

Seasonal changes in the population dynamics of hairy-footed gerbils in the Namib Desert

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The dynamics and demography of gerbil populations at three study sites in the Namib Desert dunefields are reported. Low and fluctuating rodent biomass resulted from low primary and insect productivity caused by extremely low levels of precipitation. Reproduction was strictly seasonal and temporally associated with the occurrence of seeds in the diet. However, although seeds likely triggered reproduction, they did not sustain breeding. The gerbils were primarily insectivorous but also consumed some green plant material. Insects supply the protein, and plant tissues the vitamins and minerals, necessary for the maintenance of reproduction. Precipitation drove the system, regulated primary production, and hence determined gerbil population dynamics; plane of nutrition or a reproductive trigger initiated breeding, but requires experimentation. Juvenile recruitment was postponed, despite an apparent sufficiency of food resources during reproduction, and was likely inhibited by reproduction-related aggression of adults. Extrinsic and intrinsic factors are implicated in controlling the demographic processes of gerbils in the Namib Desert dunefields.

Keywords: field technique, food, *Gerbillurus*, Namibia, population dynamics, reproduction

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Introduction

Many factors are implicated in the regulation of breeding and population density in African small mammal populations (Field 1975; Perrin 1980; Neal 1982; Perrin & Swanepoel 1987). However, examination of a relatively simple arid zone system, the Namib Desert, allowed for a focused investigation of key factors affecting gerbil populations.

Several populations of the pygmy hairy-footed gerbil *Gerbillurus tytonis* and the dune hairy-footed gerbil *G. paebe* were studied to quantify aspects of their reproduction, demography and population dynamics in relation to rainfall and diet composition (Perrin, Boyer & Boyer 1992). Causes of reproduction and variable levels of recruitment into the population are discussed.

G. paebe and *G. tytonis* are omnivorous, with much of their diet comprising arthropods and plant material but few seeds (Perrin *et al.*, 1992). A previous study (Christian 1979) showed reproduction of *G. paebe* to be extremely seasonal, and limited by the occurrence of rain. The breeding season could be extended artificially by the provision of water, although peak abundance was not significantly affected.

In this study, a positive, temporal, but lagged correlation was anticipated between the intensity and duration of precipitation, and the seasonality of reproduction and population density. Increased density would infer that rainfall stimulates primary production (plant vigour and seed production) and insect availability (Perrin *et al.*, 1992), the gerbil's plane of nutrition (Sadleir 1969), reproductive success (Perrin 1980), and hence population increase (Field 1975). Behaviour and breeding in captivity have been described for *G. p. coombsi*

(Hallet & Keogh 1971) and *G. p. paebe* (Stutterheim & Skinner 1973).

Data on plant community dynamics of the Namib Desert dunefields (Boyer 1990) are reviewed, and used with other data, on climate, seed production (Boyer 1989) and insect availability (Seely & Louw 1980) to identify predictive correlations. Results of studies of the agonistic behaviour of *G. tytonis* and *G. paebe* (Dempster & Perrin 1989 a, b, 1990) were used to enhance interpretation of demographic patterns.

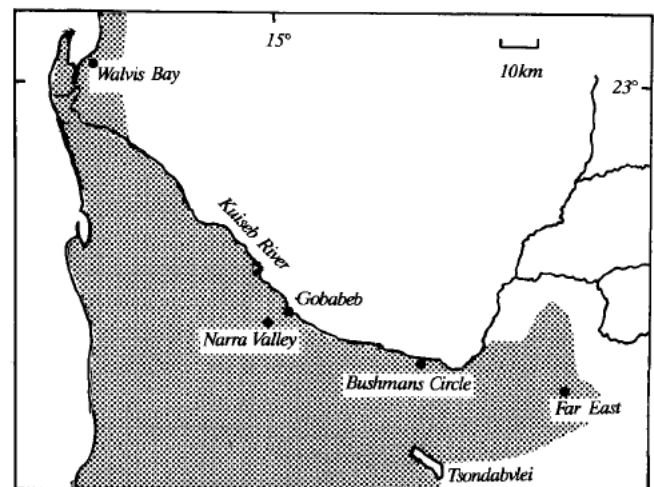


Figure 1 Map of the Namib Desert showing the position of the three study areas. Stippling represents the dunefields.

Study area

The Namib varies from extreme desert to semi-arid conditions (McGinnies, Goldman & Paycore 1977); it is a coastal desert extending from southern Angola through Namibia to the Olifants River in South Africa. The main dune system extends from the Kuiseb River to Luderitz, 400 km to the south (Figure 1) (Barnard 1973). There is a marked climatic gradient from east to west (Besler 1972) with higher rainfall on the eastern edge of the dune field. Most rainfall occurs between February and May when mean temperatures are highest (Lancaster, Lancaster & Seely 1984). Unlike other deserts, temperature extremes are relatively uncommon.

The Namib has very little vegetation and some plants are leafless, succulent or halophytic (McGinnies *et al.*, 1977). In the central Namib, short grass develops in autumn (April–June) following the summer rains. Methods used to describe, characterise, and quantify the productivity of the plant community are given in Perrin and Boyer (1994).

Methods

Gerbil capture

Rodents were sampled at three study areas across the east-west climatic gradient, at Narra Valley (23°37'S, 14°59'E), Bushman's Circle (23°42'S, 15°21'E) and Far East (23°47'S, 15°48'E), situated 48 km, 75 km, and 128 km from the coast respectively (Figure 1). Study sites were located on linear dunes that run north to south, and, except at Far East, were separated by wide interdune valleys.

The Namib supports an unusually high diversity of arthropod species for a desert ecosystem (Seely 1978). Biomasses of insects at a site near Narra Valley have been recorded at 0.01 g m² prior to rain and to 0.06 g m² after rain (Seely & Louw 1980).

Methods used to describe, characterise, and to quantify the productivity of the plant community are given in Boyer (1990), and Perrin and Boyer (1994). Repetitive live trapping of four gerbil populations (*G. paeba* at Far East, and *G. tytonis* at Far East, Bushman's Circle and Narra Valley) were undertaken between February 1984 and August 1985 in the Namib dune field. Single box traps were set on 5 × 30 station grids with 20 m spacing for two nights each month. Bait used was a mixture of peanut butter and rolled oats. At Far East and Bushman's Circle 17 trapping sessions were conducted over 19 months, while at Narra Valley only 12 sessions were completed over 17 months, owing to disturbances caused by jackals.

Since vegetation zones are stratified horizontally along the dune slopes, trap rows were placed perpendicular to the axis of the dunes. Occupied traps were processed and reset between 22h00 and 24h00. Captured animals were released immediately to reduce stress from hypothermia, and predation from jackals and owls, which also increased capture opportunity.

Animals were weighed to 0.1 g, measured, sexed and individually marked by toe-clipping. Reproductive state was assessed. Females were considered reproductively active when the nipples were enlarged or engorged, or the vulva was perforate, plugged or bloody, and the lower

abdomen swollen. Males were considered reproductively active when enlarged testes had descended to the scrotum.

