



Direct Observations of Owls and Heteromyid Rodents: Can Predation Risk Explain Microhabitat Use?

Author(s): William S. Longland and Mary V. Price

Source: *Ecology*, Vol. 72, No. 6 (Dec., 1991), pp. 2261-2273

Published by: [Ecological Society of America](#)

Stable URL: <http://www.jstor.org/stable/1941576>

Accessed: 14/12/2014 16:58

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



Ecological Society of America is collaborating with JSTOR to digitize, preserve and extend access to *Ecology*.

<http://www.jstor.org>

DIRECT OBSERVATIONS OF OWLS AND HETEROMYID RODENTS: CAN PREDATION RISK EXPLAIN MICROHABITAT USE?¹

WILLIAM S. LONGLAND

Department of Biology, University of California, Riverside, California 92521 USA and
USDA-Agricultural Research Service, 920 Valley Road, Reno, Nevada 89512 USA²

MARY V. PRICE

Department of Biology, University of California, Riverside, California 92521 USA

Abstract. Coexisting heteromyid rodent species of North American deserts differ in habitat use and in locomotory morphology. Quadrupedal species forage primarily in structurally complex microhabitats, such as under bush canopies, while bipedal species forage in open spaces. A common explanation for this morphology–microhabitat association is that species differing in morphology also differ in vulnerability to predators, that microhabitat structure affects predation risk, and that animals preferentially forage in the safest microhabitats. We tested this for two bipedal and two quadrupedal heteromyid species (matched by body size), and one cricetid species, by quantifying effects of habitat and illumination on activity and on risk of predation by Great Horned Owls.

Capture frequencies were lower for all heteromyid species than for the cricetid species, *Peromyscus maniculatus*. Heteromyid activity was lower in open habitat and under bright illumination. Illumination had no significant effect on risk, perhaps because rodents changed activity patterns under full moon to compensate for a potential increment in risk. Habitat, however, did affect risk: all species were attacked and captured more frequently in the open. Bipedal species were attacked relatively more in the open than were quadrupeds. If these results apply to all predators, they indicate that predation alone cannot account for the divergent microhabitat associations of bipedal and quadrupedal species. Bipedal heteromyids, however, escaped owl attacks more frequently than did quadrupeds of equivalent size. It is therefore conceivable that they experience lower overall risk in nature, where owls may preferentially attack more easily captured prey species when given a choice. Under these circumstances, owl predation could reinforce divergent microhabitat specializations based on some other factor, such as foraging economics, by restricting quadrupeds more strongly than bipeds to the safety of bushes.

Key words: *Chaetodipus*; community structure; desert rodents; *Dipodomys*; foraging economics; *Microdipodops*; microhabitat; moonlight; owls; risk-foraging trade-off.

INTRODUCTION

In North American deserts, widely spaced perennial plants and varied topography produce a mosaic of structurally distant patches on a variety of spatial scales. Heterogeneity such as this often provides a major axis for resource partitioning by ecologically similar species through divergent habitat or microhabitat use (Schoener 1974). Interspecific differences in habitat or microhabitat specialization can be an evolutionary or population-dynamical by-product of interactions between species such as competition or predation (Lawlor and Maynard Smith 1976, Roughgarden 1976). In very few cases, however, do we know why coexisting species are associated with different habitats or microhabitats.

Rodents of the family Heteromyidae provide a model system for studying divergent microhabitat specializations. Four of the six extant genera (Hafner and

Hafner 1983) in this ecologically uniform family of nocturnal, burrowing seed-eaters are found in North American deserts, where they form a dominant part of the granivore guild (Brown et al. 1979). Several heteromyid species often coexist, and one of the most conspicuous differences among species that might be important for coexistence involves habitat or microhabitat affinities (Rosenzweig and Winakur 1969, Brown and Lieberman 1973, Price 1978, Price and Brown 1983, Kotler and Brown 1988) that are correlated with locomotory morphology, a major axis of morphological variation in the family as a whole (Wood 1935). Bipedal kangaroo rats (*Dipodomys* spp.) and kangaroo mice (*Microdipodops* spp.) frequent open spaces (i.e., “open microhabitats”) between canopies of perennial plants in relatively flat, nonrocky terrain, whereas quadrupedal pocket mice (*Chaetodipus* spp. and *Perognathus* spp.) occur relatively more in structurally complex habitats and/or microhabitats, such as rocky slopes or areas under shrub canopies (“bush microhabitats”) (see Price 1986, Reichman and Price 1991, and references therein).

¹ Manuscript received 9 July 1990; revised 28 January 1991; accepted 12 February 1991.

² Address correspondence to first author at this address.

Explanations for the association between morphology and microhabitat affinity in heteromyid rodents generally have assumed that morphology affects an individual's ability to perform fitness-related activities in bush and open microhabitats, and that the morphology that is most fit in one microhabitat differs from the one that is best in other microhabitats. What has varied among hypotheses is the relative importance assigned to food-related and predator-related components of fitness (Price and Brown 1983, Price 1984, Reichman and Price 1991).

The "foraging economics hypothesis" suggests that competition for food resources, which limit heteromyid population densities and female reproductive success (French et al. 1974, Munger et al. 1983, Price and Endo 1989), places a fitness premium on foraging efficiency (i.e., net rate of energy harvest). If morphology affects ability to forage in different microhabitats, and animals prefer more profitable microhabitats, then foraging economics alone can account for observed patterns of microhabitat use as long as bipeds are more efficient in open microhabitats while quadrupeds are more efficient in bush microhabitats (Tilman 1982, Price 1984, Brown 1989).

The "predation risk hypothesis" suggests that predator-related mortality is an important fitness component for heteromyids, placing a premium on predator escape ability. If morphology affects escape ability in different microhabitats, and individuals prefer safer microhabitats, then predation alone can account for observed patterns of microhabitat use as long as bipeds are relatively safer in open microhabitats while quadrupeds are relatively safer in bush microhabitats (Price and Brown 1983, Price 1984).

Although much of the heteromyid literature has focused on one or the other fitness component, some investigators have considered potential effects of both foraging and predation on microhabitat use (Rosenzweig 1973, Kotler 1984b). Indeed, empirical investigations with a variety of taxa suggest that foraging behavior may generally be sensitive to the simultaneous and often conflicting fitness demands of food acquisition and predator avoidance (Milinski and Heller 1978, Sih 1980, Cerri and Fraser 1983, Mittelbach 1984, Lima et al. 1985, Lima and Valone 1986, Holbrook and Schmitt 1988, Newman et al. 1988, Pierce 1988, Werner and Hall 1988, Abrahams and Dill 1989). Utility theory (Keeney and Raiffa 1976, Stephens and Krebs 1986) provides a means of integrating these diverse fitness components into a single index of microhabitat value (Caraco 1980, Lima et al. 1985).

The utility, or fitness value, of microhabitat i (W_i) to a foraging individual can be expressed as the net rate of fitness gain. This equals the expected fitness gain from resource acquisition, multiplied by the probability of escaping predation, plus the expected fitness gain (=0) if the animal is eaten, times the probability this occurs:

$$W_i = [g_i \cdot f(g)](1 - p_i) + 0 \cdot p_i = [g_i f(g)](1 - p_i). \quad (1)$$

Here g_i is the net resource (energy) gain per unit time spent foraging in microhabitat i , $f(g)$ represents the fitness gain per unit of resource acquired, and p_i the probability of predation per unit time in microhabitat i . To maximize fitness an animal should rank microhabitats by W_i and, given a choice between alternative microhabitats, prefer that with the highest W_i . This model of microhabitat affinity reduces to the "foraging economics hypothesis" if microhabitats are equivalent in predation risk (i.e., $p_{\text{bush}} = p_{\text{open}}$) and to the "predation risk hypothesis" if microhabitats are equivalent in economic value (i.e., $g_{\text{bush}} = g_{\text{open}}$).

Here we report results of a study designed to test the predation risk hypothesis for heteromyid microhabitat affinities. We compare the risk of predation from Great Horned Owls (*Bubo virginianus*) incurred by individuals of two bipedal and two similarly sized quadrupedal heteromyid species while active in bush and open microhabitats. For predation alone to produce observed microhabitat affinities, each morphological type must be safer in the microhabitat with which it is associated: for bipeds, $p_{\text{open}} < p_{\text{bush}}$; for quadrupeds, $p_{\text{open}} > p_{\text{bush}}$. Because we measured risk from only one of the suite of heteromyid predators, our study provides only a partial test of the predation hypothesis, which is based upon total risk from all sources. We address how general our findings are likely to be in the discussion.

