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DETERMINANTS OF COMMUNITY STRUCTURE IN DESERT RODENTS:
RISK, RESOURCE AND FORAGING BEHAVIOR

The University of Arizona

Ph.D. 1983

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DETERMINANTS OF COMMUNITY STRUCTURE IN DESERT RODENTS:
RISK, RESOURCE AND FORAGING BEHAVIOR

by

Burt Philip Kotler

A Dissertation Submitted to the Faculty of the
DEPARTMENT OF ECOLOGY AND EVOLUTIONARY BIOLOGY

In Partial Fulfillment of the Requirements
For the Degree of

DOCTOR OF PHILOSOPHY

In the Graduate College

THE UNIVERSITY OF ARIZONA

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THE UNIVERSITY OF ARIZONA
GRADUATE COLLEGE

As members of the Final Examination Committee, we certify that we have read
the dissertation prepared by Burt Philip Kotler

entitled Determinants of Community Structure in Desert Rodents: Risk,
Resources and Foraging Behavior

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ABSTRACT

Communities of granivorous desert rodents are structured by habitat selection and may be influenced by either predatory risk or resources. To examine these hypotheses, I manipulated illumination using lanterns, parachute canopies, or natural moonlight and resources using seeds. Foraging behavior is risk-sensitive; increased illumination reduces foraging in open areas while adding shadows to open areas using parachutes increases foraging there. Foraging behavior is also affected by resource enrichments. Differences among species in habitat selection were determined by specific abilities to detect and avoid predators. The least vulnerable species, Dipodomys deserti, foraged heavily in the open and was largely unaffected by treatments; other species of kangaroo rats and kangaroo mice also prefer the open, but responded to both risk and resource manipulations; highly vulnerable Peromyscus maniculatus was always restricted to bushes even under the most favorable circumstances; Perognathus longimembris was restricted to bushes in the absence of P. maniculatus in 1980 and was displaced from preferred microhabitats by the presence of kangaroo rats in 1981. A correlation between auditory bullar volume and use of open habitat by the various species in this community suggests that predatory risk provides an axis along which habitat segregation occurs. Predation can shape community structure by influencing foraging decisions of individuals.

Desert rodents from North America and the Middle East have converged morphologically and perhaps in behavior and in community structure. Using desert rodent communities in the Great Basin Desert of U.S.A. and in the Negev Desert of Israel, I manipulated predatory risk in both communities and noted that foraging activity declines with increased predatory risk. Additional evidence suggests that predation also affects habitat selection behavior in both communities. Furthermore, differences in habitat utilization among species which promotes coexistence are related to morphological anti-predator specialization of the species. Predation appears to have shaped behavior and contributed to community structure in similar ways in both communities.

CHAPTER 1

RISK AND RESOURCE AND THE FORAGING BEHAVIOR OF DESERT RODENTS

Desert rodents of North America have received a great deal of attention from ecologists due to the coexistence of many species exploiting similar resources (Brown 1973, Rosenzweig 1973, Reichman 1975, M'Closkey 1978, Smigel and Rosenzweig 1974). Significant differences in foraging behavior among coexisting species have been found time and again (Rosenzweig and Winakur 1969, Brown and Lieberman 1973, Kenagy 1973a, O'Farrall 1974, Schroder and Rosenzweig 1975, Lemen and Rosenzweig 1978, Thompson 1982a). These include differences in activity times (Kenagy 1973) and habitat selection (Rosenzweig 1973, Brown and Lieberman 1973, Schroder and Rosenzweig 1975, Lemen and Rosenzweig 1975, Price 1978a, M'Closkey 1978, Wondolleck 1978). Such differences promote species coexistence, so understanding the factors which influence decisions will contribute to understanding desert rodent community structure.

Many factors are likely to influence foraging and hence lead to these foraging differences. For instance, optimal foraging theory suggests that resources may affect habitat selection behavior (e.g. MacArthur and Pianka 1966, Charnov 1976, Rosenzweig 1981), and indeed, laboratory experiments have shown differences between rodent species in

selection of patches of seeds (Mares and Williams 1977, Reichman and Oberstein 1977, Price 1978b).

Patch choice may be affected by predatory risk as well. Rosenzweig (1974) and Pearson (1976) have demonstrated this theoretically. In addition, the foraging behavior of desert rodents has been shown to be influenced by moonlight, a factor affecting predatory risk (see below). Justice (1960) and Lockard and Owings (1974a) showed that activity of the banner tailed kangaroo rat, Dipodomys spectabilis, declines with increasing moonlight, and Lockard and Owings (1974b) further showed that the use of risky, open areas declines also with increasing moonlight. Furthermore, the morphology and behavior of kangaroo rats appears geared toward avoiding predation. Anti-predator adaptations include inflated auditory bullae, the better to hear striking predators (Webster 1962) and bipedal locomotion, the better to jump out of harm's way (Eisenberg 1963).

Habitat use by other organisms is also affected by predatory risk. Crayfish (Stein 1976, 1977), sparrows (Pulliam and Mills 1977), yellow-eyed juncos (Caraco, Martindale, and Whittam 1980), and notonectids (Sih 1980) are all known to alter foraging behavior in response to predatory risk.

In this paper I demonstrate that desert rodents do indeed modify their habitat use in accordance with changes in habitat-specific predatory risk, although such behavior is also influenced by resource manipulations.

Methods

In order to examine the role of predatory risk in influencing foraging behavior and community structure, I manipulated light and shadow. Other researchers have shown that kangaroo rats alter their foraging activities in response to moonlight (Justice 1960, Lockard and Owings 1974a, 1974b), and Dice (1945, 1947) has shown that owls are more dangerous when light is present. It seems that the open, moonlit areas should be much riskier than places under bushes or in shadows, so manipulating light and shadow should correspond to manipulating predatory risk. In addition, I also manipulated seed resources.

I established two plots in June, 1980 on stabilized sand dunes in the Great Basin Desert. The study site is located 12 km south of Mina in Mineral County, Nevada at an elevation of 1343 meters. Each plot covered one square hectare and contained 100 traps divided among 25 trap stations arranged in a 5 by 5 grid. Trap stations were 20 meters apart with 4 traps placed per station in order to reduce competition for traps. I placed two traps in the open and two traps under a bush at each station. One plot served as a control, and the other was the experimental plot. I chose plots to be as similar as possible.

