The effects of owl predation on the foraging behavior of heteromyid rodents

Joel S. Brown*, **Burt P. Kotler****, **Rosemary J. Smith*****, **and William O. Wirtz II**
Pomona College, Department of Biology, Claremont, CA 91711, USA

Summary. Researchers have documented microhabitat partitioning among the heteromyid rodents of the deserts of North America that may result from microhabitat specific predation rates; large/bipedal species predominate in the open/risky microhabitat and small/quadrupedal species predominate in the bush/safer microhabitat. Here, we provide direct experimental evidence on the role of predatory risk in affecting the foraging behavior of three species of heteromyid rodents: Arizona pocket mouse (*Perognathus amplus*; small/quadrupedal), Bailey's pocket mouse (*P. baileyi*; large/quadrupedal), and Merriam's kangaroo rat (*Dipodomys merriami*; large/bipedal). Both kangaroo rats and pocket mice are behaviorally flexible and able to adjust their foraging behavior to nightly changes in predatory risk. Under low levels of perceived predatory risk the kangaroo rat foraged relatively more in the open microhabitat than the two pocket mouse species. In response to the presence of barn owls, however, all three species shifted their habitat use towards the bush microhabitat. In response to direct measures of predatory risk, i.e. the actual presence of owls, all three species reduced foraging and left resource patches at higher giving up densities of seeds. In response to indirect indicators of predatory risk, i.e. illumination, there was a tendency for all three species to reduce foraging. The differences in morphology between pocket mice and kangaroo rats do appear to influence their behavioral responses to predatory risk.

Key words: Predation – Desert rodents – Habitat selection – Optimal foraging – Predatory risk

Predators can play an important role in species coexistence and in structuring ecological communities (see Kerfoot and Sih 1987). They may influence a community by physically removing individual prey and by affecting prey behavior (Peckarsky and Dodson 1980; Sih 1980, 1982; Bellman and Krasne 1983). Behavioral reponses of prey species include

* *Present address and address for offprint requests*: University of Illinois at Chicago, Department of Biological Sciences, Chicago, IL 60680, USA
Present addresses:
** Ben-Gurion University, Blaustein Institute for Desert Research, Sede Boqer, 84990, Israel
*** University of Arizona, Department of Ecology and Evolutionary Biology, Tucson, AZ 85721, USA

shifting activity to less risky microhabitats or to less risky time periods (e.g. Milinski and Heller 1978; Werner et al. 1983; Edwards 1983; Ohman et al. 1983; Lima et al. 1985). The influence of predators on prey behavior can have important consequences on prey population dynamics and coexistence (Holt 1984; Kotler and Holt 1988). Where there is an evolutionary tradeoff between competitive ability and predator avoidance, predators can produce species coexistence: one prey species is competitively superior in safe microhabitats while the second is competitively superior in risky microhabitats. This mechanism has been proposed to explain coexistence of bipedal and quadrupedal desert granivorous rodents of the family Heteromyidae (Webster 1962; Eisenberg 1963; Rosenzweig 1973; Kotler 1984). Here we present direct experimental evidence on the effect of barn owls on the foraging behavior of three species of heteromyid rodents: Merriam's kangaroo rat (*Dipodomys merriami*, 38 grams), Bailey's pocket mouse (*Perognathus baileyi*, 33 grams), and Arizona pocket mouse (*P. amplus*, 12 grams).

Deserts are comprised of scattered shrubs in a sea of open space. These two microhabitats may differ greatly in predatory risk. Visually aided predators such as owls, foxes, and coyotes may detect and capture rodents in the open areas more easily than in or under shrubs canopies, particularly on moonlit nights (Dice 1945, 1947; Clarke 1983; Kotler 1984). The animals which exploit the different microhabitats have different attributes which appear to promote microhabitat partitioning. Kangaroo rats (*Dipodomys*) possess enlarged hindlimbs for bipedal locomotion and inflated auditory bullae for increased hearing acuity. Pocket mice (*Perognathus*) are quadrupedal with relatively smaller auditory bullae. The anti-predator morphology of kangaroo rats is thought to permit exploitation of the risky open microhabitat (Rosenzweig 1973; Kotler 1984) but may interfere with movement through the jungle gym of branches in the bush microhabitat (Thompson et al. 1980). In contrast, risk of predation may restrict pocket mice to shrubs. A number of factors, including resource distributions, risk of predation, rodent morphology, and rodent body size, are apt to affect rodent foraging behavior. Here, we study the effects of predation on the foraging behavior of heteromyid rodents which differ in body size or morphology.

We performed experiments in a semi-natural enclosure using barn owls as predators. The enclosure allowed us to perform controlled manipulations of illumination, preda-

tors, and rodent species composition. Such manipulations are often difficult to perform under field conditions. We selected three rodent species which would allow us to separate effects of morphology (locomotion and bullae inflation) from effects of body size. The experiment addresses the following questions:

1) Does risk of predation affect habitat selection by desert rodents, and is the response influenced either by the morphology or body size of the rodent species?

2) Do the rodent species respond to indirect cues of predatory risk such as light level, or do they respond directly to the presence of predators?

3) Does increasing predatory risk reduce resource patch quality and result in less time spent foraging?

4) On what time scale are the rodents able to adjust their behavior to changes in predatory risk?