We also tested for an effect of illumination. Heteromyids often exhibit lower activity and increase their use of shaded microhabitats in bright moonlight (Lockard and Owings 1974, Kaufman and Kaufman 1982, Kotler 1984a, b, Price et al. 1984, Bowers 1988, Brown et al. 1988). These shifts in behavior traditionally have been interpreted as responses to an illumination-related increase in risk from visual predators (Lockard and Owings 1974, Rosenzweig 1974, Kaufman and Kaufman 1982, Kotler 1984a, b), but only a few studies have attempted to confirm that light does increase risk (Dice 1945, Clarke 1983, Kotler et al. 1988), and these either have utilized deermice (*Peromyscus maniculatus*) under somewhat unnatural circumstances, or have used indirect estimates of activity to quantify risk per unit of activity. We used direct observation in a semi-natural enclosure to assess effects of habitat structure and illumination on activity, and expressed risk per unit of active time.

Finally, we compared risk to heteromyids with that to a cricetid rodent species (*Peromyscus maniculatus*). Heteromyids, especially bipeds, have very large middle-ear cavities (auditory bullae), which facilitate auditory detection of attacking predators (Webster and Webster 1984). Cricetids have much smaller auditory bullae. We expected, therefore, that heteromyids would outperform *P. maniculatus* at escaping owl attacks if hearing acuity is important for avoiding predators.

The experimental design thus enabled us to compare risk between: (1) open and bush microhabitats, (2) dim and brighter illumination conditions, (3) bipedal and quadrupedal heteromyids, (4) large and small heteromyids, and (5) heteromyids and *P. maniculatus*.

Risk of predation to an individual rodent can be broken down into several components:

$$P\{\text{capture/time}\} = P\{\text{encounter/time}\} \\ \times P\{\text{attack given an encounter}\} \\ \times P\{\text{capture given an attack}\}.$$

In the confines of the enclosure, an active rodent's probability of encountering an owl was assumed to be 1.0. We therefore considered two separate components of risk, i.e., the probability of being attacked by a predator per unit of time spent above ground, assuming that an encounter has occurred ($P\{A|E\}$), and the probability of being captured given that an attack occurs ($P\{C|A\}$), as well as total risk, which is the product of $P\{A|E\}$ and $P\{C|A\}$. Our measure of total risk overestimates that experienced by animals in nature to the extent that predator encounter rates were artificially high under our experimental conditions, and because owls may have been more familiar with the enclosure environment than rodents. It underestimates total risk to the extent that predators other than Great Horned Owls are important in nature.

MATERIALS AND METHODS

Experiments were conducted from August 1986 to April 1988 at the Claremont Colleges' Bernard Field Station (Claremont, California), in a $23 \times 18 \times 4$ m flight cage equipped with a rodent-proof fence. A series of perches and a temporary holding cage for raptors were at one end of the cage, and an observation tower was at the center of the opposite end. The observation platform was 2 m above the ground, and three windows made the entire cage visible from the tower. Six pairs of 60-W light bulbs suspended from the cage top were controlled by a rheostat in the observation tower.

We partitioned two adjacent 80-m² arenas in the cage with a 0.5 m high fence, which confined rodents but allowed owls easy access to either arena. Into one arena (the "bush" habitat) we transplanted 35 living brittle-bush (*Encelia farinosa*) plants, which, together with cut shrub branches inserted into 20 cm lengths of upright polyvinyl chloride (PVC) tubing, provided a shrub layer 0.5–1.0 m high. We replaced branches with fresh cuttings 10 times during the 20 mo of the experiment. Each time we replaced cuttings we ran three randomly placed line-intercept transects across the bush arena to measure canopy cover; cover (mean \pm SD) for all 30 transects was $51.5 \pm 8.1\%$. Canopy cover did not differ significantly among the different cuttings (SAS ANOVA procedure, SAS 1987: $F = 1.86$, $df = 9, 20$, $P > .10$). The second arena was an open habitat with no shrub cover. The two arenas were equally distant from

owl perches and equally visible from the observation tower.

Both arenas had 10 PVC-tube "burrows" buried in the ground at an angle of $\approx 25^\circ$ with one end opening to the surface. Rodents quickly extended the burrows and created secondary entrances from the buried ends to the surface, which we left intact. On observation nights we placed three cafeteria trays ($30 \times 45 \times 2$ cm) each containing > 50 g of wild bird seed mixed with fine sand around the center of each arena to entice rodents away from arena walls. Seed trays were placed under the edges of bush canopies in the bush arena. Trays had abundant seed (> 30 g) remaining after trials, so rodent activity should not have been affected by seed depletion during trials.

Four heteromyid species, *Dipodomys merriami* (a biped with body mass = 38.2 ± 2.9 g [mean \pm SD]), *Microdipodops megacephalus* (biped; 13.8 ± 1.3 g), *Chaetodipus baileyi* (quadruped; 32.6 ± 4.2 g), and *C. fallax* (quadruped; 18.5 ± 1.5 g) were selected to provide comparison of two body sizes within each locomotion category, and of two locomotion categories within each body size. In addition, a quadrupedal cricetid rodent species (*Peromyscus maniculatus*; 18.0 ± 0.4 g) was chosen to provide a comparison of families.

We placed four individuals (marked with uniquely numbered ear tags) of a particular species into each arena 24 h before exposure to owls to familiarize them with the arenas. We provided no food during the familiarization period, but seeds may have been available from plants in and around the flight cage or from caches made by previous occupants. After familiarization, each group of rodents was observed in the presence of owls for two consecutive nights before survivors were captured and returned to an animal colony. Occasionally, we observed the same group of individuals for four consecutive nights, in which case we added rodents of the same species to each arena after the second night to compensate for attrition. We rotated the heteromyid species used between consecutive weeks as much as possible, but fluctuations in seasonal availabilities of species sometimes prevented this. All trials with *P. maniculatus* were conducted during the last month of the experiment.

We placed two Great Horned Owls into the holding cage during the 24 h rodent familiarization periods and between consecutive observation nights. Owls were not fed in the holding cage. They were released from the holding cage ≈ 0.5 h before nightfall on nights of experimental trials. We used five individual owls during the course of the experiment, and could distinguish them based on body size, roosting locations within the cage, or behavior. One owl was used in most trials throughout the experiment. A second, used in most heteromyid observations, died near the end of the experiment and was not involved in any *P. maniculatus* trials. A third individual was used in several heteromyid trials and in all *P. maniculatus* trials. Two other

owls, available on a temporary basis, were used much less frequently ($<10\%$ of all trials). Log-linear contingency tests (SAS CATMOD procedure, SAS 1987) revealed no significant differences among owls in capture success with different prey or under different habitat or illumination conditions ($P > .14$ for all "among owl" comparisons). Effects of individual owls were therefore omitted from further data analyses.

Each trial began when we heard or saw the first rodent activity after nightfall and continued for a 3-h observation period. During trials a single observer with image-intensifying night-vision goggles (Litton, model M-802) tape recorded the following from the tower: (1) time spent in aboveground activity by focal individuals in both arenas. Whenever we saw an active rodent, we timed its activity until it re-entered a burrow or we lost sight of it. This gave an estimate of mean activity bout duration and of total activity time per trial. Total activity times were underestimated, especially in the bush arena, for three reasons. First, we do not know how many activity bouts escaped detection. Second, in some cases, two or more rodents were active simultaneously, and only one could be observed. Finally, focal animals in the bush arena often disappeared from sight behind a bush before returning to a burrow. Judging from the number of owl attacks directed at individuals other than focal animals, we estimate that we recorded $\approx 12\text{--}17\%$ of activity depending on habitat and light level. (2) Outcome of each owl attack: escape or capture. Captures were later verified by recovering rodent ear tags from regurgitated owl pellets. (3) Behavioral reaction of each attacked rodent: evasive leap or no response. (4) If possible, the duration of owl attack flights from takeoff to contact with the ground. Flight distances were measured later to calculate attack velocities.

We used the number of owl attacks on focal animals, divided by total rodent activity per trial, as an index of attack probability per encounter, $P\{A|E\}$. The probability of capture given an attack, $P\{C|A\}$, was taken as the proportion of owl attacks resulting in captures. This included all attacks, not just those directed at focal individuals. For each species and each combination of habitat and moonlight conditions, we estimated total risk as $P\{A|E\} \times P\{C|A\}$.

To investigate effects of moonlight on $P\{A|E\}$ and $P\{C|A\}$ we conducted trials under two different light intensities. In "full moon" trials the overhead lighting in the flight cage was adjusted to 3.0 lux at ground level, and natural moonlight was often present. "New moon" trials had no artificial or lunar illumination, and could therefore occur only during periods of the lunar cycle with no moonlight for ≥ 3 h following night-fall (i.e., between the fourth night after a full moon and the night of the next new moon). Thus, full and new moon trials were rotated approximately every 2 wk.

