

FACTORS AFFECTING GERBIL FORAGING BEHAVIOR AND RATES OF OWL PREDATION¹

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Abstract. We experimented on how illumination, habitat structure, and three different species of owls affected the foraging behavior of *Gerbillus allenbyi* and *G. pyramidum*, two gerbil species that coexist on sand dune habitats in the Negev Desert, Israel. We also tested how illumination and habitat structure affected rates of predation by owls on the two gerbil species. In a large aviary, we manipulated presence and absence of owls, owl species, presence and absence of illumination, and shrub cover. In response to the presence of owls or to increased illumination, gerbils foraged less, shifted foraging activity to the bush microhabitat, and quit patches at a higher giving-up density of resources. In accord with moonlight avoidance, both gerbil species suffered higher predation rates under illumination than in the absence of illumination. In addition, *G. pyramidum* distinguished among owl species, as indicated by changes in patch use and habitat selection. Habitat structure also affected foraging behavior and rates of predation. Gerbils foraged less in the open than in the bush microhabitat, foraged less when there was no cover present, and foraged less in the bush microhabitat when patches were encumbered by entangling branches. In accord with avoidance of open areas, both gerbil species suffered higher rates of predation when shrub cover was 0% than when shrub cover was 10%. With 0% cover, *G. allenbyi* suffered higher predation rates than *G. pyramidum*, but with 10% cover, rates of owl predation did not differ between gerbil species. Rates of owl predation on the two species corresponded to their natural patterns of macro- and microhabitat partitioning; relative to *G. allenbyi*, *G. pyramidum* predominates on open sand dunes and biases its behavior toward the open microhabitat. The results suggest that predation interacts with resource competition to determine the distribution and habitat separation of *G. allenbyi* and *G. pyramidum*.

Key words: aviary experiments; Barn Owls; Eagle Owls; foraging activity; foraging behavior; gerbils; habitat selection; Little Owls; optimal patch use; predation rate; rodents; seed tray experiments.

INTRODUCTION

Predation influences the ecology of prey species both directly via removal of prey animals (e.g., Morin 1983) and indirectly via predators' effects on prey behavior (e.g., Caraco et al. 1980a, b, Dill 1987, Kats et al. 1988, Abrahams and Dill 1989, Lima and Dill 1990). Direct removal of prey individuals influences population dynamics (e.g., Kerfoot and Sih 1987), prey distributions (Holt 1984), and conditions for the coexistence of species sharing a common predator (Holt 1977). Mortality inflicted by predators can have cascading effects through a food web (Kerfoot and Sih 1987). Also, such mortality determines the risk of predation that prey may consider when making foraging decisions.

In regard to behavior, predatory risk may influence the prey's foraging decisions (e.g., Peckarsky and Dod-

son 1980, Sih 1980, 1982, Dill and Fraser 1984, Lima 1985, Lima et al. 1985, Anderson 1986), travel speeds (Sih 1980, 1982), activity times (Sih 1980, 1982), and use of habitats and microhabitats (e.g., Milinski and Heller 1978, Cerri and Fraser 1983, Edwards 1983, Ohman et al. 1983, Werner et al. 1983, Lima et al. 1985, Lima 1987, Holbrook and Schmitt 1988, Nonacs and Dill 1990). In so doing, predation can increase or decrease the likelihood of species coexistence (Holt 1977, Kotler and Holt 1989). For example, it can promote species coexistence by promoting habitat partitioning in an environment that is heterogeneous with respect to predation risk (Kotler and Brown 1988). Or, it can cause competitive exclusion by forcing competing species into the same refugia (Mittelbach 1988). The influences of predatory risk on prey behavior are expected to be diverse and profound.

Sand dune inhabiting, seed-eating gerbils in the Negev Desert of Israel provide a community in which pre-

¹ Manuscript received 20 June 1990; revised 12 January 1991; accepted 14 January 1991.

dation may affect foraging behavior and species co-existence. Allenby's gerbil (*Gerbillus allenbyi*) and the greater Egyptian sand gerbil (*G. pyramidum*) commonly co-occur and are locally abundant in most sandy habitats of the Negev Desert. The species are morphologically similar, but differ in body size; mean adult masses for *G. allenbyi* and *G. pyramidum* are 25 and 39 g, respectively (Abramsky et al. 1985; animals used in the experiments presented in this paper averaged 26.5 g for *G. allenbyi* and 37.0 g for *G. pyramidum*). Both gerbils mostly consume seeds (Bar et al. 1984), live in burrows, forage at night, and do not exhibit torpor. These two species show striking patterns of habitat selection (Abramsky et al. 1985, Rosenzweig and Abramsky 1985, 1986, Abramsky and Pinshow 1989, Abramsky et al. 1990).

The two species select habitats according to soil substrate type. At large spatial scales (macrohabitat), both species prefer areas of semi-stabilized sand dunes, but differ in their secondary preferences (Rosenzweig and Abramsky 1986). Secondarily, *G. pyramidum* prefers open dunes, and *G. allenbyi* prefers stabilized sand fields. Despite these preferences, both species may also occur in the secondary habitat of the other species. At small spatial scales, both species prefer to forage at the edge of perennial shrubs (bush microhabitat) rather than in areas between shrubs (open microhabitat). Despite similar preferences, *G. pyramidum*, relative to *G. allenbyi*, biases its activity toward the open microhabitat (J. S. Brown, B. P. Kotler, and W. A. Mitchell, *unpublished manuscript*). Temporally, both species forage less in response to moonlight (Kotler 1984a).

Predatory risk may influence all of the aforementioned patterns of habitat selection in time and space. Gerbils may be more vulnerable to predation by owls in the open microhabitat and under conditions of high illumination. If so, predatory risk may explain the gerbils' preference for semi-stabilized dunes (higher in perennial ground cover), the bush microhabitat, and nights without moonlight. Kotler (1984a) and Abramsky (1988) suggested that the larger auditory bullae and larger body size of *G. pyramidum* may assist in detecting and escaping from predators. If so, then predatory risk may explain *G. pyramidum*'s predominance on open dunes (sparse in perennial ground cover) and in the open microhabitat.