Foraging activity and habitat selection of rodents were assayed by live trappings using 8 x 8 x 25 cm Sherman traps baited with mixed bird seed. I used the number of captures per night for a treatment as a measure of foraging activity for a species and the proportion of captures occurring at traps placed in the open as a measurement of habitat selection. Captured animals were identified and weighed, their

reproductive condition noted, and they were marked with ear tags and unique toe clip numbers.

I manipulated light and shadows and seed resources on the experimental grid and looked for effects on foraging activity of the various species of desert rodents. I added light by using Coleman model 200-A lanterns and Ray-O-Vac Sportsman 360 fluorescent electric lanterns. Four lanterns were used to illuminate the grid, producing light conditions similar to moonlight over most of the grid (Chapter 2).

I manipulated shadows by covering traps placed in the open with parachute canopies. I suspended the parachutes above the traps using a wooden frame. I ran parachute treatments only when the moon was up. This manipulation cast deep shadows over traps which were in open microhabitats.

The resource manipulation consisted of scattering 15 grams of mixed bird seed over a 2-3 square meter areas surrounding the traps in the open microhabitat at each trap station. This addition of seeds corresponds to the seed manipulation of Frye and Rosenzweig (1980) which in turn was based on observations of naturally occurring densities of seeds (Reichman and Oberstein 1977).

In addition to the solitary factors, I ran all pairwise combinations of experimental factors. There were 6 different treatments in addition to a control: lanterns (L), lanterns and seeds (L + S₀), lanterns and parachutes (L + P), seeds (S₀), parachutes (P), and seeds and parachutes (P + S₀). I repeated each treatment for 6 or 7 consecutive nights. I conducted live trapping on the control grid

simultaneously with trapping on the experimental grid for all treatments. I tested hypotheses using distribution-free regression methods (Maritz 1981) or t-tests.

The species present in 1980 included Merriam's kangaroo rat (Dipodomys merriami), Ord's kangaroo rat (Dipodomys ordii), Great Basin kangaroo rat (Dipodomys microps), desert kangaroo rat (Dipodomys deserti), pallid kangaroo mouse (Microdipodops pallidus), and little pocket mouse (Perognathus longimembris).

Results

Examination of the effects of individual treatments was difficult due to density changes which occurred during the course of the experiment. In many cases, changes in foraging behavior could not be attributed solely to the experimental treatments. However, I was able to make several unambiguous comparisons for both the risk and the resource manipulations.

Four of the six species responded to changes in risk. These species responded either to the addition of parachutes or to changes in moonlight.

The presence of parachutes, which increased shadows in open areas and therefore decreased risk, increased the total proportion of D. ordii captured ($t = 3.8, p < 0.001$, Table 1). Thus, decreased risk led to greater foraging activity. Parachutes also caused an increase in the use of open areas for D. merriami ($t = 3.08, p < 0.05$). Though animals did not forage more, their activity was more concentrated in the open. Finally, parachutes caused a change in the foraging activity

Table 1. Capture rates per individual and total captures for the parachute treatment. -- Increasing shadow causes significantly much greater activity in Dipodomys ordii but less in Microdipodops pallidus.

Species	<u>Total Number Captures</u>		<u>Capture Rate Per Individual</u>		d_i^1	t^2
	Experiment	Control	Experiment	Control		
<u>Dipodomys merriami</u>	45	38	.33	.47	-.003 (.08)	0.11
<u>Dipodomys ordii</u>	8	4	.66	.17	.49 (.09)	3.8***
<u>Dipodomys microps</u>	6	8	.31	.39	.08 (.24)	0.9
<u>Dipodomys deserti</u>	5	4	.46	.61	-.98 (1.99)	1.2
<u>Microdipodops pallidus</u>	6	8	.07	.15	-.11 (.13)	2.3*
<u>Perognathus longimembris</u>	7	11	.24	.25	.02 (.17)	0.08

1. Average difference (standard error) of paired observations between experimental and control grid.

2. Paired observations.

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

of M. pallidus ($t = 2.3$, $p < 0.05$). However, the parachute treatment led to fewer captures rather than more captures. This is contrary to the effect of risk on other species.

Increased moonlight, the risk factor, caused a change in total captures of both D. ordii and D. microps. To test for the effects of changing risk due to changes in moonlight, I compared total captures on the control grid for two consecutive periods (P and $P + S_0$) when populations on the grid did not change, but when the duration and intensity of moonlight did. For these two species there were more total captures (D. ordii, $t = 2.28$, $p < 0.01$; D. microps, $t = 4.65$, $p < 0.001$; Table 4) and for D. ordii proportionately more captures ($t = 2.57$, $p < 0.05$) when moonlight decreased. Hence, both manipulation of light and of shadow and changes in natural light show that these species alter foraging activity in response to changes in risk.

The two remaining species, D. deserti and P. longimembris, failed to respond to changes in risk.

Three species (D. ordii, D. microps, M. pallidus) showed significant changes in foraging behavior in response to source enrichments. All species were captured fewer times when seeds were added. The declines in captures indicates responses to seeds since seeds were also used to bait traps which were used to measure foraging activity. For D. ordii, though there were more captures on the experimental grid during the seed treatment. Owing to higher population densities there, there were significantly fewer captures per individual ($t = 3.94$, $p < 0.001$). D. microps also showed a lower rate of captures per marked animal on the experimental grid during the seed

Table 2. Capture rates per individual and total captures for the parachutes and seeds treatment. -- The positive d_i 's for Dipodomys ordii (and also for Dipodomys microps and Dipodomys merriami) suggest that risk influenced activity more than resources.