Rodents were collected as adults from various sites in California and Arizona. Large owl species (including

Great Horned Owls) and abundant owl perches occurred at all collection sites. Before being tested rodents were maintained for 2–8 d in a captive colony, where they were housed in plastic cages under a 14L:10D photoperiod and fed a mixture of wild bird seed and sunflower seed, lettuce, mealworms, and laboratory chow. Because experiments required substantial numbers of individuals, animals that were recovered after a set of trials were returned to the colony and sometimes used again later. Animals were not used in the experiment again if they had been in captivity for >6 wk, as they seemed to become unwary after several weeks. For each prey species the experiment was terminated when there was a minimum of 5 captures in each habitat or a minimum of 25 owl attacks and 2 captures in each habitat. This criterion was used for trials conducted under both illumination levels, and was fulfilled in most cases. For *M. megacephalus*, however, a shortage of animals prevented us from attaining these minimum attack and capture numbers in the bush habitat under new moon.

Data analysis

To test effects of habitat type and moonlight on activity, we used rodent species, habitat type, and light level as fixed effects and activity data (number of activity bouts, mean time per bout, total time of activity) from individual trials as dependent variables in factorial analysis of variance (ANOVA; SAS GLM procedure, SAS 1987). We eliminated data from trials in which we saw no rodent activity, because this may have resulted from habitat- or moonlight-specific observational biases or other causes unrelated to risk. Inter-specific differences were tested with Tukey-Kramer studentized range tests (SAS GLM procedure). We also analyzed data by locomotion type and by body size to test for systematic differences in activity between bipedal and quadrupedal heteromyids and between large (*D. merriami*, *C. baileyi*) and small (*M. megacephalus*, *C. fallax*) species. *Peromyscus maniculatus* was omitted from these analyses, because we did not record its activity.

Because $P\{A|E\}$ is a composite measure affected by rodent activity as well as by owl attack frequencies, we used Analysis of Covariance (ANCOVA; SAS GLM procedure) to control for variation in activity when assessing species and treatment effects on attack rate. We used the number of owl attacks on focal individuals per trial as the dependent variable, with total time of focal rodent activity per trial as a covariate, and habitat type, moonlight, and rodent species as independent variables. ANCOVAs were also run with rodent species lumped by locomotion type or body size. The Type III sums of squares indicated effects of the independent variables adjusted for rodent activity time on number of owl attacks on focal individuals. To test for homogeneity of slopes before performing ANCOVA we considered all 16 combinations of rodent species, hab-

TABLE 1. Prey activity and owl attack data (means \pm SE) from observations on focal animals of four rodent prey species. N is number of trials in which rodent activity was observed for each moonlight level and each habitat; N' = total numbers of trials conducted per moonlight level. Probability of attack ($P\{A|E\}$) is the number of owl attacks per min of observed prey activity.

Prey species	Moonlight	N'	Habitat	N	Prey activity			Owl attacks during observation of rodent activity	
					Activity bouts observed per trial	Total activity time per trial (min)	Mean time per bout (min)	Total number owl attacks	Attacks per min activity ($P\{A E\}$)
<i>Chaetodipus baileyi</i>	full	19	open	10	3.50 \pm 0.92	5.57 \pm 2.25	1.37 \pm 0.30	8	0.39 \pm 0.14
			bush	14	2.43 \pm 0.44	5.23 \pm 1.15	2.31 \pm 0.59	6	0.15 \pm 0.06
	new	20	open	7	3.57 \pm 0.90	8.99 \pm 3.00	2.47 \pm 0.44	5	0.16 \pm 0.09
			bush	6	2.17 \pm 0.40	6.68 \pm 3.04	2.55 \pm 0.93	2	0.02 \pm 0.02
<i>Chaetodipus fallax</i>	full	28	open	12	3.42 \pm 0.90	3.69 \pm 1.08	1.19 \pm 0.32	6	0.19 \pm 0.09
			bush	15	3.93 \pm 0.56	14.43 \pm 4.46	3.93 \pm 1.32	2	0.02 \pm 0.02
	new	22	open	16	3.13 \pm 0.50	7.10 \pm 1.26	2.43 \pm 0.42	12	0.13 \pm 0.06
			bush	9	1.56 \pm 0.24	6.41 \pm 2.85	3.06 \pm 1.22	2	0.02 \pm 0.02
<i>Dipodomys merriami</i>	full	19	open	9	6.22 \pm 2.47	10.52 \pm 6.73	0.99 \pm 0.50	23	3.20 \pm 1.77
			bush	14	5.79 \pm 1.47	20.11 \pm 4.68	4.70 \pm 1.46	8	0.06 \pm 0.03
	new	17	open	10	2.60 \pm 0.50	4.54 \pm 1.58	1.60 \pm 0.44	10	0.50 \pm 0.24
			bush	14	2.43 \pm 0.52	4.69 \pm 1.03	2.33 \pm 0.49	2	0.05 \pm 0.04
<i>Microdipodops megacephalus</i>	full	13	open	7	10.71 \pm 2.07	1.73 \pm 0.54	0.15 \pm 0.03	7	0.43 \pm 0.20
			bush	6	9.00 \pm 2.41	8.92 \pm 2.45	1.63 \pm 0.92	6	0.17 \pm 0.14
	new	15	open	7	7.00 \pm 2.04	4.08 \pm 1.61	0.57 \pm 0.14	7	0.89 \pm 0.43
			bush	6	3.83 \pm 0.91	18.17 \pm 14.46	3.98 \pm 2.86	6	0.06 \pm 0.04

itat type, and moonlight as "treatments," and tested effects of treatment and total activity times on numbers of owl attacks in each trial using the SAS GLM procedure. This analysis indicated homogeneous slopes ($F = 0.48$, $df = 15, 130$, $P > .65$ for the treatment \times total activity interaction), so we proceeded with ANCOVA.

To test for a time effect on rodent activity and $P\{A|E\}$ in the above ANOVAs and ANCOVAs, we divided data from the 20-mo experiment into several arbitrary time blocks (i.e., five 4-mo, four 5-mo, or two 10-mo blocks), and repeated the analysis with blocks added to fixed effects. Block effects were insignificant in all cases (P values ranged from .14 to .79), while the significance of other terms in the models remained virtually unchanged. Therefore, we report results of analyses lacking time blocks. Also, activity and attack data were log transformed to satisfy the homoscedasticity and normality assumptions of the above analyses.

We conducted a series of log-linear factorial contingency analyses (SAS CATMOD procedure) using pooled data from all trials to test effects of habitat and illumination on $P\{C|A\}$ among all rodent species (including *P. maniculatus*), among the four heteromyid species, and between subsets of species (i.e., *P. maniculatus* vs. heteromyids, bipedal vs. quadrupedal heteromyids, large vs. small heteromyids). For $P\{C|A\}$ analyses, we compared numbers of owl attacks resulting in capture with those resulting in escape.

We compared total risk ($P\{A|E\} \times P\{C|A\}$, or estimated numbers of captures per minute of prey activity) between open and bush habitats and between full and new moon trials across all four heteromyid species

with Wilcoxon matched-pairs signed-ranks tests, and used a Kruskal-Wallis test to compare the ranking of total risk among heteromyid species across all combinations of habitat type and moonlight (SAS NPAR1WAY procedure). We also tested for concordance among heteromyid species in ranking of total risk across all habitat/moonlight combinations using a Friedman two-way ANOVA (Siegel 1956). Finally, we estimated habitat-specific survival rates ($1 - \text{total risk}$), and compared ratios of open : bush survival rates for quadrupedal vs. bipedal heteromyid species with a Wilcoxon two-sample test (Sokal and Rohlf 1981).

To examine potential effects of moonlight- and microhabitat-specific risk on heteromyid behavior, we ranked mean values of activity variables (number of activity bouts observed, time per activity bout, and total activity) among all combinations of rodent species, habitat, and moonlight, and tested these for correlations with $P\{C|A\}$ rankings (Spearman rank correlations; Siegel 1956). Because we assessed $P\{C|A\}$ independent of rodent activity observations, but used activity measures to calculate $P\{A|E\}$ and total risk estimates, we did not test the latter risk variables for correlations with activity.

RESULTS

Rodents appeared to forage normally in the flight cage, and occasionally exhibited other behaviors found in nature such as sand bathing and mating. Owls initiated attacks ≈ 15 m from experimental arenas, which was sufficient to attain attack speed. When heteromyids escaped, it was with a last split-second leap perpen-

TABLE 2. Results of factorial ANOVAs testing for effects of rodent species (four heteromyid species), habitat type (open or bush), and moonlight ("new" or "full moon") on rodent activity variables and a factorial ANCOVA testing the same effects on number of owl attacks to focal animals per trial with rodent activity time as a covariate.