Here, we performed aviary experiments with the two gerbil species and three species of owls as predators. We tested the effects of sand dune habitat, microhabitat structure, illumination, and owl species on the foraging behavior of *G. allenbyi* and *G. pyramidum*. In addition, we tested the effects of illumination and cover on predation rates by owls to see how changes in gerbil foraging behavior influenced actual predation rates.

We predict that both species will experience higher rates of predation in the presence of added illumination and in the absence of cover. This effect should be greatest for *G. allenbyi*. In response, both species should

spend less time foraging, avoid the open microhabitat, and use food patches less intensively in the presence of increased predatory risk. The avoidance of the open microhabitat should be strongest for *G. allenbyi*. We predict that *G. pyramidum* may show a preference for loose, sandy substrates and *G. allenbyi* may show a preference for more stable substrates. Because of its small body size, *G. allenbyi* should be less affected by changes in the entangling structure of the bush microhabitat. We expect the gerbils to differentiate among owl species. Gerbils may be most wary of Barn Owls, a rodent specialist. Furthermore, large gerbils may be more wary of large Eagle Owls and small gerbils more wary of Little Owls.

METHODS

During the summer of 1988 we performed manipulations of owl species, illumination, cover, substrate, seed resources, and the populations of two gerbil species in a large outdoor aviary (measuring 18 × 23 × 5 m) at the Mitrani Center for Desert Ecology, Sede Boqer Campus of Ben-Gurion University, Israel. The aviary had a natural earth floor and was divided into halves of equal size by a 50 cm high rodent-proof fence. Within each half, equal portions of the floor were covered by a substrate of sand or loess (across which habitat selection behavior changes dramatically in nature). The aviary contained 13 perches for owls (distances to the closest perch were <5 m) and six lights (one located in each corner and midway along the longest sides of the aviary) controlled by a rheostat. When lights were in use, we set light levels to that of a full moon.

We provided cover in the aviary with piles of cut brush. When simulating a desert environment with 10% shrub cover, we placed 16 brush piles in each half of the aviary. For the experiment examining the effect of cover on gerbil foraging (see below, this section), the removal of brush piles from one of the halves simulated a desert environment with 0% shrub cover. In each experiment, we placed half of the brush piles on 15 cm tall trellises; these trellises permit gerbils to pass underneath without having to negotiate the "jungle gym" of branches frequently present in the bush microhabitat. To facilitate testing for effects of entangling vegetation on gerbil foraging behavior, we rotated the trellises among brush piles midway through designated experimental rounds.

For the different experiments, we established various populations of gerbils. Prior to experimentation and data collection, rodents were given three nights to acclimate to the aviary under conditions of no owls and no artificial illumination. To facilitate acclimation, we placed 25 plastic irrigation tubes (5 cm in diameter and 35 cm long) with one end buried in the ground in each half of the aviary. In seeking shelter, the gerbils used these tubes to start burrows, dug their own burrows, used burrows dug by other gerbils in previous experimental rounds, or burrowed under seed trays.

We provided resources to the gerbils in metal trays ($45 \times 60 \times 2.5$ cm) filled with 6 g of millet seeds mixed into 6 L of sifted sand. In each half of the aviary, we placed 16 pairs of trays at stations. We placed one tray of each pair beneath a "shrub" (bush microhabitat), and the other 1 m away in the open (open microhabitat). The distribution of seeds created identical foraging opportunities for the gerbils save for microhabitat (within stations), substrate or bush structure (among stations), or predatory risk (among nights).

Rodents foraged readily in seed trays. Following a night of foraging, we distinguished among trays that had been foraged (sand covered by spoor [tracks] and thoroughly excavated by digging), trays that had only been visited (few spoor and no signs of digging), and trays that were ignored (no spoor). In foraged trays, we sifted the remaining seeds from the sand, weighed the seeds, and recharged trays with 6 g of millet. We quantified gerbil foraging by the number of foraged trays and by the amount of seed left behind in foraged trays. These provide measures of foraging effort and costs during the night (Brown 1988).

We refer to the seeds remaining in a tray as the *giving-up density* (GUD, Brown 1988). When the rate of seed harvest in a patch declines with the amount of seeds remaining (as is the case for gerbils in these seed trays, Kotler and Brown 1990), the forager's GUD should reflect various components of foraging costs including energy costs, costs arising from predatory risk, and missed opportunity costs. An optimal forager should quit harvesting a food patch when benefits from additional foraging equal the sum of these costs (Brown 1988). Differences in GUDs between microhabitats and different predator treatments measure differences in the gerbils' perceived predatory risks (see Brown et al. 1988).

For predators, we used: two Eagle Owls (*Bubo bubo*, 1700 g), one at a time; four Barn Owls (*Tyto alba*, 370 g), two at a time; or three Little Owls (*Athene noctua*, 130 g), three at a time. The rotation of Barn Owl and Eagle Owl individuals reduced effects arising from individual idiosyncrasies. In using different numbers of owls for the different owl species, we reduced disparities in predator biomass among predator treatments. After nights with owls, we removed owls from the aviary and held them individually in boxes until we recovered their spit (i.e., regurgitated) pellets. To document captures of gerbils, we examined pellets for long bones, skulls, and ear tags (each rodent was marked with a sequentially numbered tag).

We measured predation rates either by comparing the proportion of a gerbil species in the diet of owls to the proportion in the aviary population, or by comparing the number of gerbils killed per unit mass of seeds harvested (an estimate of time spent foraging). We prefer the second of these estimates because it better estimates vulnerability per unit time exposed to predators and because it is the appropriate estimate

with regard to species coexistence. Potential interactions between the gerbils is based on seed removal rather than relative abundances.

The nature of the seed trays introduces two biases into our relative estimates of foraging time among species and among illumination treatments. First, because *G. pyramidum* has a faster seed harvest rate in these trays than does *G. allenbyi* (Kotler and Brown 1990), amount of seed harvested from trays overestimates *G. pyramidum*'s foraging time relative to *G. allenbyi*'s. This bias will make *G. allenbyi* appear more vulnerable to predation per unit mass of seeds harvested. Second, because harvest rates decline as seeds are depleted, more than twice as much time is required to harvest twice as many seeds (Kotler and Brown 1990). Hence, treatments with high amounts of seed harvest will underestimate total foraging time relative to treatments with lower amounts of seed harvest. Because more seeds are harvested under no-illumination than high-illumination treatments, this bias will make rodents on dark nights appear relatively more vulnerable to predation.

