387	6.60	1.46
	Z2		32.0	2.56	1.832	19.08	0.87
	Z3		19.2	1.31	1.622	14.75	1.01
	Z4		17.2	2.00	0.050	2.69	0.40
Nara Valley	Z5		26.4	2.02	1.564	18.39	0.88
	Z6		26.9	3.01	1.625	17.75	0.92
	Z1		8.5	1.00	0.004	0.57	2.45
	Z2		11.1	2.11	0.372	10.12	1.86
	Z3		9.6	1.15	0.279	9.42	0.84
	Z4		8.9	1.00	0.019	2.43	0.22
	Z5		22.1	1.00	0.023	2.36	1.03

Z1 = West interdune plain, Z2 = West dune base, Z3 = West dune plinth, Z4 = dune crest, Z5 = East dune plinth, Z6 = East dune base

Table 3 Partial correlation coefficients: *G. tytonis* habitat selection against habitat parameters for all study areas combined

Habitat <i>Y</i>	Sp. div. $X_1 = +0.4363$	Biomass $X_2 = -0.0092$	Cover $X_3 = +0.0904$	Soil $X_4 = -0.4696$
Probability	0.006	0.00 (N.S.)	0.010	0.005

Habitat = rodent habitat selection, Sp. div. = plant species diversity, Biomass = plant biomass, Cover = plant cover, Soil = soil penetrability

Table 4 Correlation coefficients between gerbil habitat occupation and individual habitat parameters

	Species	Locality	Variable	Correlation coefficient (<i>r</i>)	Probability level (<i>p</i>)
Habitat generalists	<i>G. paeba</i>	Far East	Plant sp. diversity	-0.92	0.076 (NS)
	<i>G. tytonis</i>	Far East	Plant sp. diversity	+0.87	0.134 (NS)
			Soft substrate	+0.97	0.023
Habitat specialist	<i>G. tytonis</i>	Bushman's Circle	Plant sp. diversity	+0.82	0.045
			Plant cover	+0.82	0.044
	<i>G. tytonis</i>	Nara Valley	Plant sp. diversity	+0.83	0.079
Habitat specialist	<i>G. tytonis</i>	All	Plant sp. diversity	+0.64	0.011
			Soft substrate	+0.51	0.048

the dunefield were compared ($n = 158$), a significant negative correlation was observed ($r = -0.82$, $p < 0.001$). The inverse relationship demonstrated that population dynamics were not synchronised but there was no evidence of competitive exclusion. In areas of sympatry on the dunes, the demographic patterns of the two species populations were independent ($r = -0.26$; $p > 0.05$).

The total population density of *G. paeba* ($n = 47$) in all habitats was surprisingly and significantly correlated with the population confined to the dune habitat ($r = 0.84$; $p < 0.001$). Since the interdune plains are the preferred habitat of *G. paeba* (Boyer 1985), and *G. tytonis* is behaviourally dominant over *G. paeba* (Dempster & Perrin 1989, 1990), it appears

that during periods of high *G. paeba* and low *G. tytonis* density, suboptimal dune habitats are colonised by *G. paeba*.

Discussion

At Far East, *G. tytonis* preferred habitat zones with high plant species diversity, but avoided compacted soils, whereas *G. paeba* avoided areas with high plant species diversity and preferred habitats with low plant species diversity.

G. tytonis only showed a preference for non-compacted or soft shifting sand at Far East, and the dune crest zone. It may prefer soft substrata for burrow construction since its psammophilous adaptations include large hairy feet for locomotion on dunes, which may reduce its capacity for burrowing in

compacted soils. However, *G. tytonis* construct more complex burrows than *G. paeba* (Downs & Perrin 1989). The preference of *G. tytonis* for areas with high plant species diversity may be associated with the varied phenological characteristics of the individual plant species that provide a greater continuity of food resources (Boyer 1988), since the gerbils eat large amounts of plant material (Perrin, Boyer & Boyer 1992).

At Bushman's Circle, in the absence of *G. paeba*, *G. tytonis* selected habitats with a high plant species diversity. This suggests that the presence of *G. paeba*, which preferred areas of low plant species diversity, did not influence habitat selection of *G. tytonis* in areas of syntopy. There is no competitive release and *G. tytonis* does not invade habitats usually occupied by *G. paeba*.

Plant biomass and plant cover were significantly correlated ($r = 0.98$; $p = 0.002$) and *G. tytonis* preferred habitat zones with high plant biomass and cover at Bushman's Circle, but at no other study areas. This was probably caused by high predation pressure (Hughes *et al.* 1994) at Bushman's Circle, since it is adjacent to the Kuiseb River, a known predator refuge with a high density of predators (Boyer 1988). Cover is known to provide protection for gerbils in desert ecosystems (Hughes *et al.* 1994).

At Nara Valley, *G. tytonis* showed no preference for any of the measured habitat parameters, possibly owing to large foraging ranges and low capture rates (densities) at this site. Use of the western dune plinth by *G. tytonis*, an area of high plant species diversity, was unexpectedly low, probably because many plants were dead or photosynthetically inactive. These interpretations are more parsimonious than invoking competitive release.

Generally, *G. tytonis* preferred habitats with loose soils and high plant species diversity. High plant species diversity was associated with the dune crest and the eastern plinth at Far East, where star dunes occur, but with the western dune base of the linear dunes at Bushman's Circle and Nara Valley. At all study areas, loose soils were associated with the dune crest and the dune plinth. Prime habitat occurred for *G. tytonis* on the dune crest at Far East, where *G. paeba* is segregated by habitat differences and behaviour (Dempster & Perrin 1990). In the Namib, *G. paeba* prefers (relatively) compacted soils which appears to contradict unquantified reports in the literature. Either the substrates of the Namib dunefields are generally more penetrable or *G. paeba* is displaced to sub-optimal habitat by *G. tytonis*.

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