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Ecology, Vol. 75, No. 5. (Jul., 1994), pp. 1397-1405.

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PREDATION RISK AND COMPETITION AFFECT HABITAT SELECTION AND ACTIVITY OF NAMIB DESERT GERBILS¹

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Abstract. Microhabitat partitioning based on microhabitat-specific predation rates has been well documented as a mechanism of coexistence in desert rodents. In the Namib Desert, two species of rodent, a nocturnal dune hairy-footed gerbil, *Gerbillurus tytonis*, and a diurnal striped mouse, *Rhabdomys pumilio*, co-occur in a vegetated island in the dune sea. The species show a marked preference for the same microhabitat, although gerbils also inhabit a second microhabitat where predation risk is greater. We provide direct experimental evidence for the role of predation risk and both inter- and intraspecific competition in affecting foraging behavior and habitat selection of gerbils. Using two techniques (tracking and seed trays), we were able to show that gerbils decrease foraging activity in vegetated areas during periods of increased illumination (full-moon periods). Removal of a potential competitor, the striped mouse, as well as removal of conspecifics, resulted in a significant increase in gerbil foraging activity. We propose that high susceptibility to predation results in a shared preference for the safest habitat and leads to competition for limited resources.

Key words: community ecology; competition; desert rodents; foraging behavior; habitat selection; Namib Desert; predation risk.

INTRODUCTION

Predation and competition may interact to structure communities (Kotler and Holt 1989). Preferred habitats, where predation risk is low, may be competed for by several species. Predation may influence competition directly by inflicting mortality on one or more potentially competing prey populations (density-mediated effect) and/or by altering prey behavior and the intensity of competition by forcing prey species to occupy the same habitat where predation risk is low (behaviorally mediated effect).

Competitive interactions can be affected directly by predation if different risks are associated with different activities. Foraging behavior can be altered markedly by predation risk and may lead to habitat partitioning in species differing in susceptibility to predation, thereby allowing for competitive coexistence (Caswell 1978, Sih 1980, Hanski 1983, Werner et al. 1983). Where habitat partitioning occurs in the absence of exploitative competition or aggressive interference, it has been termed "short-term apparent competition" (Holt and Kotler 1987).

Desert rodents are well suited to studies of the effects of predation and competition on community organization for the following reasons. (1) Predation risk has been shown to cause a marked change in nocturnal desert rodent activity (e.g., Kotler 1984a, b, 1985a, Brown et al. 1988, Kotler et al. 1988). (2) Competition between sympatric rodent species has been demonstrated by removal experiments, resulting in density increases, habitat shifts, or activity changes in the remaining species (e.g., Holbrook 1979, Abramsky and Sella 1982, Brown and Munger 1985, Mitchell et al. 1990).

Much literature is available on coexistence of desert rodents from North America and Israel (e.g., Price 1978a, b, Kotler 1984a, b, c, 1985a, b, Brown 1988, 1989a, b). However, there is a paucity of similar work from Africa and Asia, which prompted this study in the Namib Desert of Africa.

At the study site in the Namib Desert, Namibia, a high density of dune hairy-footed gerbils, *Gerbillurus tytonis*, lives in a vegetated island in the dune sea. The gerbils travel between isolated patches of vegetation and presumably incur great risk of predation by predators such as jackals and raptors. Only one other species of rodent was present in the "island," the striped mouse, *Rhabdomys pumilio*, which is widespread in many habitats in sub-Saharan Africa (Smithers 1983). It is more commonly associated with dense vegetation and probably reached the "island" from the riparian vegetation of the Kuiseb riverbed 1 km away. These species, which are similar in size (Table 1) and opportunistic omnivores, are vulnerable to predation and may compete for the predator-restricted habitat. We

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TABLE 1. Morphological characteristics of gerbils and striped mice.

Characteristic	Gerbils	Striped mice
Body mass (g)	28	43
Hind foot length/ body length (%)	31	20
Locomotion	Saltatorial/ quadrapedal	Quadrapedal
Auditory bullae	Slightly inflated	No inflation
Activity	Nocturnal	Diurnal

concentrated our study on the gerbil because it is a specialist in the desert dune habitat, while the striped mouse is a habitat generalist. We predicted that, if interspecific competition had a negative effect on habitat selection and activity of either species in this habitat, it would be through detrimental effects on the gerbil by the larger, invasive striped mouse.

