Tropical Zoology 7: 299-308, 1994

The effect of rodents on plant recruitment and production in the dune fields of the Namib Desert

M.R. PERRIN[1] and D.C. BOYER[2]

[1] *Department of Zoology and Entomology, University of Natal, Private Bag X01, Scottsville 3209, Republic of South Africa*

Received 3 March 1992, accepted 16 October 1993

The biomass of invertebrates at Narra Valley in the Namib Desert was estimated; rodents removed about 10% of the total invertebrate biomass each month. This level of predation surely has a major impact on local invertebrate communities.

On certain interdune plains in the Eastern Namib rodents consumed all the green plant material that was locally available; plant growth was adversely affected. At other sites green plant availability and its utilization by rodents indicated that rodent herbivory has little impact on primary production. When rodents graze selectively on individual species or on preferred plant parts, such as growing points, growth and reproduction of these plants will be affected.

The removal of sufficient seeds to have a negative impact on certain dune plant species occurred for short periods only, though the effects are unknown.

KEY WORDS: rodents, plant utilization, desert.

INTRODUCTION

In North America, deserts rodents are often granivorous (REICHMAN 1977, MARES & ROSENZWEIG 1978, BROWN et al. 1979), and occur in such densities that

[2] Present address: Ministry of Fisheries and Marine Resources, P.O. Box 912, Swakopmund, Namibia.

their effect on plant resources, particularly seeds, has been sufficient to impact on the structure of the plant communities (CHEW & CHEW 1970, SOHOLT 1973).

The aim of this study was to determine the impact of granivory and herbivory by the dune hairy-footed gerbil *Gerbillurus tytonis* Bauer & Niethammer 1960 and the pygmy hairy-footed gerbil *Gerbillurus paeba* A. Smith 1836 on the vegetation of the central and eastern area of the Namib Desert dunefields. However, diet analysis (PERRIN et al. 1992) determined that for certain time periods, Namib Desert rodents are predominantly insectivorous. In the light of this finding, it was felt that rodents may have a major impact on the system through the removal of invertebrates. Therefore, where data were available, the degree of utilization of invertebrates was estimated.

This paper collates and interprets data bases collected during a larger study (BOYER 1988, 1989; PERRIN et al. 1992; PERRIN & BOYER in prep.) by examining the availability of resources and the demand made by rodents on these resources.

METHODS

The Namib. Conditions in the Namib Desert vary from extreme to moderate (MCGINNIES et al. 1977). In the north there is no seasonality to precipitation; in the south winter precipitation occurs.

The Namib 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 dunefield. Most rainfall occurs between February and May, when mean temperatures are highest, while June to September is somewhat cooler than the period October to January (LANCASTER et al. 1984). The Namib has very little vegetation and some plants are leafless, succulent or halophytic (MCGINNIES et al. 1977). In the inner Namib a short grass develops in autumn (April-June) following the summer rains.

Study area. Rodents were sampled at three study areas situated 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, 75 and 128 km from the coast respectively.

Vegetation was relatively sparse at all sites with plant crown cover ranging from 1.5% at Narra 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 area at Far East was dominated by two grass species, *Cladoraphis spinosa* and *Stipogrostis ciliata* while *Hermania minimifolia* was uncommon (BOYER 1989). Narra Valley had one dominant species *Stipogrostis subulicola*, although *Trianthema hereroensis* constituted 25% of the total plant cover. At Bushman's Circle four plant species were relatively common, *S. sabulicola, S.* cf. *namaquensis, S. lutescens* and *Centropodia glauca*. *S. ciliata* was the dominant plant species on the interdune plains at each study site.

Origin of data. Rodent populations dynamics and diets were monitored from early 1984 to mid-1985, whereas resource abundance was quantified between January and December 1985. Resource abundance showed some degree of seasonality during 1985, and as meteorological conditions during 1984 were similar to those of 1985, the resource abundance data for 1985 were used to estimate resource dynamics in 1984 (BOYER 1988).

Availability of resources. The net availability of three resource types was determined: the total mass of seeds found in the substrate and the mass of seeds present on perennial plants were summed to give the total mass of seeds available; the amount of green plant material derived from all perennial plant species was computed; and invertebrate biomass; although only available from the Narra Valley study site. Plant material produced by plants germinating during the study periods was

minimal, and insignificant relative to the amounts available on the perennial plants, and was excluded from analyses.