Data analysis

The Jolly-Seber (JS) capture-mark-recapture population model was used to estimate population density and recruitment (birth and immigration), and loss (mortality and emigration) from the population (Jolly 1965; Seber 1965). Population density was also enumerated as the minimum number alive (MNA) following the method of Krebs (1966). Recruitment computed by the programme approximated the product of the number of pregnant females in the population and litter size, and estimated the total (trappable plus untrappable) sub-adult population. The mean of the MNA and JS estimates was used as the best indicator of density.

Snap trapping using Museum Special traps was conducted at 2 km to 5 km from each study site. One hundred traps baited with peanut butter were set on five lines with 20 m spacing. Information was collected on stomach contents, reproductive states, and emigration of marked animals from the live trapping grids.

Demography

Natal recruitment was estimated from the reproductive activity of the adult population and by analysing the cohort structure of the population, using the programme (Jolly 1965; Seber 1965). Animals first caught as sub-adults maturing to adult size were assumed to have been born in the study populations.

Since no simple field method for age determination of live rodents exists, individuals were placed in relative body mass classes viz. < 10 g (juveniles), 10–15 g (sub-adults), > 15 g (adults).

The plant community

Vegetation was sparse at all sites with crown cover ranging from 1.5% at Narra Valley to over 7% at Far East and Bushman's Circle. Hill's (1973) species diversity index estimated the effective number of plant species present in each community, and accounted for diversity and evenness of species by weighting for proportional abundance. The highest diversity index was 3.01 (ie. three effective species). At Narra Valley most vegetation zones comprised a single species; most plant species were grasses. Some green vegetative material was available at all times at Far East and Bushman's Circle. For plant species occurring on the lower dune slopes, peak periods of growth occurred after the rains. Total plant production was estimated at 200 kg ha⁻¹ year⁻¹ at Far East and Bushman's Circle, while at Narra Valley it was minimal (Boyer 1989, 1990).

The amount of photosynthetically active vegetation was estimated visually, and yielded an estimate of the total proportion of live active to dead material on the plant, and was termed plant vigour.

Using the same plants used to assess primary production, seed production was determined by direct enumeration. To estimate substrate seed reserves, two sand samples were collected, one under the grass canopy and the second from open

Table 1 Relative abundance of rodents at three study sites in the central Namib dune field

Site	Species	Density ha ⁻¹		Biomass g ha ⁻¹	
		Min.	Max.	Min.	Max.
Far East	<i>G. tytonis</i>	0.3	6.3	7	175
	<i>G. paeba</i>	1.0	7.7	22	140
	<i>D. auricularis</i>	—	0.2	—	—
Bushman's Circle	<i>G. tytonis</i>	2.8	18.2	44	413
	<i>G. paeba</i>	—	0.2	—	—
	<i>T. paedulus</i>	—	0.2	—	—
	<i>H. africae australis</i>	—	0.2	—	—
Narra Valley	<i>G. tytonis</i>	0.8	7.8	19	198

Table 2 Relative densities of *Gerbillurus* populations from various study sites

Species	Minimum	Maximum	Study Site	Reference
<i>G.p. exilis</i>	< 0.7 ha ⁻¹	3.3 ha ⁻¹	Coastal dunes	Ascaray <i>et al.</i> 1991
<i>G.p. paeba</i>	< 0.4 ha ⁻¹	3.4 ha ⁻¹	Goraris	Christian (1979)
<i>G.p. paeba</i>	< 0.4 ha ⁻¹	3.2 ha ⁻¹	Far East	This study
<i>G.p. paeba</i>	< 0.1 ha ⁻¹	9.5 ha ⁻¹	Namib dunes	This study

sand. Each sample approximated 100 cm³. Seeds present in the samples were removed using a flotation technique (Reichman 1975). In most species, seed production was correlated with vegetative growth.

Results

Rodent species occurrence

Gerbillurus paeba and *G. tytonis* were captured at Far East

Table 3 Mean body mass (g) ± SE of gerbils at three study sites in the central Namib dune field

	<i>G.p.</i> at F.E.	<i>G.t.</i> at F.E.	<i>G.t.</i> at B.C.	<i>G.t.</i> at N.V.
Mean mass	22.2	24.9	22.7	24.3
Sample size	178	168	376	167
Standard error	± 0.30	± 0.42	± 0.23	± 0.38

G.p. = *G. paeba*, *G.t.* = *G. tytonis*, F.E. = Far East, B.C. = Bushman's Circle, N.V. = Narra Valley

(Table 1). Only three short-tailed gerbils *Desmodillus auricularis* were captured on the live trapping grid, while snap-trapping on the adjacent gravel plains caught four individuals. As *D. auricularis* constituted only 0.67% (5 out of 600) of all live captures, and 2.3% (4 out of 169) of the snap-trap captures, its contribution to community structure was insignificant.

Gerbillurus tytonis, *G. paeba*, and a single tree rat *Thalomys nigricauda* were trapped at Bushman's Circle. Two *G. paeba* representing 0.5% of the total captured, were vagrants from the ephemeral Kuiseb River, 2 km from the study site. Similarly, the *T. paedulus* was likely dispersing between two river systems, the Kuiseb and the Tsondab. The tracks of one African porcupine *Hystrix africae australis* which passed through the site were noted. The Bushman's Circle and Narra Valley rodent communities comprised only one effective species, *G. tytonis* (Table 1).

Density estimates

The MNA estimate and JS model generated similar population estimates except during periods of high recruitment (February to April 1985) (Figures 2 and 3). Both estimates indicated the same seasonal population trend but higher densities were generated by the JS model. Densities fluctuated within and between populations but peaks were tied to rainfall

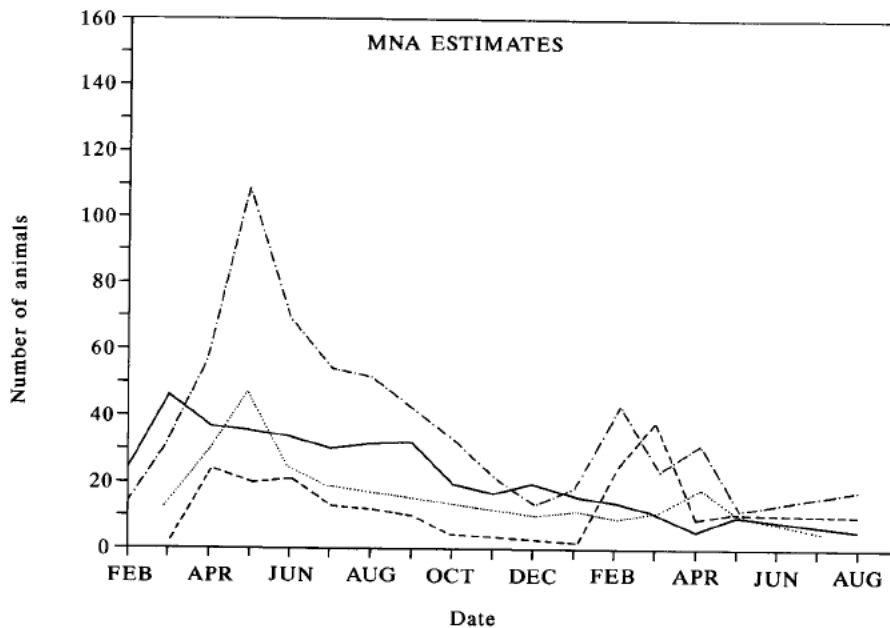


Figure 2 Minimum number alive (MNA) (Krebs 1966) density estimates of gerbils in the Namib dunes: *G. paeba* at Far East —, *G. tytonis* at Far East -----, *G. tytonis* at Bushman's Circle , *G. tytonis* at Narra Valley

