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Foraging efficiencies of competing rodents: why do gerbils exhibit shared-preference habitat selection?

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ABSTRACT

Two coexisting gerbil species, *Gerbillus allenbyi* (26 g) and *G. pyramidum* (40 g), exhibit shared-preference optimal habitat selection. In a mosaic of stabilized sands and semistabilized dunes, both species primarily prefer the semistabilized-dune habitat. We hypothesized that foraging benefit, due to the lower amount of loess in the semistabilized dunes, is the underlying cause for this preference. We tested this by measuring foraging efficiencies (giving-up density of seeds) in both manipulated foraging substrates (sand and loess) and natural habitats (semistabilized dunes, stabilized sands, and loess plateau). We also compared harvest rates on sand and loess. We used the loess substrate and loess plateau habitat to exaggerate the effect of loess on the gerbils' foraging behavior. Regarding foraging substrate, gerbils had significantly higher foraging efficiencies on sand in the field. They also had significantly higher harvest rates on sand in the laboratory. Regarding habitats, both species were more efficient in semistabilized dunes than in stabilized sands or loess plateau. Additional results suggested that the area surrounding a foraging patch had an important role in predator avoidance. We concluded that the semistabilized-dune habitat allowed gerbils to forage more efficiently in a patch, because it is easier to dig for seeds in the sandy substrate found there, and because gerbils enjoyed lower predatory risk traveling to and from the seed patch. The results supported the hypothesis that foraging benefit is the basis of the shared-preference habitat selection of the gerbil species.

INTRODUCTION

Habitat selection has been suggested to have an important role in community organization (e.g., MacArthur and Wilson 1967, Schoener 1974, Rosenzweig 1981, 1991, Grant 1986). Schoener (1974, 1986) showed that among three modes of resource partitioning -- food, habitat, and time -- habitat partitioning was found to be the most common one. Indeed, the existence of different habitats (or microhabitats) was often essential for understanding desert rodent communities (see for reviews Rosenzweig 1977, Price 1986, Kotler and Brown 1988).

Rosenzweig (e.g., 1979, 1981, 1989) developed a theory of *interspecific density-dependent optimal habitat selection* (hereafter, optimal habitat selection) for two competing species (see also Brown and Rosenzweig 1986). The theory builds on the intraspecific habitat selection theory of Fretwell and Lucas (1970, Fretwell 1972), and optimal patch use theory (Charnov 1976, Brown 1988). The theory assumes that individuals of each of the competing species choose the habitat set that maximizes their fitness. This choice is affected by the density and distribution of each species. Practically, the theory allows one to describe different optimal behavioral strategies (i.e., different habitat preferences) in a two-species-system state space by using lines (i.e., isolegs) which separate regions of the state space in which each strategy is preferred (see for details Rosenzweig 1981, 1985, 1989, 1991). The number and shapes of the isolegs provide information about the species' competitive relationships and behavioral preferences. They also suggest hypotheses about mechanisms of coexistence between the species (e.g., Rosenzweig 1981, 1985, 1991, Rosenzweig and Abramsky 1986, Abramsky et al. 1990, 1991, 1992, Ziv et al. 1993).

Optimal habitat selection and its isolegs have been studied in two gerbil species -- the greater Egyptian sand gerbil, *Gerbillus pyramidum*, and Allenby's gerbil, *G. allenbyi* (=*G. andersoni allenbyi*; Ritte et al. 1976, Harrison and Bates 1991). These two species are the most common among five rodent species of the gerbilline subfamily that live in the sandy habitats of the Negev Desert in Israel (Zahavi and Wahrman 1957, Abramsky et al. 1985).

They are nocturnal, inhabiting burrows during the day and collecting and consuming seeds and vegetative material while foraging during the night. Both species are mostly granivorous (seed consumption of 85.3% and 89.6% for *G. pyramidum* and *G. allenbyi*, respectively; Bar et al. 1984) and show a diet overlap value of 0.92 (Bar 1982).

Based on their isolegs and the habitat information, Rosenzweig and Abramsky (1986) hypothesized that the two species share the same primary habitat preference -- semistabilized dunes. This hypothesis has been confirmed experimentally (Abramsky et al. 1990). Where two habitat types occur (i.e., semistabilized dunes and stabilized sands), the habitat selection of the species follows the shared preference pattern (Abramsky et al. 1990). In the absence of its competitor, each species prefers the semistabilized dunes. We do not know the underlying cause of the shared preference. Why do both species, at low densities, prefer the same habitat type? What is better about the semistabilized habitat?