The goals of this study were to: (1) examine the effect of predation risk on foraging efficiency, activity, and habitat selection in the nocturnal dune hairy-footed gerbil, *G. tytonis*; (2) determine, by removal experiments, the influence of intraspecific and interspecific competition (with the striped mouse, *R. pumilio*) on gerbil activity.

By examining whether predation risk (as indicated by lunar periodicity, i.e., moonlight [Kotler 1984a]) affects habitat selection, as well as investigating competition between the two species, it may be possible to present a comprehensive picture of how predation and competition interact to structure this Namib Desert rodent community. Because the study site was a vegetated "island" in a dune sea, it was unnecessary to erect enclosures for the removal experiments to study the effects of competition. We thereby avoided interference with the natural movement of predator and prey populations within the "island." Thus, any effect of competition could not be construed as an artifact of the size of enclosure in which the animals were constrained. Using an "island" also permitted effective competitor-removal experiments because immigration was rare.

METHODS

Study site

The study site was an isolated "island" of vegetation, $\approx 1 \times 0.35$ km in size, situated in an interdune valley between two parallel linear dunes. It lies at the northern end of the Namib sand sea, 5 km northwest of the Namib Desert Research Unit of Namibia at Gobabeb (23°24' S, 15°03' E) and was separated by 1 km of sand dune and interdune plains from the usually dry Kuiseb riverbed. The vegetation consists predominantly of the perennial grass *Stipagrostis sabulicola* and to a lesser extent, the endemic nara, *Acanthosicyos horrida*, both of which occur in distinct, monospecific clumps on sandy hummocks throughout the site. *S. sabulicola* is

a spiky grass, which grows in tufts and may reach a height of 2 m. Seeds are produced during summer after sufficient rain has fallen. Nara has leaves reduced to sharp thorns and grows in dense tangled bushes up to 1.5 m tall (Robinson 1976) and a few metres wide (Craven and Marais 1986). Female plants produce melons, which ripen in the summer months (October to February) and are commonly eaten by rodents, Ostriches, and jackals.

Predators

Nocturnal predators at the study site included black-backed jackals, *Canis mesomelas*, which were regular nightly visitors (J. J. Hughes, *personal observations* of tracks and animals), and Spotted Eagle Owls, *Bubo africanus* (one pair observed roosting and foraging there for many years). Diurnal predators were predominantly raptors: Pale Chanting Goshawks, *Melierax canorus*, and Rock Kestrels, *Falco tinnunculus*. Reptilian predators present were the Namib sand snake, *Psammophis leightoni namibensis*, and the sidewinding adder, *Bitis peringueyi*. No data are available on the abundances of these predators.

Assessment of relative activity

Three techniques, live-trapping, sand-tracking, and seed-tray giving up densities (GUDs), were used in several experiments from May 1989 to February 1990 to assess relative activity of the gerbil under different conditions. Approximately equal numbers of trap, track, and seed-tray stations were arranged in the three recognized microhabitats: nara, grass, and open areas (> 1.5 m from vegetation). The number of new moon and full moon nights on which each technique was performed for the different experiments is shown in Table 2.

Live-trapping

Two Elliot live traps (32 × 10 × 9 cm), baited with peanut butter mixed with rolled oats, were placed 1.5–2 m apart at each trapping station. Approximately 30–

TABLE 2. Number of new moon (N) and full moon (F) nights on which each technique was performed in predation risk and interspecific competition experiments.

	N	F	Total
Predation risk			
Live-trapping	4	3	7
Tracking	4	4	8
Seed trays	2	2	4
Interspecific competition			
Removal			
Live-trapping	2	2	4
Tracking	2	1	3
Seed trays	1	2	3
Reintroduction			
Live-trapping	1	1	2
Tracking	2	1	3
Seed trays	1	1	2

36 traps (15–18 stations) were laid in each of the three microhabitats (open, grass, and nara) in a grid design, with 10 m between the lines. Traps were set at sunrise for day-trapping and at sunset for night-trapping.

Sand-tracking

Kotler (1985a) and Mitchell et al. (1990) have used sand-tracking to measure the effects of predation risk and competition on the activity of desert rodents. Counting the number of crossings of smoothed areas of sand by these rodents enables direct quantification of a population's relative or actual activity (travel, exploration, foraging) within and between microhabitats with a minimum of interference. In this study, sand-tracking entailed smoothing two 45 × 45 cm patches of sand (separated by 1.5–2 m) using a squeegee (a strip of thick rubber on a handle) at 20 stations in nara, grass, and open areas at sunset. The next morning, at sunrise, rodent activity at each plot was scored according to the number of tracks left in the sand. A single track that completely crossed a patch received a score of 1, an incomplete crossing (a track cutting across the edge of a smoothed square) received a score of 0.5, while no activity received a score of 0. The maximum score for a tracking plot was 4 because it was impossible to accurately assess the true number of rodent crossings greater than this.