Variable	Source of variation	df	ss	F	P
Activity bouts observed per trial	Species	3, 146	3.136	10.32	.0001
	Habitat	1, 146	0.369	3.65	.058
	Species \times habitat	3, 146	0.180	0.59	.620
	Moonlight	1, 146	1.045	10.32	.002
	Species \times moonlight	3, 146	0.469	1.54	.206
	Habitat \times moonlight	1, 146	0.250	2.47	.118
	Species \times habitat \times moonlight	3, 146	0.238	0.78	.505
Total activity time per trial	Species	3, 146	0.186	0.16	.925
	Habitat	1, 146	2.515	6.40	.013
	Species \times habitat	3, 146	2.566	2.18	.093
	Moonlight	1, 146	0.007	0.02	.896
	Species \times moonlight	3, 146	0.578	0.49	.689
	Habitat \times moonlight	1, 146	4.175	10.63	.001
	Species \times habitat \times moonlight	3, 146	0.396	0.34	.799
Mean time per activity bout per trial	Species	3, 146	4.588	6.63	.0003
	Habitat	1, 146	4.812	20.86	.0001
	Species \times habitat	3, 146	1.991	2.88	.038
	Moonlight	1, 146	1.219	5.29	.023
	Species \times moonlight	3, 146	0.124	0.18	.910
	Habitat \times moonlight	1, 146	2.381	10.32	.002
	Species \times habitat \times moonlight	3, 146	0.090	0.13	.942
Attacks to focal animals per trial	Species	3, 145	648.171	2.58	.056
	Habitat	1, 145	1920.760	22.96	.0001
	Species \times habitat	3, 145	281.772	1.12	.342
	Moonlight	1, 145	1.843	0.02	.882
	Species \times moonlight	3, 145	341.422	1.36	.257
	Habitat \times moonlight	1, 145	66.189	0.79	.375
	Species \times habitat \times moonlight	3, 145	32.835	0.13	.942
	Activity	1, 145	1209.900	14.46	.0002

dicular to the owl's trajectory, followed by retreat to a burrow. Owls usually transferred captured prey from talons to beak and flew to a perch to eat it.

Attack velocities (mean \pm SD) for the open arena were 7.13 ± 0.96 ($N = 6$) and 8.40 ± 0.63 m/s ($N = 4$) during new and full moon trials, respectively, which is a marginally significant difference ($t = 2.30$, $df = 8$, $P = .05$). Bush arena velocities were 4.67 and 5.50 m/s under new and full moon, respectively, but only one flight was measured under each light level. The new moon/bush arena value did not differ significantly from open arena values under new moon ($t = 2.37$, $df = 5$, $.05 < P < .10$; see Sokal and Rohlf 1981:231), but the full moon/bush arena value was significantly slower than open arena values under full moon ($t = 4.12$, $df = 3$, $P < .05$). There is some suggestion, then, that both darkness and bush canopies cause owls to reduce attack velocity.

Heteromyid activity patterns

Effects of species, habitat, and moonlight.—Table 1 summarizes activity data for the four heteromyid species, and Table 2 gives results of ANOVAs testing effects of rodent species, habitat type, and moonlight on activity.

There was a significant difference among heteromyid species in number of activity bouts per trial, because

M. megacephalus and *D. merriami* were observed more frequently than the other two species. There was also a significant species effect on mean bout length: *C. baileyi* and *C. fallax* generally had longer bouts than the bipedal species. Thus, species that were active more frequently tended to have shorter bouts. The opposing trends in bout frequency and bout duration canceled one another, yielding no significant species differences in total activity time per trial.

Habitat had significant effects on total activity time and mean time per bout, and a marginally significant effect on number of bouts per trial. Activity times for all species were generally greater in the bush habitat, but bouts were observed more frequently in the open habitat. There was also a significant species \times habitat interaction for mean time per bout, because bout lengths differed between habitats more for *M. megacephalus* than other species.

All species were observed in significantly more bouts during full moon than new moon trials, but mean bout lengths were significantly shorter under full moon. This trade-off between bout frequency and bout length yielded an insignificant moonlight effect on total activity time per trial. There was a significant habitat \times moonlight effect on mean bout length and on total activity time; the discrepancy in activity times between habitat types was generally greatest under full moon conditions.

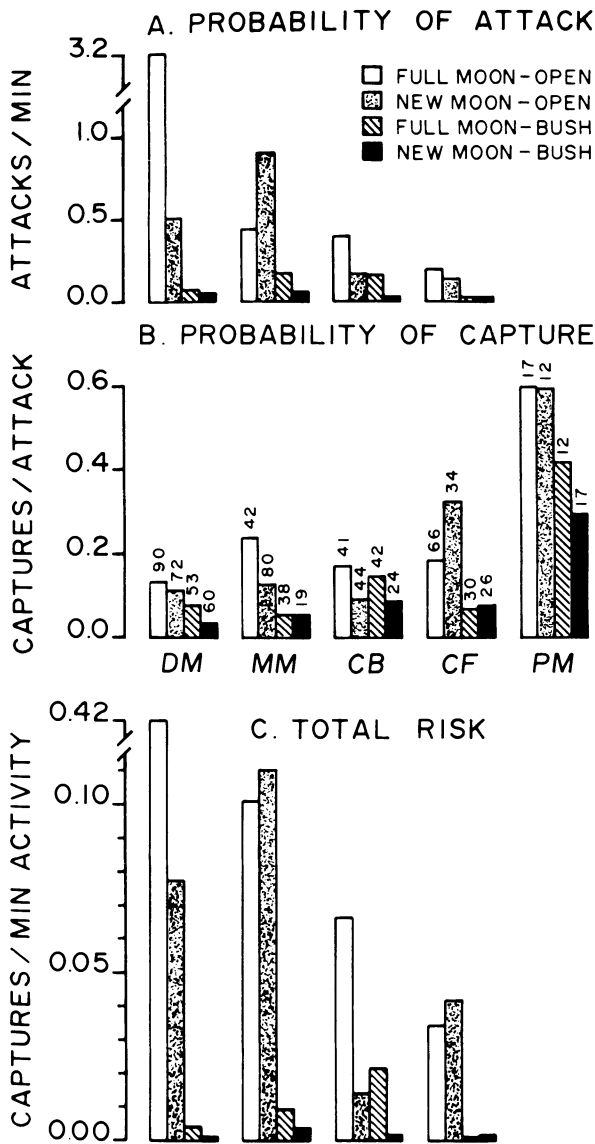


FIG. 1. (A) Probability of owl attack, (B) probability of capture given attack (numbers above bars are total numbers of attacks), and (C) total risk of predation for four heteromyid rodent species. Species are *Dipodomys merriami* (DM), *Microdipodops megacephalus* (MM), *Chaetodipus baileyi* (CB), *C. fallax* (CF), and *Peromyscus maniculatus* (PM).

Comparison of bipedal and quadrupedal species.—Bipedal heteromyids were observed in significantly more bouts per trial than quadrupeds ($F = 12.77$, $df = 1, 154$, $P < .001$), but mean bout length was significantly greater for quadrupeds ($F = 8.87$, $df = 1, 154$, $P < .005$). There were no significant biped–quadruped differences in total activity time per trial ($F = 0.17$, $df = 1, 154$, $P > .65$), but there was a significant locomotion type \times habitat interaction for this variable ($F = 6.32$, $df = 1, 154$, $P < .02$) and for mean bout length ($F = 25.44$, $df = 1, 154$, $P < .002$), because between-

habitat activity time differences were greater for bipeds than for quadrupeds.

Comparison of large and small species.—The two small heteromyid species (*M. megacephalus* and *C. fallax*) were observed in significantly more bouts per trial than the two larger species ($F = 4.11$, $df = 1, 154$, $P < .05$). This was due to the frequent activity of *M. megacephalus*. There were no other significant differences in activity of large and small species.

Probability of attack ($P\{A|E\}$)

$P\{A|E\}$ among heteromyid species.—Numbers of attacks on focal rodents per minute of activity ($P\{A|E\}$) are summarized in Table 1 and Fig. 1. An ANCOVA testing effects of species, habitat, and moonlight on $P\{A|E\}$ (i.e., on number of attacks to focal individuals, controlling for variation in rodent activity) revealed a marginally significant species effect (Table 2). *Microdipodops megacephalus* was attacked more frequently than other species.

ANCOVA indicated that $P\{A|E\}$ was significantly higher in the open than the bush habitat, but moonlight had no consistent effect on $P\{A|E\}$ (Table 2). The ANCOVA model had no significant interaction terms (Table 2), so among-species and between-habitat differences in $P\{A|E\}$ were independent of one another and of moonlight.

Comparison of bipedal and quadrupedal heteromyids.—Although bipeds were attacked more often than quadrupedal heteromyids (Table 1), this effect was not significant (ANCOVA: $F = 2.55$, $df = 1, 153$, $P > .10$). There also were no significant interactions between locomotion type and habitat or moonlight.