We hypothesize that habitat preference depends primarily on foraging benefits. That is, where both semistabilized dunes and stabilized sands exist, individuals of both species benefit more from foraging in the semistabilized dunes. Foraging benefits may result from two different foraging components: higher harvest rate and higher foraging efficiency. We hypothesize that these components vary with foraging substrate. By foraging efficiency, we mean the amount of food resources left by optimal foragers in a patch after a night of foraging: the less left behind, the greater the efficiency (Brown 1988; see methods). Hence, where harvest rate describes how fast a forager can deplete a food resource at high and moderate resource densities, foraging efficiency describes the extent of resource depletion by a forager given some constraints (Brown 1988). We assume that higher foraging benefits correlate with higher fitness and therefore are favored by natural selection. This assumption agrees with the assumption of optimal habitat selection theory (Rosenzweig 1981) as well as optimal foraging theories (Stephens and Krebs 1986).

We test the hypothesis by concentrating on the differences between the semistabilized dunes and stabilized sands. Danin (1978) showed that the two habitats differ in the proportion of loess in the soil (semistabilized dune soil has less loess than stabilized sands) and that this difference strongly affects different plant association characteristics (see methods). We examine how loess affects two aspects of foraging for *G. allenbyi* and *G. pyramidum*: 1) the effect of foraging substrate (i.e., where gerbils are taking their seeds), and 2) the influence of the substrate surrounding each foraged patch (i.e., where travel between patches and escape from predators are important) (e.g., Price 1986, Kotler and Brown 1988). We measure harvest rates and foraging efficiencies on two different foraging substrates (i.e., loess and sand) to test the effect of foraging substrate. We also measure foraging efficiencies in distinct habitat types (i.e., semistabilized vs. stabilized dunes, and semistabilized vs. loess plateau) to test the influence of the substrate surrounding each foraged patch.

Based on our hypothesis, that benefits differ between the habitats, we predict that: 1) both gerbil species benefit more from foraging on sand than loess (therefore, we predict that harvest rates and foraging efficiency will be higher on sand than on loess, and 2) both gerbil species benefit more from foraging within an area of semistabilized dunes than either stabilized dunes or loess plateau habitats (therefore, we predict that foraging efficiency will be higher in the semistabilized dunes than in the stabilized dunes or the loess plateau habitats).

METHODS

Study area and habitat types

We conducted three independent experiments to test the above predictions. The first two experiments measured foraging efficiencies (i.e., GUDs; see below) in the field, while the third experiment measured harvest rates in the lab.

The two field experiments occurred in a sandy area of Holot Mashabim Nature Reserve, northwestern Negev Desert, Israel (31°01' N, 34°45' E). The sandy area contains patches of semistabilized dunes and stabilized sands. A plant association of *Artemisia monosperma* grows in semistabilized dunes and one of *Retama raetam* (retam - a leguminous shrub) in stabilized sands. These two habitat types differ in the amount of loess in the soil and in the organic soil crust which comes from stabilization (Danin 1978). Loess is a loosely consolidated sediment formed from wind-deposited silt (Sawkins et al. 1978). It is common in the Negev Desert (e.g., Issar et al. 1984) and it is characterized by particles smaller than 0.062 mm (Danin 1978). Stabilized sands habitat has approximately 12% loess where semistabilized dunes habitat has only about 2% loess (Danin 1978).

The sandy area often ends abruptly and is replaced with loess plateau habitat (a flat area containing a high fraction of small loessal particles in the soil). Wind carries the small particles and deposits them in patches within the sandy areas. Loess plateau habitat has a firmer soil surface than stabilized sands. *Noaea mucronata* (Chenopodiaceae) and *Thymelaea hirsuta* (Thymelaeaceae) grow in the loess plateau habitat.

Animal tracks and species identification

Prior to the field experiments, we captured rodents on field grids using Sherman live traps and marked individuals with species-specific toe clips -- outer toe of the right or left hind foot for *G. allenbyi* or *G. pyramidum*, respectively. In the field experiments, we identified tracks of each species in seed trays by size and shape of tracks and by the species-specific marks (toe clips). In this manner, we could identify the species identity of the last forager that exploited a tray, and therefore, the species responsible for the amount of seeds left behind in each tray. Tracks left in the sand around the tray at a station also told us which species visited the tray the previous night. This method has been successfully used in other studies on these species (e.g., Abramsky et al. 1990, 1991, Brown et al. 1994, Kotler et al. 1993b, Ziv et al. 1993).

Seed trays and foraging efficiencies

We used aluminum trays (45 X 60 X 2.5 cm deep) as artificial resource patches in all the experiments. Each tray was filled with 3 g of millet seeds mixed thoroughly into 5 l of sifted substrate, either sand or loess (see below). In the two field experiments, we replaced the seeds in all the trays every night and sifted the sand from each tray to recover its remaining seeds the next morning. Later, we cleaned and weighed the non-harvested seeds. The amount of seeds remaining in a tray after a night of foraging is called the "giving-up density" (GUD; Brown 1986, 1988, see also Kotler and Brown 1988).