Species	Total Number Captures		Capture Rate Per Individual		d_i^1	t^2
	Experiment	Control	Experiment	Control		
<u>Dipodomys merriami</u>	57	54	.40	.36	.12	(.17) 1.73
<u>Dipodomys ordii</u>	9	5	.59	.38	.21	(.19) 2.68*
<u>Dipodomys microps</u>	6	9	.28	.48	.20	(.28) 1.78
<u>Dipodomys deserti</u>	6	4	.37	.40	-.03	(.20) 0.41
<u>Microdipodops pallidus</u>	6	8	.11	.29	-.18	(.20) 2.21*
<u>Perognathus longimembris</u>	11	14	.24	.25	-.01	(.13) 0.17

1. Average difference (standard error) of paired observations between experimental and control grid.

2. Paired observations.

* $p < 0.05$.

Table 3. Capture rates per individual and total captures for the seed treatment. -- Where significant effects were found, species increased their exploitation of the enriched microhabitat. A negative d_i indicates a positive response to the seeds.

Species	<u>Total Number Captures</u>		<u>Capture Rate Per Individual</u>		d_i^1	t^2
	Experiment	Control	Experiment	Control		
<u>Dipodomys merriami</u>	74	65	.35	.42	-.06 (.09)	1.71
<u>Dipodomys ordii</u>	11	5	.27	.36	-.27 (.17)	3.94***
<u>Dipodomys microps</u>	7	9	.17	.44	-.28 (.16)	4.19***
<u>Dipodomys deserti</u>	6	3	.43	.23	.20 (.36)	1.37
<u>Microdipodops pallidus</u>	6	8	.08	.15	-.19 (.15)	3.00
<u>Perognathus longimembris</u>	15	15	.36	.36	0 (.20)	0

1. Average difference (standard error) of paired observations between experimental and control grid.

2. Paired observations.

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Table 4. Average captures per night for two levels of moonlight. -- Moonlight causes a decrease in the foraging activity of Dipodomys ordii and Dipodomys microps. A comparison of captures on the control grid during high (1 July to 7 July) amounts and low (8 July to 18 July) of moonlight shows the effect of moonlight on foraging activities. Population increases for Dipodomys merriami and Perognathus longimembris during the two periods prevented comparisons for these species.

	1 July to 7 July 1980 (High Moonlight)	8 July to 13 July 1980 (Low Moonlight)	t
<u>Dipodomys merriami</u>	19.00	22.67	-
<u>Dipodomys ordii</u>	0.86	2.00	2.28**
<u>Dipodomys microps</u>	3.14	4.33	4.65***
<u>Dipodomys deserti</u>	2.43	2.00	0.96
<u>Microdipodops pallidus</u>	1.28	2.17	0.77
<u>Perognathus longimembris</u>	2.71	3.50	-

* p < 0.05

** p < 0.01

*** p < 0.001

treatment than on the control grid at the same time ($t = 4.19$, $p < 0.001$, Table 3) as did M. pallidus ($t = 3.0$, $p < 0.05$). Also, M. pallidus had a lower capture rate per animal for the parachute treatment ($t = 2.33$, $p < 0.05$) and for the parachutes and seeds treatment ($t = 2.21$, $p < 0.05$, Table 2). Both P and P + S_o should have increased total captures if animals were responding at all to changes in risk. The decreased capture rates suggest that the changes in foraging behavior for M. pallidus is due to something other than experimental factors, perhaps the behavior of other species.

To assess the effect of the manipulations on habitat selection behavior, I first ranked the treatments according to their expected effect on habitat utilization and then tested to see if changes in behavior for each species could be explained by treatment rank. The lantern treatment was the only manipulation which involved an increase in risk. It should have forced animals to restrict their foraging more to bushes which provide shadow and shelter; it was assigned the arbitrary rank of 4--the highest of any treatment. The remaining treatments should have led to less extreme avoidance or even preference of the open. Two other treatments also involved lanterns: L + S_o and L + P. These included, in addition to the lanterns, a factor (either seeds or parachutes) which enhanced the attractiveness of the open microhabitat and should have helped to draw animals more into the open. Since animals should not have shown as strong an avoidance of the open as with just lanterns, both L + S_o and L + P were assigned the rank of 3. Treatments without lanterns, but with other factors to make the open more attractive were assigned even lower ranks. The parachute

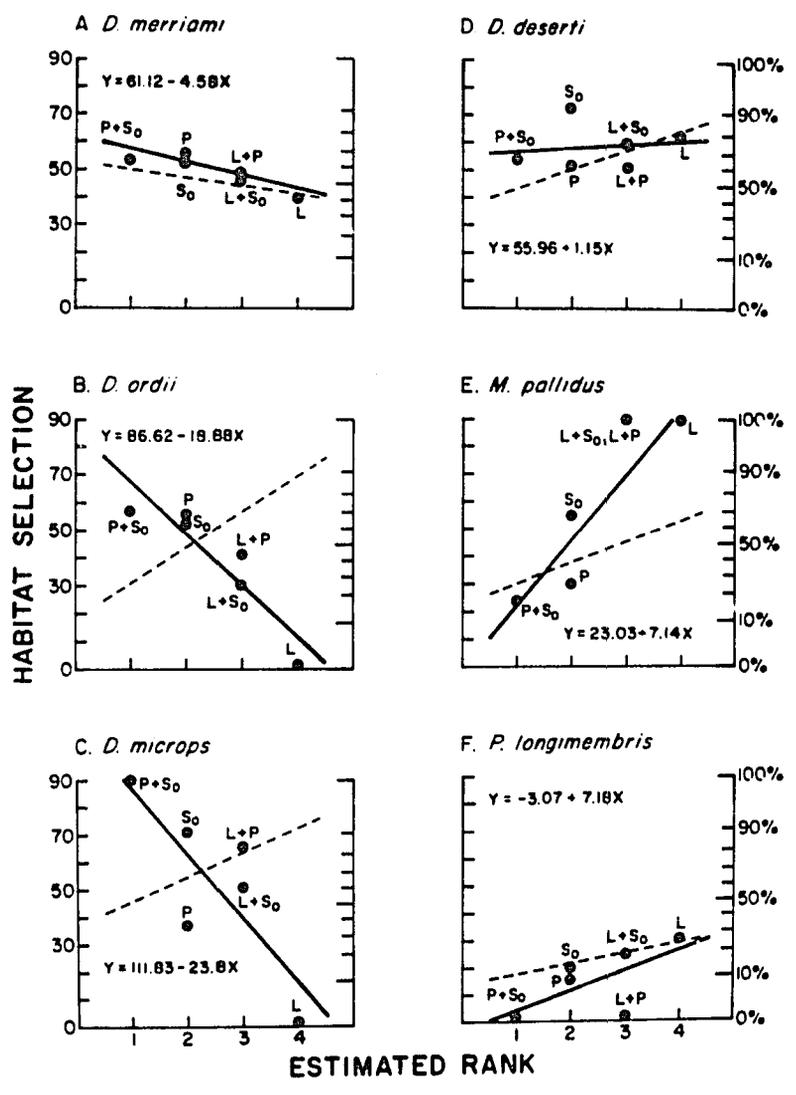
treatment and the seed treatment were given ranks of 2, and the combined treatment of parachutes and seeds which should have increased the attractiveness of the open most of all was given the rank of 1. Thus, the rankings indicate the predicted likelihood of animals avoiding the open.