We could differentiate between the tracks of *G. tytonis* and *R. pumilio* by the greater depth of the imprint left by the larger striped mouse and by the tail-drag marks it left in the sand. It was seldom necessary to differentiate between the species' tracks because *R. pumilio* is largely diurnal; the squares were smoothed in the evening after this species' afternoon activity and tracks were read the following morning prior to its morning activity period.

GUDs

A number of studies have estimated the effects of predation and competition on the activity of rodents using seed-tray "giving-up densities" (GUDs) (Brown 1988, 1989a, b, Mitchell et al. 1990, Kotler et al. 1991). Seed trays provide uniform foraging opportunities that allow measurement of foraging efficiency under different environmental conditions. Twenty circular seed trays (45 cm in diameter and 2.5 cm deep), filled with 3 L of sifted sand into which was mixed 5 g of pre-weighed millet seed, were laid in pairs (separated by 1.5–2 m) in nara, grass, and open areas, at sunset. The following morning the sand was sieved, debris removed, and the remaining seed collected.

Assumptions of seed-tray technique

The use of seed trays for assessing GUD was based on several assumptions (Brown 1988, 1989b): (1) rodents harvest seeds from a patch until the benefit of foraging there no longer outweighs the costs, (2) rodents do not become satiated when feeding in a single patch,

and (3) GUD results are not distorted by multiple foragers (sand-tracking revealed that virtually all rodents foraged alone in this study).

An important attribute of this technique is that rodents foraging in the trays face diminishing returns to harvesting with increased time spent in the patch (Brown 1988). The use of seed trays therefore mimics the situation in the natural environment where energy input is required for harvesting. Seed trays do not provide "free food" because rodents must search through the sand matrix as they would in their natural habitat. In addition, the millet seed used in the seed trays, although slightly larger than the average grass seed normally encountered by the rodents (J. J. Hughes, *personal observation*), falls within the range of seed sizes naturally available. We could differentiate between species using the trays by the deeper imprints of the heavier striped mouse and the tail-drag marks it left in the sand. As was the case with the tracking data, seed trays were made available and removed outside of the usual activity period of the diurnal striped mouse. Thus, we seldom needed to determine which species had used the trays.

Predation risk and habitat selection

To investigate habitat selection in gerbils, relative activity within each microhabitat was quantified by laying traps (30–36), track stations (40), and seed trays (20) in nara, grass, and open areas. The effect of predation risk on gerbil activity was monitored by performing the experiment on both full moon and new moon occasions, making the assumption that increased lunar illumination is tantamount to increased risk of predation, particularly in deserts where cloud cover is minimal and infrequent (see Price et al. 1984, Kotler 1985b). The experimental protocol involved running trapping, tracking, and seed trays every 2 wk on successive nights during new and full moon periods (Table 2).

Competition

Intraspecific competition.—Perturbation experiments facilitate assessment of the effect of intraspecific competition on per capita gerbil activity (i.e., total number of crossings per tracking station divided by population size). The Petersen capture–recapture method (Krebs 1989), when applied to five consecutive nights of live-trapping data, just prior to removal of the first 25% of the population, indicated a total population size of 62 gerbils for the study area. In order to effect a stepwise reduction of 25% of the total population, 15 or 16 gerbils were removed on three occasions, each 3 d apart. Sand-tracking was used on the third night after each removal session to assess any changes in per capita activity.

Interspecific competition.—Perturbation experiments were also used to determine the effects of interspecific competition on per capita gerbil activity. The

entire population of striped mice was removed from the study site by live-trapping during the course of a week until none was captured. Any changes in activity of the remaining gerbils were monitored by subsequent live-trapping, sand-tracking, and seed-tray experiments over a period of 2 mo, beginning a few days after striped mouse removal (Table 2). Trapping enabled monitoring of striped mouse immigration and removal of intruders. After 2 mo, the striped mice were reintroduced to the study site and gerbil activity further monitored, in the same way, over the course of the following month (Table 2).