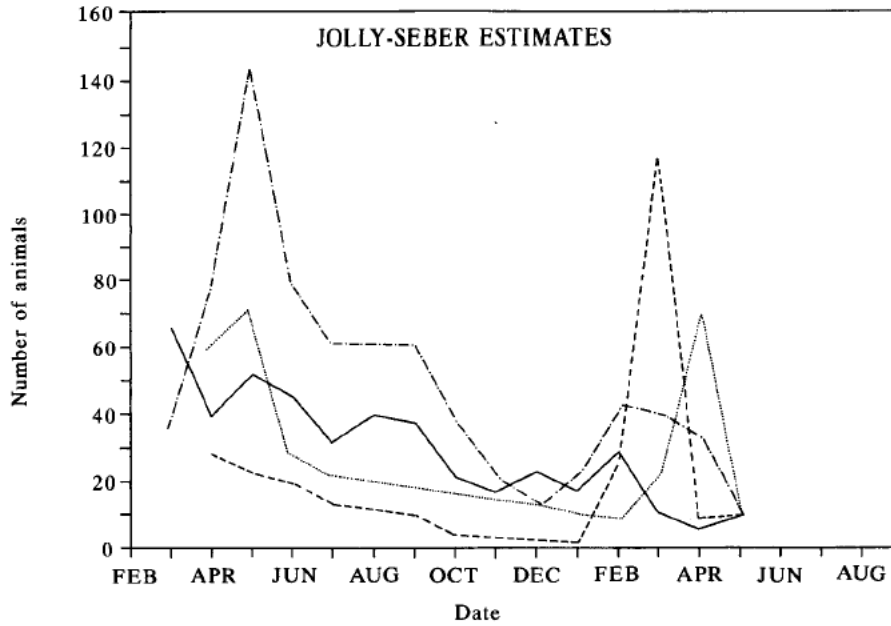


Figure 3 Jolly-Seber density estimates (Jolly 1965; Seber 1965) of gerbils in the Namib dunes: *G. paeba* at Far East —, *G. tytonis* at Far East -----, *G. tytonis* at Bushman's Circle, *G. tytonis* at Narra Valley

Table 4 Percentage of the populations that were sexually active on the trapping grids

Species	Sex	Site	February 1984				Sampling occasions						March 1995			
			18	19	5	4	10	8	38	28	62	100	100	100	100	89
<i>G. paeba</i>	M	Far East	18	19	5	4	10	8	38	28	62	100	100	89	60	72
	F		34	26	4	32	3	—	—	6	—	—	100	80	80	14
<i>G. tytonis</i>	M	Far East	—	—	17	50	41	22	56	74	100	100	100	100	73	100
	F		—	—	11	—	—	—	—	39	—	—	—	—	20	6
<i>G. tytonis</i>	M	Bushman's Circle	50	29	43	58	53	66	81	85	100	100	100	100	100	89
	F		10	26	26	10	—	—	—	—	6	—	17	68	83	34
<i>G. tytonis</i>	M	Narra Valley	—	40	14	10	—	—	—	—	—	—	100	80	100	67
	F		—	40	14	10	—	—	—	—	—	—	100	80	100	67

Table 5 Summary of the diet composition of four gerbil populations in the Namib dunefield

Dietary component	Far East		Bushman's Circle		Narra Valley			
	<i>G. paeba</i>		<i>G. tytonis</i>		<i>G. tytonis</i>			
	$\bar{x} \pm \text{s.e. (42)}$	$\bar{x} \pm \text{s.e. (46)}$	$\bar{x} \pm \text{s.e. (74)}$	$\bar{x} \pm \text{s.e. (74)}$	$\bar{x} \pm \text{s.e. (36)}$	$\bar{x} \pm \text{s.e. (36)}$		
Seeds	3.8	1.2	7.9	2.4	17.1	2.3	10.4	2.1
Plants	40.6	3.9	36.4	4.0	45.9	3.3	28.0	4.8
Inverts	52.9	4.3	52.6	4.8	33.6	3.2	58.9	4.9
Unknown	3.0	0.5	2.2	0.3	3.2	0.3	2.8	0.5
Other	0.0		2.0	1.0	0.0		0.5	0.5

From Perrin *et al.*, 1992

events (Figure 4 and Figure 5).

The population density of *G. paeba* ranged from 7.7 ha⁻¹ to <1 ha⁻¹ (Table 1), similar to the maximum and minimum densities of *G. tytonis* at Far East and Narra Valley. The density of *G. tytonis* was considerably higher at Bushman's Circle, varying from 2 to 17 ha⁻¹. Comparative data for other *Gerbillurus* populations in arid zone environments are summarised in Table 2.

Biomass

The body masses of *G. paeba* and *G. tytonis* at Far East exhibited small but significant differences (Table 3), and members of the *G. tytonis* population at Bushman's Circle had a significantly lower mean body mass ($p < 0.05$) than other *G. tytonis* populations (Table 3).

The maximum rodent biomass at Far East, where *G. paeba* and *G. tytonis* coexisted, was 315 g ha⁻¹ (Table 1), however,

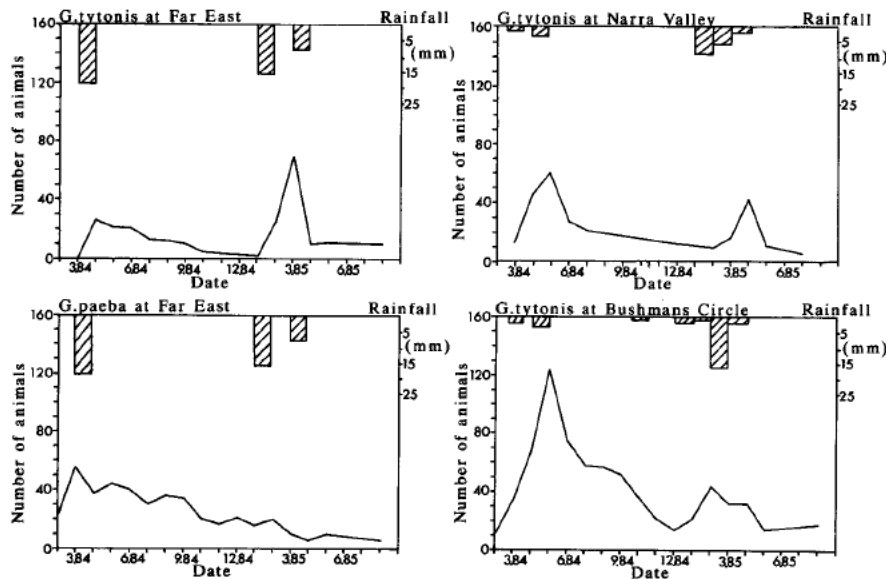


Figure 4 Population dynamics in relation to rainfall (histograms) events. **A** *G. tytonis* at Far East, **B** *G. paeba* at Far East, **C** *G. tytonis* at Narra Valley, **D** *G. tytonis* at Bushman's Circle.