We used GUD values to determine the foraging efficiency of a species. Brown (1988) split foraging results into four rate components: harvest, H, metabolic cost, C, predation cost (i.e., energetic costs associated with the probability of being eaten), P, and missed opportunity costs of foraging, MOC. Brown showed that an optimal forager should leave a patch when:

$$H=C+P+MOC \tag{1}$$

When Eq. 1 is satisfied, the ratio between the benefits and costs of foraging equals 1. If a forager leaves a patch before or after Eq. 1 is satisfied, it obtains a lower net energy gain. Consequently, the GUD value is a measure of the foraging efficiency of an individual because it determines to what density a forager can most profitably depress the seeds of a patch (see detailed development and description of the theory in Brown 1986, 1988, 1989a, 1989b, 1992). GUDs are appropriately comparable between closely-related situations and are independent of population density, where identical numbers of individuals have access to trays in both habitats or soil types, as is the case in our experiments. GUDs are species-specific measures, because at the end of a night, when animals quit foraging and missed opportunity costs of resources diminish, the species-specific characteristics (e.g., metabolic rate and risk of predation) determine the lowest resource density that can be profitably harvested. The species whose individuals have a lower GUD is the more efficient forager (Tilman 1982, Vance 1985, Brown 1988). The GUD method for determining foraging efficiencies has been previously used in other studies on foraging behavior of these species (e.g., Kotler et al. 1991, 1993a, Kotler 1992, Brown et al. 1994).

We used local sand in trays containing sand substrate, but we brought the loess substrate from another location (Sede Zin, 40 km south of Beer Sheva) where soil contained approximately 60% of loess (Dan et al. 1973). Notice that the stabilized sands have only 12.5% loess (Danin 1978). While the stabilized sands habitat has soil crust, the loess substrate lacks it. However, the need for sifting the substrate to recover the remaining amount of seeds after a night of foraging forced us to break the soil crust of the stabilized sands. This changed the characteristics of this habitat type. But, the high percentage of loess in this substrate gave it the firm structure that affected forging by rodents like that of the stabilized sands. And, soil crust is mainly a product of a high amount of loess in the soil (Danin 1978). We therefore think that the loess from Sede Zin reflected accurately the difference between the stabilized sands and semistabilized dunes. We also believe that using the loess substrate might reflect, if anything, an underestimation of the differences between the habitats rather than an overestimation. This is because of the important role of the soil crust in the stabilized sands (Danin 1978).

Experiments

GUDs on different substrates in the semistabilized dunes and stabilized sands (The semistabilized dunes - stabilized sands experiment)

For the first field experiment, we established two square grids of 16 stations (4 X 4) with 40 m between stations. Each grid contained both stabilized and semistabilized habitats. We located eight stations in each habitat. We placed two seed trays at each station. One seed tray contained sand and the other loess.

The species ratios (density of *G. allenbyi* / density of *G. pyramidum*) in the two grids were similar (4.7 and 4.5). The ratios are typical of these habitat types (e.g., Ziv et al.

1993). Animals were allowed to acclimate to the experimental treatment for 3 days before data were collected. We collected data for analysis for 6 days.

GUDs on sand substrate in the semistabilized dunes and loess plateau (The semistabilized dunes - loess plateau experiment)

We conducted the second experiment across a transition between the semistabilized dunes and the loess plateau habitat. We wanted to examine the effects of both escape substrate (Brown et al. 1994) and the risk of predation on patch use of gerbils in the different habitats.

We established four pairs of rows which crossed and were perpendicular to the habitat border. Each row contained 6 stations, 3 in the sandy habitat and 3 in the loess habitat. The stations were located 5, 10, and 15 meters from the habitat border. Each station contained a seed tray (Figure 1 shows the experimental design). We had two replicates of this experiment.

Three pairs of rows each received a different treatment. The fourth pair served as control (i.e., no treatment on either row of the pair). Also, in each of the experimental pairs, one row served as treatment and the other row as control. Treatments included: a) shelters between seed trays (to reduce the risk of moving between trays and escaping to cover), b) shelters on seed trays (to reduce the risk of foraging in trays), and c) change of substrate around the seed trays (to examine the effect of needing to cross a particular substrate to reach safety).

For manipulation c, each station of each habitat type was surrounded by the other habitat type's substrate. That is, in the sandy habitat, we ringed trays, approximately 2.5 m in diameter, with small-sized stones to mimic the hard substrate of loess. In the loess, we made a 2 X 30 m strip of sand running from the habitat boundary and past the last tray in the loess. All seed trays, in all 8 rows, held sand as the foraging substrate. The species density ratio (*G. allenbyi / G. pyramidum*) in the sandy habitat (i.e., semistabilized dunes) was 4.8, a typical ratio in that habitat type. We captured most of the individuals (25 individuals; 86%) of both species in the sandy habitat.

Animals were allowed to acclimate to the experimental treatment for 3 days before data were collected. We collected data for analysis for 9 days.

Harvest rate on loess substrate
(The harvest rate experiment)

The third experiment measured the harvest rates of the two species in the laboratory. We captured 6 individuals of each species near the field research area. We introduced them into a six-compartment wooden arena, one to each compartment. Each compartment (70 X 55 cm) held a nest box and a seed tray with room for movement on both sides of the seed tray. Before measuring harvest rates, we allowed rodents to adjust to the experimental conditions for several days.