Since the experiments were run simultaneously with the controls, I also had 6 estimates of control habitat use for each species. I assigned these the same ranks as their experimental counterparts. I then tested to see if selection of the open habitat during experimental treatments changed significantly with estimated rank of the treatments for each species relative to any changes which may have occurred on the control plot for reasons other than the experimental treatments. I fit lines to the control data and to experimental data for each species using non-parametric regression techniques (Maritz 1981), and tested whether the experimental data differed significantly from the regression line for the control data. The experimental data should have showed a more negative slope than the control data since the experiments with higher ranks were designed to make the open less attractive. I also tested for trends in the differences between experimental and control values for each treatment using the distribution-free isotonic regression technique of Chacko and Shorack (see Lehmann 1975).

For the four Dipodomys species, the experimental data differed significantly from the line fit through the control data (Fig. 1). The slopes of the regression lines for the experimental data were more negative, indicating that these animals tended to avoid open areas when

Figure 1. Risk and resources both affect foraging behavior of desert rodents. -- All four kangaroo rat species show a significant shift into open habitat as rank is increased and risk decreased. All other species show nonsignificant trends toward foraging more in bushes.

- a. D. merriami, $Q = 6.11$, $p < 0.01$.
- b. D. ordii, $Q = 6.79$, $p < 0.01$.
- c. D. microps, $Q = 5.22$, $p < 0.05$.
- d. D. deserti, $Q = 5.84$, $p < 0.01$.
- e. M. pallidus.
- f. P. longimembris.



light was added, but foraged more heavily in the open when shadow and when seeds were added. These trends are also significant by Chacko-Shorak test for D. ordii ($K' = 22.77$, $p \ll 0.001$), D. microps ($K' = 14.87$, $p = 0.001$), and D. deserti ($K' = 18.48$, $p < 0.001$).

In the case of the remaining two species, M. pallidus and P. longimembris, the lines did not differ significantly, and the slopes for the experimental data were, if anything, higher than for the controls.

Discussion

These experiments are consistent with the hypothesis that foraging behavior in desert rodents is risk-sensitive; changes in light and shadow lead to predictable changes in foraging activity and habitat selection regardless of whether the change in illumination is due to lanterns, parachutes, or the shifting phase of the moon. Increased illumination leads to decreased foraging, particularly in open areas lacking both shadow and cover; conversely, experimentally augmented shadow in open areas increases foraging activity. Under natural conditions, risk changes over the course of the night with the rising and the setting of the moon and the shifting of shadows and clouds. It also changes over the course of the month with the phase of the moon. Since animals constantly experience changing habitat-specific risk of predation, they can be expected to make appropriate facultative shifts in the utilization of microhabitats that afford different degrees of protection. Consequently, it is no surprise that they possess the behavioral flexibility to respond to the experimental manipulations.

Foraging behavior is also affected by resources. The foraging activity of three species was significantly altered by the addition of seeds in the open. While it is unclear from these experiments that resource enrichment resulted in the expected increase in foraging activity, the enrichment clearly caused some changes in foraging behavior. Furthermore, other experiments have shown that desert rodents increase foraging activity in response to resource enrichments (Chapter 3) and shift their activity into the enriched microhabitat (Chapter 2).

Since foraging activity and harvesting rates of desert rodents can be shown experimentally to be altered by predatory risk or resources separately, one may wonder if these two factors may interact to influence foraging behavior. The ranking of treatments for analysis was based on the assumption that they do, and indeed, the relation between habitat selection and predicted effect of the treatment (rank) was significant for all the kangaroo rat species. This suggests that for the kangaroo rats, microhabitat selection changes in response to both risk and resources.

Microdipodops pallidus is an exception to these patterns in the larger kangaroo rats. M. pallidus combines the small size of a pocket mouse with the inflated auditory bullae and bipedal locomotion of a kangaroo rat. Rather than having an increased foraging rate in response to the parachute treatment, M. pallidus foraged less. Moreover, it spent a smaller portion of what little time it did forage in the open. In addition, the regression of habitat selection on estimated rank for the experimental treatment did not have a higher

slope than the controls. Rather than increase foraging in the open in response to seeds or parachutes, M. pallidus tended to forage more in the bushes.

If M. pallidus is responding to the treatments, then it appears actually to avoid the predicted preferred microhabitat (less risky, more resources). Instead, I suggest that M. pallidus is responding to the kangaroo rats. As the abundant kangaroo rats shift their foraging in response to the experimental treatments, they may exclude the small M. pallidus from the preferred microhabitat, either by direct aggressive interference or by depleting the food supply by their foraging activities.

P. longimembris failed to respond significantly to the experimental treatments. Instead, it spent most of its time foraging under bushes, where 84% of all captures were recorded (Table 5), even when seeds or parachutes were added to increase the attractiveness of the open microhabitat. It seems that the lack of extreme development of anti-predator adaptations (Webster 1975) renders pocket mice inferior to kangaroo rats in detecting and escaping predators, with the result that P. longimembris always forages near bushes even under the least risky circumstances. Though they cross open areas while traveling from bush to bush, they seem to do so only rarely.