For each round of experiments, we placed 12 *G. allenbyi* and 8 *G. pyramidum* in the aviary. These numbers maintain approximately equal biomasses of each species (corrected for metabolic rates measured at 25°C; Y. Linder, unpublished manuscript), make measurements of patch use by the two species roughly comparable, and roughly equilibrate the combined value of each gerbil species to the predators. Following an experimental round, all surviving gerbils were removed from the aviary. For each round, we used different individuals and switched the halves of the aviary containing *G. allenbyi* and *G. pyramidum*. To keep gerbil densities constant from night to night, we replaced gerbils captured by owls with new animals. A concern arises over whether newly added gerbils are more susceptible to subsequent owl predation than resident gerbils. This was not the case; of the 42 captures that occurred in each experiments, only 6 were newly added gerbils and 36 were gerbils with two or more nights of experience.

In the first experiment, we manipulated the presence or absence of Barn Owls and the presence or absence of artificial illumination (moonlight vs. starlight levels of illumination) (Table 1). For this experiment, each half of the aviary possessed 16 brush piles, half of which were placed on trellises. Prior to a round, 12 *G. allenbyi* were introduced into one half, and 8 *G. pyramidum* were introduced into the other half of the aviary. The four experimental treatments included all combinations of the presence (+) and absence (-) of owls and illumination. We ran three rounds of 16 nights each. An experimental round consisted of: 5 nights of +lights, +owls; 5 nights of -lights, +owls; 3 nights of +lights, -owls; and 3 nights of -lights, -owls. The extra nights with owls increased sample sizes for comparing predation rates. The nightly order of treatments within a

TABLE 1. Design of the three experiments. The columns describe manipulations of the three experimental variables. An entry of “+/-” indicates manipulations of presence and absence, and “+” indicates presence only.

	Experimental treatments		
	Owl species	Illumination	Trellises
Experiment 1	<i>Tyto alba</i> : +/-	+/-	+/-
Experiment 2	<i>Athene noctua</i> , <i>Tyto alba</i> , or <i>Bubo bubo</i> : +/-	+/-	+
Experiment 3	<i>Tyto alba</i> : +	+	+/-

round was randomized with the constraint that nights near full moon had lights present and that owls were present for no more than 2 consecutive nights. This interspersed the combinations of the experimental factors among days. Data from this experiment were used to test for the effects of Barn Owls, illumination, trellises, and substrate on gerbil foraging.

In the second experiment, we manipulated the presence of different owl species: Eagle Owls, Barn Owls, and Little Owls (Table 1). The arrangement of gerbils and brush piles was the same as the first experiment. We ran two rounds of 16 nights each. Each round consisted of four sessions. Each session consisted of 4 nights: 1 night for each of the three owl species followed by a night with no owls. The nightly order of owl species within a session was randomized. In each round, two sessions had added illumination and two did not. Data from this experiment were used to test for the effects of owl species, illumination, trellises, and substrate on microhabitat selection and patch use by gerbils.

In the third experiment, we manipulated the presence and absence of brush piles (cover) between halves of the aviary (Table 1). For this experiment, we introduced 4 *G. pyramidum* and 6 *G. allenbyi* to each side of the aviary (total of 8 *G. pyramidum* and 12 *G. al-*

lenbyi in the aviary, as in the previous experiments). One side of the aviary received 16 brush piles (10–15% cover) while the other received none (0% cover). We used Barn Owls as predators, and ran two rounds of 6 nights each. Each night received owls and added illumination. After the first round, we trapped gerbils from the aviary, and switched the halves of the aviary receiving 10% and 0% cover. The results of this experiment test for the effects of bush vs. open microhabitats and test for the effects of shifting sand dune habitats with close to 0% cover vs. semi-stabilized sand dune habitats with 10–15% cover on gerbil foraging behavior.

To study factors influencing predation rates, we used the first experiment to test for the effects of illumination, and the third experiment to test for the effects of cover; too few gerbil captures occurred during the second experiment to test for differences among the three owl species.

RESULTS

Effects of owls and illumination on foraging behavior and predation rates

In this section, we analyzed data from the first experiment. We used a four-way log-linear model to test for the effects of owls and lights on activity (number of trays foraged) and microhabitat selection. We organized frequency data on the presence and absence of foraging in trays by experimental round, microhabitat, treatment, and gerbil species (Table 2). We performed separate tests for each species. We pooled frequency data over temporal replicates and experimental rounds in order to avoid empty cells. The four variables in the model were owls, illumination, microhabitat (bush/open), and presence/absence of foraging.

The two gerbil species had similar patterns of microhabitat selection. Both foraged more trays in the bush microhabitat than in the open (“microhabitat ×

TABLE 2. Number of seed trays foraged per night by rodents for the first experiment.*

Microhabitat		Experimental round					
		1		2		3	
		Light		Light		Light	
		-	+	-	+	-	+
<i>Gerbillus allenbyi</i>							
- owls	Bush	15.33	14.33	16.0	15.67	15.00	13.33
	Open	6.33	1.33	5.67	0	1.0	0.67
+ owls	Bush	14.20	11.20	9.80	10.00	10.16	9.60
	Open	0	0.20	0	0	0	0
<i>Gerbillus pyramidum</i>							
- owls	Bush	14.00	14.00	14.00	15.33	13.67	12.33
	Open	1.67	2.00	7.00	0.33	2.67	1.00
+ owls	Bush	11.00	8.60	8.60	6.40	9.20	6.00
	Open	0.40	0.20	0.60	0.20	0.20	0

* We present the data as number of trays foraged per night rather than total number of foragings for ease of visual comparisons (numbers of nights per cell are not equal).