Statistical analysis

Kruskal–Wallis nonparametric tests (Sokal and Rohlf 1981) were used to analyze tracking data as the tracking plots were often saturated with tracks resulting in a skewed distribution of data. Analysis of variance (ANOVA) (Sokal and Rohlf 1981) was used on logarithmically transformed GUDs (following Brown 1988).

RESULTS

Habitat selection

Habitat selection and activity.—Gerbils exhibited significant habitat preferences. Nara was the most preferred microhabitat, followed by grass, while open areas were the least preferred (Table 3).

Effects of moonlight.—Gerbil activity was significantly reduced in increased moonlight as shown by sand-tracking ($H = 26.1$, $P < 0.05$) and seed-tray data ($F_{1,18} = 158.2$, $P < 0.001$) (Fig. 1). Both techniques revealed greater gerbil activity during new moon for all microhabitats combined and for open, grass, and nara microhabitats analyzed separately (Table 4). Increased illumination did not affect gerbil capture rate. There was no significant difference between the number of individuals caught on new moon and full moon nights ($\chi^2 = 0.113$, $df = 1$, $P > 0.05$). There was a significant interaction between microhabitat and moon effects on the capture data ($F_{2,14} = 7.771$, $P = 0.02$).

Competition

Intraspecific competition.—Reduction in the number of gerbils present resulted in a significant increase in per capita activity (measured by tracking) after each removal stage across all microhabitats ($H = 30.25$, P

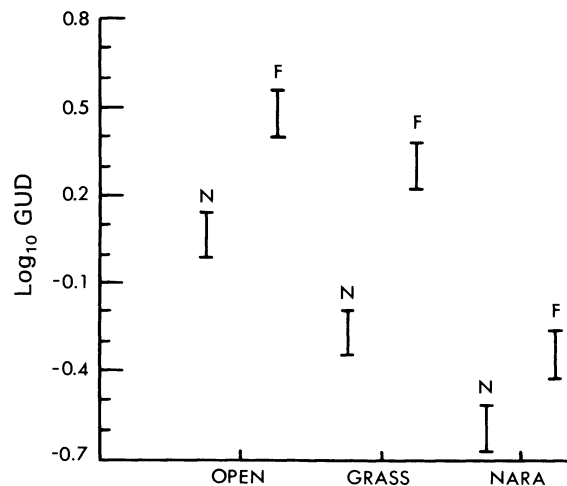


FIG. 1. The effect of predation risk on relative gerbil activity (\log_{10} giving-up seed densities [GUDs]). New moon is denoted by N and full moon by F and the vertical bars represent 95% confidence intervals.

< 0.001). However, the increase in per capita activity was significant for the grass ($H = 8.80$, $P < 0.05$) and nara ($H = 81.9$, $P < 0.001$) microhabitats only (Table 5). There was no significant change in per capita activity in open areas ($H = 2.36$, $P > 0.05$). There was a significant increase in per capita activity after each successive removal stage in the nara microhabitat ($P < 0.05$). In the grass microhabitat, the increase in per capita activity was significant after each removal stage except the last (i.e., after removal of the last 25% of rodents, $P < 0.05$).

Interspecific competition.—Gerbil activity, as measured by sand-tracking data, increased following removal of striped mice from the study area ($P < 0.05$). After subsequent reintroduction of the mice, gerbil activity then decreased significantly (Kruskal–Wallis test on tracking data; $H = 11.05$, $P < 0.05$). A three-way ANOVA (testing for the effects of habitat, moon phase, and species presence) on logarithmically transformed GUDs produced similar results ($F_{1,14} = 15.79$, $P < 0.001$; data from all microhabitats, with new and full moon data pooled).

When the Kruskal–Wallis test was applied to tracking data for each microhabitat separately, the increase in gerbil activity following competitor removal and the

TABLE 3. Effect of habitat on gerbil activity, as indicated by median number of tracks per 45×45 cm tracking station and mean ± 1 SE seed-tray GUDs (giving-up [seed] densities). Kruskal–Wallis tests were performed on tracking data and ANOVA on seed-tray GUDs (log transformed prior to analysis).

Technique	Microhabitats			
	Open	Grass	Nara	All
Tracking†	0	2	3.5	2***
Seed trays‡	2.24 ± 0.16	1.49 ± 0.15	0.45 ± 0.06	1.43 ± 0.09 ***

*** $P < 0.001$.

† Units are number of track crossings per 0.2 m^2 .

‡ Units are grams of seed remaining in each seed tray.