I have demonstrated here that foraging behavior in desert rodents is responsive to changes in illumination and resources. In particular, kangaroo rats alter their use of microhabitats in accordance with changes in predatory risk. The pocket mice and kangaroo mice of the same community do not fit the pattern, however. Pocket mice tend

Table 5. Habitat use of the species of Tonopah Junction, 1980. -- Dipodomys deserti and Perognathus longimembris show the most extreme habitat preferences. Trapping effort was equal in the bush microhabitat and in the open microhabitat so the percentage of captures in the open indicates the specialization of the species on that habitat.

Species	Percentage of Captures in Open
<u>Dipodomys merriami</u>	53.65
<u>Dipodomys ordii</u>	44.81
<u>Dipodomys microps</u>	69.88
<u>Dipodomys deserti</u>	77.50
<u>Microdipodops pallidus</u>	50.73
<u>Perognathus longimembris</u>	16.24

to forage only under bushes, and kangaroo mice utilize whichever microhabitat the kangaroo rats are not using.

The differences between species in response to these experiments corresponds roughly to their development of anti-predator morphologies. This suggests that the differences among species in microhabitat selection which are so important to species coexistence (e.g. Brown and Lieberman 1973, Rosenzweig 1973, Lemen and Rosenzweig 1978) are due to segregation along a gradient of predatory risk. I examine this more closely in Chapter 2.

CHAPTER 2

RISK-SENSITIVE FORAGING AND DESERT RODENT COMMUNITY STRUCTURE

Desert rodent communities in North America have received a great deal of attention from ecologists due to the coexistence of many species exploiting similar seed resources (e.g. Rosenzweig 1973, Brown 1973, Smigel and Rosenzweig 1974, Reichman 1975, M'Closkey 1978, Price 1978a and 1978b). Field studies have addressed modes of competitive coexistence focusing on how species partition space and food. Significant differences in utilization of habitats and microhabitats have been found repeatedly (Rosenzweig and Winakur 1979, Brown and Lieberman 1973, Rosenzweig 1973, Rosenzweig, Smigal and Kraft 1975, Shroder and Rosenzweig 1975, Lemen and Rosenzweig 1978, Stamp and Ohmart 1978).

Kangaroo rats in general exploit open areas while pocket mice and deer mice (Peromyscus) mostly restrict their foraging to bushes and other cover. For example, Lemen and Rosenzweig (1978) demonstrated that in desert grasslands Ord's kangaroo rat (Dipodomys ordii) uses open areas while the silky pocket mouse (Perognathus flavus) restricts its foraging mostly to grassy areas. Such differences are believed to promote coexistence. To understand community structure in desert rodents, it is necessary to understand the causes of such differences.

Two hypotheses have been suggested to account for differences in habitat selection among species.

One suggests that kangaroo rats prefer open microhabitats because their bipedal locomotion allows them to exploit efficiently large, scattered clumps of seeds (Reichman and Oberstein 1977, Hutto 1978, Price 1978a). Quadrupedal deer mice and pocket mice restrict their foraging to bushes; there, they are able to harvest seeds which may be spatially more predictable but less dense (Reichman and Oberstein 1977). Quadrupedal locomotion also aids in climbing and maneuvering in bushes (Rosenzweig et al. 1975). According to this hypothesis, the ultimate cause of coexistence lies in differential exploitation of seed resources and microhabitats by species in accordance with their body size and locomotor abilities.

The second hypothesis proposes that habitat selection is enforced by predatory risk; foraging is risk-sensitive (Caraco, Martindale, and Pulliam 1980; Caraco, Martindale, and Whittam 1980). Risk sensitivity as discussed in the literature refers to how animals respond to variance in profit, particularly in regard to variance in resource acquisition (marginal revenue; Caraco 1980, Real 1981). However, profit is the difference between revenue and cost. Hence, animals which respond to variance in cost are also risk-sensitive. Since the costs of predation are incurred all at once, the variance of the probability of predation increases directly with the probability itself. Therefore, animals which respond to changes in predatory risk forage in a risk-sensitive manner in every sense of the phrase.

Applied to desert rodents, the predatory risk hypothesis proposes that quadrupedal rodents prefer to forage in dense vegetation because of the great danger from predators in open microhabitats (Rosenzweig 1973). Bipedal kangaroo rats are better able to exploit open areas because they are better able to detect and escape predators (Webster 1962, Eisenberg 1963). Their anti-predator adaptations include inflated auditory bullae, the better to hear approaching predators, and bipedal locomotion, the better to escape attacks. Without such adaptations, foraging in the open would be just too risky even though open microhabitats may contain rich seed resources. Individuals ought to alter their habitat utilization in accordance with habitat-specific changes in mortality risk. Also, predatory risk and predator avoidance may provide an axis along which microhabitat segregation among species can occur. Such partitioning may occur for three reasons. First, predatory risk may be greater in the open than under bushes. This would be true if most predators locate prey visually and pursue them. Second, some anti-predator morphologies may be effective in one microhabitat but not in another. For example, bipedal locomotion may reduce agility under bushes (Rosenzweig 1973). Third, the types of predators most often encountered in various microhabitats may differ. Such qualitative differences in predatory risk may select for very different strategies on the part of the prey. So long as predatory risk differs qualitatively or quantitatively among microhabitats, predatory risk can promote habitat selection differences among species.

To see how these factors affect desert rodents, I manipulated both resources and predatory risks and noted their effects on foraging

activity and, in particular, on microhabitat selection behavior for six species of rodents in a Great Basin sand dune community.

Methods

I established two study plots in May 1981 on stabilized sand dune habitat in the Great Basin Desert. The study site is located at Tonopah Junction, 12 km south of Mina in Mineral County, Nevada at an elevation of 1343 meters. Species present in summer 1981 were Merriam's kangaroo rat (Dipodomys merriami), Ord's kangaroo rat (Dipodomys ordii), Great Basin kangaroo rat (Dipodomys deserti), pallid kangaroo mouse (Microdipodops pallidus), little pocket mouse (Perognathus longimembris), southern grasshopper mouse (Onychomys torridus), pinon mouse (Peromyscus truei), and white-footed deer mouse (Peromyscus maniculatus). These species differ greatly in body size and morphology (Table 6). The predators at this site include long-eared owls (Asio otus), coyotes (Canis latrans), kit foxes (Vulpes macrotis), and gopher snakes (Pituophis melanoleucus). With the exception of gopher snakes, these predators actively pursue their prey and locate prey largely by vision, producing a gradient of increasing predatory risk from under bushes to open microhabitats. I set up two 5 by 5 grids, each of which covered one square hectare and contained 100 live traps divided equally among 25 stations. Trap stations were 20 meters apart. At each trap station, I placed two traps in both of the two microhabitats recognized in this study: open areas and under bushes. One plot served as a control and the other as the experimental plot on a rotating basis.