TABLE 3. The effects of owls, lights, and microhabitat on foraging activity of two *Gerbillus* species. The last two columns give *G* test results from a four-way log-linear model of the frequency data from Table 2.

	df	<i>G. allenbyi</i>	<i>G. pyramidum</i>
Owls × lights × microhabitat × presence/absence	1	9.60**	0.87
Owls × lights × presence/absence	1	1.81	2.00
Owls × microhabitat × presence/absence	1	3.15*	2.99*
Lights × microhabitat × presence/absence	1	8.79**	7.34**
Owls × presence/absence	1	200.88***	158.72***
Lights × presence/absence	1	17.56***	22.86***
Microhabitat × presence/absence	1	1118.71***	704.18***

* *P* < .05, ** *P* < .01, *** *P* < .001; one-tailed test.

presence/absence” of Table 3). In the presence of owls or illumination, both foraged fewer seed trays (“owls × presence/absence” and “lights × presence/absence,” respectively), and a greater proportion of foragings occurred in the bush microhabitat (“owls × microhabitat × presence/absence,” and “lights × microhabitat × presence/absence,” respectively). Gerbils treated the bush microhabitat as less risky in response to both direct (owls) and indirect (illumination) cues of predatory risk.

We used a sign test to determine the effect of microhabitat on GUDs. For each species, we compared the mean GUD in the bush and open microhabitats at each station. In accord with the previous analysis, for both species mean GUD was lower in the bush tray than in the open tray at all 32 stations (*P* < .001; Table 4).

We used partially hierarchical ANOVAs to determine the effects of owls and lights on the gerbils’ GUDs. Table 4 gives mean GUDs for the first experiment by round, gerbil species, and the four combinations of owls and illumination. Because the experimental design is partially hierarchical, partially nested, and partially blocked, we performed separate ANOVAs for each species and experimental round. Because of the paucity of open foragings, we only analyzed GUDs in the bush microhabitat. (Inspection of Table 4 confirms

that GUDs in the open follow the same trends as GUDs in the bush microhabitat.) In each analysis, GUD is the dependent variable, owls and illumination are the group variables, days are a subgroup variable nested within the group variables, and seed tray stations comprise a variable fully crossed with both the group and subgroup variables. In accord with the previous log-linear analysis, both species’ GUDs increased in the presence of owls and lights (Table 5), although the effect of illumination was not significant for *G. pyramidum* during the first round. Both gerbil species perceived a higher predatory risk when owls and lights were present.

To determine whether actual predation rates corresponded to the gerbils’ perceived costs of predation, we used nights with Barn Owls in the first experiment to test for the effects of gerbil species and illumination on predation rates. Barn Owls captured a total of 19 gerbils: 7 *G. pyramidum* and 12 *G. allenbyi*. Furthermore, 12 captures occurred under added illumination: 4 *G. pyramidum* and 8 *G. allenbyi* (Fig. 1).

Predation rates did not differ between gerbil species. When comparing rates based on the proportion of each species in the prey population, the expected numbers of *G. allenbyi* and *G. pyramidum* among the 19 captures were 11.4 and 7.6 animals, respectively ($\chi^2 = 0.08$, *P* > .5). There were 0.0177 *G. allenbyi*/g seed

TABLE 4. Giving-up seed densities (GUDs, in grams of millet) by species, round, treatment, and microhabitat for the first experiment. The sample sizes are 48 seed trays per microhabitat for treatment combinations without owls and 80 seed trays for those with owls. + means presence, - means absence.

		Experimental round					
		1		2		3	
		Light		Light		Light	
Microhabitat		-	+	-	+	-	+
<i>G. allenbyi</i>							
- owls	Bush	2.95	3.52	4.32	4.70	3.33	3.58
	Open	5.87	5.90	5.65	6.00	5.87	5.96
+ owls	Bush	3.64	5.02	4.96	5.16	4.10	4.64
	Open	6.00	6.00	6.00	6.00	6.00	6.00
<i>G. pyramidum</i>							
- owls	Bush	3.71	3.53	4.36	4.64	4.22	4.41
	Open	5.97	5.95	5.79	5.98	5.64	5.89
+ owls	Bush	4.49	4.91	4.79	5.27	4.93	5.35
	Open	5.99	5.99	5.99	5.99	5.98	6.00

TABLE 5. The effects of owls and lights on giving-up seed densities in experiment 1. Each column represents the results of a partially hierarchical ANOVA. The error terms are given as mean sums of squares. All other entries in the table are *F* ratios.

	df	<i>Gerbillus allenbyi</i>			<i>Gerbillus pyramidum</i>		
		Round 1	Round 2	Round 3	Round 1	Round 2	Round 3
Group variables							
Lights	1	25.20***	10.32**	16.82**	1.65	6.69*	9.94*
Owls	1	24.43***	39.34***	70.96***	46.62***	13.38**	56.03***
Lights × owls	1	3.27	1.77	1.77	3.54	0.73	1.15
Subgroup variable							
Days	12	3.84***	0.61	0.63	1.92*	1.42	0.68
Error 1	12	35.46	5.34	8.56	17.97	16.39	8.60
Crossed variable							
Station	15	22.75***	6.04***	27.86***	36.39***	12.61***	12.21***
Station × group	45	2.91***	1.86**	1.38	2.49***	1.52*	1.23
Error 2	180	138.65	130.59	203.34	140.27	173.07	188.26

* $P < .05$, ** $P < .01$, *** $P < .001$.

and 0.0180 *G. pyramidum*/g seed harvested. On this basis the expected captures of *G. allenbyi* and *G. pyramidum* were 10.9 and 8.1 animals, respectively ($\chi^2 = 0.26$, $P > .5$).

Predation rates were higher in the presence of illumination. When comparing rates based on the proportion of individuals, the effect is not significant; the expected number of captures was 9.5 individuals for each of the two illumination treatments ($\chi^2 = 1.32$, $P > .05$). However, based on gerbils captured per unit of seed mass harvested, predation rates were dramatically higher under illumination than under no illumination. With artificial illumination capture levels were 0.0314 *G. allenbyi*/g seed and 0.0203 *G. pyramidum*/g seed harvested. Without artificial illumination the numbers of gerbils captured were 0.0094 *G. allenbyi*/g seed and 0.0099 *G. pyramidum*/g seed harvested. On this basis, the expected numbers of captures under the presence and absence of artificial illumination were 7.3 and 11.7 individuals/g, respectively ($\chi^2 = 4.91$, $P < .025$, one-tailed test).