Comparison of large and small heteromyids.— $P\{A|E\}$ did not differ between large and small heteromyids (ANCOVA: $F = 1.31$, $df = 1, 153$, $P > .25$), but there was a marginally significant body size \times moonlight interaction ($F = 3.79$, $df = 1, 153$, $P = .053$); large species were attacked relatively more than small species under full, but not under new moon (Table 1).

Probability of capture given attack ($P\{C|A\}$)

$P\{C|A\}$ among all species.—Capture probability per attack ($P\{C|A\}$) is given in Fig. 1 for all five rodent species. Contingency analysis indicated that $P\{C|A\}$ did not differ significantly among heteromyid species ($\chi^2 = 2.90$, $df = 3$, $P > .40$). On average, owls captured heteromyids in only 12.4% of attacks, but captured *P. maniculatus* in 46.6%. Addition of *P. maniculatus* to the analysis produced a significant species effect ($\chi^2 = 45.43$, $df = 4$, $P < .0001$). Moreover, with rodent species grouped by family, $P\{C|A\}$ of the heteromyids as a whole was significantly lower than for *P. maniculatus* ($\chi^2 = 43.20$, $df = 1$, $P < .0001$). The overall order of decreasing vulnerability was: *P. maniculatus* > *C. fallax* > *C. baileyi* > *M. megacephalus* > *D. merriami*. This is the exact inverse of the rank order of absolute

TABLE 3. Total risk of owl predation (number of captures per minute of activity) to four heteromyid rodent species in two habitat types under two moonlight levels, differences in total risk between habitats, and between-habitat survival probability ratios.

Prey species	Moonlight	Total risk*			Ratio: $\frac{1 - p_{\text{open}}}{1 - p_{\text{bush}}}$
		Habitat		Difference between habitats	
		Open	Bush		
<i>Chaetodipus</i>	full	0.0245	0.0117	0.0128	0.9870
<i>baileyi</i>	new	0.0072	0.0042	0.0030	0.9970
<i>Chaetodipus</i>	full	0.0247	0.0007	0.0240	0.9760
<i>fallax</i>	new	0.0342	0.0027	0.0315	0.9684
<i>Dipodomys</i>	full	0.0323	0.0022	0.0301	0.9698
<i>merriami</i>	new	0.0245	0.0010	0.0235	0.9765
<i>Microdipodops</i>	full	0.0952	0.0058	0.0894	0.9101
<i>megacephalus</i>	new	0.0307	0.0015	0.0292	0.9708

* Total risk estimates are the product of $P\{A|E\}$ and $P\{C|A\}$ from Fig. 1, and were used as p_i values to calculate survival probability ratios.

auditory bullar volume among these five species (Webster and Webster 1975, Kotler 1984b; Spearman rank correlation: $r_s = -1.0$, $P < .01$; Siegel 1956). $P\{C|A\}$ values ranked among all combinations of heteromyid species, habitats, and light levels were inversely correlated with ranks of mean activity bout times ($r_s = -0.608$, $N = 16$, $P < .01$) and total activity times ($r_s = -0.493$, $P < .05$), but there was no rank correlation between $P\{C|A\}$ and activity bout frequency ($r_s = 0.043$, NS).

There was a significant habitat effect on $P\{C|A\}$ whether or not the analysis was restricted to heteromyids ($\chi^2 = 11.31$ and 14.29 , $df = 1$, $P < .001$ for analyses without and with *P. maniculatus*, respectively). All species had a higher probability of being captured when attacked in the open.

Moonlight had no significant effect on $P\{C|A\}$ for heteromyids alone ($\chi^2 = 0.95$, $df = 1$, $P > .30$) or when *P. maniculatus* was included ($\chi^2 = 1.21$, $df = 1$, $P > .25$). *Chaetodipus fallax* was captured more often under new than full moon in both habitats, whereas all other species had higher $P\{C|A\}$ under full moon in both habitats, but moonlight still had no significant effect on $P\{C|A\}$ if *C. fallax* was omitted from the analysis ($\chi^2 = 2.50$, $df = 1$, $P > .10$).

There were no significant interaction terms in analyses of $P\{C|A\}$ for heteromyids or for all five rodent species ($P > .35$ for all interactions).

$P\{C|A\}$ of bipedal vs. quadrupedal heteromyid species. — $P\{C|A\}$ of bipedal heteromyids as a group tended to be lower than for quadrupeds, but this was not quite significant ($\chi^2 = 3.36$, $df = 1$, $P = .067$). Within each body size category, however, bipeds had lower $P\{C|A\}$ than quadrupeds; capture rates for *D. merriami* were significantly lower than for the two quadrupeds ($\chi^2 = 4.30$, $df = 1$, $P < .04$), and those for *C. fallax* were significantly higher than the two bipeds ($\chi^2 = 3.96$, $df = 1$, $P < .05$). Interactions involving locomotion type and habitat or moonlight were not significant ($P > .50$).

$P\{C|A\}$ of large vs. small heteromyid species. — The two bipedal species did not differ significantly in $P\{C|A\}$ ($\chi^2 = 1.15$, $df = 1$, $P > .25$), nor did the two quadrupedal species ($\chi^2 = 0.76$, $df = 1$, $P > .35$). Size also had no effect on capture rates when the two large and small heteromyids were compared ($\chi^2 = 1.83$, $df = 1$, $P > .15$), and there were no significant interactions involving body size ($P > .20$).

Total risk ($P\{A|E\} \times P\{C|A\}$)

Total risk among heteromyid species. — Estimates of total risk, derived as $P\{A|E\} \times P\{C|A\}$, are shown in Fig. 1 and Table 3. Like $P\{A|E\}$ and $P\{C|A\}$, total risk for the four heteromyid species was significantly higher in open than bush habitat (Wilcoxon's $Z = 3.20$, $P = .001$), but did not differ significantly between new and full moon trials (Wilcoxon's $Z = 0.58$, $P = .53$). Omission of *C. fallax*, the only species for which total risk was higher under new than full moon, did not alter these results.

Rankings of total risk across the four combinations of habitat and moonlight did not differ significantly among heteromyid species (Kruskal-Wallis test: $H = 0.46$, $df = 3$, $P > .90$), but were instead significantly concordant (Friedman two-way ANOVA by ranks: $\chi^2 = 8.7$, $df = 3$, $P = .014$). The overall ranking of decreasing risk among moonlight/habitat conditions was: full moon/open > new moon/open > full moon/bush > new moon/bush, suggesting that a habitat \times moonlight interaction affects risk in a qualitatively consistent way for the four heteromyid species.

Total risk for bipedal vs. quadrupedal heteromyid species. — Total risk estimates for bipeds and quadrupeds of similar size did not differ significantly (Wilcoxon signed-ranks test for paired quadrupedal and bipedal species: $T = 12$, $N = 8$, $P \gg .05$). The proportional decrease in expected survival rates from using open microhabitats relative to bushes tended to be greater for bipeds than for quadrupeds, although not signifi-

cantly so (Table 3; Wilcoxon two-sample test: $U_s = 12$, $N_{1,2} = 4$, $P > .10$).

DISCUSSION

Microhabitat-specific predation risk

Our results demonstrate that desert rodents are attacked and captured more frequently, and therefore experience greater risk of predation by Great Horned Owls in open than in bush microhabitats. It makes sense for owls to avoid attacking prey in the bush habitat, because they had significantly lower capture success there. Not only did bush canopies interfere directly with owl attacks (owls collided with shrubs on several occasions when attacking prey in the bush arena), but judging from attack velocities, owls were more cautious when attacking prey in the structurally complex habitat. This provided rodents with more time to detect and react to an oncoming owl.

Heteromyids responded to this risk differential between habitats by engaging in more frequent, but shorter activity bouts in the open arena. Total activity time per trial was significantly shorter in the open. Thus, higher risk was associated with reduced activity.

These results agree well with two previous studies (conducted in the same owl flight cage and with two of the same rodent species as our experiment) that used indirect estimates of rodent activity (seed removal from feeding trays) rather than direct observation. Kotler et al. (1988) found that rodents incurred significantly higher rates of owl predation per unit of seed harvested in an open than a shrubby habitat, and Brown et al. (1988) found that the presence of owls caused heteromyids to reduce seed removal rates, especially in open habitat. The correspondence between these results and the present study suggests that seed removal provides a convenient index of microhabitat-specific activity for heteromyids.

Illumination and predation risk

Effects of illumination on risk are not as clear as those of habitat. We found no significant differences between full and new moon trials in either $P\{A|E\}$ or $P\{C|A\}$, although both were usually higher under full moon (Table 1, Fig. 1), and owls attacked at faster velocities in full moon trials. The only statistical evidence for an effect of moonlight on risk came from the concordance among rodent species in ranking patterns of risk across moonlight levels and habitat types; for all species except *C. fallax* risk was highest in the open under full moon and lowest in the bush under new moon (Table 3).