An approximation of invertebrate resource utilization was made using animal biomass data from SEELY & LOUW (1980); they reported two animal biomass figures for dunes in the vicinity of Narra Valley. One figure (0.013 g m^{-2}) was measured in 1975 at the end of an extended dry period of at least 13 years and the second (0.063 g m^{-2}) immediately following a period of substantial rainfall in 1976. This represented a reduction in biomass of 0.004 g m^{-2} per year during the period of minimal rain. The last rainfall event to stimulate plant germination prior to the present study at Narra Valley was in 1979 (M.K. SEELY pers. comm.), 5 years prior to the study. This represented a reduction of animal biomass of 0.020 g m^{-2} (or 32%) from the post-rain biomass figure of about 0.063 g m^{-2}. Interestingly plant biomass figures at Narra Valley were about 33% below SEELY & LOUW's (1980) post-rain plant biomass figure. A maximum animal biomass figure of 0.043 g m^{-2} was computed.

Utilization of resources. The amount of each resource type eaten per month was computed from data on individual rodent consumption, rodent density (PERRIN & BOYER in prep.) and diet (PERRIN et al. 1992). Food consumption rates were determined using laboratory feeding trials. An average consumption rate of 0.095 g g body $mass^{-1}$ day^{-1} was used.

The resources removed from the dune area and the interdune area at Far East are presented separately. At the other sites, where only one species of rodent occurred, the areas were not differentiated.

RESULTS

Production

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 Narra 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 Narra Valley it was minimal (BOYER 1988).

Seed production was temporally correlated with vegetative growth in most species. This occurred following rainfall in the dune base species and immediately prior to the rainy season for those on the upper dune slopes. Sub-surface seed reserves were greatest at the eastern site, ranging from 01.77 g m^{-2} under the plant canopies to 0.57 g m^{-2} in open areas, and were least in the west (<0.1 g m^2 in all habitats). Seasonal differences were not significant between any of the sites (BOYER 1988).

The Namib Desert supports an unusually high diversity of arthropod species (SEELY 1978). Biomasses of insects at a site near Narra Valley have been recorded at 0.01 g m^{-2} prior to rains, to 0.06 g m^{-2} after rain (SEELY & LOUW 1980).

Resource utilization at the study sites

Far East-Interdune plains. Invertebrates were the most utilized resource throughout the year on the interdune plains (Fig. 1). Green vegetation was rarely available but utilization figures of over 100% were recorded for 4 months.

Seeds were more abundant on the interdune plants at Far East than in any other area, but as seeds formed a small proportion of the diet of the rodents, the percentage of seeds utilized was less than at the other sites (Fig. 2).

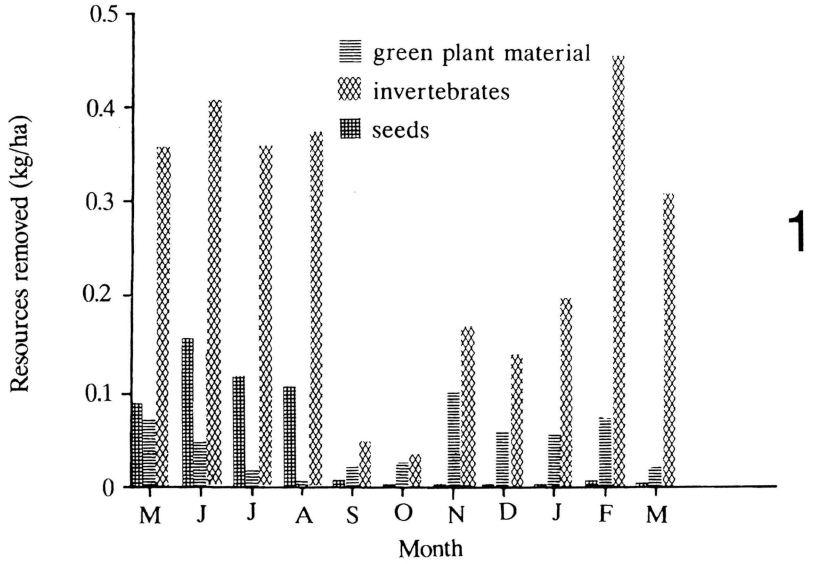

Fig. 1. — Resource utilization by gerbils on the interdune plains at Far East.