Table 6. The desert rodent community at Tonopah Junction in 1981.

	Locomotion	Body Size (g)	Bullar Volume (mm ³)	Relative Bullar Inflation ¹
<u>Dipodomys merriami</u>	Bipedal	42	1859	.58
<u>Dipodomys microps</u>	Bipedal	65	1824	.43
<u>Dipodomys deserti</u>	Bipedal	100	3496	.53
<u>Microdipodops pallidus</u>	Bipedal	12	1262	.65
<u>Perognathus longimembris</u>	Quadrupedal	7	252	.29
<u>Peromyscus maniculatus</u>	Quadrupedal	18	77	.07

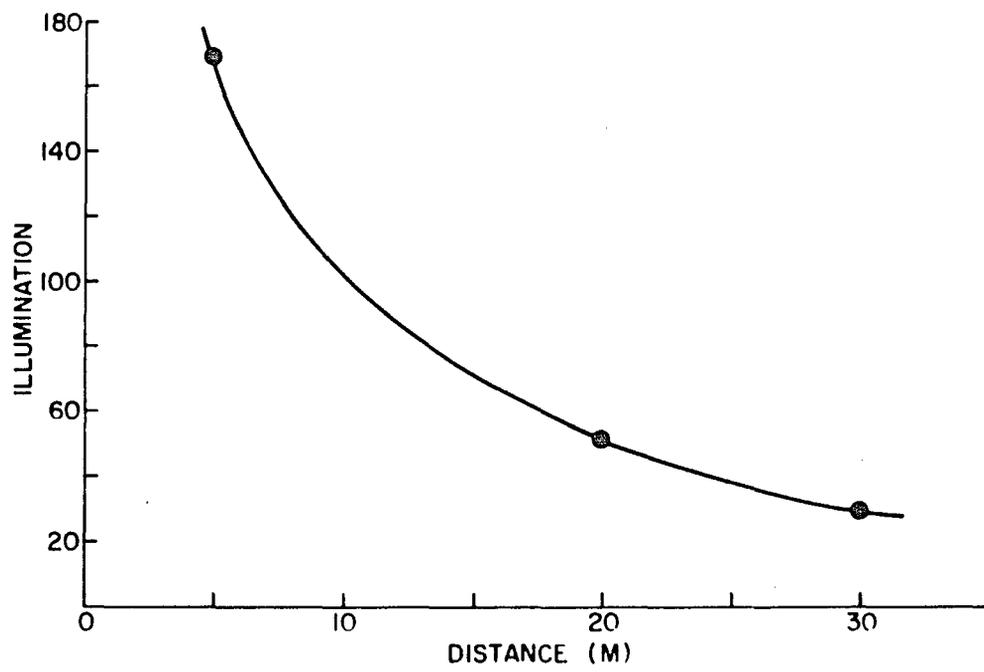
1. Relative bullar inflation = bullar volume / total skull volume.

Foraging activity and habitat selection of rodents were assayed by live trapping using 8 x 8 x 25 cm Sherman traps baited with mixed bird seed (millet, wheat and sorghum). Captured animals were identified as to species and weighed, reproductive condition was noted, and individuals were marked with both ear tags and unique toe-clip numbers.

To overcome the difficulties of studying predation and its effects under field conditions, I chose instead to manipulate a factor which nocturnal rodents should associate with predatory risk: illumination. Animals foraging in moonlight are not only easier to see, they also cast shadows, and the contrast of light and shadow should be more easily spotted by predators. For example, important rodent predators such as long-eared owls (Asio otus) have been shown to be much more dangerous when light is present (Dice 1945, 1947). Altering levels of illumination is tantamount to altering predatory risk.

I manipulated light by illuminating the experimental grid with Coleman Model 200-A gasoline lanterns and Ray-O-Vac Sportsman 360 electric fluorescent lanterns. Four lanterns were used to illuminate the grid, producing light intensities similar to natural moonlight over most of the grid (Fig. 2). I manipulated resources by adding bird seed to either shrub areas or open areas in densities corresponding to naturally occurring seed clumps (Reichman and Oberstein 1977). Hence, the manipulations correspond to light levels and resource densities which the animals encounter in nature. Performing seed enrichments in both the open and under bushes allowed me to examine whether

Figure 2. Illumination of the experimental grid from lanterns is similar to natural moonlight. -- Only traps in the open at the four stations containing lanterns are illuminated by intensities brighter than full moonlight (100 on the illumination scale). The thirteen stations which are at 20 m from a lantern receive slightly less illumination than from a half-full moon and the remaining 9 stations which are 30 m from a lantern receive only two-thirds of that. Starlight measured approximately 10 on the illumination scale.



microhabitat has an effect on responses to resources for the various species.

In addition to the main factors of lanterns (\underline{L}), seeds in the open (\underline{S}_o), and seed in bushes (\underline{S}_b), I also ran pairwise combinations of factors (lanterns + seeds in open, $\underline{L} + \underline{S}_o$; lanterns + seeds in bush, $\underline{L} + \underline{S}_b$). The set of five treatments was repeated seven times over a two-month period. I randomized both the order of treatments within each set of which plot contained the experimental treatment on any given night. In contrast to the 1980 experiments (Chapter 1) when the treatments included two levels of risk (manipulations of light and shadow) and only one resource enrichment, in 1981 I performed only one type of predatory risk manipulation but performed two types of seed enrichments. Thus, the experiments of 1980 and 1981 were similar enough to serve as replicates yet different enough to examine new hypotheses.