5) Does the tangle of branches under bushes affect foraging behavior either as a function of rodent morphology or rodent body size?

A companion paper (Kotler et al. ms.) examines the effects of illumination, microhabitat, rodent body size, and rodent morphology on predation rates by barn owls.

Methods

We performed all experiments during the summers of 1984 and 1985 in a large enclosure at the Bernard Field Station of the Claremont Colleges, Claremont, CA. The owl and rodent proof enclosure measures $25 \times 18 \times 3.5$ meters. It has an earth floor, a bank of six lights controlled by rheostat, and an observation tower. The enclosure is divided in half by a low (50 cm) rodent proof fence. We cleared the enclosure of all low brush and ground vegetation (several trees and large shrubs remained). In each half of the enclosure, we uniformly distributed 16 piles of cut brush. This simulated a desert habitat of about 10–15% total shrub cover. Every 5 days we replaced the brush piles with fresh cuttings to maintain life-like shrub cover. In the enclosure, perches were available for the barn owls, and numerous natural and artificial (half-buried PVC piping) burrows were available to the rodents.

We supplied resources to the rodents in aluminum trays (45 cm on a side, 2.5 cm deep) which were filled with 6 grams of millet mixed randomly into three liters of sifted dirt. We placed 16 pairs of seed trays in each half of the enclosure. To test for the effect of microhabitat on rodent foraging, we placed one tray of a pair under a brush pile (bush microhabitat) and the other tray a short distance away in the open microhabitat. To test for the effect of tangled shrub cover on foraging, we set 8 of the 16 brush piles on wood trellises 15 cm high. The trellis leaves the tray completely shaded but unobstructed by branches or leaves. Following a night of experiments, we examined each tray for footprints, digs, and other signs of foraging activity. We then sifted the remaining seeds from each tray which had been foraged. To measure the number of seeds harvested from each tray, we cleared the collected seeds of debris and weighed them.

All rodents used for each summer's experiments were collected over a two day period from a single site near Tucson, Arizona. When not in the enclosure, the rodents were individually caged and fed millet and fresh vegetables. Before being placed in the enclosure the rodents were ear tagged, sexed, and weighed. The predators were captive barn owls (*Tyto alba*) which had been raised and trained to capture rodents in the enclosure. Three owls were placed in the enclosure at dusk on owl treatment nights. On other nights the owls were kept in a smaller enclosure and fed lab rats, mice, and chicks. Following nights with predators, we held the owls in boxes until they regurgitated their pellets. Long bones, skulls, and ear tags from the owls' pellets identified the rodents captured the previous night (see Kotler et al. ms.).

To distinguish the roles of morphology and body size in determining the effect of predatory risk on rodent foraging behavior, we conducted two experiments. In the first, we held morphology constant while varying body size. We stocked twenty Arizona pocket mice, *Perognathus amplus* (small and quadrupedal, 12 g.), in one half of the enclosure and 10 Bailey's pocket mice, *P. baileyi* (large and quadrupedal, 33 g.), in the other half. Following the first experiment all rodents were trapped from the enclosure. These animals were not used for the subsequent experiment. In the second experiment, we held body size constant (approximately) while varying morphology. We stocked 8 Merriam's kangaroo rats, *Dipodomys merriami* (large and bipedal, 38 g.), in one half of the enclosure and 10 *P. baileyi* in the other half. The rodent densities approximately equalize the total metabolic requirements of the rodents in each half. (Daily metabolic requirements scales $M^{0.75}$ where M is body mass [Calder 1984]). Before each experiment, the rodents were given one night to acclimate to the enclosure. During this night, all rodents readily established burrows in the PVC piping, in natural burrows, or under seed trays.

For each experiment, the treatments included the four combinations resulting from the presence and absence of predators (three barn owls) and the presence and absence of artificial illumination (six floodlights set to approximate the light intensity of a full moon). We shuffled the ordering of treatments so that 1) the ordering was interspersed (Hurlbert 1984), 2) there were never two consecutive nights of owls plus lights, and 3) the treatments without lights would tend to occur during the week before and after the new moon. Prior to nights with predators, we added an additional rodent of each species to the enclosure. These additions minimize the effect on foraging caused by the physical removal of rodents by owls. Following nights with owls, we made appropriate additions (or subtractions) of rodents in the enclosure to maintain original population numbers. Each experiment ran for 16 nights. To factor out the effect of tray location, we switched the trellised and untrellised trays following the 8th night of each experiment.

We used the above protocol for experiments run during the summer of 1985. We completed a similar experiment in 1984. The 1984 experiment included the four treatments resulting from the presence and absence of owls (two barn owls in this case) and the presence and absence of artificial illumination (six red floodlights at full intensity). We replicated each treatment three times and within each replicate we randomized the ordering of treatments. In one half of the enclosure we added 8 *D. merriami*, and in the other we added 20 *P. amplus*. Each half of the enclosure received 15 pairs of trays and each tray was filled with 7 grams of millet mixed into 3 liters of sifted dirt. In this experiment the artificial illumination was not meant to mimic the natural intensity of moonlight. The illumination allowed us to test whether red lights affect the behavior of the rodents

and owls (Langeford [1983] reports that the behavior of *Dipodomys ordii* is unaffected by red light) and to make direct behavioral observations of the rodents and the owls from the observation tower.