The lack of an illumination effect on risk seems surprising in light of previous studies, in which desert rodents increase use of bush microhabitats or decrease activity as illumination intensity increases (Blair 1943, Lockard and Owings 1974, Kaufman and Kaufman 1982, Kotler 1984a, b, Price et al. 1984, Bowers 1988,

Brown et al. 1988). Such shifts generally have been assumed to reflect a response to increased predation risk under bright moonlight.

We also observed light-related changes in rodent activity. Activity bouts were fewer but significantly longer under new moon. Total activity and bout duration both differed more between habitats under full than new moon; rodents were relatively more active in the open habitat under new moon. These shifts in activity paralleled activity differences between bush and open arenas, suggesting that light-related changes in risk were responsible for activity differences between new and full moon trials.

If rodents modify activity to compensate for illumination-dependent changes in risk, however, it becomes difficult to determine whether moonlight actually does increase potential risk. To date there is little unequivocal evidence that it does. Dice (1945) observed that captive owls more accurately located dead deer mice as illumination increased, but of course could not determine whether the ability of the mice to detect approaching predators was correspondingly improved. Clarke (1983) used *P. maniculatus* as prey to quantify owl foraging behavior and a component of risk (number of escapes per owl attack) under three light levels. Her results are similar to ours: rodent activity decreased and the time required for an owl to locate and capture mice decreased with increasing illumination, as expected, but escapes per attack remained essentially unchanged. Perhaps the best evidence comes from Kotler et al.'s (1988) experiment in the same owl cage as our study; owl predation rates per unit of seed harvested by heteromyids were higher under full moon than new moon. Because they did not directly monitor activity, however, it remains possible that light affected foraging rates (seeds removed per unit active time), if animals were more vigilant or foraged in fewer trays for example, but did not affect capture rates per unit of activity. Again, shifts in behavior may obscure effects of light level on potential risk.

The potential effect of light on risk may depend on the extent to which rodents (and their predators) rely on two different sensory modes, vision and hearing. Those species that rely mainly on vision should be better at detecting predators as illumination increases, but species with sensitive hearing may not be much affected by light. For kangaroo rats at least, hearing is very important in detecting attacking owls and snakes (Webster 1962). Sensitivity to the low-frequency sounds made by these predators is correlated among heteromyid genera with volume of the middle-ear cavities (Webster and Strother 1972), and experimental reduction of auditory bullar volume increases vulnerability to snake and owl attacks (Webster 1962). Indeed, the ranking of $P\{C|A\}$ for the five rodent species tested in this study was inversely related to auditory bullar volume, and the extent to which four heteromyid species used risky open microhabitats in Kotler's (1984b) field

experiment was directly correlated with bullar volume. Even for heteromyids, however, vision enhances ability to detect and escape from attacking predators (Webster and Webster 1971, 1984). The net effect of illumination on risk should therefore be determined by the relative degrees to which light enhances prey localization by predators and predator detection by prey. Species with smaller middle-ear cavities would be expected to rely more on vision than those with highly inflated middle ears, and thus may actually find owl predators to be less dangerous as illumination increases. This may explain why *C. fallax*, with smaller auditory bullae and a higher average capture rate than other heteromyids tested, was the only species for which $P\{C|A\}$ and total risk were higher under new than full moon.

Combined effects of habitat and illumination on heteromyid behavior

Inverse rank correlations between $P\{C|A\}$ and two measures of rodent activity (mean duration of activity bouts and total activity) imply that those heteromyid species that experience higher levels of risk may compensate by reducing activity, and that species tend to adjust activity in different habitats and under differing moonlight conditions in response to variation in vulnerability to predators. Based on our results, the potential effect of habitat type on $P\{C|A\}$ seems considerably stronger than that of moonlight. By changing activity as experimental conditions changed, heteromyids were apparently able to offset potential effects of illumination on $P\{C|A\}$, but similar activity adjustments did not nullify the habitat effect.

Modification of activity patterns would be an effective antipredator strategy only if risk is associated with activity level, and there is some evidence of this for kangaroo rats. Apparent intersexual differences in vulnerability to Great Horned Owl predation were associated with activity differences in a Great Basin Desert population of *D. ordii*: males had longer movement distances and were captured by owls more frequently than females (Longland and Jenkins 1987). In a Sonoran Desert population of *D. merriami*, the probability an individual fell prey to a vertebrate predator was directly correlated with movement distances (Daly et al. 1990).

Morphology-related and species-specific predation risk

Results of this study demonstrate remarkable abilities of heteromyid rodents to avoid Great Horned Owl predation. $P\{C|A\}$ ranged from 3.3 to 23.8% for bipedal heteromyids, and 6.7 to 32.4% for quadrupedal pocket mice (Fig. 1). *Peromyscus maniculatus* individuals, by contrast, were captured in 29.4–58.8% of attacks, significantly more often than the heteromyid species. Low capture rates of the heteromyids can therefore be attributed to their superior escape abilities

rather than to inferior marksmanship by our owls. Webster (1962) reported similar evasive abilities when *D. merriami* individuals were attacked by Barn Owls (*Tyto alba*) or rattlesnakes (*Crotalus cerastes*).

We also found evidence that capture rates were higher for quadrupedal than for bipedal heteromyids. *Dipodomys merriami* had significantly lower $P\{C|A\}$ than the two quadrupeds combined, and *C. fallax* had significantly higher $P\{C|A\}$ than the two bipeds. Owls may capture bipedal species less often either because bipeds, by virtue of their larger middle-ear cavities, more readily detect attacking owls (Webster and Webster 1984), or because bipeds are better at evading attacks of predators after detecting them (Bartholomew and Caswell 1951). Kotler (1985) provided field evidence that bipedal heteromyids are captured less by Long-eared Owls (*Asio otus*) than quadrupedal species, but he lumped data for pocket mice and *P. maniculatus* in the quadrupedal class. In a similar field study, Longland (1983) found that two heteromyids (*D. ordii* and *Perognathus parvus*) and two cricetids (including *P. maniculatus*) were captured by Great Horned Owls in proportions that differed significantly from their relative abundances in the local rodent community; the heteromyids (especially *D. ordii*) were under represented in owl diets, while the cricetids were over represented. From this, one would expect $P\{C|A\}$ to be lower for bipedal than for the quadrupedal heteromyids and lower for heteromyids in general than for *P. maniculatus*, and this is what we observed.

In contrast to the $P\{C|A\}$ results, bipeds had higher (although not significantly higher) $P\{A|E\}$ than quadrupeds. Perhaps bipeds attract the attention of owls more than quadrupeds because they move faster (Djavidan and Garland 1988), or because their hopping gait is more conspicuous. While pocket mice were also seen moving saltatorially without being startled during the experiment, this was not their usual gait.

Field study results often suggest that Great Horned Owls prefer large rodent prey over smaller ones (Korschgen and Stuart 1972, Marti 1974, Longland 1983). Similarly, in the same owl cage that we used, Kotler et al. (1988) found evidence of higher Barn Owl predation rates on *C. baileyi* than on a smaller pocket mouse species (*Perognathus amplus*). This is to be expected as long as larger prey are not so much more difficult to catch or handle that they provide the predator with a smaller net energy return. Although we found no effect of rodent body size on $P\{A|E\}$, we cannot directly assess whether prey size preferences existed, because we did not present owls with a choice of prey species. However, we can assess whether $P\{C|A\}$ is likely to be enough lower for the two large species to make them less profitable to the owls than the small species. Overall, *M. megacephalus* was 1.35 times as likely to be captured as *D. merriami*, and *C. fallax* was 1.45 times as likely to be captured as *C. baileyi* (Fig. 1). The mass ratio for the two bipeds was 2.75, and

for the two quadrupeds 1.76. It seems, then, that Great Horned Owls should prefer the larger species, since the increment in energy value is greater than the cost in failed attacks. In nature, where different prey are available, owls may exhibit such preferences.

Finally, bipedal and quadrupedal heteromyids responded differently to risk. Overall, bipeds and quadrupeds did not differ significantly in total risk or in total activity, but they did differ in components of risk and activity. Bipeds, which experienced higher $P\{A|E\}$ than quadrupeds, were involved in significantly more activity bouts per trial. Quadrupeds, which experienced higher $P\{C|A\}$ than bipeds, had significantly longer times per bout. Perhaps the frequency and duration of activity bouts have different effects on the two components of risk, $P\{A|E\}$ and $P\{C|A\}$. Regardless of reasons for the apparent sensitivity of rodent activity to risk, the behavioral flexibility shown here in response to variation in risk should have important consequences for heteromyid foraging efficiency.