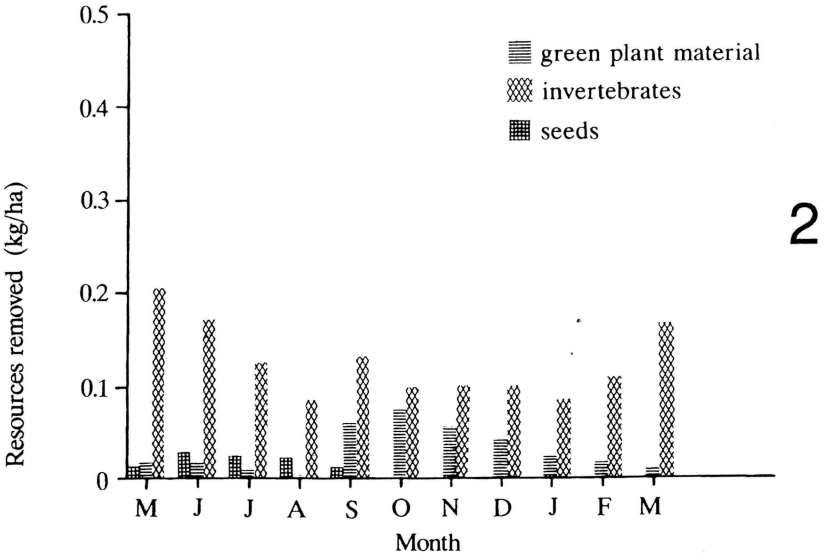

Fig. 2. — Resource utilization by gerbils on the dune at Far East.

In the dunes at Far East, invertebrates were the major trophic resource while seeds were of secondary importance during the first half of the study and green plant material during the second half (Fig. 2). Since fewer seeds were available on the dunes

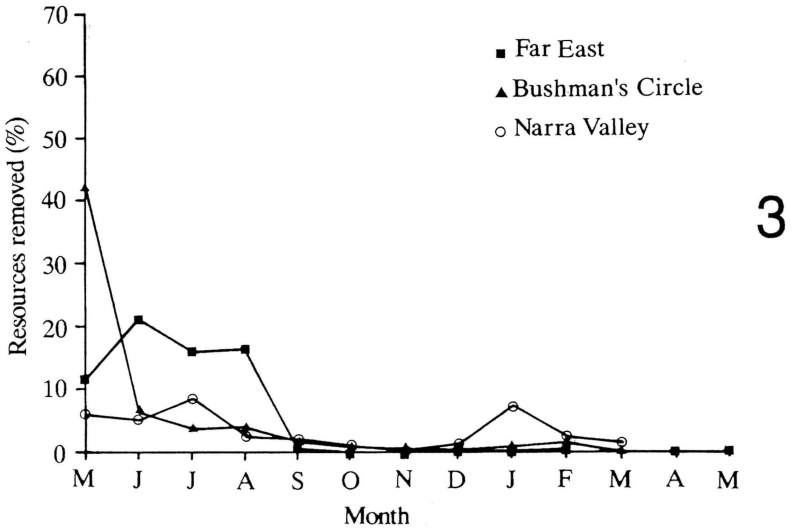

Fig. 3. — Percentage utilization of seeds available to gerbils.

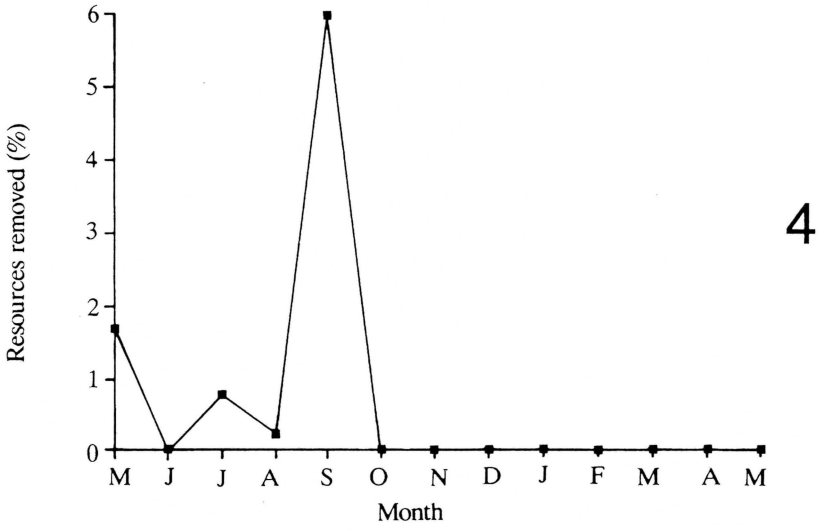

Fig. 4. — Percentage utilization of green plant material by gerbils on the interdune plains at Far East.