The presence of illumination increased rates of Barn Owl predation. In response both gerbil species decreased their foraging activity, increased their GUDs, and shifted their foraging toward the bush microhabitat.

Effects of owl species on foraging behavior

We used a four-way log-linear model on data from the second experiment to test for the effects of owl species on gerbil foraging activity and microhabitat selection. We organized frequency data on the presence and absence of foraging in seed trays by round, owl species, illumination level, microhabitat, and gerbil species (Table 6). We performed separate tests for each gerbil species. We pooled frequency data over temporal replicates and experimental rounds. The four levels of the model were owl species, illumination, microhabitat (bush/open), and presence/absence of foraging. We did

not include data from nights without owls because the question of interest was the effect of different owl species.

Patterns of microhabitat utilization in response to owl species were similar for the two gerbil species (Table 7). In accord with data from the first experiment: both species foraged fewer trays under conditions of high illumination ("lights × presence/absence"), foraged fewer trays in the open microhabitat ("microhabitat × presence/absence"), and shifted their microhabitat use toward the bush under conditions of high illumination ("lights × microhabitat × presence/absence").

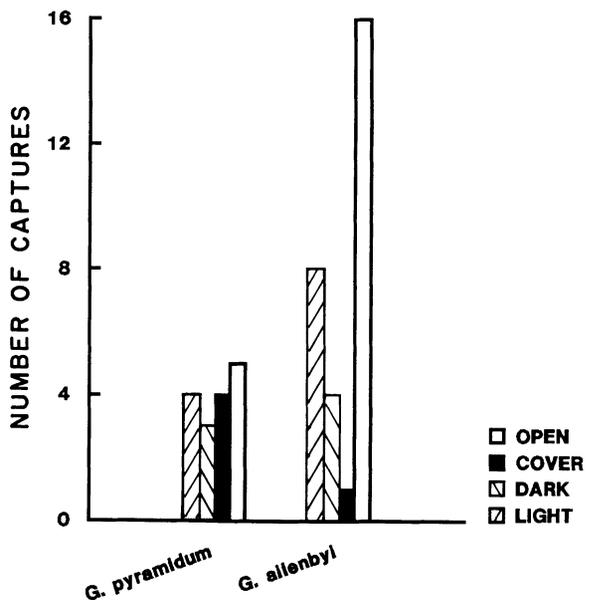


FIG. 1. The numbers of gerbils captured under each of the experimental treatments and for each species. The first and second bars give captures under high (LIGHT) and low (DARK) illumination, respectively. The third and fourth bars give captures under 10% (COVER) and 0% (OPEN) cover, respectively.

TABLE 6. Number of seed trays foraged per night by rodents when exposed to different species of owls. The data are arranged by rodent species, round, experimental treatment, and microhabitat.

Owl species	Micro-habitat	Experimental round			
		1		2	
		Light		Light	
		-	+	-	+
<i>Gerbillus allenbyi</i>					
<i>Athene noctua</i>	Bush	15	9.5	15	7
	Open	4	4	3	3.5
<i>Tyto alba</i>	Bush	13.5	10	13.5	7.5
	Open	0	0	0	0
<i>Bubo bubo</i>	Bush	13.5	12	14	9
	Open	0	0	1.5	0
No owls	Bush	14.5	15	15	9.5
	Open	1.0	0.5	1.5	0
<i>Gerbillus pyramidum</i>					
<i>Athene noctua</i>	Bush	14.5	8	14	12
	Open	7.5	10.5	2.0	2.0
<i>Tyto alba</i>	Bush	10	8	13.5	7.5
	Open	0	0	0	0
<i>Bubo bubo</i>	Bush	12.5	8.5	10.5	10.5
	Open	0	0	0.5	0
No owls	Bush	14.5	11	14	8
	Open	3.0	1.5	2.0	0

In response to owl species, both gerbils foraged more trays in the presence of Little Owls and foraged the fewest trays in the presence of Barn Owls ("owl species × presence/absence"). Furthermore, both gerbil species altered their habitat selectivities in response to different owl species ("owl species × microhabitat × presence/absence"); selectivity for the bush microhabitat was least extreme in the presence of Little Owls. Because we introduced different numbers of individuals for each owl species, it is possible that the effects of owl species are actually the effect of numbers of predators. Had this been the case, the number of trays foraged should have been fewest with Little Owls and highest with the Eagle Owls, and selectivity for the bush microhabitat should have been highest with Little Owls. This was not the case. As revealed by changes in foraging activity, both gerbil species appear to differentiate among predator species.

To test for the effects of owl species and illumination on the gerbils' GUDs, we used a nested ANOVA. Table 8 gives mean GUDs for the second experiment by round, gerbil species, owl species, and illumination. We performed a separate ANOVA for each gerbil species. Because of the paucity of open foragings, we only analyzed GUDs from the bush microhabitat. In each analysis, GUD is the dependent variable, owl species and illumination are the group variables, and days is a subgroup variable nested within the group variables. We also performed two orthogonal a priori comparisons. In the first, we compared the three treatments with owls to the one treatment without owls. In the second we compared GUDs among the three treatments with owls (Table 9).

As before, both gerbil species increased their GUDs in response to both illumination and the presence of owls (first planned comparison, Table 9). Only *G. pyramidum* altered its GUD significantly in response to owl species (second planned comparison). The mean GUD of *G. pyramidum* was highest in the presence of Barn Owls and lowest in the presence of Eagle Owls. This provides additional evidence that *G. pyramidum* perceived two Barn Owls as a greater risk than three Little Owls or one Eagle Owl.

Overall, both gerbil species altered foraging activity most in response to Barn Owls and least in response to Little Owls. Consistent with the hypothesis that *G. pyramidum* is better at detecting owl predators, *G. pyramidum* reacted more strongly than *G. allenbyi* to changes in owl species.