Predation risk, microhabitat selection, and community structure

Recall that, in terms of Eq. 1, the "pure" predation hypothesis for heteromyid microhabitat choice requires that $p_{\text{open}} < p_{\text{bush}}$ for bipedal heteromyids and $p_{\text{open}} > p_{\text{bush}}$ for quadrupeds. The concordant rankings of microhabitat-specific risk reported here do not support the hypothesis that divergent microhabitat associations of bipedal and quadrupedal heteromyids can be explained solely on the basis of risk of predation (at least by Great Horned Owls). Because $P\{A|E\}$ and $P\{C|A\}$ were both greater in open than bush habitat for all rodent species tested (i.e., $p_{\text{open}} > p_{\text{bush}}$), predation risk is a viable explanation for the use of bushes by pocket mice, but cannot explain biped microhabitat affinities. Furthermore, differences between habitat types in $P\{A|E\}$, $P\{C|A\}$, and total risk tended to be higher for bipeds than quadrupeds (Fig. 1, Table 3), so the quadrupedal species (especially *C. baileyi*, which incurred the smallest increases in risk in the open relative to the bush arena) should gain least in terms of survival probability by restricting activity to bushes. Thus, any adaptive explanation for the use of open microhabitats by bipedal heteromyid species must invoke some factor(s) other than, or in addition to, risk of owl predation.

Perhaps another predator is more common or more dangerous around bushes than in open spaces. The extent to which our results apply to predators other than Great Horned Owls is unknown. Other owl species as well as snakes and mammalian carnivores occur with heteromyids in North American deserts. Comparison of observed escapes from owls in this experiment with Webster's (1962) observations of heteromyids and rattlesnakes suggests that these rodents have evolved different responses to these two important predators.

In our experiments all heteromyids escaped with leaps perpendicular to the flight path of an attacking owl. Webster (1962) also noted last-second evasive leaps by *D. merriami* under attack by rattlesnakes and Barn Owls, but reported that snakes were evaded with vertical or backward leaps relative to strike trajectory. These differing responses may be appropriate considering constraints on maneuverability of the two predators. Owls cannot make last-second lateral adjustments in attack trajectory (M. Konishi, California Institute of Technology, Pasadena, *personal communication*), but can easily glide further if a rodent were to leap backward in relation to attack trajectory. Snakes, however, can make lateral corrections in mid-strike (H. Greene, University of California, Berkeley, *personal communication*), but cannot change strike distance. A last-second backward leap with respect to a snake's trajectory would therefore cause the snake to fall short of the intended prey, while a lateral leap in response to an owl attack would remove the target from the line of attack.

Although these observations imply that snake predation may have influenced the evolution of heteromyid behavior, effects of snakes on microhabitat- and moonlight-specific risk to heteromyids are currently unknown. Snakes are ambush predators like owls, but unlike owls (and probably unlike mammalian carnivores) may attack from under bushes and are not visual predators, so moonlight should not affect their strike accuracy. It is likely, then, that among the cast of predators encountered by heteromyids, snakes have the most potential for imposing constraints on microhabitat use different from those imposed by owls, but we must complete ongoing experiments with rattlesnakes to address this possibility.

It is certainly possible, perhaps probable, that open microhabitats are consistently riskier than bushes, regardless of the predator community. If so, the only adaptive explanation for bipeds to use open microhabitats is that by doing so they gain enough in some fitness component to offset the cost of reduced survival probability. If bipeds harvest seeds more efficiently from open than from bush microhabitats, for example, and this enhances reproductive potential, a trade-off between the survival and reproduction components of fitness may produce a net fitness advantage to individuals that use open microhabitats. Expressed in terms of Eq. 1, this would occur if:

$$W_{\text{open}} > W_{\text{bush}}$$

or

$$[g_{\text{open}}f(g)](1 - p_{\text{open}}) > [g_{\text{bush}}f(g)](1 - p_{\text{bush}}),$$

which reduces to

$$\frac{1 - p_{\text{open}}}{1 - p_{\text{bush}}} > \frac{g_{\text{bush}}}{g_{\text{open}}}. \quad (2)$$

The left side of Eq. 2 represents the ratio of open to

bush survival probabilities, the right side the ratio of bush to open rate of fitness gain. Net fitness gain in risky open areas will be greater than in bush microhabitats for individuals of any species for which this inequality holds. If it holds for individuals of bipedal species, but not for quadrupeds, then a trade-off between foraging economics and predation risk may maintain the divergent microhabitat affinities of heteromyid species.

Our data suggest that relative risk in open microhabitats is greater for bipeds than quadrupeds. To satisfy Eq. 2, then, relative fitness gain through foraging in open spaces must also be greater for bipeds. Little is known about consequences of this morphological difference for foraging performance, but it is certainly possible for morphology to influence the degree to which foraging rates are affected by such seed-patch characteristics as seed density or soil texture (Price 1983, Price and Podolsky 1989).

The risk differential between microhabitats can be influenced not only by morphology, as our $P\{C|A\}$ data suggest, but also by predator abundance, which determines the probability of encountering a predator. By introducing two owls into a relatively small enclosure, we maximized encounter rates in our experiments. In nature encounter rates would be much lower, and this would have the effect of multiplying p_i values in the left-hand side of Eq. 2 by some fraction. The net effect would be to lower the discrepancy between microhabitats in predation risk, and hence reduce the differential in fitness gain that would balance predation costs. Because conditions favoring use of the risky habitat are less stringent the lower the absolute risk, this would facilitate use of open microhabitats, especially by species with low $P\{C|A\}$.

Divergence among heteromyid species in microhabitat selection has important implications for community structure. The number and relative abundances of coexisting heteromyid species can be predicted from habitat structure, because relative availability of preferred microhabitats dictates the relative abundance of species (Price 1978, Price and Waser 1984) and because habitat complexity dictates the diversity of available microhabitats (Rosenzweig and Winakur 1969). To the extent that morphology dictates microhabitat use, and microhabitat use similarity dictates coexistence probability, then not only are species number and relative abundance affected by microhabitat, but phenotypic characteristics of coexisting species are as well. Understanding the structure of desert heteromyid communities may therefore hinge on understanding the mechanisms underlying microhabitat use.

ACKNOWLEDGMENTS

We thank Cathy Endo for extensive help with collecting rodents in the field and with maintenance of the owl flight cage. Thoughtful comments by Joel Berger, Joel Brown, Steve Jenkins, Burt Kotler, Len Nunnery, Dave Reznick, Nick Waser, and an anonymous reviewer helped improve the manu-

script. We are grateful to Clyde Eriksen, Karen Mosher, and Bill Wirtz of the Claremont Colleges for use of the flight cage at Bernard Field Station, and to Tom Baker and Lyle Gaston of the Department of Entomology, UC Riverside, for use of their night-vision goggles. The research was submitted by W. S. Longland in partial fulfillment of requirements for the Ph.D. degree in the Department of Biology, UC Riverside, and was supported by NSF grant BSR-8407602 (to M. V. Price), grants from the American Society of Mammalogists, Sigma Xi, the Los Angeles Audubon Society, the Frank Chapman Memorial Fund (American Museum of Natural History), the UC Riverside Graduate Division, the Bernard Field Station (to W. S. Longland), and grants from the UC Riverside Academic Senate (to both authors). This paper is a contribution of the USDA, Agricultural Research Service, Landscape Ecology of Rangelands Unit, Reno, Nevada.

LITERATURE CITED

- Abrahams, M. V., and L. M. Dill. 1989. A determination of the energetic equivalence of the risk of predation. *Ecology* 70:999-1007.
- Bartholomew, G. A., and H. H. Caswell, Jr. 1951. Locomotion in kangaroo rats and its adaptive significance. *Journal of Mammalogy* 32:155-169.
- Blair, W. F. 1943. Activities of the Chihuahua deer-mouse in relation to light intensity. *Journal of Wildlife Management* 7:92-97.
- Bowers, M. A. 1988. Seed removal experiments on desert rodents: the microhabitat by moonlight effect. *Journal of Mammalogy* 69:201-204.
- Brown, J. H., and G. A. Lieberman. 1973. Resource utilization and coexistence of seed-eating rodents in sand dune habitats. *Ecology* 54:788-797.
- Brown, J. H., O. J. Reichman, and D. W. Davidson. 1979. Granivory in desert ecosystems. *Annual Review of Ecology and Systematics* 10:201-227.
- Brown, J. S. 1989. Desert rodent community structure: a test of four mechanisms of coexistence. *Ecological Monographs* 59:1-20.
- Brown, J. S., B. P. Kotler, R. J. Smith, and W. O. Wirtz II. 1988. The effects of owl predation on the foraging behavior of heteromyid rodents. *Oecologia (Berlin)* 76:408-415.
- Caraco, T. 1980. On foraging time allocation in a stochastic environment. *Ecology* 61:119-128.
- Cerri, R. D., and D. F. Fraser. 1983. Predation and risk in foraging minnows: balancing conflicting demands. *American Naturalist* 121:552-561.
- Clarke, J. A. 1983. Moonlight's influence on predator/prey interactions between short-eared owls (*Asio flammeus*) and deer mice (*Peromyscus maniculatus*). *Behavioral Ecology and Sociobiology* 13:205-209.
- Daly, M., M. Wilson, P. R. Behrends, and L. F. Jacobs. 1990. Characteristics of kangaroo rats, *Dipodomys merriami*, associated with differential predation risk. *Animal Behaviour* 40:380-389.
- Dice, L. R. 1945. Minimum intensities of illumination under which owls can find dead prey by sight. *American Naturalist* 79:385-416.
- Djawdan, M., and T. Garland, Jr. 1988. Maximal running speeds of bipedal and quadrupedal rodents. *Journal of Mammalogy* 69:765-772.
- French, N. R., B. G. Maza, H. O. Hill, A. P. A. Schwanden, and H. W. Kaaz. 1974. A population study of irradiated desert rodents. *Ecological Monographs* 44:45-72.
- Hafner, J. C., and M. S. Hafner. 1983. Evolutionary relationships of heteromyid rodents. *Great Basin Naturalist Memoirs* 7:3-29.
- Holbrook, S. J., and R. J. Schmitt. 1988. The combined effects of predation risk and food reward on patch selection. *Ecology* 69:125-134.