than the interdune plains, the proportion used was higher, particularly during the first four months of the study (Fig. 3). The demand for green material was insignificant compared to the amount available (Fig. 4).

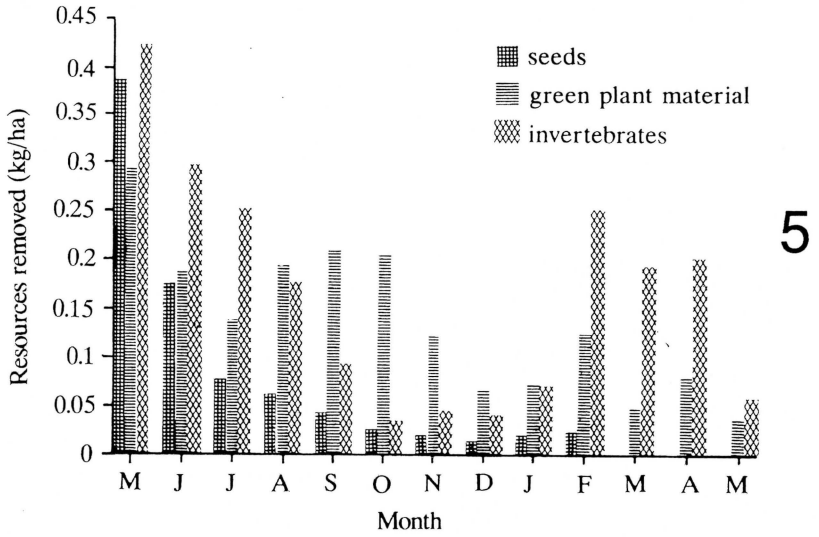

Fig. 5. — Resource utilization by gerbils at Bushman's Circle.

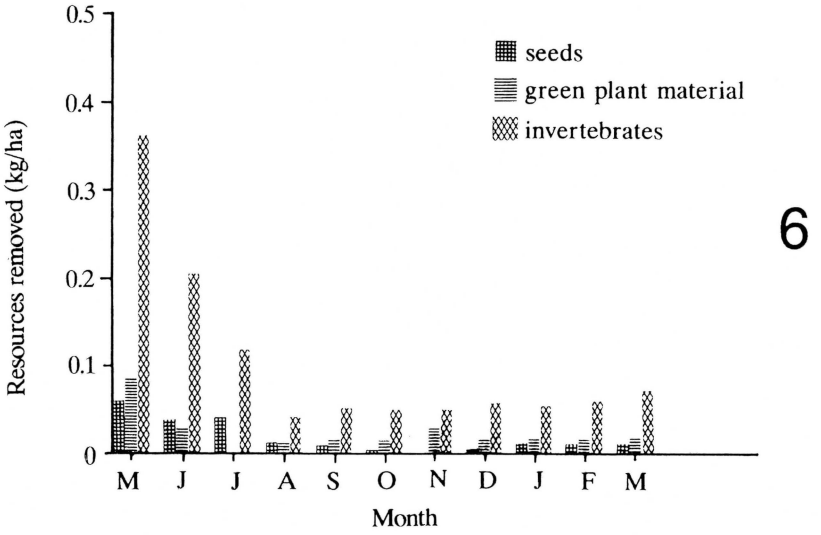

Fig. 6. — Resource utilization by gerbils at Narra Valley.

Bushman's Circle. Invertebrates were again the most utilized resource, with over 2 kg ha^{-1} being eaten during 13 months (Fig. 5). However, from August 1984 to January 1985 green plant material formed a larger part of the diet than invertebrates.