Measuring foraging behavior

We used seed trays to measure the foraging behavior of the rodents in the enclosure. A seed tray presents the forager with two related decisions. First, the forager must decide whether to accept or reject the opportunity to forage. Second, if the forager elects to harvest seeds from the tray, then it must decide when to cease foraging in the tray. Because of the large amount of dirt in the trays, the rate at which rodents find seeds is positively related to the number of seeds in the tray. As an individual forages a tray, its harvest rate declines. An individual should cease foraging when the benefits from additional foraging balance the perceived costs of additional foraging. The costs of foraging include metabolic costs, risk of predation, and the missed opportunity cost from not engaging in alternative activities. Thus, the density of seeds remaining after a night of foraging, the giving up density (GUD), is an indicator of the rodent's perception of foraging costs and predatory risk. This technique has been applied with success to a natural community of desert rodents (see Brown 1988 for a more complete discussion of the technique).

We can use GUD data resulting from forages in seed trays to test whether the behavior of the rodents is consistent with the assumption that the foragers' GUD's are an indication of the costs and benefits of foraging. The location of a tray should influence perceived costs of foraging independent of the experimental treatment. In the enclosure, tray location influences factors such as topography, exposure, surrounding substrate, proximity to burrow, relationship to other trays, relationship to artificial and natural vegetation, and amounts of natural shading. For all of these reasons animals should tend to rank trays consistently regardless of treatment. If the foragers do not rank trays consistently this means either that the trays are, by coincident, remarkably similar with respect to extrinsic factors that influence the value of a tray (highly unlikely!), or that the foragers are not consistent and do not have GUD's which reflect accurately their perceived costs and benefits of foraging.

Providing that the consistency tests show that GUD's reflect the costs and benefits of foraging, both GUD's and the number of trays foraged can be used to test a variety of hypotheses. We can use the presence and absence of foraging in seed trays to measure habitat use and, in particular, to test for the effects of predators and illumination on the use of the bush and open microhabitat. We can use changes in GUD's in response to the experimental treatments to test for the rodents' assessment of predatory risk. The experimental treatments should have little (predictable) effect on the metabolic costs of foraging or the missed opportunity cost of not engaging in alternative activities. Thus, an increase in GUD's, in response to an experimental treatment, indicates a higher perceived risk of predation. Similarly, the microhabitat with the lower perceived risk of predation should have the lower GUD (when comparing trellised bush trays with open trays). The tangle of branches within a seedtray may interfere with foraging and decrease the forager's harvest rate. If this is so, then, for each experimental treatment, trellised trays should have a lower GUD than untrellised trays.

Results

The results of the experiments can be divided into three categories. The first, consistency, examines whether the results obtained can be attributed to an animal's assessment of patch quality and subsequent utilization of patches according to a GUD rule. The second, examines whether the experimental treatments affect habitat use (choice of bush or open, trellised or untrellised trays). The third category examines the intensity with which the rodents use a patch (their GUD's). We present comparisons between foraging in trellised and un-trellised trays after we present the results from the other experimental factors.

The first category of results is in response to the question: Is there a significant effect of station (tray location) on the foraging behavior of the rodents, independent of experimental treatment? For each bush tray, we calculated the average GUD by experimental treatment and species. A Friedman's Randomized Block test was used to assess whether a species ranks (according to GUD's) bush trays (14 and 15 d.f. for the 1984 and 1985 experiments respectively) similarly from one treatment to the next. For each species, there was a significant concordance of tray use across treatments (*P. baileyi* [first session 1985], $X^2 = 46.0$, $P < 0.001$; [second session], $X^2 = 42.5$, $P < 0.001$; *P. amplus* [1984], $X^2 = 50.1$, $P < 0.001$; [1985], $X^2 = 43.7$, $P < 0.001$; *D. merriami* [1984], $X^2 = 54.6$, $P < 0.001$; [1985], $X^2 = 39.0$, $P < 0.001$). Thus, stations with lower GUD's within one experimental treatment also tend to have lower GUD's within other treatments (also see results of Table 5).

The preference for certain bush stations may not result from the station's characteristics but from the idiosyncracies of individual rodents which happen to reside and forage in different parts of the enclosure. We can factor out the effect of individual by comparing the rankings of stations by *P. baileyi* for the two experiments. (Recall, that different sets of animals were used for each experiment). To determine the composite preference for a bush station within the two experiments, we summed each station's rank (with respect to average GUD) across the four treatments. A Spearman rank correlation of composite preference between *P. baileyi* in the two experiments showed a significant positive correlation ($r_s = 0.6596$, 15 d.f., $P < 0.01$, one-tailed test). Thus, the two separate populations of *P. baileyi* ranked their GUD's of bush stations similarly. The results support the assumption that GUD's measure a forager's assessment of patch quality.