I used total capture of a species on a given night as an indicator of its foraging activity and the proportion of captures in the open as an indicator of microhabitat use. All statistical tests on proportions were performed on angularly transformed data. D. ordii, O. torridus, and P. truei were excluded from the data analysis because there were too few captures for meaningful statistical treatment. I tested hypotheses using t-tests with standard errors measured directly from data. Comparisons were made between data from a given treatment and its particular control.

Table 7. Species differ in mean habitat use. -- Habitat use of the species as measured by the percentage of captures occurring in the open (based on control data) show that kangaroo rats forage more in the open and pocket mice and deer mice frequent bushes. Angular transformation of the percentages (along with standard errors) are also given.

Species	Habitat Selection Value	
	Percentage	Angular Transformation
<u>Dipodomys merriami</u>	56.0	49.26 (3.78)
<u>Dipodomys microps</u>	59.0	52.68 (1.97)
<u>Dipodomys deserti</u>	95.0	82.35 (11.89)
<u>Microdipodops pallidus</u>	63.0	55.34 (2.24)
<u>Perognathus longimembris</u>	40.0	36.76 (15.39)
<u>Peromyscus maniculatus</u>	23.0	26.68 (3.99)

Results

The results described in this paper are based on 7000 trap nights and 1775 animal captures. The six species commonly captured differed significantly in habitat selection (Kruskal-Wallis test, $H = 47.64$, $p \ll 0.001$; Table 7). Among the kangaroo rats, D. deserti has the greatest preference for the open and differs significantly from D. merriami ($t = 2.68$, $p < 0.05$), though D. merriami and D. microps do not differ significantly from each other in microhabitat use. M. pallidus falls within the range of habitat use of the various kangaroo rat species. P. maniculatus shows the greatest preference for bushes, and its mean habitat use value is significantly less than that of the kangaroo rats ($t = 5.503$, $p < 0.001$). Habitat use in P. longimembris is quite variable and is intermediate to that of P. maniculatus and the kangaroo rats. Due to its high variance of habitat use, P. longimembris is not significantly different from that of P. maniculatus nor the kangaroo rats. Kangaroo rats and kangaroo mice were captured more frequently in the open, and the remaining species are captured more often around bushes. As in so many other communities of desert rodents, there are significant differences among species in habitat use.

An important question is whether the experimental treatments did, in fact, affect foraging behavior. The nature of the experimental design affords an opportunity to test for overall treatment effects on habitat selection behavior for each species.

Each of the five experimental treatments had a predicted effect on habitat selection. Some should have caused an increase in the use

of open habitats; others should cause a decline. For example, S_o should draw animals more into the open, and S_b should draw them into the bushes; L should force them into bushes. If the treatments were effective, then the variance among the means of the treatment effects should be large compared to variance among controls (which were run simultaneously).

The variance among the means for habitat selection for the experimental treatments is indeed significantly greater than the variance among the controls for the four bipedal species: D. merriami, D. microps, D. deserti and M. pallidus (Table 8). The Siegel-Tukey test in Table 3 does not give a significant value for D. merriami. However, the test is sensitive to differences between the means of the groups being compared (Siegel and Tukey 1960). Ansari and Bradley's W corrects for this, and shows that the variance among the experimental means is in fact greater than the variance among the control means for D. merriami ($W = 6, p < 0.05$; Ansari and Bradley 1960). For D. microps, the variance among the experimental means is 51 times greater than the variance among the control means. The large variance of the experimental means for D. deserti is mostly due to one treatment ($L + S_b$), but most treatments contribute to the large variance found for D. merriami, D. microps, and M. pallidus. Habitat selection for all four species is therefore responsive to the experimental manipulations of both illumination and resources. In contrast, the variance among the control means is actually greater than the variance among the experimental means for the quadrupedal species P. longimembris and P.

Table 8. Habitat selection (percentage of captures occurring in the open) means for the experimental treatments and their controls. -- Siegel-Tukey R values testing if the variance among the means of the experimental treatments is greater than the variance among the means of the controls are given. The greater variance among the experimental mean shows that the experimental treatments affect habitat selection for each bipedal species. There is no corresponding difference for the quadrupedal species.

Species	Level	Treatment						R
		L	S _b	S _o	L+S _b	L+S _o	S	
<u>Dipodomys merriami</u>	Experiment	37.0	44.0	69.0	49.3	30.0	14.80	
	Control	53.0	50.0	56.0	66.0	54.0	6.10	20**
<u>Dipodomys microps</u>	Experiment	41.0	36.0	71.0	47.0	76.0	18.30	
	Control	53.0	50.0	56.0	66.0	54.0	6.10	20**
<u>Dipodomys microps</u>	Experiment	41.0	36.0	71.0	47.0	76.0	18.30	
	Control	58.0	55.0	60.0	61.0	60.0	2.39	15***
<u>Dipodomys deserti</u>	Experiment	90.0	88.0	100.0	34.0	100.0	361.90	
	Control	100.0	100.0	80.0	100.0	88.0	9.21	18.7*
<u>Microdipodops pallidus</u>	Experiment	57.0	45.0	85.0	84.0	60.0	17.63	
	Control	68.0	66.0	64.0	58.0	61.0	3.97	18.0*
<u>Perognathus longimembris</u>	Experiment	56.0	53.0	45.0	45.0	27.0	11.28	
	Control	28.0	35.0	47.0	22.0	67.0	17.82	32.0
<u>Peromyscus maniculatus</u>	Experiment	18.0	13.0	20.0	12.0	20.0	3.85	
	Control	27.0	22.0	28.0	16.0	21.0	4.69	22.5

* Siegel-Tukey test.

** Significance by Ansari-Bradley test, $p < 0.05$.

* $p < 0.05$; ** $p < 0.01$.

maniculatus. The experimental treatments apparently had little or no effect on their habitat use.

If treatments influence foraging activity as predicted, then the mean number of captures per night should be lower for each experimental treatment. If increased illumination means increased predatory risk and foraging is risk-sensitive, then animals should reduce their foraging activity in response to lanterns. Also, I would expect animals to spend more time foraging in rich patches and so animals should increase their foraging activity in response to the seed enrichments. However, foraging activity was measured by the numbers of captures in traps which used seed as bait. Animals may have spent foraging time collecting the scattered seeds instead of (or in addition to) entering traps; the result is that even with an increase in foraging activity, there may have been fewer experimental captures in response to seed enrichments. Hence, the different treatments should all reduce or have little effect on the average number of nightly captures.