Rodents foraged on trays in the presence of an observer. The observer timed cumulative foraging time (but not time spent traveling or time inactive in the tray) for each rodent. Time was measured using a different stopwatch for each gerbil.

We interrupted foraging rodents after predetermined foraging time periods, removed the seed tray, and sifted the loess to recover the remaining millet seeds. We chose time periods to cover a large range of times and a wide range of resource densities. We used these to construct an entire harvest rate curve (i.e., the grams of seed eaten in a given time). Also, we designed the harvest rate experiment similarly to allow comparison of our results with results of a previous harvest rate experiment on the same two species (Kotler and Brown 1990) in which sand was used instead of loess as the foraging substrate.

RESULTS

Habitats and foraging efficiencies

The semistabilized dunes - stabilized sands experiment: We used a factorial ANOVA including the factors day (blocking variable), habitat, substrate and species to test for their effect on GUDs (Table 1). Species did not differ significantly in GUDs. Also, we did not find significant differences in GUDs of each species between the two habitat types (no habitat * species interaction; Table 1). So, we lumped data of both species to test the effect of habitat on gerbils' GUDs. GUDs differed significantly between the semistabilized dunes and the stabilized sands (Table 1). They averaged 0.5 g and 0.62 g in the semistabilized and stabilized habitats, respectively. Individuals of each species had lower GUDs in the semistabilized dunes than in the stabilized sands (Figure 2a). Therefore, foragers benefit more from resource patches occurring in the semistabilized dunes habitat.

The semistabilized dunes - loess plateau experiment: We used the loess plateau habitat to exaggerate the characteristics of the stabilized habitat (see methods). We compared GUDs from seed trays located in the semistabilized dunes with those located in loess plateau habitat (Table 2). For this comparison, we used only data from the control seed trays to avoid possible effects of treatments (see methods). We found no significant difference in GUDs between species. And, both species appeared to treat the habitats similarly (no species * habitat interaction; Table 2). We had too few data points for *G. pyramidum* to rule out Type II error (N=14 for both habitats). However, when data of both species were lumped together, foragers of both species left significantly lower GUDs in the semistabilized than in the loess plateau habitat. The GUDs in the semistabilized habitat were about half those in the loessal habitat (Figure 2b). Hence, foragers were always more efficient when they foraged in trays located in semistabilized dunes.

The sharp transition between the semistabilized dunes and loess plateau habitats allowed us to test the change in GUDs as a function of the distance from the habitat border (see methods). We did this analysis to examine the effect of the location of a seed tray between and within habitats. Because of the few data points for *G. pyramidum* in the control seed trays, we used only *G. allenbyi*'s data points.

We found a significant negative correlation between GUDs and the distance from the habitat border for each habitat (Figure 3; N=108, r=0.288, p=.003 for sand, and N=47, r=0.338, p=.02 for loess). Individuals of *G. allenbyi* left fewest seeds in the 25m station of the sandy habitat (GUDs=0.35). Because all seed trays in both habitats contained sand as foraging substrate, it suggests that the substrate surrounding a tray has an important role in foraging efficiency.

Two more results from this experiment support the significance of the risk of predation to foraging behavior. First, foragers in the loessal plateau habitat left lower GUDs in seed trays covered by shelters than in uncovered control seed trays (paired t-test; N=60, t=2.118, p=.042). Second, change of the surrounding substrate around seed trays in the semistabilized habitat (i.e., ringing trays in the sandy habitat with small rocks) resulted in significantly higher GUDs (paired t-test within semistabilized dunes; N=82, t=2.077, p=.044). These results suggest that the higher GUDs on the loess arise, at least in part, from the risk of predation to a forager. Predation risk may force a forager to flee over rocks and other obstacles and experience lower probability of survivorship due to fewer shelters in the loessal habitat.

We found no significant differences in the other treatments. We suspect that at least one treatment -- adding shelters between trays -- was not designed well enough to find differences between GUDs. In addition, the presence of a high shrub density in the semistabilized dunes might decrease the difference between covered and uncovered trays in that habitat type.

Substrates and foraging efficiencies

To test the effect of foraging substrate on the foraging efficiency of the gerbils, we measured GUDs in seed trays containing either loess or sand as foraging substrates. We measured the GUDs in loess and sand in the semistabilized dunes - stabilized sands experiment. GUDs in the two foraging substrates differed significantly (Table 1). They averaged 0.9 and 0.22 on the loess and sand substrates, respectively. These results hold regardless of the habitat surrounding the seed trays (i.e., stabilized sands or semistabilized dunes. Figure 4; t=11.42, df=227, p<.001 for *G. allenbyi*, and t=165.72, df=144, p<.001 for *G. pyramidum*). We found no significant interaction of species and substrate.