To test for the effects of owls and lights on microhabitat selection, a log-linear model was applied to the number of trays foraged in the bush and open microhabitat. Data on number of trays foraged is organized by experiment, experimental treatment, and rodent species (Table 1). Each species was tested separately (Table 2). For this test, frequency data was pooled over temporal replicates and experimental session. In response to the presence of owls, all species shift their microhabitat utilization away from the open and towards the bush microhabitat. In response to lights both pocket mouse species shift their relative use of microhabitats away from the open. The kangaroo rat spe-

Table 1. The number of seedtrays foraged by rodents. Data is arranged by rodent species, experimental session, experimental treatment, and microhabitat. Session I refers to 1984 for *D. merriami* and *P. amplus* and to the first experiment of 1985 for *P. baileyi*. Session II refers to the first experiment of 1985 for *P. amplus* and to the second experiment of 1985 for *P. baileyi* and *D. merriami*. The columns and rows reflect the level of owl and light treatment. The entries preceding and following a comma refer to the bush (B) and open (O) microhabitats respectively. Each entry is the sum of replicates within the session

Session		I		II	
Microhabitat		B, O	B, O	B, O	B, O
Light\Owls		−	+	−	+
P. amplus	−	45, 11	37, 3	58, 10	75, 0
	+	42, 6	31, 1	48, 1	65, 0
P. baileyi	−	47, 7	61, 0	40, 3	54, 2
	+	44, 2	56, 0	37, 1	42, 0
D. merriami	−	40, 31	31, 3	42, 26	50, 3
	+	33, 28	23, 1	32, 23	40, 0

Table 2. The effects of owls and light on microhabitat selection. The columns are the three species and the rows are the G-tests (with William's correction) resulting from the three-way log-linear model of the frequency data from Table 1. All G values have one degree of freedom

	P. amplus	*D. merriami*	*P. baileyi*
Light × Owls × Microhabitat	0.00	2.89	0.00
Lights × Owls	0.01	0.32	0.22
Owls × Microhabitat	20.33***	79.08***	10.19**
Light × Microhabitat	5.59*	0.00	3.95*

* $P<0.05$, ** $P<0.01$, *** $P<0.001$

cies did not shift its use of microhabitats in response to lights.

To test for differences between *P. amplus*, *P. baileyi*, and *D. merriami* in microhabitat utilization we used separate G-tests (with William's correction) for each experimental session. The number of bush and open forages (Table 1) provided the data. In the absence of owls, kangaroo rats show relatively greater use of the open microhabitat than the small pocket mice, *P. amplus*, (G = 22.46, $P<0.001$ [1984 data]) and the large pocket mice, *P. baileyi* (G = 35.26, $P<0.001$). When owls are present there is no difference in relative use of microhabitats between kangaroo rats and pocket mice. The two pocket mouse species do not differ in their relative microhabitat use.

We used the number of seeds harvested from trays to test for the rodents' microhabitat preferences, and to test for the effects of owls and illumination on the rodents' foraging behavior. For pairs of seed trays, Table 3 gives the number of stations at which the bush or open microhabitat had the lower remaining density of seeds (GUD's at a station were averaged over temporal replicates). Regardless of experimental treatment, both pocket mice and kangaroo rats preferred the bush microhabitat.

For each experiment and experimental treatment Table 4 gives mean GUD's (grams) by species, microhabitat, and session. To test for the effects of owls and illumination

Table 3. Number of seed tray stations at which the bush (B) or the open (O) microhabitat had the lower giving-up density of seeds. Each tray station had one tray in the bush microhabitat and one in the open microhabitat. Data is obtained by averaging the giving up densities of a tray over the replicates of a given session and experimental treatment. See Table 1 for an explanation of sessions I and II. A " + " indicates the presence of owls or illumination and a " − " indicates the absence of owls or illumination. Independent of experimental treatment, all three species have lower GUD's in the bush microhabitat (sign test)

(Light Owls)		(− −)		(− +)		(+ −)		(+ +)	
		B	O	B	O	B	O	B	O
P. amplus	I	15	0	15	0	15	0	11	0
	II	16	0	16	0	16	0	16	0
		***		***		***		***	
P. baileyi	I	16	0	16	0	16	0	15	0
	II	16	0	16	0	16	0	15	0
		***		***		***		***	
D. merriami	I	11	3	10	4	13	0	8	0
	II	14	2	14	2	15	0	14	0
		**		**		***		***	

** $P<0.01$, *** $P<0.001$

Table 4. Giving-up densities (GUD's) by species, session, treatment, and microhabitat. The columns are the owl treatments and the rows are the illumination treatments. A " − " indicates the absence of owls (or illumination) and a " + " indicates the presence of owls (or illumination). Sessions I and II are explained in Table 1. The entries are the average GUD's (grams of millet) for trays in the bush and open (in parentheses) microhabitat

Session		I		II	
	Light\Owls	−	+	−	+
P. amplus	−	3.35	4.64	2.42	3.89
		(6.78)	(6.92)	(5.80)	(6.00)
	+	3.77	5.21	3.22	4.25
		(6.83)	(7.00)	(5.99)	(6.00)
P. baileyi	−	3.35	4.32	3.89	4.71
		(5.86)	(6.00)	(5.92)	(5.98)
	+	3.46	4.38	3.82	5.16
		(5.97)	(6.00)	(5.96)	(6.00)
D. merriami	−	4.95	5.75	4.16	5.17
		(6.22)	(6.96)	(5.52)	(5.99)
	+	5.55	6.06	4.63	5.28
		(6.59)	(7.00)	(5.38)	(6.00)

on GUD's, we used a partially-hierarchical ANOVA (Brownlee 1965) for each experimental session and for each species (Table 5). Each ANOVA includes the effects of owls, lights, days, and station on bush GUD's. For the ANOVA, the four combinations of owls and lights are the group factor. Because of nesting, days are a subgroup factor within the group factor. And, stations are a factor that is fully crossed with both the group and the subgroup factors. To insure normality of the data and homogeneity of the cell variances the data for the ANOVA's are the arcsine transformation of the proportion of seeds removed from