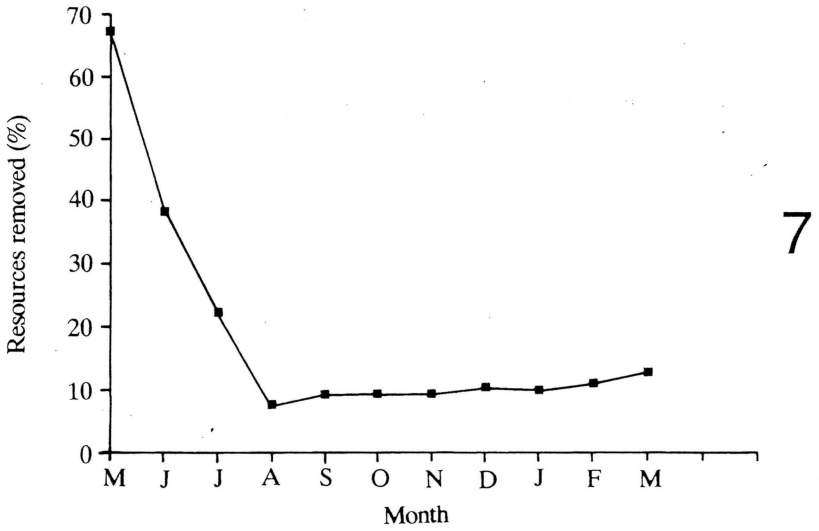

Fig. 7. — Percentage utilization of invertebrates by gerbils at Narra Valley.

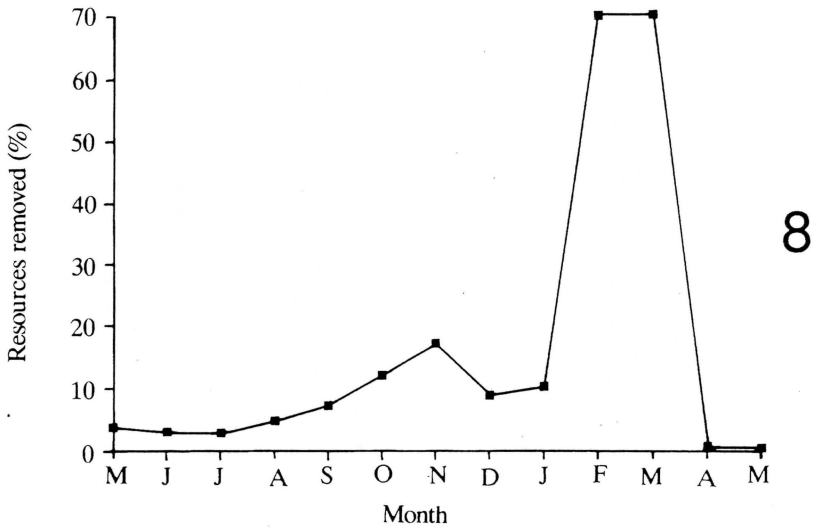

Fig. 8. — Predicted percentage utilization of green material of *C. glauca* if it were the sole food resource.

Despite the demand for plant tissues being greater than at other sites, utilization was always less than 0.2% of availability.

Narra Valley. Invertebrates were by far the most important food resource (Fig. 6). At high rodent population densities, early in the study, a large proportion of the

estimated invertebrate population was being removed (Fig. 7). Although demand was later reduced, often 10% of the invertebrate biomass was consumed.

Generally, seeds formed a smaller part of resource utilization than green plant material, but resulted in 1 to 8% of available seeds being consumed. Removal of green material was insignificant relative to the amount available.

DISCUSSION

Do rodents have an impact on green vegetation? Desert rodents generally consume less than 1% of the available annual primary production (GOLLEY 1960, GRODZINSKI & GORECKI 1967, WIEGART & EVANS 1967). CHEW & CHEW (1970) and SOHOLT (1973) reported 9.5 and 10.7% of available primary production being removed by rodents from North American deserts, whereas SOHOLT (1973) indicated that if green plant parts are eaten selectively, these levels of herbivory can have a large impact on total primary production.

The pressure on green plant resources was low at all sites in the Namib dunefields except on the interdune plants at Far East. Little green material was available but the gerbils included large amounts in their diet. This indicated that foraging on the dunes had occurred. The demand for green vegetative parts was intense, such that the reproductive success of *Stipogrostis ciliata*, the only perennial plant species in the habitat, was probably adversely affected.