TABLE 4. The effects of increased illumination on gerbil activity, shown by median number of tracks per tracking station and mean \pm 1 SE GUDs (giving-up [seed] densities). Kruskal-Wallis tests were performed on tracking data and ANOVA on seed-tray GUDs.

Technique	Microhabitats			
	Open	Grass	Nara	All
Tracking†				
New moon	0.5***	2.5***	3.5**	2***
Full moon	0	2	3	1
Seed trays‡				
New moon	1.32 \pm 0.18	0.69 \pm 0.11	0.27 \pm 0.02	0.77 \pm 0.07
Full moon	3.18 \pm 0.2	2.37 \pm 0.21	0.63 \pm 0.12	2.12 \pm 0.15

** $P < 0.01$, *** $P < 0.001$ for comparisons within habitats between new and full moon. all such comparisons of seed-tray GUDs were highly significant ($P < 0.001$).

† Units are number of track crossings per 0.2 m².

‡ Units are grams of seed remaining in each seed tray.

decrease following subsequent reintroduction was significant for the grass microhabitat only ($H = 11.64$, $P < 0.05$) (Table 6). In the nara microhabitat, there was a significant increase in gerbil activity after striped mouse removal ($H = 20.25$, $P < 0.05$), but the decrease in activity after competitor reintroduction was not significant ($P > 0.05$). The level of activity in the least preferred, open microhabitat was not significantly altered after removal or reintroduction of striped mice ($H = 0.66$, $P > 0.50$).

When GUDs from grass and open microhabitats were analyzed separately, no significant change was found in GUDs either after competitor removal or reintroduction (Open $F_{1,17} = 1.83$, $P > 0.20$; Grass $F = 1.6$, $P > 0.20$). In the nara microhabitat, GUDs decreased significantly after striped mice reintroduction ($F_{2,17} = 5.46$, $P < 0.05$) (Fig. 2).

Trapping data

The number of gerbils captured differed significantly between open and nara microhabitats ($\chi^2 = 25.5$, $df = 1$, $P < 0.0001$) and the grass and nara microhabitats

($\chi^2 = 14.6$, $df = 1$, $P < 0.0001$). Gerbils were most frequently caught in nara and least frequently in open areas. The difference in capture success, however, was not significant between the open and grass microhabitats ($\chi^2 = 1.74$, $df = 1$, $P > 0.05$). Increased illumination did not affect gerbil capture rate. There was no significant difference between the number of individuals caught on new moon and full moon nights ($\chi^2 = 0.113$, $df = 1$, $P > 0.05$).

Of 92 *R. pumilio* captures, 85 were in nara clumps, seven in grass and none in the open microhabitat. Seventy-one of the 92 captures of this species were from day trapping. Significantly more of the nocturnal captures were on new moon nights ($\chi^2 = 3.86$, $df = 1$, $P < 0.05$). The abundance of *R. pumilio* was significantly positively correlated with both the size and density of nara clumps ($r^2 = 0.66$; $P < 0.0005$). Both factors were significantly correlated with *R. pumilio* abundance (nara density: $F_{1,15} = 23.08$; nara clump size: $F_{1,15} = 23.22$; Hughes 1990).

DISCUSSION

Microhabitat selection

Nara was the preferred microhabitat of both striped mice and gerbils. Analysis of tracking and GUD data showed a significant difference in the amount of gerbil activity occurring in nara, grass, and open microhabitats. The open microhabitat was the least preferred microhabitat. Live-trapping data, however, did not reveal a difference in densities between grass and open areas for gerbils but did show that striped mice inhabited nara clumps almost exclusively. Striped mice tended to restrict activity to the cover of the nara bushes, and pathways between nara clumps were direct (J. J. Hughes, *personal observation*). Dependence of striped mice on cover, usually dense grass in other habitats, has been widely reported (e.g., Nel and Rautenbach 1975, Christian 1980, David and Jarvis 1983), as has the tendency to form runways (Bond et al. 1980). Both are important strategies for reducing susceptibility to predation.