Table 5. The effects of owls and light on bush giving-up-densities by species and session. The columns are the species and the sessions. Sessions I and II are explained in Table 1. Each column represents the results of a separate partially-hierarchical ANOVA. In the analyses the group factors are the combinations of light and owls. The subgroup (nested) factor is day. The factor crossed with both the group and nested factors is station. The error term ("Error 1") for the group factors is the mean sum of squares (entered in the Table) for among subgroups within groups. The error term ("Error 2") for the subgroup and crossed factors is the mean sum of squares (entered in the Table) within subgroups. Entries in parentheses give the degrees of freedom. The dependent variable is the arcsine transformation of the proportion of seeds removed from a seed tray

Species Session	*P. amplus*		*P. baileyi*		*D. merriami*	
	I	II	I	II	I	II
Owls	48.4***	28.9***	37.6***	28.9***	35.4***	18.3**
	(1)	(1)	(1)	(1)	(1)	(1)
Light	6.4*	6.0*	0.5	1.6	18.9***	0.8
	(1)	(1)	(1)	(1)	(1)	(1)
Owls × Lights	0.4	0.3	0.0	1.0	0.6	2.1
	(1)	(1)	(1)	(1)	(1)	(1)
Days	1.7	2.8**	1.3	1.2	1.3	1.9*
	(8)	(12)	(12)	(12)	(8)	(12)
Error 1	220	439	268	443	80	496
	(8)	(12)	(12)	(12)	(8)	(12)
Station	19.6***	7.1***	13.6***	3.1***	53.0***	4.1***
	(14)	(15)	(15)	(15)	(14)	(15)
(Owls/Light) × Station	1.1	0.7	0.8	0.5	1.9**	0.9
	(42)	(45)	(45)	(45)	(42)	(45)
Error 2	132	159	213	375	59.8	263
	(112)	(180)	(180)	(180)	(112)	(180)

$* P < 0.05, ** P < 0.01, *** P < 0.001$

a tray. In the bush microhabitat, the presence of owls resulted in a significant decrease in seeds harvested by all three rodent species. Artificial illumination resulted in a decrease in seeds harvested by *P. amplus* during both sessions and by *D. merriami* during its 1984 session. Artificial illumination did not effect the GUD's of *P. baileyi* during either session or *D. merriami* during its 1985 session.

As an alternative test for the effects of the four treatments on the GUD's of the different rodent species, we used a Friedman's Randomized Block Test on mean bush and open GUD's to assess concordance of species' rankings. GUD's across stations and temporal replicates for each species, microhabitat, experimental treatment, and session were averaged to provide a single data point (see Table 4). For both microhabitats, each species ranks the treatments similarly (Table 6). Furthermore, sign tests can be applied to these ranks in Table 6 to test for the effects of owls and lights. Increasing owls for a fixed level of illumination increases GUD's in both microhabitats (12 of 12, $P < 0.01$; and 12 of 12, $P < 0.001$ comparisons for the bush and open microhabitats respectively). Similarly, increasing illumination for a fixed level of owls increases GUD's (11 of 12, $P < 0.02$; and 9 of 10 [2 ties], $P < 0.02$ comparisons for the bush and open microhabitats respectively).

We used presence and absence of foraging in bush trays and GUD's in bush trays to test for effects of trellises on the rodent's foraging behavior (Table 7). With respect to

Table 6. Treatment rankings by species and microhabitat based upon mean GUD's. Increasing ranks indicate increasing mean GUD's. All six sets of experimental animals (3 species and 2 replicates of each species) ranked experimental treatments similarly (Friedman's Randomized Block Test); *P.b.* = *P. baileyi*, *P.a.* = *P. amplus*, and *D.m.* = *D. merriami*

Bush microhabitat

Owls	Light	Body-size comparison		Morphology comparison		1984 Data	
		P.b.	P.a.	P.b.	D.m.	P.a.	D.m.
−	−	1	1	1	1	1	1
−	+	2	2	2	2	2	2
+	−	3	3	4	3	3	3
+	+	4	4	3	4	4	4

$X^2 = 17.00, 3$ d.f., $P < 0.001$

Open microhabitat

Owls	Light	Body-size comparison		Morphology comparison		1984 Data	
		P.b.	P.a.	P.b.	D.m.	P.a.	D.m.
−	−	1	1	1	2	1	1
−	+	2	2	2	1	2	2
+	−	3.5	3.5	3	3	3	3
+	+	3.5	3.5	4	4	4	4

$X^2 = 16.00, 3$ d.f., $P < 0.01$

Table 7. The effects of trellises on habitat use and patch quality. Habitat use is given as the proportion of trays of each type (trellised or untrellised) foraged. Patch quality is measured by the mean GUD in trays of each type. While all three species have lower GUD's in trellised trays, only *P. baileyi* and *D. merriami* bias their habitat selection in favor of trellised trays

Species	Proportion of trays foraged		Giving-up density (g)	
	Trellised	Untrellised	Trellised	Untrellised
P. amplus	0.930	0.914	3.274	4.026**
P. baileyi	0.913	0.742***	3.379	4.615***
P. baileyi	0.801	0.471***	3.805	5.291***
D. merriami	0.772	0.463***	4.343	5.472**