Table 6 Growth rates of subadult *G. paeba* and *G. tytonis*. Figures in parentheses indicate sample size

	Growth rate	<i>G. paeba</i>	<i>G. tytonis</i>
Body mass	g/day ⁻¹	0.4 (21)	0.4 (16)
	%	1.8	1.6
Head-body	mm/day ⁻¹	1.7 (6)	1.4 (11)
	%	1.8	1.5
Tail	mm/day ⁻¹	3.0 (6)	2.3 (11)
	%	2.8	1.8
Hind foot	mm/day ⁻¹	1.0 (6)	0.9 (11)
	%	3.6	2.7

From Boyer 1989

at Bushman's Circle, where only *G. tytonis* occurred, a higher biomass was recorded.

Reproduction

At Far East, female *G. paeba* reproduced from December to April (Table 4) and juvenile recruitment occurred from February to June (Figure 6). However, population density did not increase during either breeding seasons. At the same locality, very little breeding was recorded in female *G. tytonis* (Table 4) but its population increased during each summertime breeding season (Figure 3). Immigration accounted for the large population increase and there was no emigration. Female *G. paeba* were sexually active for longer than female *G. tytonis*, but their population declined during the second breeding season. So, while reproduction failed in *G. tytonis*, numbers increased through immigration, yet in the syntopic *G. paeba* population, many animals were reproductively active but the population declined.

At Bushman's Circle and Narra Valley *G. tytonis* reproduced during the summer rains (Table 4).

The percentage of adult females breeding (fertility) varied markedly between populations (Table 4). Maximal rates were attained for a few months by *G. paeba* at Far East and *G.*

tytonis at Narra Valley, whereas fertility was very low in the *G. tytonis* population at Far East. Males of each population were sexually mature for longer than females. In each population males had scrotal testes during the cool, dry winters. Throughout summer the proportion of breeding males decreased owing to sub-adult recruitment.

Detailed studies (Perrin *et al.* 1992) have shown no marked seasonal changes in the diet composition of *G. paeba* and *G. tytonis*, and no differences between the species (Table 5). However, changes that were apparent, particularly in the use of green plants and seeds, were likely implicated in the initiation and maintenance of reproduction. Plant vigour, the production of new growth, and the seeding of grasses were triggered by rainfall (Perrin *et al.*, 1992).

Data are presented which summarise seasonal changes in plant vigour at Far East (Figure 6) and Bushman's Circle (Figure 7), and seed production at Bushman's Circle (Figure 8) and Narra Valley (Figure 9). Although some grasses retained vigour throughout the year (*S. sabulicola* at Bushman's Circle, *E. spinosa* at Far East), growth was markedly seasonal in others (*S. lutescens* and *C. glauca* at Bushman's Circle, *S. ciliata* at Far East). Seed production by *S. sabulicola* was significant and seasonal at Bushman's Circle and Narra Valley. Plant vigour and seed production were pronounced during the breeding seasons of the gerbils.

On the dunes at Far East, seed production and seed reserves were low, but some ephemerals germinated, and perennials showed growth during the gerbil's breeding season. On the interdune plains, seed reserves were the highest recorded but no green vegetation was available for food. This suggested that green plant material, rather than seeds, was important in the timing of reproduction.

At Bushman's Circle, plant growth was concurrent with seed production, which occurred prior to gerbil reproduction. Although seeds may have been implicated in the onset of breeding, seed production was largely confined to the interdune plains whereas the gerbils were resident on the dunes. Reproduction occurred in *G. tytonis* at Narra Valley

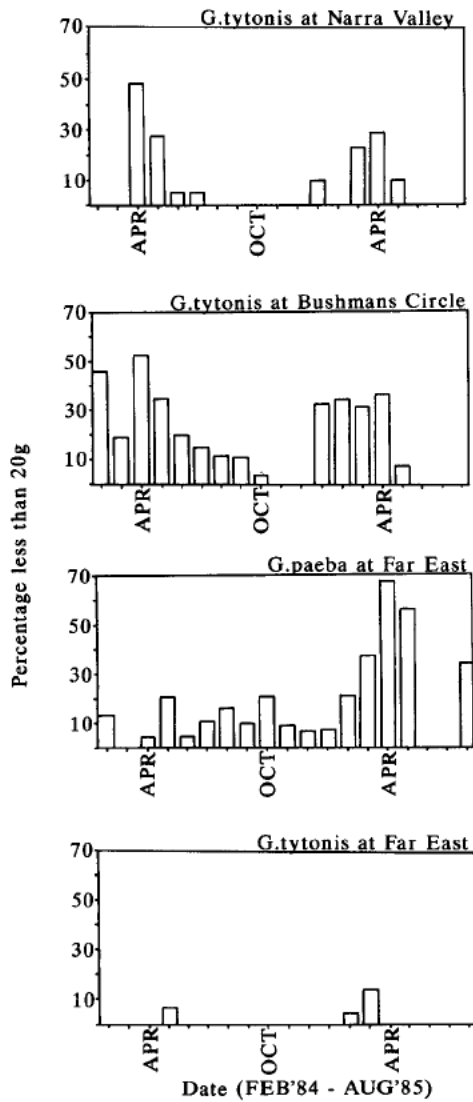


Figure 5 Juvenile recruitment of gerbils in the Namib dunes. **A** *G. tytonis* at Narra Valley, **B** *G. tytonis* at Bushman's Circle, **C** *G. paeba* at Far East, **D** *G. tytonis* at Far East.

despite low levels of seed production and little plant growth.

Recruitment

The seasonal appearance of low mass animals in the populations, caused by recruitment through reproduction, was closely tied to rainfall events (Figure 10). Recruitment was seasonal in all populations but varied considerably between populations. Development of the study species (Table 6) suggested juvenile recruitment into the trappable population was delayed beyond the time required to achieve independence, perhaps by one or two months. Failed and deferred recruitment may be explained by inadequate nutrition or social behaviour.

The relationships between actual and computed sub-adult recruitment and population density are shown for the synoptic species populations at Far East (Figures 11 and 12). Recruitment of *G. paeba* showed slight inverse density dependence, suggesting fertility and reproductive capacity

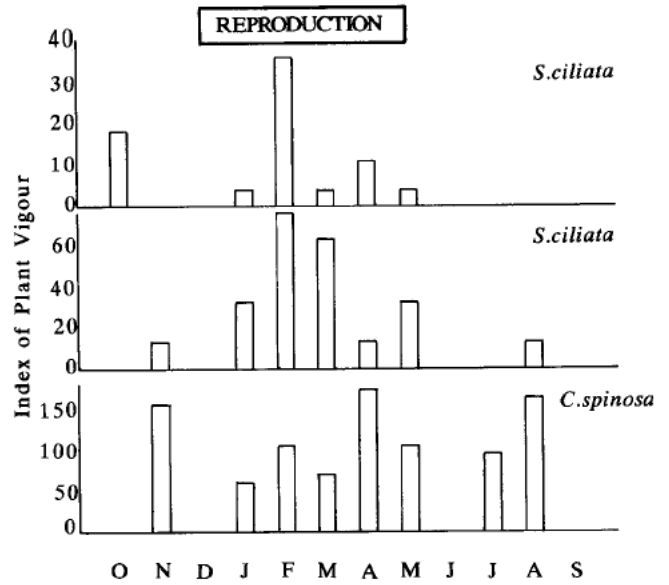


Figure 6 Indices of plant vigour at Bushman's Circle. The box labelled REPRODUCTION identifies the period when the gerbils were breeding. The upper reference to *S. ciliata* refers to the dunes and the latter to the interdune plains.