The above results also hold when we examined each habitat separately. In each habitat, foragers of each species left significantly lower GUDs on sand than on loess (Table 3; t=6.96, df=103, p<.001 and t=9.39, df=121, p<.001 for *G. allenbyi* in semistabilized dunes and stabilized sands, respectively; t=5.04, df=48, p<0.001 and t=5.67, df=35, p<0.001 for *G. pyramidum* in semistabilized dunes and stabilized sands, respectively). Hence, for any individual, foraging efficiency in the sand foraging substrate is much higher than that in the loess foraging substrate, resulting in higher benefit from foraging on sand.

Harvest rates

We measured the harvest rates of the species in the laboratory under constant conditions and without predation. The experiment allowed us to compare harvest rates on a loess foraging substrate (current experiment) with harvest rates on a sand foraging substrate from a previous experiment (Kotler and Brown 1990). Using the methods of this paper, we re-analyzed the previous experiment's data to allow for comparison. We used multiplicative regression (i.e., log-log transformation) to test the effect of foraging time periods (independent variable) on the amount of seeds harvested (dependent variable) by both species in both substrates. We used this linear transformation only after we found that the original harvest rate curves (that were not log-log transformed) showed diminishing returns of seeds harvested over time. All four analyses resulted in high correlations and regression lines were significantly different from zero (Figures 5a and 5b; N=109, r=0.92, p<.001; N=103, r=0.93, p<.001; N=100, r=0.95, p<.001; N=115, r=0.91, p<.001 for *G. allenbyi* on loess, *G. allenbyi* on sand, *G. pyramidum* on loess, and *G. pyramidum* on sand, respectively). We then tested for differences between the harvest rate regression lines (both intercept values and slopes; Zar 1984).

Overall, Individuals of both species had significantly higher harvest rates on sand than loess (Figures 5a and 5b). Most important, intercept values were significantly higher on sand than on loess substrate (t=8.48, p<.001, and t=5.843, p<.001 for *G. allenbyi* and *G. pyramidum*, respectively). Logarithmic slopes were significantly lower on sand than on loess substrate (t=5.43, p<.001, and t=2.5, p<.02, for *G. allenbyi* and *G. pyramidum*, respectively). So, for a given seed density, gerbils had to spend less foraging time on sand than loess in order to harvest identical amount of seeds.

DISCUSSION

The shared-preference habitat selection pattern shows how two species select two habitat types in a density-dependent manner, when both prefer the same primary habitat type (Pimm et al. 1985, Rosenzweig 1985). Results of previous study (Abramsky et al. 1990) showed that *G. allenbyi* and *G. pyramidum* follow the predictions of the modeled pattern. In this paper we present evidence revealing the cause of the shared preference in these gerbils. Our results show that both species benefit most from foraging in semistabilized dunes. The advantage results from two differences. Gerbils recover seeds faster and more efficiently from a sand substrate. And they forage more efficiently when foraging in resource patches surrounded by sandy habitat. We think that the latter reflects lower predation risk.

Our study and that by Brown et al. (1994) show that *G. allenbyi* and *G. pyramidum* identify accurately differences between the habitats. Both in laboratory experiments (harvest rate measurement) and in the field (giving-up density measurement), the species show significant differences in harvest rates and foraging efficiencies on different substrates and habitats. Studies on rodent species of the southwest deserts of North America showed also that rodents accurately identify differences between habitats (or microhabitats; Lawhon and Hafner 1981, Price and Heinz 1984). In addition, Price and Heinz (1984) demonstrated that soil characteristics of a microhabitat affect the foraging choices of heteromyid rodents, and that seed harvest rates are affected by soil attributes (see review Price 1986).

The present study tests the effect of two components of foraging: foraging substrate in which foragers need to dig for seeds (i.e., seed patch), and area around a seed patch. In regard to foraging substrate, the two species should prefer sand over loess. Most potential seed resources for gerbils are buried in the first 10 cm or less (Abramsky 1983). So, gerbils must often dig to get their seeds. Sand is easier to dig because loess contains small particles that tightly adhere. When water wets the loess substrate, due to rainfall and dew, the ground becomes even harder. Afterward, bacteria and ground algae occupy the upper ground level resulting in a hard biological soil crust (Danin 1978). This makes sand even more advantageous than loess for gerbils. That is why the two species forage more efficiently and have higher harvest rates on sand than on loess.

The stabilized sands contain a larger fraction of loess component than the semistabilized dunes (Danin 1978). So, foragers should find it more difficult to dig for seeds in stabilized sands. In other words, foraging on a loess substrate in stabilized sands increases the costs for gerbils. This may result in lower net energy gain from foraging on the loess substrate which occurs in the stabilized sands habitat.

Higher harvest rates on sand than loess suggest that our results contradict the study of Price and Heinz (1984). They found significantly higher harvest rates on a fine soil. However, this apparent contradiction may result from differences between local soil characteristics in the different environments and does not necessarily reflect a disagreement.