$** P < 0.01, *** P < 0.001$

habitat selection, both the large pocket mouse and the kangaroo rat bias their selection towards trellised trays while the small pocket mouse does not differentiate between trellised and untrellised shrubs in selecting trays (G-test for heterogeneity; *P. baileyi*, G = 44.2, $P < 0.01$ [combining data from both experiments]; *D. merriami*, G = 27.9, $P < 0.001$; *P. amplus*, G = 0.21, $P > 0.5$). With respect to patch use, all three species had lower GUD's in the trellised trays (two-tailed sign test; *P. baileyi* [both experiments combined] $t_s = 4.0$, 31 d.f., $P < 0.001$; *P. amplus*, $t_s = 3.0$, 15 d.f., $P < 0.01$; *D. merriami*, $t_s = 3.5$, 15 d.f., $P < 0.01$). (The sign test uses 1985 data to compare the mean GUD at a station when it was trellised with when it was not trellised; recall

that we switched trellises half way through each experiment.)

Discussion

In these experiments, we offered the rodents *identical* resource patches in each microhabitat and in each experimental treatment. The use of these patches by the rodents permits us to answer the original five questions of this investigation.

1) Risk of predation does influence habitat use by desert rodents. Both pocket mice and kangaroo rats revealed their perception of greater predatory risk in the open by foraging bush trays to a lower GUD. In addition, all three rodent species shifted their habitat use to nearly complete avoidance of the open in response to the presence of barn owls. This response is particularly appropriate since the rate of predation on these rodents by barn owls is higher in the open microhabitat (Kotler et al. unpublished work).

It is well known that kangaroo rats utilize the open microhabitat relatively more than pocket mice (Rosenzweig and Winakur 1969; Brown and Lieberman 1973; Price 1978; Kotler 1984). Evidence from field experiments implicate predators as the cause of this habitat selectivity (Rosenzweig 1973; Thompson 1982; Kotler 1984). Our experiments lend support to this hypothesis that predators create habitat heterogeneity. In the enclosure, when there were no predators, the kangaroo rat differed from the two pocket mouse species in habitat utilization. Presumably under conditions of no perceived predation risk both microhabitats would have been treated equally by all three species. Similarly at very high levels of predatory risk all three species showed exclusive use of the safer bush-microhabitat. Under intermediate levels of *perceived* predatory risk (the no-owl experimental treatments or perhaps natural levels of predatory risk), however, kangaroo rats use the open microhabitat proportionately more than the two pocket mouse species.

2) Since owls are more effective predators when illumination is provided (Clarke 1983; Kotler et al. ms.), rodents may use light as an indirect cue of predatory risk. This should be particularly true for rodent species which cannot accurately assess the actual approach or presence of predators. Lockard and Owings (1974) found that the kangaroo rat *D. spectabilis* decreased its activity on moonlit nights and Price et al. (1984) noted that captures of *D. merriami* shifted towards the bush microhabitat on nights near full moon. More specifically, Kotler (1984) showed that shifts in habitat utilization, decreases in activity, and use of the risky open microhabitat were related to the morphology of the rodent species; species with inflated auditory bullae and bipedal locomotion responded less to artificial illumination than quadrupedal species. Our results corroborate Kotler's view that this pattern of illumination avoidance is in response to increased perceived predatory risk. All three species increase their GUD's when artificial illumination was present (although using ANOVA this effect was not significant for *P. baileyi* and only significant for *D. merriami* during the 1984 session). Furthermore, both pocket mouse species shift their activity away from the risky open microhabitat in response to illumination whereas the kangaroo rat does not. This suggests that kangaroo rats may use their extraordinary auditory acuity (Webster 1962; Webster and Webster 1971) to detect the presence of predators in the general vicinity and need not rely as much on less accurate indirect cues to assess the true risk of predation.

3) Both direct (presence of owls) and indirect (illumination) cues of predatory risk affected the amount of seeds harvested. Increased risk of predation resulted in animals raising their GUD's in both microhabitats. If animals equilibrate the costs and benefits of foraging then, the increased GUD's show that desert rodents can treat risk of predation as a foraging cost.

4) Both pocket mice and kangaroo rats are able to adjust their foraging behavior on a nightly basis to changes in direct and indirect cues of predatory risk. Presumably, while foraging the rodents are constantly using environmental cues to update their perception of risk.

5) The tangle of branches which may be found under shrubs does affect the foraging behavior of desert rodents. Placing brush piles on trellises decreased the GUD's of all three species. A jungle-gym of branches either increases foraging costs or, more likely, slows the forager's harvest rate. However, only the larger pocket mouse species and the kangaroo rat actually biased their habitat selection away from shrubs with obstructions.

With respect to the body size and morphology of the rodents, body size appears to influence the ability to successfully negotiate the tangle of branches often found in the bush microhabitat while morphology (bipedality and inflated auditory bullae) appears to influence the avoidance and assessment of predatory risk.