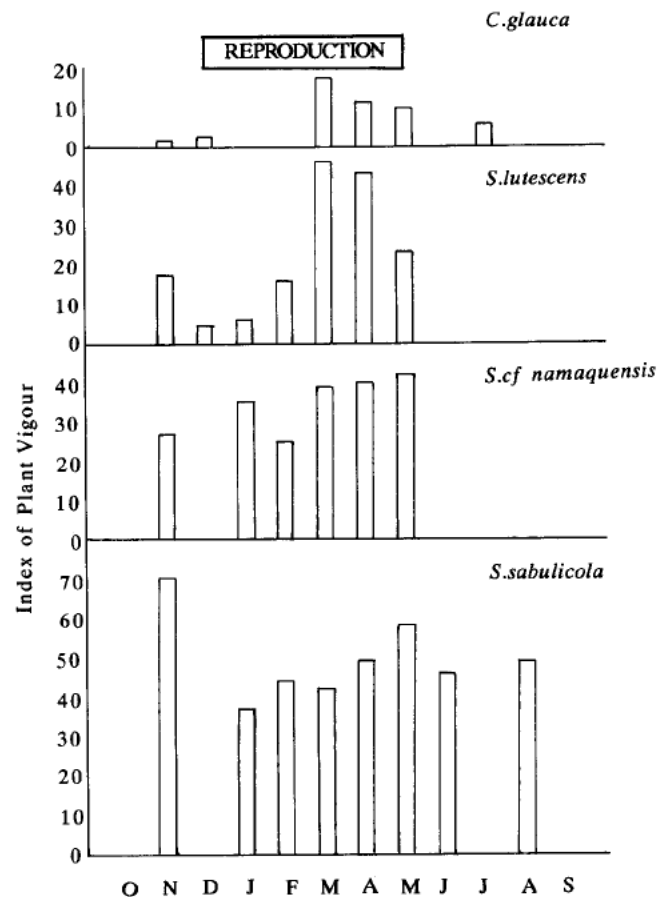


Figure 7 Indices of plant vigour at Far East. The box labelled REPRODUCTION identifies the period when the gerbils were breeding.

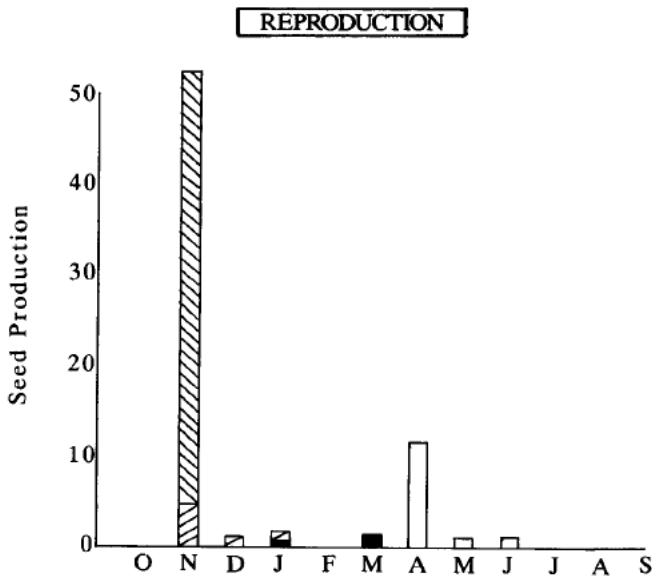


Figure 8 Seed production at Bushman's Circle. Solid = *S. cf. namaquensis*, open = *S. sabulicola*, left slash = *S. lutescens* and right slash = *C. glauca*. The box labelled REPRODUCTION identifies the period when the gerbils were breeding.

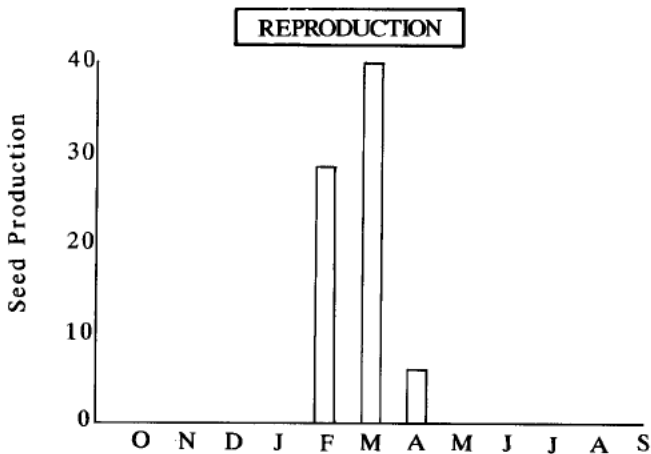


Figure 9 Seed production of *S. sabulicola* at Narra Valley. The box labelled REPRODUCTION identifies the period when the gerbils were breeding.

of breeding females were adversely affected by high densities.

Survivorship

Survival was higher in winter than during the summertime breeding season for all populations (Figures 13 and 14). Mortality affected recruits and overwintered adults of each sex. Since reproduction occurred during the season of greatest primary production and nutritional sufficiency, and since mortality was high when density was high, mortality was likely socially-induced.

Immigration and emigration

At Far East and Bushman's Circle snap trapping at the periphery of the grid failed to catch marked individuals, indi-

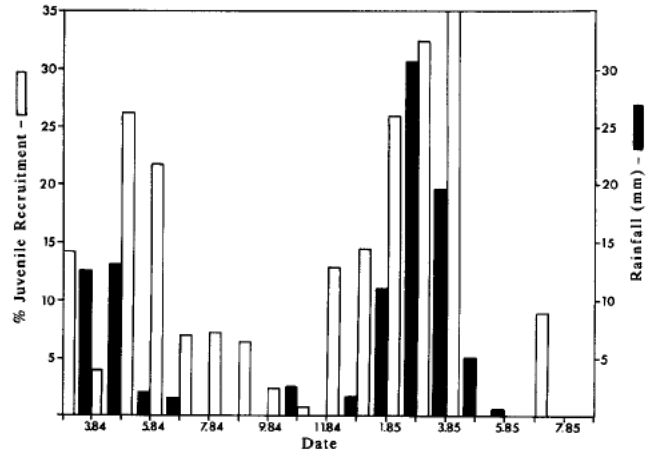


Figure 10 Patterns of rainfall and recruitment (the sum of all populations).