Daily afternoon winds expose and redistribute seed resources and, as consequence, cause a daily seed renewal regime. Because sand is much more mobile than loess covered with soil crust, this regime should be most pronounced in the semistabilized dunes. Hence, in addition to the easier-to-dig and less energetically demanding substrate, the semistabilized habitat may provide more available and richer seed patches with more rapid renewal than the stabilized habitat (Kotler at al. 1993). Price and Reichman (1987), and Price and Heinz (1984) found differences between habitats and microhabitats in seed abundances in the southwest deserts of North America and suggested that these differences have an important role in heteromyid microhabitat preferences (see review Price 1986).

In regard to area around a seed patch, the semistabilized dunes habitat also plays an important role. Regardless of foraging substrate, the rodents always have higher foraging efficiencies when the area around the resource patch is the semistabilized dunes. What makes the surrounding area so influential? We think that the surrounding area has an important influence on the ability of the species to flee from predators (i.e., escape substrate). Several studies have shown that predation plays an essential role in rodent communities (e.g., Kotler 1984, 1985, Brown et al. 1988, Thompson 1982a, b). Predation may also affect the gerbils' behavior (Kotler et al. 1991, Kotler 1992).

The semistabilized dunes may provide better escape substrate across which to flee to cover. This may result from the rodents adaptations for the sandy substrate (e.g., hairy feet). In addition, the semistabilized habitat provides a high density of shrubs and many burrows. Shrubs and burrows as well as better escape substrate, may yield higher probability of survival and can permit rodents to forage for longer time periods and exploit more resources.

To use a patch optimally, a forager should quit harvesting when its benefit equals the costs, including costs of predation (Brown 1986, 1988). As cost of predation increases, the equality between benefits and costs occurs at a higher resource level. As a result, the forager quits foraging at a higher resource density (Brown 1988). That is why, increasing predatory risk decreases foraging efficiency.

In sum, the results of the present study show that both species forage more efficiently, and as a result can gain higher net resources, in the semistabilized dunes. This is because of two factors -- higher foraging gain in a sand substrate and lower predation risk in the sandy area surrounding the seed patches. Therefore, the two important factors of foraging advantage and predation risk (see reviews Price 1986, Kotler and Brown 1988) combine to benefit rodents most in the semistabilized dunes. That is the basis of their shared preference habitat selection pattern.

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LITERATURE CITED

Abramsky, Z. 1983. Experiments of seed predation by rodents and ants in the Israeli desert. - Oecologia 57:328-332.

Abramsky, Z., Brand, S., and Rosenzweig, M. L. 1985. Geographical ecology of gerbilline rodents in the sans dune habitats of Israel. - Journal of Biogeography 12:363-372.

Abramsky, Z., Rosenzweig, M. L., Pinshow, B., Brown, J. S., Kotler, B. P., and Mitchell, W. A. 1990. Habitat selection: an experimental field test with two gerbil species. - Ecology 71:2358-2369.

Abramsky, Z., Rosenzweig, M.L., and Pinshow, B. 1991. The shape of a gerbil isocline measured using principles of optimal habitat selection. - Ecology 72:329-340.

Abramsky, Z., Rosenzweig, M. L., and Subach, A. 1992. The shape of a gerbil isocline: an experimental field study. - Oikos 63:193-199.

Bar, Y. 1982. Diet composition and similarity of Gerbillidae species in Holot Agur and Holot Shunra. - M.Sc. thesis, Ben-Gurion University of the Negev, Beer-Sheva (In hebrew with an english abstract).

Bar, Y., Abramsky, Z., and Gutterman, Y. 1984. Diet of Gerbilline rodents in the Israeli desert. - Journal of Arid Environment 7:371-376.

Brown, J. S. 1986. Coexistence on a resource whose abundance varies: a test with desert rodents. - Ph.D. dissertation, University of Arizona, Tucson.

Brown, J. S. 1988. Patch use as an indicator of habitat preference, predation risk, and competition. - Behavioral Ecology and Sociobiology 22:37-47.

Brown, J. S. 1989a. Coexistence on a seasonal resource. - American Naturalist 133:168-182.

Brown, J. S. 1989b. The role of resource variability in structuring desert rodent communities. - Ecological Monographs 59:1-20

Brown, J. S. 1992. Patch use under predation risk: I. Models and predictions. - Annales Zoologici Fennici 29:301-309.

Brown J. S., and Rosenzweig, M. L. 1986. Habitat selection in slowly regenerating environments. - Journal of Theoretical Biology 123:151-171.

Brown, J. S., Kotler, B. P., Rosmery, S. J., and William, W. O. 1988. The effects of owl predation on the foraging behavior of heteromyid rodents. - Oecologia 76:408-415.

Brown, J. S., Kotler, B. P., and Mitchell, W. A. 1994. Patch use as the basis for the structure of a Negev Desert granivore community. - Ecology, In press.

Charnov, E. L. 1976. Optimal foraging: the marginal value theorem. - Theoretical Population Biology 9:129-136.