- Kaufman, D. W., and G. Kaufman. 1982. Effect of moonlight on activity and microhabitat use by Ord's kangaroo rat (*Dipodomys ordii*). *Journal of Mammalogy* **63**:309–312.
- Keeney, R. L., and H. Raiffa. 1976. Decisions with multiple objectives: preferences and value tradeoffs. John Wiley & Sons, New York, New York, USA.
- Korschgen, L. J., and H. B. Stuart. 1972. Twenty years of avian predator—small mammal relationships in Missouri. *Journal of Wildlife Management* **36**:269–282.
- Kotler, B. P. 1984a. Effects of illumination on the rate of resource harvesting in a community of desert rodents. *American Midland Naturalist* **11**:383–389.
- . 1984b. Risk of predation and the structure of desert rodent communities. *Ecology* **65**:689–701.
- . 1985. Owl predation on desert rodents which differ in morphology and behavior. *Journal of Mammalogy* **66**:824–828.
- Kotler, B. P., and J. S. Brown. 1988. Environmental heterogeneity and the coexistence of desert rodents. *Annual Review of Ecology and Systematics* **19**:281–307.
- Kotler, B. P., J. S. Brown, R. J. Smith, and W. O. Wirtz II. 1988. The effects of morphology and body size on rates of owl predation on desert rodents. *Oikos* **53**:145–152.
- Lawlor, L. R., and J. Maynard Smith. 1976. The coevolution and stability of competing species. *American Naturalist* **110**:79–99.
- Lima, S. L., and T. J. Valone. 1986. Influence of predation risk on diet selection: a simple example in the grey squirrel. *Animal Behaviour* **34**:536–544.
- Lima, S. L., T. J. Valone, and T. Caraco. 1985. Foraging-efficiency—predation-risk trade-off in the grey squirrel. *Animal Behaviour* **33**:155–185.
- Lockard, R. B., and D. H. Owings. 1974. Seasonal variation in moonlight avoidance by bannertail kangaroo rats. *Journal of Mammalogy* **55**:189–193.
- Longland, W. S. 1983. Prey selection by great horned owls (*Bubo virginianus*) in central Nevada. Thesis. University of Nevada, Reno, Nevada, USA.
- Longland, W. S., and S. H. Jenkins. 1987. Sex and age affect vulnerability of desert rodents to owl predation. *Journal of Mammalogy* **68**:746–754.
- Marti, C. D. 1974. Feeding ecology of four sympatric owls. *Condor* **76**:45–61.
- Milinski, M., and R. Heller. 1978. The influence of a predator on the optimal foraging behavior of sticklebacks (*Gasterosteus aculeatus* L.). *Nature* **275**:642–644.
- Mittelbach, G. G. 1984. Predation and resource partitioning in two sunfishes (Centrarchidae). *Ecology* **65**:499–513.
- Munger, J. C., M. A. Bowers, and W. T. Jones. 1983. Desert rodent populations: factors affecting abundance, distribution, and genetic structure. *Great Basin Naturalist Memoirs* **7**:91–116.
- Newman, J. A., G. M. Recer, S. M. Zwicker, and T. Caraco. 1988. Effects of predation hazard on foraging “constraints”: patch-use strategies in grey squirrels. *Oikos* **53**:93–97.
- Pierce, C. L. 1988. Predator avoidance, microhabitat shift, and risk-sensitive foraging in larval dragonflies. *Oecologia* (Berlin) **77**:81–90.
- Price, M. V. 1978. The role of microhabitat in structuring desert rodent communities. *Ecology* **59**:910–921.
- . 1983. Ecological consequences of body size: a model for patch choice in desert rodents. *Oecologia* (Berlin) **59**:384–392.
- . 1984. Microhabitat use in rodent communities: predator avoidance or foraging economics? *Netherlands Journal of Zoology* **34**:63–80.
- . 1986. Structure of desert rodent communities: a critical review of questions and approaches. *American Zoologist* **26**:39–49.
- Price, M. V., and J. H. Brown. 1983. Patterns of morphology and resource use in North American desert rodent communities. *Great Basin Naturalist Memoirs* **7**:117–134.
- Price, M. V., and P. R. Endo. 1989. Estimating the distribution and abundance of a cryptic species, *Dipodomys stephensi* (Rodentia: Heteromyidae), and implications for management. *Conservation Biology* **3**:293–301.
- Price, M. V., and R. H. Podolsky. 1989. Mechanisms of seed harvest by heteromyid rodents: soil texture effects on harvest rate and seed size selection. *Oecologia* (Berlin) **81**:267–273.
- Price, M. V., and N. M. Waser. 1984. On the relative abundance of species: post-fire changes in a coastal sage scrub rodent community. *Ecology* **65**:1161–1169.
- Price, M. V., N. M. Waser, and T. A. Bass. 1984. Effects of moonlight on microhabitat use by desert rodents. *Journal of Mammalogy* **65**:353–356.
- Reichman, O. J., and M. V. Price. 1991. Ecological aspects of heteromyid foraging. In J. H. Brown and H. H. Genoways, editors. *Biology of heteromyid rodents*. American Society of Mammalogists, Shippensburg, Pennsylvania, USA, *in press*.
- Rosenzweig, M. L. 1973. Habitat selection experiments with a pair of coexisting heteromyid rodent species. *Ecology* **54**:111–117.
- . 1974. On the optimal above-ground activity of bannertail kangaroo rats. *Journal of Mammalogy* **55**:193–199.
- Rosenzweig, M. L., and J. Winakur. 1969. Population ecology of desert rodent communities: habitats and environmental complexity. *Ecology* **50**:558–572.
- Roughgarden, J. 1976. Resource partitioning among coexisting species—a coevolutionary approach. *Theoretical Population Biology* **9**:388–424.
- SAS. 1987. SAS/STAT guide for personal computers. Version 6 edition. SAS Institute, Cary, North Carolina, USA.
- Schoener, T. W. 1974. Resource partitioning in ecological communities. *Science* **185**:27–39.
- Siegel, S. 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill, New York, New York, USA.
- Sih, A. 1980. Optimal behavior: can foragers balance two conflicting demands? *Science* **210**:1041–1043.
- Sokal, R. R., and F. J. Rohlf. 1981. Biometry. W. H. Freeman, San Francisco, California, USA.
- Stephens, D. W., and J. R. Krebs. 1986. *Foraging theory*. Princeton University Press, Princeton, New Jersey, USA.
- Tilman, D. 1982. Resource competition and community structure. Princeton University Press, Princeton, New Jersey, USA.
- Webster, D. B. 1962. A function of the enlarged middle-ear cavities of the kangaroo rat, *Dipodomys*. *Physiological Zoology* **35**:248–255.
- Webster, D. B., and W. F. Strother. 1972. Middle ear morphology and auditory sensitivity of heteromyid rodents. *American Zoologist* **12**:727.
- Webster, D. B., and M. Webster. 1971. Adaptive value of hearing and vision in kangaroo rat predator avoidance. *Brain, Behavior and Evolution* **4**:310–322.
- Webster, D. B., and M. Webster. 1975. Auditory systems of Heteromyidae: functional morphology and evolution of the middle ear. *Journal of Morphology* **146**:343–376.
- Webster, D. B., and M. Webster. 1984. The specialized auditory system of kangaroo rats. *Contributions to Sensory Physiology* **8**:161–196.
- Werner, E. E., and D. J. Hall. 1988. Ontogenetic habitat shifts in bluegill: the foraging rate—predation risk trade-off. *Ecology* **69**:1352–1366.
- Wood, A. E. 1935. Evolution and relationships of the heteromyid rodents with new forms from the Tertiary of western North America. *Annals of the Carnegie Museum* **24**:73–262.