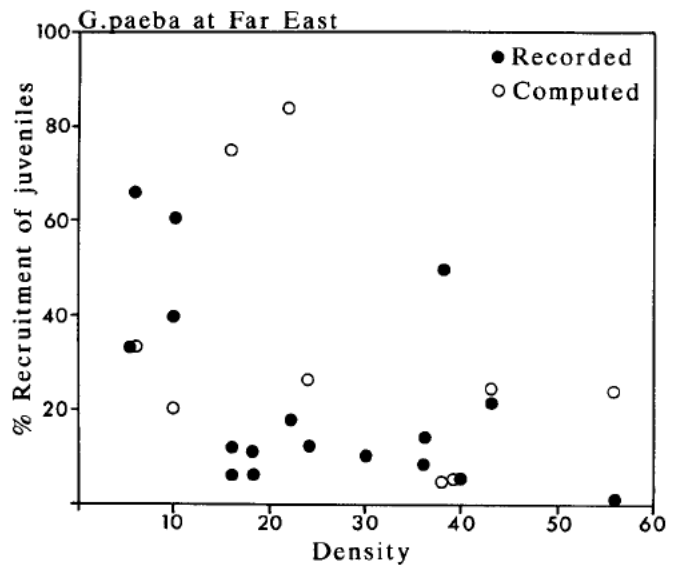


Figure 11 Density and recruitment: *G. paeba* at Far East.

cating that emigration was low. At Narra Valley, however, five of nine *G. tytonis* snap trapped 1 km south of the grid in May were marked animals. Of these, three had been captured on the grid 48 h earlier and one within 24 h, suggesting high emigration.

Discussion

Parallel studies

To fully interpret the results, it is necessary to briefly review three prior studies of the demography of *G. paeba*.

Nel's (1983) long-term studies of the population dynamics of arid zone rodents in the Kalahari demonstrated that *G. paeba* populations fluctuate widely; that explosive increase in numbers results from effective summer rains; and that annual density peaks occur in dry mid-winter. Although the population increased exponentially it declined over several years with variable patterns of numerical oscillation (Figure 15). This long-term pattern exemplifies the trends shown by the four populations studied in the Namib Desert.

Christian's (1979) study clearly demonstrated that population increase in *G. paeba* was triggered by rainfall, and that

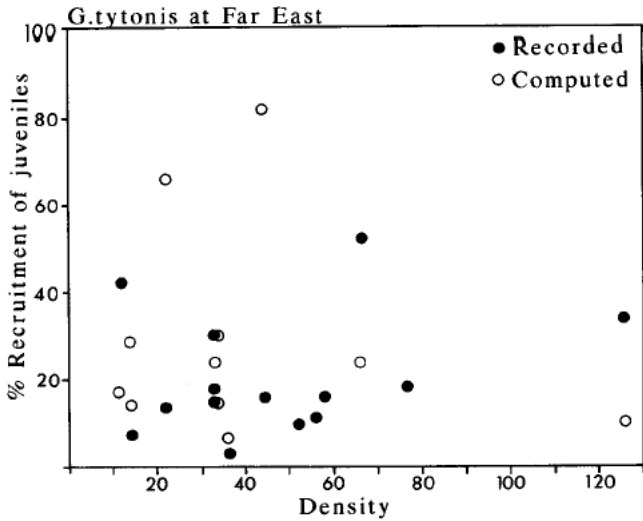


Figure 12 Density and recruitment: *G. tytonis* at Far East.

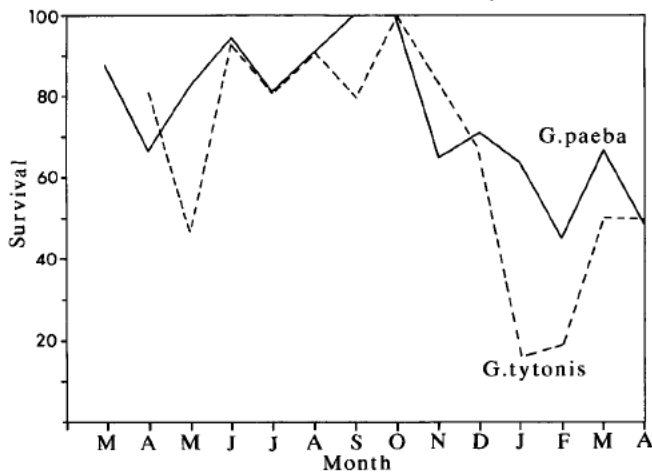


Figure 13 Survivorship: *G. paeba* and *G. tytonis* at Far East.

provision of free water extends the breeding season (Figure 16) and increases the number of breeding females (Figure 17). The effect of supplying free water mirrored that of rainfall on plants. It caused vegetative growth and gerbil reproductive activity, likely by increasing plane of nutrition. However, population density did not increase, suggesting that an intrinsic factor, such as agonistic behaviour, regulates reproduction and density (Turner & Iverson 1973; Perrin 1981).

A detailed study of a coastal population of *G.p. exilis* (Ascaray, Perrin, McLachlan & Els 1991) demonstrated that breeding was seasonal, that males were sexually mature for much longer than females, and that juvenile recruitment into the trappable population was delayed (Figure 18). Breeding, however, although seasonal, was not correlated with rainfall, because significant rains occurred throughout the year (Figure 18).

Species occurrence

Rodent species number and diversity in the Namib dunes are considerably lower than in arid ecosystems of North America. Brown (1973) recorded five sympatric rodent species occurring

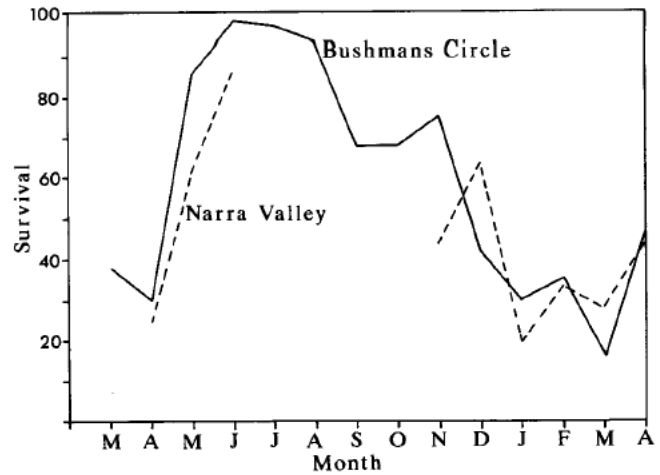


Figure 14 Survivorship: *G. tytonis* at Bushman's Circle and Narra Valley.