Dan, J., Moshe, R., and Alperovitch, N. 1973. The soils of Sede Zin. - Israel Journal of Earth-Sciences 22:211-227.

Danin, A. 1978. Plant species diversity and plant succession in a sandy area in the Northern Negev. - Flora 167:400-422.

Fretwell, S. D. 1972. Population in a seasonal environment. - Princeton University Press, Princeton, NJ.

Fretwell, S. D., and Lucas, H. L. 1970. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. - Acta Biotheoretica 14:16-36.

Grant, P. R. 1986. Ecology and evolution of Darwin's finches. - Princeton University Press, Princeton, NJ.

Harrison, D. L., and Bates, P. JJ. 1991. The mammals of Arabia. - Harrison Zoological Museum.

Issar, A., Karnieli, A., Bruins, H. J., and Gilead, I. 1984. The quaternary geology and hydrology of Sede Zin, Negev, Israel. - Israel Journal of Earth Sciences 33:34-42.

Kotler, B. P. 1984. Risk of predation and the structure of desert rodent communities. - Ecology 65:689-701.

Kotler, B. P. 1985. Owl predation on desert rodents which differ in morphology and behavior. - Journal of Mammalogy 66:824-828.

Kotler, B. P. 1992. Behavioral resource depression and decaying perceived risk of predation in two species of coexisting gerbils. - Behavioral Ecology and Sociobiology 30:239-244.

Kotler, B. P., and Brown, J. S. 1988. Environmental heterogeneity and the coexistence of desert rodents. - Annual Review of Ecology and Systematics 19:281-307.

Kotler, B. P., and Brown, J. S. 1990. Rates of seed harvest by two gerbilline rodents. - Journal of mammalogy 71:591-596.

Kotler, B. P., Brown, J. S., and Hasson, O. 1991. Factors affecting gerbil foraging behavior and rates of owl predation. - Ecology 72:2249-2260.

Kotler, B. P., Brown, J. S., Slotow, R. H., Goodfriend, W. L., and Strauss, M. 1993a. The influence of snakes on the foraging behavior of gerbils. - Oikos 67:309-316.

Kotler, B. P., Brown, J. S., and Subach, A. 1993b. Mechanisms of species coexistence of optimal foragers: temporal partitioning by two species of sand dune gerbils. - Oikos 67: 548-556.

Lawhon, D. K., and Hafner, M. S. 1981. Tactile discriminatory ability and foraging strategies in kangaroo rats and pocket mice (Rodentia: Heteromyidae). - Oecologia 50:303-309.

MacArthur, R. M., and Wilson, E. O. 1967. The theory of island biogeography. - Princeton University Press, Princeton, NJ.

Pimm, S. L., Rosenzweig, M. L., and Mitchell, W. A. 1985. Competition and food selection: field test of theory. - Ecology 66:798-807.

Price, M. V. 1986. Structure of desert rodent communities: a critical review of questions and approaches. - American Zoologist 26:39-49.

Price, M. V., and Heinz, K. M. 1984. Effects of body size, seed density, and soil characteristics on rates of seed harvest by heteromyid rodents. - Oecologia 61:420-425.

Price, M. V., and Reichman, O. J. 1987. Spatial and temporal heterogeneity in Sonoran Desert soil seed pools, and implication for heteromyid rodent foraging. Ecology 68:1797-1811.

Ritte, U., Haim, A., and Neufeld, E. 1976. Use of electrophoretic patterns of hemoglobin for identification of Israeli gerbils (genus *Gerbillus*, Rodantia: Gerbillinae). - Israel Journal of Zoology 25:52-60.

Rosenzweig, M. L. 1977. Coexistence and diversity in heteromyd rodents. - In: Stonehouse, B. and Perrins, C. (eds.), Evolutionary biology. Macmillan, London, pp. 89-99.

Rosenzweig, M. L. 1979. Optimal habitat selection in two-species competitive system. - Fortschritte der Zoologie 25:283-293.

Rosenzweig, M. L. 1981. A theory of habitat selection. - Ecology 62:327-335.

Rosenzweig, M. L. 1985. Some theoretical aspects of habitat selection. - In: Cody, M. L. (ed.), Habitat selection in birds. Academic Press, New York, pp. 517-540.

Rosenzweig, M. L. 1989. Habitat selection, community organization, and small mammal studies. - In: Morris, D. W., Abramsky, Z., Fox, B. J., and Willig, M. R. (eds.), Patterns in the structure of mammalian communities. Texas University Press, Lubbock, pp. 5-21.

Rosenzweig, M. L. 1991. Habitat selection and population interactions: the search for mechanism. - American Naturalist 137:5-28.

Rosenzweig, M. L., and Abramsky, Z. 1986. Centrifugal community organization. - Oikos 46:339-348.

Sawkins, F. J., Chase, C. G., Darby, D. G., and Rapp, G. Jr. 1978. The evolving earth. - Macmillan, New York, NY.