With the exception of the interdune plains at Far East, rodents have little impact on green plants although selective grazing of plant growth points could stunt growth. Saharan gerbils selectively remove new growth from certain bushes (DALY & DALY 1975) and in California *Perognathus* spp. selectively browse the desert herb *Polygola deserticum* reducing all aerial parts of plants until they are unable to reproduce (MEEHAN et al. 1977). Such selective herbivory was observed at Bushman's Circle where green material produced by *Centropodia glauca* was preferred over that of other species. If the rodents grazed this species exclusively, offtake would be very high prior to the rains and during periods of vegetative growth (Fig. 8). Such levels of herbivory must be regarded as high and probably detrimental to growth and reproduction. CHEW & CHEW (1970) have shown that the pruning of shrubs by rodents (2% of the primary production) can increase productivity, and NOTT (1985) recorded a similar effect when *Trianthema hereroensis* in the Namib was browsed by gemsbok *Oryx gazella* (Linnaeus 1758).

Do rodents have an impact on seeds? Selective removal of seeds from the system could have serious consequences for primary production and species diversity. However, the utilization of seeds was low. Little seasonality of seed availability suggests that replenishment rates were negligible or consistent. Seed production during the study was low, and at Far East and Narra Valley, restricted to summer (BOYER 1988, 1989) so the replenishment of seed reserves was minimal. The gradual utilization of seeds did not significantly reduce the available seed reserves. At all sites granivory only reached high levels for short periods of time.

Does resource availability affect rodent communities? The high degree of dietary overlap between *G. tytonis* and *G. paeba* at Far East cannot be explained by

opportunism. Seeds were relatively abundant on the interdune plants but green plant material was generally absent. Despite this *G. paeba* ate more green material than seeds. It is suggested that green vegetation was eaten as a water source, rather than for its nutritional value (PERRIN et al. 1992).

The regular pattern of occurrence of seeds in the rodents' diet suggested some dependence on seed production, rather than the use of seed reserves from the substrate. However, no clear temporal pattern of resource availability and resource use could be discerned.

The timing of reproduction in each rodent population coincided with increased plant vigour (PERRIN & BOYER in prep.). Although increased plant vigour may be a cue for the onset of rodent reproduction (BEATLEY 1969), increase in invertebrate availability might also be significant. Seed production followed rodent reproduction and was highest at Bushman's Circle, the site with the highest rodent recruitment rate, suggesting that seeds may be an important factor in successful rodent recruitment.

Do rodents affect plant communities? Insects are one of the main animal life forms in many arid systems, including the Namib (SEELY 1978). Many insects are herbivorous, and their removal by rodents may benefit the individual growth of plants. However, in the Namib, many insects are detritivores, and in the absence of microbial action due to the aridity of the system, are the main decomposers of plant material (NOY-MEIR 1974, LOUW & SEELY 1982). Removal of the detritivores might be detrimental to energy and nutrient flow for the entire system.

The low availability of green plant material on the interdune plains at Far East might have been caused by rodent herbivory. Utilization of green vegetation far exceeded supply, and is explained by the rodents foraging on adjacent dunes.

Seed reserves in the substrate were not depleted by rodents, and had little impact at the plant community level. Sonoran rodents consume certain seeds preferentially, to increase energy intake, and for other dietary reasons (REICHMAN 1977). Species-specific selection of seeds by rodents in the Namib could affect plant species composition.

Abandoned rodent seed caches can improve conditions for seed germination and plant survival (SOHOLT 1973, REICHMAN 1979). Although seed caches were not found in *G. tytonis* or *G. paeba* burrows in the Namib, dried plant parts, including seeds, frequently accumulated in subterranean runways. Captive gerbils readily cache food but its significance in nature is unknown.

Plant biomass is affected locally in the Namib dune system by herbivorous gerbils, particularly when densities are high. The distribution of plant species, and the occurrence of areas of high and low plant species diversity appear not to be significantly affected by rodents. They are more likely determined by abiotic factors such as rainfall, fog precipitation, soil moisture holding capacity, soil percolation rates, and wind regimes.

REFERENCES

BARNARD W.S. 1973. Duinformasies in die sentrale Namib. *Tegnikon,* December: 2-13.