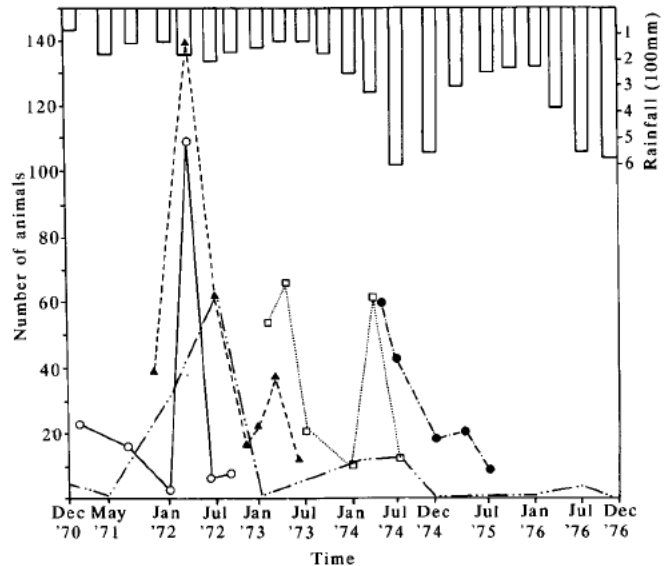


Figure 15 Demographic patterns: *G. paeba* in the Kalahari (.....) (years) (Nel 1983) in relation to rainfall (histogram); other sites in months, *G. tytonis* at Far East o—o, *G. tytonis* at Bushman's Circle Δ- - - Δ, *G. tytonis* at Narra Valley □.....□, *G. paeba* at Far East *-----*

in the dune ecosystems of the southwestern United States. The low species number of the gerbils of the Namib is attributed to biogeographical isolation, as the dunes are separated from those of the Kalahari by hundreds of kilometres of barren gravel plains, and low productivity. Low productivity, with simple habitats in the dunes, provide very few rodent niches.

Biomass

Similarly, the *Gerbillurus* biomass of the Namib dune ecosystem is low compared with other deserts (Chew & Chew 1970; Soholt 1973; French, Grant, Grodzinski & Swift 1976).

The Namib is more arid than North American midwest deserts and receives only 10% to 30% of its rainfall (Pietruska & Seely 1985). Precipitation is also highly unpredictable (Pietruska & Seely 1985) whereas in North American

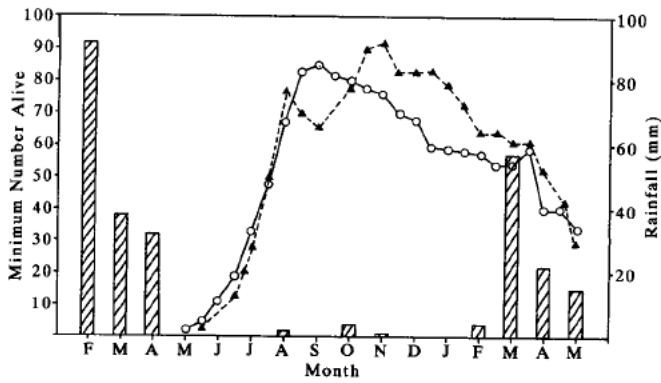


Figure 16 Population dynamics of *G. paeba* at Gorraris in the Namib in relation to rainfall (histogram): water supplementation \circ — \circ and control Δ — Δ (Christian 1979).

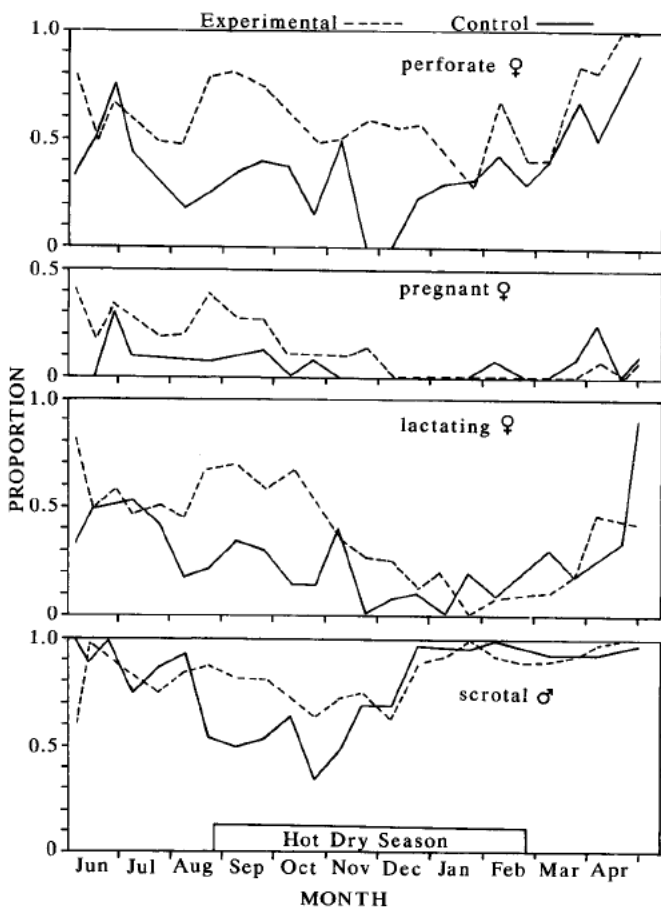


Figure 17 Effect of supplemental water on the breeding biology of *G. paeba* – (Christian 1979).

deserts annual rainfall is more certain certain (Brown 1973). Variability in biomass is attributable to the stochasticity of the climatic and biotic events within desert ecosystems (Rosenzweig & Winakur 1969).

The biomass of gerbils at Bushman's Circle was equivalent to that at Far East although it is in a lower rainfall isohyet. Christian (1980) monitored populations of rodents at Gorraris (25°18'S, 15°44'E) 120 km inland from the Atlantic coast in Namibia following good rains, and an increase in density of

G. paeba from zero to 59 ha⁻¹, at a dunes site was recorded. Jarvis (pers. comm.) reported a biomass of >2 800 g ha⁻¹ for coexisting *G. tytonis* and *G. paeba* in an area adjacent to Christian's (1980) site. The dunes were well vegetated following two years of above-average rainfall and the density may approximate maximum carrying capacity (Jarvis pers. comm.). Biomasses recorded by Christian (1979) for a rodent community at the same study site are an order of magnitude greater (3 000g ha⁻¹) than those recorded for *G. paeba* at Far East or for *G.p. exilis* on coastal dunes (Ascaray *et al.*, 1991) (Table 2).

Diet and reproduction

Seasonal reproduction in African rodents has often been associated with diet changes, particularly increased protein intake, caused by selective feeding on seeds or insects (Field 1975; Perrin 1980; Neal 1982; Perrin & Swanepoel 1987). Inclusion of seeds in the diet of gerbils in the Namib Desert corresponded with the most successful period of breeding of three *Gerbillurus* populations. However, there was a poor correlation between seed availability and consumption, and the largest biomasses of seeds were recorded from substrates on the interdune plains, rather than on the dunes (Boyer 1989; Perrin & Boyer 1994). Seed densities were generally very low throughout the ecosystem and were insufficient to maintain breeding (Downs & Perrin 1990a).

Since the gerbil's diets comprised predominantly insects (Perrin *et al.*, 1992), their protein demand for reproduction, even during pregnancy and lactation (Kaczmarek 1966), was not critical. While energy demands can be met by varied and various dietary components, green plant tissues can be critical in supplying vitamins and minerals essential for reproduction (Sadleir 1969).