Throughout, we have been assuming that the rodents' GUD's in seed trays measure changes in perceived predatory risk. This assumption should not be taken lightly especially given the un-naturally high densities of rodents and owls, and the transient nature of these populations in the enclosure. (Natural densities in such a small area would be 0.5–4 rodents and perhaps three tail feathers of a barn owl!) The rodents appeared to acclimate quickly to the enclosure. Burrows (both natural and artificial) were abundant and readily occupied by the rodents. From the observation tower we also observed the rodents' activity. (We tried to keep such observations to a minimum, lest we disturb the rodents' and owls' behavior). When active aboveground, the rodents did little else but forage in the seed trays. Furthermore, we noted no unusual behavior which might render the results an artifact of the enclosure's confines or of the high rodent density. We increased the density of rodents prior to owl treatments so that any decreases in foraging behavior would not be the result of a lowered rodent density. We used three barn owls to increase the sample size of rodent captures. The rates of predation by the owls is reported elsewhere (Kotler et al. unpublished work).

Analysis of the data supports the assumption that GUD's measured the rodents' perception of costs and benefits of foraging. We demonstrated that all species ranked treatments similarly. In accordance with predation risk, the rodents had higher GUD's under the combined treatment of owls and illumination than under the presence of either of the single factors by themselves. Similarly, the rodents had lower GUD's under the combined treatment of no owls and no illumination than under the presence of either of the single factors (see Table 5). A second test for consistency asks whether animals rank trays similarly over the different treatments. Spatial differences in tray location should influ-

ence the costs and benefits of a tray independent of treatment. For all three species there was a significant effect of station on GUD's. In fact, two entirely different groups of *P. baileyi* (from each of the experiments) gave the same ranking of stations and the same response to the experimental treatments. The simplest and predicted explanation for these results is that animals exploit patches by balancing harvest rates with metabolic costs, predation costs, and missed opportunity costs. (If anything, the contrivances of the enclosure should have made it more difficult to obtain consistent and repeatable results.)

In the bush and open microhabitat, the GUD's, from the same seed trays placed in a natural community, are 0.621 and 0.357 for *D. merriami*, and 0.325 and 0.428 for *P. amplus* (Brown 1986, data are for July 1984). These GUD's are much lower than those measured in the enclosure. This suggests that even during the no owl and no illumination treatment the rodents were more "frightened" then they would be in a natural setting. The additional fright may represent a wariness to any strange or new surroundings or it may represent a natural response to additional cues of predatory risk from the areas near the enclosure (the enclosure is part of a raptor rehabilitation center). Although the GUD's measured in the enclosure are higher than those measured in a natural community, the consistency and repeatability of the experimental results indicate their qualitative validity.

Foraging costs and microhabitat partitioning

Two well documented patterns among coexisting species of desert rodents are a non-random pattern of body size (Brown 1973; Simberloff and Boecklen 1981; Bowers and Brown 1982) and a pattern of two distinct morphologies represented by kangaroo rats and pocket mice. In addition, only 2 of approximately 25 species in the genus *Perognathus* have mean body weights greater than 30 grams and only 2 of approximately 24 bipedal heteromyids have body weights less than 30 grams. The results of our experiment suggest an explanation for this corrolation between body size and morphology. Our results show that body size and not morphology appears to influence the effectiveness with which a rodent can exploit the bush microhabitat. A larger species will find the bush microhabitat, relative to the open, less valuable than a smaller species. Once forced to rely relatively more on the open microhabitat it may be to the advantage of that species to evolve a kangaroo-rat-like morphology which allows the forager to more accurately detect and assess predatory risk. In fact, our results show that morphology and not body size influences the use of the open microhabitat. While our experiments offer a possible explanation for why kangaroo rats tend to be large and pocket mice tend to be small, they do not suggest any reason for being large or small. Proposed explanations for body size patterns include a tradeoff between interference and exploitative competitive abilities (Frye 1983) and a tradeoff between foraging speed and foraging efficiency (Brown 1986).

A word of caution is necessary. The results concerning the effects of body size and morphology on foraging behavior are based on only three species and two comparisons. Further experiments with other species are merited to eliminate the possibility that our results are peculiar to our choice of species.

The role of predation

The behavioral responses of prey to the presence of predators can lead to an additional interaction among predators (Charnov et al. 1976). If desert rodents reduce their foraging activity or cease foraging in open patches following the passage of an owl through an area, then a second owl or predator may not encounter prey which can be successfully attacked. Simply through its effect on prey behavior a predator may depress the success of another even when prey numbers have not changed. In terms of isocline models of predator-prey interactions (Rosenzweig and MacArthur 1963), a predator species whose individuals interact via prey behavior will have a positively sloped isocline. This will tend to stabilize the dynamics of the predator-prey interaction (see Ives and Dobson 1987).

The behavioral responses of prey to their predators can have important influences on the role of predators on community structure (Kotler and Holt 1988). In particular, the effect of predators on the behavior of their prey may be more important than the actual capture and removal of prey by the predators. Merely the threat of predation may be sufficient to create microhabitat distinctions and resource heterogeneity (of course, death by predation must occur to make this threat credible). Both of these effects of predators create opportunities for greater species diversity. Rather than viewing predator mediated coexistence and competitive coexistence as alternative hypotheses, this study encourages an integrated approach where predation plays an often critical role by influencing, inhibiting, or promoting competitive coexistence. In the case of desert rodents, any model of competitive coexistence based upon foraging economics or habitat partitioning must consider the effects of predators.