BEATLEY J.C. 1969. Dependence of desert rodents on winter annuals and precipitation. *Ecology* 50: 721-724.

BESLER H. 1972. Klimaverhaltrisse und klimageomorphologische Zonierung der zentralen Namib (Suidwestafrika). *Stuttgarter Geographische Studien* 83: 1-209.

BOYER D.C. 1988. Effect of rodents on land productivity and recruitment in the dune area of the Namib Desert. *M.Sc. Thesis, University of Natal,* 232 pp.

BOYER D.C. 1989. Some characteristics of the plant communities of three dunes situated across a climatic gradient in the Namib Desert. *Madoqua* 16: 141-148.

BROWN J.H., REICHMAN O.J. & DAVIDSON D.W. 1979. Granivory in desert ecosystems. *Annual Review of Ecology and Systematics* 10: 201-227.

CHEW R.M. & CHEW A.E. 1970. Energy relationships of the mammals of a desert shrub (*Larrea tridentata*) community. *Ecological Monographs* 40: 1-21.

DALY M. & DALY S. 1975. Socioecology of Saharan gerbils especially *Meriones libycus*. *Mammalia* 39: 289-312.

GOLLEY F.B. 1960. Energy dynamics of a food chain in an old field community. *Ecological Monographs* 30: 187-206.

GRODZINSKI W.G. & GORECKI A. 1967. Daily energy budgets of small rodents, pp. 295-314. In: Petrusewicz K., Edit. Secondary productivity of terrestrial ecosystems. Vol. 1. *Warsaw: Panstowe Wydamnictwo Naukowe,* 379 pp.

LANCASTER J., LANCASTER N. & SEELY M.K. 1984. Climate of the central Namib Desert. *Madoqua* 14: 5-61.

LOUW G.N. & SEELY M.K. 1982. Ecology of desert organisms. *London: Longman*: 194 pp.

MARES M.A. & ROSENZWEIG M.L. 1978. Granivory in North and Southern African deserts: rodents, birds and ants. *Ecology* 59: 235-241.

MCGINNIES W.G., GOLDMAN B.J. & PAYCORE P. 1977. Deserts of the World. *Tucson, Arizona: University of Arizona Press,* 788 pp.

MEEHAN T.E., RUNDEL P.W., AMBROSE R., BAKER G. & RAPPAPORT A. 1977. The influence of intense selective browsing by pocket mice (*Perognathus*) on the spatial distribution of *Polygala deserticum* in Baja California. *American Midland Naturalist* 97: 489-495.

NOTT K. 1985. An autecological study of a Namib dune succulent *Trianthema hereroensis*. *M.Sc. Thesis, University of Natal, Pietermaritzburg, RSA,* 147 pp.

NOY-MEIR I. 1974. Desert ecosystems: higher trophic levels. *Annual Review of Ecology and Systematics* 5: 195-214.

PERRIN M.R. & BOYER D.C. (in prep.). Population biology of gerbils in the Namib Desert.

PERRIN M.R., BOYER H. & BOYER D.C. 1992. The diets of the hairy-footed gerbils *Gerbillurus paeba* and *G. tytonis* from the dunes of the Namib Desert. *Israel Journal of Zoology* 38: 373-383.

REICHMAN O.J. 1977. Optimization of diets through food preferences by heteromyid rodents. *Ecology* 58: 454-457.

REICHMAN O.J. 1979. Desert granivore foraging and its impact on seed densities and distributions. *Ecology* 60: 1085-1092.

SEELY M.K. 1978. The Namib Dune Desert; an unusual ecosystem. *Journal of Arid Environments* 1: 117-128.

SEELY M.K. & LOUW G.N. 1980. First approximation of the effect of rainfall on the ecology and energetics of a Namib Desert dune ecosystem. *Journal of Arid Environments* 3: 25-54.

SOHOLT L.T. 1973. Consumption of primary production by a population of kangaroo rats (*Dipodomys merriami*) in the Mojave Desert. *Ecological Monograph* 43: 357-376.

WIEGERT R.G. & EVANS F.C. 1967. Investigations of secondary productivity in grasslands, pp. 499-518. In: Petrusewicz K., Edit. Secondary productivity of terrestrial ecosystems. Vol. II. *Warsaw: Panstwowe Wydawnictwo Naukowe,* 381-879 pp.