Schoener, T. W. 1974. Resource partitioning in ecological communities. - Science 185:27-39.

Schoener T. W. 1986. Resource partitioning. - In: Anderson, D., and Kikkawa, J. (eds.), Community ecology: pattern and process. Blackwell Scientific, Oxford, pp. 91-126.

Stephens, D. W., and Krebs, J. R. 1986. Foraging theory. - Princeton University Press, Princeton, NJ.

Thompson, S. D. 1982a. Structure and species composition of desert heteromyid rodent species assemblages: effects of a single habitat manipulation. - Ecology 63:1313-1321.

Thompson, S. D. 1982b. Microhabitat utilization and foraging behavior of bipedal and quadropedal heteromyid rodents. - Ecology 63:1302-1312.

Tilman, D. 1982. Resource competition and community structure. - Princeton University Press, Princeton, NJ.

Vance, R. R. 1985. The stable coexistence of two competitors for one resource. - American Naturalist 126:72-86.

Zahavi, A., and Wharman, J. 1957. The cytotaxonomy, ecology, and evolution of the gerbils and jirds of Israel (Rodentia: Gerbillinae). - Mammalia 21:341-380.

Zar, J. H. 1984. Biostatistical analysis. - Prentice-Hall Inc., New Jersey.

Ziv, Y., Abramsky, Z., Kotler, B. P., and Subach, A. 1993. Interference competition, and temporal and habitat partitioning in two gerbil species. - Oikos 66:237-246.

TABLE 1: Factorial ANOVA for the semistabilized dunes - stabilized sands experiment, testing the effects of habitat type, foraging substrate, and species on GUD. The day variable is treated as a block.

Source	SS	df	F	P
Day	14.04	5	18.93	<.001
Habitat	1.07	1	7.26	.007
Substrate	26.07	1	157.76	<.001
Species	0.27	1	1.86	.137
Habitat * Substrate	0.308	1	2.076	.151
Habitat * Species	0.006	1	0.041	.839
Substrate * Species	0.097	1	0.652	.420
Error	44.94	303		

TABLE 2: Factorial ANOVA between species and habitat for the semistabilized dunes - loess plateau experiment, testing the effects of species and habitat type on the GUD. The day variable is treated as a block.

Source	**SS**	**df**	**F**	**P**
Day	12.25	8	9.84	<.001
Species	0.22	1	1.45	.230
Habitat	3.39	1	21.81	<.001
Species * Habitat	0.16	1	1.04	.307
Error	24.41	157		

TABLE 3: Giving-up density values (Mean ± S.E.) of the semistabilized dunes - stabilized sands experiment.

	Semistabilized dunes		**Stabilized sands**	
	Sand	**Loess**	**Sand**	**Loess**
G. allenbyi	0.21 ±0.066 (n=49)	0.83 ±0.061 (n=56)	0.27 ±0.060 (n=59)	1.04 ±0.057 (n=65)
G. pyramidum	0.18 ±0.069 (n=27)	0.69 ±0.075 (n=23)	0.19 ±0.076 (n=22)	0.86 ±0.092 (n=15)

FIGURE LEGENDS

FIGURE 1: The semistabilized dunes - loess plateau experimental design. Squares represent seed trays. Filled squares indicate manipulated seed trays. The dotted line represents the habitat border and numbers on the right-hand side are distances from the habitat border (loess plateau seed trays are represented by negative signs, i.e., -5, -15, -25). Each seed tray line has different treatment as indicated above each line. Treatments are: TL = shelters between trays, TY = shelters on seed trays, CH = change of substrate around the seed trays, and CO = control.

FIGURE 2: *G. allenbyi* and *G. pyramidum* shared lower GUDs in the semistabilized dunes than in either stabilized sands or loess plateau. (A) Semistabilized dunes (semistab.) and stabilized sands (stab.). (B) Semistabilized dunes and loess plateau. Data (± S.E.) of each graph obtained from different experiment (see methods).

FIGURE 3: *G. allenbyi* in the semistabilized dunes had lower GUDs when it foraged at trays further from the loess-sand border than when it foraged closer to the border (broken line). *G. allenbyi* in loess plateau had lower GUDs when it foraged at trays closer to the border than when it foraged further from the border (solid line). Values of X axis indicate distance in meters from loess-sand border. Negative signs are of those stations located in the loess plateau habitat. Note that although each regression has 3 locations only, each of these location values represents an average of many replicates (see text).

FIGURE 4: *G. allenbyi* and *G. pyramidum* shared lower GUDs on the sand substrate than on the loess substrate. Data (± S.E.) obtained from the semistabilized dunes - stabilized sands experiment.

FIGURE 5: Regression analyses testing the effect of time ($\log_{10}$-transformed) on seed harvesting ($\log_{10}$-transformed) for *G. allenbyi* (5a) and *G. pyramidum* (5b) on loess and sand substrates. Note, intercept values are $\log_{10}$-transformed. Data for the sand substrate were taken from Kotler and Brown 1990.