References

Belman KL, Kranse FB (1983) Adaptive complexity of interactions between feeding and escape in crayfish. Science 221:779–781

Bowers MA, Brown JH (1982) Body size and coexistence in desert rodents: chance or community structure? Ecology 63:391–400

Brown JH (1973) Species diversity of seed eating desert rodents in dune habitats. Ecology 54:775–787

Brown JH, Lieberman G (1973) Resource utilization and coexistence of seed-eating rodents in sand dune habitats. Ecology 54:788–797

Brown JS (1986) Coexistence on a resource whose abundance varies: a test with desert rodents. Unpublished PhD Dissertation, Univ Arizona, Tucson, 231 pp

Brown JS (1988) Patch use as an indicator of habitat preference, predation risk, and competition. Behav Ecol Sociobiol 22:37–47

Brownlee KA (1965) "Statistical Theory and Methodology in Science and Engineering, 2nd Edition". Wiley, New York, New York

Calder WA III (1984) "Size, Function, and Life History". Harvard Univ Press, Cambridge, Massachusetts

Charnov EL, Orians GH, Hyatt K (1976) Ecological implications of resource depression. Amer Natur 110:247–259

Clarke JA (1983) Moonlight's influence on predator/prey interactions between short-eared owls (Asio flammeus) and deermice (Peromyscus maniculatus). Behav Ecol Sociobiol 13:205–209

Dice LR (1945) Minimum intensities of illumination under which owls can find dead prey by sight. Amer Natur 79:385–416

Dice LR (1947) Effectiveness of selectivity by owls of deer mice (Peromyscus maniculatus) which contrast with their color background. Contr Lab Vert Biol Univ Mich No 34 20 pp

Edwards J (1983) Diet shifts in the moose due to predator avoidance. Oecologia (Berlin) 60:185–189

Eisenberg JF (1963) The behavior of heteromyid rodents. Univ Calif Publ Zool Vol 69, iv+100 pp

Frye RJ (1983) Experimental field evidence of interspecific agression between two species of kangaroo rats (Dipodomys). Oecologia (Berlin) 47:323–327

Holt RD (1984) Spatial heterogeneity, indirect interactions, and the coexistence of prey species. Amer Nat 124:377–406

Hurlbert SH (1984) Pseudoreplication and the design of ecological field experiments. Ecol Monogr 54:187–211

Ives AR, Dobson AP (1987) Antipredator behavior and the population dynamics of simple predator-prey systems. Amer Natur 130:431–447

Kerfoot WC, Sih A, eds. (1987) "Predation, Direct and Indirect Impacts on Aquatic Systems". University Press of New England, Hanover, New Hampshire

Kotler BP (1984) Risk of predation and the structure of desert rodent communities. Ecology 65:689–701

Kotler BP, Holt RD (1988) Predation and competition: the interaction of two types of species interaction. Oikos (in press)

Langeford A (1983) Pattern of nocturnal activity of male Dipodomys merriami (Heteromyidae). Southwest Natur 28:341–346

Lima SL, Valone TJ, Caraco T (1985) Foraging efficiency-predation risk tradeoff in the gray squirrel. Anim Behav 33:155–165

Lockard RB, Owings DH (1974) Seasonal variation in moonlight avoidance by bannertail kangaroo rats. J Mammal 55:189–193

Milinski M, Heller R (1978) Influence of a predator on the optimal foraging behaviour of sticklebacks (Gasterosteus aculeatus L.). Nature 275:642–644

Ohman MD, Frost BW, Cohen EB (1983) Reverse diel vertical migration: an escape from invertebrate predators. Science 220:1404–1407

Peckarsky BL, Dodson SI (1980) Do stonefly predators influence benthic distributions in streems? Ecology 61:1275–1282

Price MV (1978) The role of microhabitat specialization in structuring desert rodent communities. Ecology 58:1393–1399

Price MV, Waser NW, Bass TA (1984) Effects of moonlight on microhabitat use by desert rodents. J Mammal 65:353–356

Rosenzweig ML (1973) Habitat selection experiments with a pair of coexisting heteromyid rodent species. Ecology 62:327–335

Rosenzweig ML, MacArthur RT (1963) Graphic representation and stability conditions of predator-prey interactions. Amer Nat 97:209–223

Rosenzweig ML, Winakur J (1969) Population ecology of desert rodent communities: habitat and environmental complexity. Ecology 50:558–572

Sih A (1980) Optimal behaviour: can foragers balance two conflicting demands? Science 210:1041–1043

Sih A (1982) Foraging strategies and the avoidance of predation by an aquatic insect, Notonecta hoffmanni. Ecology 63:786–796

Simberloff D, Boecklen W (1981) Santa Rosalia reconsidered: size ratios and competition. Evolution 35:1206–1228

Thompson SD (1982) Microhabitat utilization and foraging behavior of bipedal and quadrupedal heteromyid rodents. Ecology 63:1303–1312

Thompson SD, MacMillen RE, Burke EM, Taylor CR (1980) The energetic cost of bipedal hopping in small mammals. Nature 287:223–224

Webster DB (1962) A function of the enlarged middle ear cavities of the kangaroo rat, Dipodomys. Physiol Zool 35:248–255

Webster DB, Webster M (1971) Adaptive value of hearing and vision in kangaroo rat predator avoidance. Brain Behav Evol 4:310–322

Werner EE, Gilliam JF, Hall DJ, Mittlebach GG (1983) An experimental test of the effects of predation risk on habitat use in fish. Ecology 64:1540–1548