Effect of trellises

At any given time, half of the trays in the bush microhabitat had trellises added that elevated the brush pile 15 cm over the tray. Trellises gave gerbils unencumbered access to the tray while still providing cover from owls. To test for the effect of trellises, we used data from the third round of the first experiment and the first round of the second experiment. Halfway through each of these rounds, trellises were moved to stations whose bushes were previously untrellised. Also, recall that between rounds gerbil species were switched between halves of the aviary. Over these two rounds,

TABLE 7. The effects of owl species, lights, and microhabitat on foraging activity of two *Gerbillus* species. The last two columns give *G* test results from a four-way log-linear model of the frequency data in Table 6 (excluding data when no owls were present).

	df	<i>G. allenbyi</i>	<i>G. pyramidum</i>
Owl species × lights × microhabitat × presence/absence	2	6.07*	4.76
Owl species × lights × presence/absence	2	1.38	7.94
Owl species × microhabitat × presence/absence	2	27.89***	57.39***
Lights × microhabitat × presence/absence	1	11.45***	21.90***
Owl species × presence/absence	2	16.82***	32.70***
Lights × presence/absence	1	35.07***	21.39***
Microhabitat × presence/absence	1	384.08***	247.64***

* *P* < .05, *** *P* < .001; two-tailed test.

TABLE 8. Giving-up seed densities (GUDs, in grams of millet) by species, round, treatment, and microhabitat for the second experiment. The sample size for each entry is 32.

Owl species	Micro-habitat	Experimental round			
		1		2	
		Light -	Light +	Light -	Light +
<i>G. allenbyi</i>					
<i>Athene noctua</i>	Bush	4.07	4.72	4.05	5.17
	Open	5.85	5.68	5.96	5.83
<i>Tyto alba</i>	Bush	4.01	4.72	4.01	5.13
	Open	6.00	6.00	6.00	6.00
<i>Bubo bubo</i>	Bush	3.82	4.89	3.08	5.26
	Open	6.00	6.00	6.00	6.00
No owls	Bush	3.38	3.97	2.68	4.28
	Open	5.90	5.99	5.98	5.00
<i>G. pyramidum</i>					
<i>Athene noctua</i>	Bush	4.73	5.09	4.93	5.57
	Open	5.78	5.33	5.97	5.94
<i>Tyto alba</i>	Bush	4.88	5.44	4.90	5.59
	Open	6.00	6.00	5.99	5.94
<i>Bubo bubo</i>	Bush	4.14	4.82	4.60	5.18
	Open	5.43	6.00	6.00	6.00
No owls	Bush	4.31	4.32	3.82	5.03
	Open	5.85	6.00	5.92	6.00

each station experienced each combination of trellis and gerbil species for eight nights.

To test for the effect of trellises, we used a paired *t* test that compared a gerbil species' mean GUD at a station when the shrub pile over the tray was trellised, and when it was not. We performed a separate test for *G. allenbyi* and *G. pyramidum*. Both gerbil species lowered their GUDs in response to trellises. The mean difference between untrellised GUDs and trellised GUDs was 0.523 g ($t_{31} = 2.71, P < .025$) and 0.859 g ($t_{31} = 6.04, P < .001$) for *G. allenbyi* and *G. pyramidum*, respectively. Maneuvering through jungle gyms of branches while foraging in the bush microhabitat entails either an increase in foraging cost or a decrease in harvest rate.

We used an ANCOVA to test whether gerbil species differed in their responses to trellises. Mean untrellised GUD at a station was the dependent variable, mean trellised GUD at a station was the covariate, and gerbil species was the group variable. The mean value of the covariate differed significantly between gerbil species ($F_{1,62} = 11.95, P < .001$); *G. allenbyi* had a lower GUD than *G. pyramidum*. As expected from a significant effect of station on GUD, untrellised GUDs at stations were positively correlated with their trellised GUDs ($F_{1,60} = 41.07, P < .001$), and the slope of this relationship did not differ between gerbil species ($F_{1,60} = 1.75, P > .05$). There was a significant effect of species on intercepts; the untrellised GUD intercept of *G. pyramidum* was higher than that of *G. allenbyi* ($F_{1,61} = 70.0, P < .001$). *G. pyramidum* was more adversely affected by the tangle of shrubs than was *G. allenbyi*; in response to trellising, the GUD of *G. pyramidum*

decreases more than that of *G. allenbyi*. The larger species is more adversely affected by the tangle of branches under shrubs than the smaller species.

Effect of substrate

Each half of the aviary contained portions of sandy and loessal substrates. On each side of the aviary, half of the stations were on sand and half on loess. To test for the effect of the surrounding substrate on GUDs within seed trays, we used data from the last round of the first experiment and the first round of the second experiment. Over the two rounds, each gerbil species had 16 nights to forage at each of the 32 stations. For each species, we calculated its mean GUD at each station. Using one-way ANOVAs, we compared the GUDs from stations on sandy substrate with stations on loess. For neither species were the differences significant. For *G. allenbyi*, GUDs averaged 4.344 g on loess and 3.646 g on sand ($F_{1,31} = 2.97, P < .10$); for *G. pyramidum*, GUDs averaged 4.812 g on loess and 4.733 g on sand ($F_{1,31} = 0.08, P > .75$). Natural patterns of habitat selection were not reflected in how *G. allenbyi* and *G. pyramidum* use sandy and loessal substrates in the aviary; instead, their shared primary preference for semi-stabilized sandy habitat is at best only hinted at.

Effect of perennial shrub cover on foraging activity and predation rates

In the third experiment, the halves of the aviary simulated desert conditions with 0 or 10% cover. This corresponds to comparisons between bush and open microhabitats or between shifting sand and semi-stabilized habitats. The experiment allowed us to test for the effect of cover on gerbil foraging behavior (without regard to species) and to test how cover affects rates of predation on the two species of gerbils.

TABLE 9. The effects of owl species and lights on giving-up seed densities in experiment 2. A = *Athene noctua*, T = *Tyto alba*, B = *Bubo bubo*, N = no owls. The error terms are given as mean sums of squares. Other entries in the table are *F* ratios.

	df	<i>Gerbillus allenbyi</i>	<i>Gerbillus pyramidum</i>
Group variables			
Lights	1	34.83***	17.05***
Owl species†	3	5.80**	7.08**
A, B, and T vs. N	1	14.64***	14.14***
A vs. B vs. T	2	1.39	3.54*
Lights × owl species	3	0.31	0.05
Subgroup variable			
Days	24	2.10	1.86
Error	480	984.58	676.55

* $P < .05$, ** $P < .01$, *** $P < .001$.