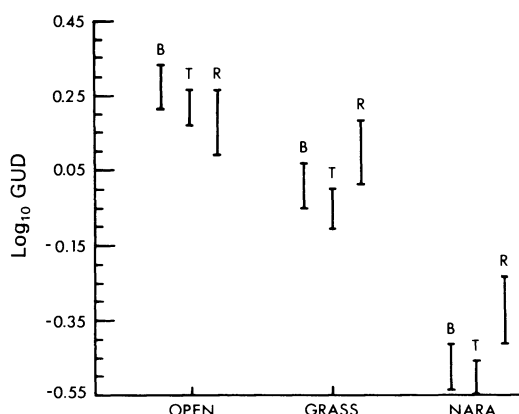


FIG. 2. The effect of striped mice removal and reintroduction on relative gerbil activity (\log_{10} GUDs). Symbols above the 95% confidence interval bars represent rodents present at the study site: both (B) species, gerbils (T) only, and striped mice reintroduced (R).

TABLE 5. The effect of gerbil removal on per capita gerbil activity. For Kruskal–Wallis tests, the tracking scores at each site are ranked across all habitats from largest to smallest. The Kruskal–Wallis average rank represents the average rank for each habitat and is, thus, an average score for each tracking site in that habitat.

Microhabitat	Number of gerbils present	Per capita activity	Kruskal–Wallis average rank
Open	62	0.0095	104.96
	46	0.0060	97.13
	31	0.010	100.95
	16	0.0313	110.64
Grass	62	0.028	76.35
	46	0.044	91.41
	31	0.063	108.70
	16	0.070	100.70
Nara	61	0.052	45.54
	46	0.080	100.00
	31	0.104	142.04
	16	0.149	161.21

In all microhabitats, gerbils foraged less on moonlit nights, when predation risk was presumably greater, than on moonless nights and avoided the open microhabitat where they were most exposed to predators. Alteration of foraging efficiency under different conditions can be understood using the “giving-up-density” (GUD) approach. Reduced gerbil activity within each microhabitat on moonlit nights can be interpreted as reflecting the higher risk of predation on these nights. With respect to seed trays, the higher foraging cost lowers the net benefit of staying and harvesting millet to a similar level to that found on new moon nights, resulting in higher GUDs. Similar results have been obtained for North American and Israeli desert rodent communities (Kotler 1984a, b, 1985a, Brown 1988, 1989b).

Corroboration of GUDs with sand-tracking data lends further support for the usefulness of this technique in measuring foraging behavior (Mitchell et al. 1990). In another study, we have shown that GUDs were not influenced by prior knowledge of seed tray location or by climatic conditions (Hughes 1990).

The observed habitat selection in these rodents is likely determined by predation risk, food availability, and dietary preference. Predation risk constitutes one of the most important foraging costs. Risk of predation affects activity of nocturnal rodents, their habitat use, and quitting patch harvest rates (see, e.g., Kaufman and Kaufman 1982, Price et al. 1984, Brown 1988). The thorny nara provides a refuge from mammalian and avian predators; using this habitat is therefore likely to be advantageous.

In this Namib Desert rodent community, striped mice are quadrupedal while gerbils exhibit a more saltatorial gait. This is likely to influence their choice of habitat. Saltatorial locomotion in gerbils may enable rapid changes in direction, thereby facilitating escape from predators (Eisenberg 1975). In addition, gerbils

possess slightly inflated auditory bullae, which may enhance sound detection (Webster and Strother 1972). Both these features likely confer an advantage to the gerbils over striped mice in allowing the use of a wider range of habitats (nara + grass [gerbils] vs. nara only [striped mice]) without higher levels of predation.

Dietary preferences and availability of resources are other likely determinants of habitat selection. Differences in diet between rodents have been invoked as the cause of density shifts between microhabitats in response to manipulation of vegetation structure (Rosenzweig 1973, Price 1978b). Cafeteria choice tests and fecal analysis (Hughes 1990) suggest striped mice and gerbils are omnivorous and exhibit similar food preferences. Striped mice ate a much wider variety of food items than gerbils (including nara plant parts), which may allow them to restrict their activity to nara clumps, thereby avoiding the high predation levels that would be incurred in other microhabitats. Seeds may be important to both species when the grass *Stipagrostis sabulicola* produces seeds for a relatively short period after sufficient rainfall in the summer. During this period, there was a marked increase in the use of the grass microhabitat by striped mice, although this was not quantified.

Food resources tend to be concentrated at vegetation clumps either in the form of the plant itself, as wind-blown detritus and seeds, or associated insects. Fielden (1989) found the biomass of excavated invertebrates from vegetation clumps on a dune slope near the study site to be 100 times that of unvegetated areas. It is therefore not surprising that nara is the microhabitat most preferred by rodents, because it acts as a trap for wind-blown seeds, produces edible plant parts (melons and flowers), is a source of insects, and confers likely benefits in terms of predator avoidance.