Gerbillurus paeba and *G. tytonis* are known to switch between food types, which may represent opportunism or individual optimisation (Perrin *et al.*, 1992). Studies of the diet of *G. paeba* undertaken in the Alexandria dunefield (Ascaray 1986) and the Karoo (Kerley 1989, 1992) in South Africa also suggest that *G.paeba* is an opportunistic omnivore. During the hot, dry part of the year, green plant material was consumed in the absence of other preferred food types (Perrin *et al.*, 1992) or as a source of moisture and nutrition (Downs & Perrin 1990a). However, Degen, Kam, Hazan and Nagy (1986) have shown that such diet selection is necessary for the survival of desert dwelling omnivores.

More metabolizable energy and metabolic water is derived from insects than dry vegetation per unit mass of dry matter, but not per unit mass of fresh matter (Degen *et al.*, 1986). Desert rodents, therefore, improve their water economy by altering diet composition, eating green vegetation, as well as through physiological responses (e.g. allantoin production, Downs & Perrin 1991). Plant diets, unlike insect diets, however, do not generate much nitrogenous waste, which also favours water conservation. Several omnivorous desert rodent species have been shown to possess high rates of water turnover through selecting green plant material and succulents (Grubbs 1980; Karasov 1983).

Diet influences the availability of water to *G. paeba* and *G. tytonis* and causes concomitant changes in water turnover rate and urine concentration (Downs & Perrin 1990a, b, c, 1991).

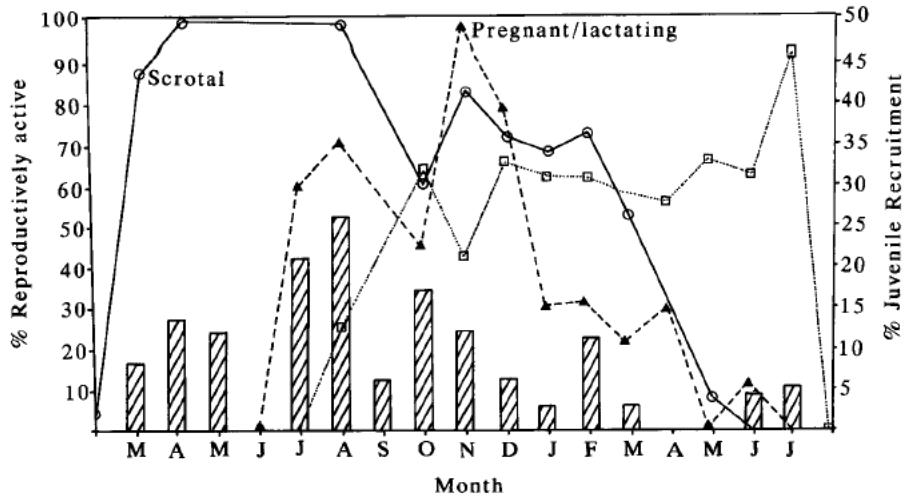


Figure 18 Reproductive activity (males \circ — \circ : females Δ - - Δ), juvenile recruitment (histogram) and immigration \square \square in a coastal *G. p. exilis* population – (Ascaray *et al.*, 1991).

Downs and Perrin (1990a) have shown that *G. tytonis* and *G. paeba* cannot survive under laboratory conditions on air-dried seeds without water supplementation. It is, therefore, suggested that green vegetation is an essential component of the diet of *G. paeba* (and *G. tytonis*) to maintain water balance and reproduction.

Seasonality of reproduction in *Gerbillurus* populations is probably dependent on diet composition, water availability, and hence rainfall. Ascaray (1986) suggested that breeding in *G. paeba exilis* in the relatively mesic Alexandria dunefields, which receive substantial rains throughout the year, was initiated by an increase in the availability and consumption of arthropods (which are high in protein and fat content: Phelps, Struthers & Moyo 1975), while Christian (1979) proposed that periods of increased water availability determined the seasonality of reproduction of *G. paeba* in the Namib Desert. Both interpretations are valid owing to differences in diet quality and environmental water availability.

For Namib populations of *Gerbillurus*, water availability is more important than protein availability. Water may act as the proximate cue in initiating reproduction, by improving plane of nutrition (Field 1975; Neal 1982), by causing the flushing of grasses, and/or the liberation of a hormonal trigger from flushing grasses (Linn 1991). A potential strategy for southern African rodents to maximise reproductive success is to cue breeding activity to rainfall and subsequent vegetative growth via a secondary plant compound such as 6-methoxybenzoxazolinone (6 MBOA) (White & Bernard 1999). However, 6 MBOA is not a major stimulant of reproduction in several species (Linn 1991; White & Bernard 1999) and seasonal breeding occurs in response to multiple environmental cues. Such a reproductive strategy and omnivory permit an opportunistic reproductive response to the unpredictable environment of the southern African region (White & Bernard 1999).

Recruitment and density

Gerbillurus paeba and *G. tytonis* are highly aggressive species (Dempster & Perrin 1989a, b) and agonistic behaviour has been implicated in competitive exclusion between the species pair (Boyer 1985). Adequate nutrition and sufficient

water are necessary for reproduction in *Gerbillurus* populations but they may not be sufficient to enable juvenile recruitment. It has been shown that reproduction-related aggression adversely affects juvenile recruitment in rodent populations (Turner & Iverson 1973; Turner, Perrin & Iverson 1975; Perrin 1981); and that the ecological specialist *G. tytonis* dominates the ecological generalist *G. paeba* in staged laboratory encounters (Dempster & Perrin 1990). Agonistic behaviour of gerbils, perhaps from immigrants, may impact negatively on juvenile recruitment; and population density relative to resource availability may determine levels of interaction and recruitment. This inference results from the interpretation of the data collected at Far East where *G. tytonis* and *G. paeba* coexist.

A high level of immigration in *G. tytonis* was associated with a decline in the density in *G. paeba*, despite a high level of, but failed reproduction in, the resident population of *G. tytonis*. In the Namib dunes the two species are generally segregated by habitat differences, with *G. paeba* preferring a compacted substrate and low plant species diversity, while *G. tytonis* selects for shifting sands and a high plant species diversity, which is normally associated with dune crest habitats (Boyer 1985, 1989). The synchronous increase in *G. tytonis* density and decline in *G. paeba* suggests behavioural dominance by *G. tytonis* over *G. paeba*. It is thought that above average rains at Far East before the study commenced allowed *G. paeba* to enter the dunes. Although *G. paeba* is as physiologically well adapted to the desert environment as *G. tytonis* (Downs & Perrin 1990 a, b, c, 1991), it generally occupies more mesic environments than its congener (De Graaff 1981). As rainfall declined at Far East, conditions would have shifted to favour *G. tytonis*, which is well adapted to foraging in the Namib dunes (Hughes 1991; Hughes, Ward & Perrin 1995).

Extrinsic (climatic) and intrinsic (behavioural) factors interact to determine the density fluctuations of *G. tytonis* in the Namib Desert. The low survival and deferred recruitment of *Gerbillurus* species in the breeding season, before trophic resources have declined to winter levels, suggest the operation of density-dependent agonistic behaviour.

Experiments are required that quantify agonistic behaviour in relation to (manipulated) densities of the two species over an annual cycle (in which trophic resources are controlled) to substantiate or negate the hypothesis (Perrin 1981).

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