† The analysis includes two planned comparisons. The first (A, B, and T vs. N) tests for the effects of owls vs. no owls. The second (A vs. B vs. T) tests for the effect of owl species on GUDs.

We tested for the effect of cover on patch use as follows. On each night there were four classes of seed trays: B_c , bush tray in cover half; O_c , open tray in cover half; B_{nc} , bush tray in no cover half; and O_{nc} , open tray in no cover half. Of course, in the no cover half there is no difference between bush and open trays other than to keep account of those trays that would have been under brush piles had brush piles been present. However, these last two classes are a useful accounting device because they permit us to make independent comparisons of how: removing a brush pile affects GUDs (comparison of B_c and B_{nc}), and having cover affects GUDs in the open microhabitat (comparison of O_c and O_{nc}).

We used the 12 nights as replicates and within a night averaged the 16 trays of a particular class. This procedure yielded 48 data points. We analyzed these data using a two-way Kruskal-Wallis test. In descending order of mean GUD: $O_c > B_{nc} > O_{nc} > B_c$. The bush microhabitat had a significantly lower GUD than the open (comparing B_c and B_{nc} with O_c and O_{nc} ; $H_{1,44} = 14.63$, $P < .001$), but there was no difference in the rankings of GUDs between the cover and no-cover halves (comparing B_c and O_c with B_{nc} and O_{nc} ; $H_{1,44} = 0.80$, $P > .80$). However, there was a significant interaction effect between microhabitat and cover ($H_{1,44} = 17.52$, $P < .001$). This comes about because in the bush microhabitat GUDs increase as cover is removed ($B_{nc} > B_c$), while in the open microhabitat GUDs decline ($O_{nc} < O_c$).

In summary, when cover was present, GUDs were significantly lower in the bush microhabitat and foraging was shifted strongly away from the open microhabitat. (Of the 301.598 g of seed harvested from the 10% cover treatment, only 0.288 g was taken from the open microhabitat.) In the absence of cover, the gerbils partially compensated by foraging more in the open microhabitat (which should now be of equal value to the "bush"), although on all 12 experimental nights, far more seeds were harvested from the cover half than from the no-cover half of the aviary.

The third experiment also tested for the effect of cover on rates of predation. On the cover side of the aviary, 1 *G. allenbyi* and 4 *G. pyramidum* were captured by owls over the course of the experiment; on the side without cover, 16 *G. allenbyi* and 5 *G. pyramidum* were captured (Fig. 1). By both measures (relative proportion of individuals in the prey population or number killed per gram of seeds harvested), rates of predation were significantly higher when cover was absent. When comparing rates based on the relative proportion of individuals, the expected numbers of captures under the presence and absence of cover were 13.0 *G. allenbyi* and 13.0 *G. pyramidum*, respectively ($\chi^2 = 9.84$, $P < .001$, one-tailed test). The numbers of gerbils captured per unit of seed mass harvested were 0.023 individuals/g with cover and 1.152 individuals/g in the absence of cover. On this basis the expected

number of captures in the presence and absence of cover were 24.0 and 2.0 individuals, respectively, even more significant than the previous test. In addition, in the absence of cover, the rate of predation on *G. allenbyi* increased more than on *G. pyramidum* (G test of heterogeneity, $G = 5.48$, 1 df, $P < 0.25$).

When given a choice, gerbils restricted their foraging to the bush microhabitat. Thus the 0 and 0% cover treatments provided a comparison of predation rates on animals foraging in the open vs. the bush microhabitats (although the gerbils had to traverse the open microhabitat to travel from tray to tray). We conclude that predation rates on gerbils were higher when there was no vegetation cover and that predation rates were higher in the open microhabitat, especially for *G. allenbyi*. Avoidance of open habitats or open microhabitats provides a behavioral means for gerbils to reduce predatory risk.

There is little evidence that differences in rates of predation between the gerbil species were directly due to body size. We noted whether smaller individuals of each species were more or less susceptible to capture. We identified 30 captures from ear tags, and scored each individual for whether it was larger or smaller than averaged size for the species. Of 21 captured individuals of *G. allenbyi* thus scored, 14 were smaller than average; of 9 individuals of *G. pyramidum*, 5 were smaller than average. Neither of these trends was significant.

DISCUSSION

The gerbils *G. allenbyi* and *G. pyramidum* treat predatory risk as a foraging cost. A gerbil facing a higher risk of predation should require a higher harvest rate in order to exploit a patch profitably (Gilliam and Fraser 1987, Brown 1988). As a result, a gerbil depleting the resources of a risky patch will reach a balance between harvest rate and foraging costs at a higher resource density than one exploiting a safer patch. As perceived predatory risk increases, gerbils should become more selective towards safer habitats, and should cease foraging resource patches at higher resource densities (giving-up density, GUD).

Predation rates by Barn Owls on gerbils increased with illumination (also see Clarke 1983, Dice 1945, 1947, Kotler et al. 1988) and increased when shrub cover was reduced from 10 to 0%. Accordingly, in response to the presence of owls or added illumination, both gerbil species increased their GUDs, foraged fewer patches, and shifted their foraging activity toward the bush microhabitat. These results parallel those for kangaroo rats (*Dipodomys merriami*) and pocket mice (*Perognathus* sp.) under similar experimental conditions (Brown et al. 1988) and under field conditions (Rosenzweig 1973, Kotler 1984b, Price et al. 1984). Moonlight avoidance has been documented for a variety of rodent taxa (Blair 1943, Lockard and Owings

1974, Butynski 1984, Kotler 1984a, Price et al. 1984, Alkon and Saltz 1988).

Indirect cues of predatory risk such as illumination (in the absence of owls) may be more important to *G. allenbyi* than to *G. pyramidum*. Inspection of Table 3 reveals that *G. allenbyi* increased its GUD equally in response to owls or illumination, while *G. pyramidum* responded more strongly to owls than to illumination. One interpretation: *G. pyramidum* is superior at detecting predators and relies less than *G. allenbyi* on indirect cues. This ability may be due to *G. pyramidum*'s larger auditory bullae (for heteromyid rodents see Webster 1962, Webster and Webster 1971). This interpretation is consistent with results obtained for heteromyid rodents; kangaroo rats (larger auditory bullae) responded less to indirect cues of predatory risk than did pocket mice (smaller auditory bullae) (Brown et al. 1988).