Validity of live-trapping

Live-trapping was unsuitable for quantifying the effect of predation risk on gerbil activity. This was indicated by similar trap success at new and full moon, which contrasts with the results of tracking and seed-

TABLE 6. The effect of striped mice removal on per capita gerbil activity. Symbols in column 2 represent the presence of both species (B); gerbils only (T); and both species after reintroduction of striped mice (R).

Microhabitat	Species presence	Number of track sites	Kruskal–Wallis average rank
Open	B	247	229
	T	108	239
	R	112	239
Grass	B	293	250
	T	113	305
	R	118	250
Nara	B	293	237
	T	118	300
	R	111	284

tray GUDs. The lack of a difference in capture success between new and full moon may result from a constant rate of prey capture by visually oriented, nocturnal predators (jackals/owls) regardless of light intensity, thereby eliciting no change in the rodents' foraging behavior. Alternatively, trapping is not a suitable technique for detecting behavioral changes. The differences detected in gerbil behavior between new and full moon nights using the other techniques (sand-tracking and seed trays) indicates the latter scenario is true.

In addition, live-trapping was not entirely reliable for monitoring habitat selection because it overestimated use of the open microhabitat. The latter finding is supported by Kotler's (1985b) results that live-trapping overestimated activity of *Peromyscus maniculatus* in open areas in the Great Basin Desert in North America. Live traps, like seed trays, constitute resource patches. However, the latter produce a graded response in the form of GUDs, while live traps yield an all-or-nothing response. The trapped animal is removed from the system for the remainder of the night/day of foraging and cannot contribute to interference or resource depletion. The use of more sensitive techniques such as seed-tray GUDs and tracking does not interfere with the foragers' normal activity patterns.

Competition

Evidence for competition usually occurs by density shifts or habitat shifts in response to changes in competitor density (Grant 1972). Density changes indicate the strength of competition while habitat shifts indicate the resources over which competition occurs (Lemen and Freeman 1987). A number of studies have demonstrated "compensatory" density shifts under conditions of reduced competition (Krebs et al. 1969, Munger and Brown 1981, Brown and Munger 1985). Brown and Munger (1985) showed density of a rodent population to be regulated by limited food resources (demonstrated by seed addition) and interspecific competition (demonstrated by selected species removal). Many studies have revealed rodent microhabitat shifts in response to manipulated competitor densities and/or vegetation structure (e.g., Koplin and Hoffman 1968, Price 1978b, Thompson 1982, Bowers et al. 1987) and natural rodent fluctuations (Frye 1983, Larsen 1986). Studies on birds, such as those by Grubb and Greenwald (1982), Lima (1985) and Lima et al. (1987), as well as fishes (Werner et al. 1983), have also revealed responses to vegetation structure (see review by Lima and Dill 1990).

The intraspecific removal experiment revealed gerbil activity to be density dependent. As the number of conspecifics decreased, per capita activity (measured by tracks) of the remaining gerbils significantly increased in grass and nara microhabitats (Table 5). In the open microhabitat, no significant change in per capita activity was noticed, although the trend was in the predicted direction. However, this may have been

a consequence of increasing darkness after full moon. The fact that intraspecific competition was not manifested in the open microhabitat is indicative of the use of open areas as corridors between resource patches.

Changes in relative activity that occurred following competitor removal may be explained in terms of a decrease in missed opportunity cost of foraging elsewhere (i.e., over all microhabitats in which gerbils are active). In the absence of competitors, foraging becomes more valuable relative to other fitness-enhancing activities, such as maintenance and territory defence. This results in increased per capita gerbil activity, which is reflected by lower GUDs and greater number of tracks. Laboratory-staged encounters revealed a high level of social intolerance in *G. tytonis*, lending additional support for intraspecific competitive behavior (Dempster and Perrin 1989).

After competitor removal, the increase in gerbil activity should be greater in nara than in either grass or open microhabitats because of the combined effect of increased resource abundance and lower missed-opportunity costs (MOC). However, as a result of track site "satiation" (track sites had an upper limit of four crossings) and seed-tray depletion (maximum of 5 g of millet), this could not be detected. The increase in gerbil activity measured in the nara was similar to that for the grass microhabitat.

Increased gerbil activity recorded in grass clumps, despite the absence of striped mice, occurred because higher resource levels in the nara apparently resulted in decreased MOC in all foraged microhabitats. The consequence of this was increased patch use and lowered optimal quitting harvest rates. Thus, removal of competitors from one microhabitat can have a spill-over effect in another where the competitor is absent. In this case, removal of striped mice from the nara microhabitat resulted in an increase in gerbil activity in the grass microhabitat. This is the reverse of what would be expected under the centrifugal community organization mooted by Rosenzweig and Abramsky (1986) for a shared habitat-preference system such as the one we studied. Under that schema, removal of a competitor should result in negative isolegs (lines in a state space of animal densities such that some aspect of a species' habitat selection is constant at every point along that line). That is, niche contraction towards the single preferred habitat should occur. The result of our study is congruent with the niche compression hypothesis (niche expansion after competitor removal) of MacArthur and Pianka (1966), although this latter theory applies to distinct-preference systems. Brown and Rosenzweig (1986) have shown that, in a distinct-preference system where there is spatial and/or temporal variation in resource density, niche shifts can behave "perversely": increases in a competitor's density may increase or decrease niche breadth. Whether niche expansion or compression will occur depends on the nature of the system and what the species' densities are

in that system. No general conclusions are possible (Brown and Rosenzweig 1986). It would appear that further theoretical work on the changes expected in shared-preference systems is required to elucidate the expected changes in habitat selection when competitors are removed.

In the open microhabitat, no change in foraging activity was measured, perhaps because the high predation cost of foraging continued to outweigh the decreased MOC or that food availability in this microhabitat was very low.

It is important to note that the increase in activity that occurred in the absence of competitors returned to the prerulevel level after competitor reintroduction. This eliminates the possibility that increased gerbil activity occurring after competitor removal was a seasonal effect related to altered food availability, climate, or reproductive stage.

An increase in gerbil activity following competitor removal is congruent with the optimization model for a forager trying to maximize net energy gain but subject to a time constraint on all activities (energy maximization). Here, it is assumed that animals forage until the marginal benefit of foraging equals the marginal cost of foraging. This contrasts with the "energy requirement" hypothesis (time minimization), which assumes animals forage to satisfy an energy requirement in the shortest possible time. This latter hypothesis predicts that animals should increase foraging effort following increased competitor density (Mitchell et al. 1990). The reasoning behind the latter hypothesis is that, as a result of resource depletion by competitors, the forager must "work harder" (increase foraging time) in order to satisfy its energy requirement. Where the goal of foraging is to maximize fitness and where the marginal value of energy is high (a likely condition under strong competition), energy maximizers should decrease foraging effort in response to increased competition. In exploitative competition, competitors deplete resources and lower the marginal benefit of foraging more than the marginal cost of foraging (Mitchell et al. 1990). Thus, optimal foraging time is decreased as is activity. In our study, removal of striped mice increased the benefit of foraging to gerbils (as resources became more available), accounting for the observed increase in gerbil activity in the vegetated areas.

Interspecific competition has been similarly demonstrated (using sand-tracking) between two species of gerbils in the Negev Desert (Mitchell et al. 1990). In that study, densities of *Gerbillus allenbyi* were altered relative to two densities of a competitor, *G. pyramidum*. Per capita activity of *G. allenbyi* was reduced at higher *G. pyramidum* densities.

*Type of density-dependent
interspecific interaction*

Temporal segregation in activity of striped mice and gerbils in the Namib Desert rodent community elim-

inates the likelihood of aggressive interference influencing the intensity of competitive interaction. However, exploitative competition is probable because daily resource renewal of plant parts and insects is likely to be limited as a result of low overall biomass in the Namib (Seely and Louw 1980). High dietary and spatial overlap leading to exploitative competition between striped mice and gerbils appears to account for the observed competitive interaction.

Short-term apparent competition may produce results indistinguishable from exploitative competition (Holt and Kotler 1987). However, gerbils and striped mice are temporally segregated and have different predators (owls/jackals vs. diurnal raptors/snakes), suggesting that short-term apparent competition does not operate in this community.

ACKNOWLEDGMENTS

We thank the Director, Dr. M. K. Seely, and staff of the Desert Ecological Research Unit of Namibia at Gobabeb for the use of facilities, accommodation and for all assistance given during the course of the fieldwork. We are grateful to Dr. B. P. Kotler for his valuable input and suggestions. Financial assistance was provided by the Foundation for Research Development (FRD). D. Ward was the Jacob Blaustein post-doctoral fellow at the Jacob Blaustein Institute for Desert Research, Sede Boqer, Israel, during the period of this study.

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