In response to the different species of owls, only *G. pyramidum* significantly altered its GUD. Based on GUDs, *G. pyramidum* perceived Barn Owls as most dangerous and Eagle Owls as least dangerous. The more fine-tuned response of *G. pyramidum* provides additional evidence for its superior ability to detect predators. Alternatively, *G. allenbyi* may also be able to detect and differentiate among the predators, but it may have perceived little difference in the level of threat. Unfortunately, we did not have sufficient numbers of captures (two captures by Eagle Owls and no captures by the other two owl species) to differentiate among the threats posed by the different owl species.

Both gerbil species had lower GUDs in seed trays under trellised than under untrellised brush piles. Under the latter, the obstruction created by surface branches and leaves may hinder harvest rates or increase energy costs. Interestingly, the smaller gerbil, *G. allenbyi*, was less affected than the larger, *G. pyramidum*. The present result accords with that for heteromyid rodents under similar conditions; *Perognathus amplus*, a 7-g pocket mouse, was less adversely affected by untrellised brush piles than either *Perognathus baileyi*, a 33-g pocket mouse, or *Dipodomys merriami*, a 38-g kangaroo rat (Brown et al. 1988). Smaller species of granivorous rodents may have a foraging advantage among the jungle gym of vegetation in the bush microhabitat.

Predation costs and habitat partitioning

The three results that (1) *G. allenbyi* suffers higher predation rates under conditions of 0% cover than does *G. pyramidum*, (2) *G. allenbyi* is less adversely affected by the tangle of branches under shrubs, and (3) predation rates are higher in the open microhabitat, are consistent with known patterns of habitat use by the two gerbil species in the field. In sand dune habitats of the Negev Desert, *G. pyramidum* reached peak densities on semi-stabilized sand dunes (areas of moderate perennial plant cover), was slightly less abundant (al-

though relatively the most abundant) on open dunes (areas of low perennial plant cover), and was least abundant on stabilized sand (areas of highest plant cover); *G. allenbyi* was most abundant on stabilized sand and least abundant on open dunes (Abramsky et al. 1985, Rosenzweig and Abramsky 1985, 1986). This pattern has been confirmed at a site with semi-stabilized dunes and stabilized sand fields using three independent measures of habitat use: sand tracking, live-trapping, and seed trays (Abramsky and Pinshow 1989, Abramsky et al. 1990; J. S. Brown, B. P. Kotler, and W. A. Mitchell, *unpublished manuscript*). To account for this pattern, Rosenzweig and Abramsky (1986) proposed a model of centrifugal community organization wherein both species prefer the semi-stabilized dune habitat, but have different secondary habitat preferences.

The centrifugal community organization of the gerbil species may result from the combined effects of predatory risk and resource competition. In terms of relative advantages, *G. pyramidum* may be less susceptible to predation in open habitats (see *Results: Effect of perennial shrub cover*), and *G. allenbyi* may have the higher energy efficiency of seed harvest (Kotler and Brown 1990). Both gerbil species may prefer habitats with semi-stabilized sand because of: high seed production by annual plants, favorable digging conditions in sand lacking soil crusts, and ample shrubs for safety from predators. *G. allenbyi* may rank habitats with open sand (little perennial vegetation) last because of high predation rates in open habitats, and *G. pyramidum* may rank this habitat second because of the rarity of its competitor and its lower susceptibility to predation in open habitats. *G. allenbyi* may rank habitats with stabilized sand second because of the availability of safe cover, and *G. pyramidum* may rank this habitat last because of the abundance of *G. allenbyi* and the presence of soil crusts.

Caveats

In evaluating these aviary experiments certain artificialities arise: rodent densities were 5 to 40 times natural densities, predator densities were many more times natural, brush piles may mimic some but not all aspects of shrubs, and millet in seed trays may represent an unusual food source under unusual circumstances. These features may compromise the use of GUDs to measure perceived predatory risk. We feel that this is unlikely.

Gerbils appeared to acclimate quickly to the aviary. They immediately occupied natural or artificial burrows and foraged in the seed trays. Based on tracks in the sand, most aboveground activity by gerbils was directed toward exploiting seed trays. Previous work under aviary (Brown et al. 1988) and natural conditions (Brown 1988, 1989, Brown and Mitchell 1989, Mitchell and Brown 1990) has supported the assumption that the foraging behavior of rodents in these seed trays is

based upon cost-benefit considerations that are consistent with fitness maximization. We purposely minimized direct observations because the presence of an observer alters the rodents' foraging behaviors. The behavioral consistency of several sets of gerbils in these experiments argues for the validity of the results. Both species of gerbils responded appropriately to nightly changes in predation regime, and the results reported here parallel those for heteromyid rodents tested under aviary conditions (Brown et al. 1988).

Conclusions

Increasingly, authors are considering the importance of predators for shaping the foraging behavior of their prey. For many systems, the threat of predation may be more important than the act of predation in mediating and influencing the interactions among prey species (see Kotler and Holt 1989). In these systems, predators have been shown to be an additional cost of an animal's behavior (Abrahams and Dill 1989). As a cost, predation influences when, where, and how much an animal forages.

Predatory risk may combine with resource competition and habitat structure to influence the organization of communities. Specifically, changes in prey activity time, patch use, and habitat selection in response to predation may differ among prey species and may influence prey species distributions, relative abundances, and coexistence (Kats et al. 1988). Predatory risk creates additional axes of environmental heterogeneity in time and space that may promote prey-species coexistence.

ACKNOWLEDGMENTS

We thank Matthew Goldowitz for assistance with data collection. We thank Z. Abramsky, W. A. Mitchell, and M. L. Rosenzweig for valuable discussion. Two anonymous reviewers and S. Holbrook provided useful comments. B. P. Kotler is a Bat-Sheva de Rothschild fellow. This work was supported by the United States-Israel Binational Science Foundation (grant 86-00087). The Jacob Blaustein International Center for Desert Studies provided financial assistance for J. S. Brown. This is publication number 110 of the Mitrani Center for Desert Ecology.

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