The means of the experimental treatments for nightly captures (Table 9) are significantly lower than the control means for D. merriami and D. microps. This substantiates the strong effect of the treatments on those species.

To provide an overview of how the six species responded to the experimental treatments, I have ordered treatments according to their expected effect (estimated rank) on habitat selection for each species (see Appendix) and graphed them against the mean habitat selection value for each treatment. I used distribution-free regression

Table 9. Mean number of nightly captures for experimental treatments and their controls. -- Significantly lower experimental means indicate that the experimental treatments affect the amount of foraging activity.

Species	Level	Treatment					\bar{X}	t
		L	S _b	S _o	L+S _b	L+S _o		
<u>Dipodomys merriami</u>	Experiment	6.14	5.43	5.71	4.57	4.14	5.20	4.48***
	Control	7.14	6.14	7.29	6.43	7.14	6.83	
<u>Dipodomys microps</u>	Experiment	2.43	2.14	2.71	3.00	2.86	2.63	2.93**
	Control	3.14	3.71	3.1	3.57	3.86	3.60	
<u>Dipodomys deserti</u>	Experiment	1.14	0.36	0.86	0.57	0.43	0.77	0.11
	Control	0.71	0.57	0.86	0.57	0.71	0.77	
<u>Microdipodops pallidus</u>	Experiment	2.71	3.86	3.00	2.29	3.57	3.09	0.77
	Control	4.43	4.14	2.86	2.29	3.00	3.34	
<u>Perognathus longimembris</u>	Experiment	2.43	2.29	1.86	1.71	1.86	2.03	0.46
	Control	2.43	2.00	1.57	1.71	2.14	1.97	
<u>Peromyscus maniculatus</u>	Experiment	8.71	9.57	9.86	7.86	8.71	8.94	1.09
	Control	12.00	9.00	8.57	10.86	11.00	10.29	

* p < 0.05

** p < 0.01

***p < 0.001

techniques (Maritz 1981) to fit lines to the points (Fig. 3).

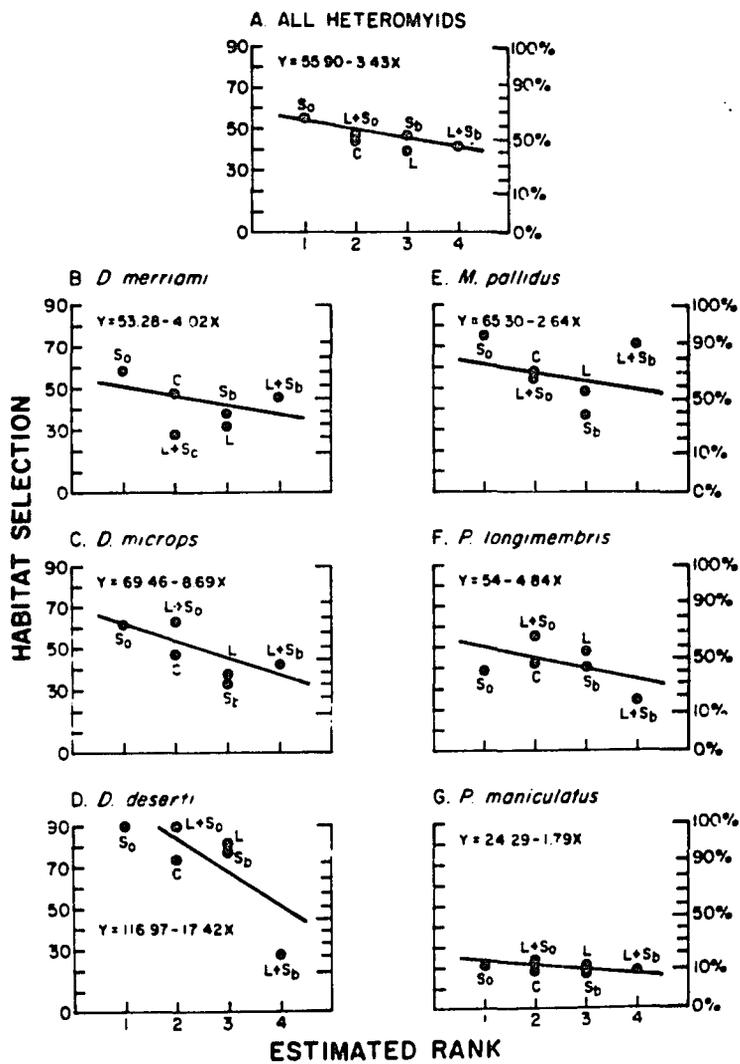
Treatments which should have led animals to forage in the open were assigned low values on the estimated rank (independent) axis, and those which should have forced or drawn animals into the bush more were given higher values. Treatments which were expected to have similar effects, but which could not be ranked with certainty with respect to each other were assigned the same rank. Because of the arbitrary nature of assigning estimated ranks, I will not present p values.

When animals belonging to the family Heteromyidae are pooled, there is a strong negative relationship between habitat selection and estimated rank (Fig. 3a). Seed treatments increased foraging in the enriched microhabitat, and lanterns forced animals to forage more in the bushes. Examining the graphs for each species reveals similar results; in fact, the slopes of the lines are negative for all six species. Furthermore, the trends indicated by the lines are significant by Chaco-Shorak test (see Lehmann 1975) for the kangaroo rats, D. merriami ($K' = 6.05$, $p = 0.037$), D. microps ($K' = 6.747$, $p = 0.035$), and D. deserti ($K' = 9.993$, $p = 0.009$).

The regression lines fall into three groups based on slope and intercept. Differences in intercept are indicative of the habitat selection differences already noted, and the slope indicates how much animals can alter behavior in response to changing risk and resources. The first group contains only D. deserti, the largest of the kangaroo rats in the community. It shows the highest intercept and the steepest slope (Fig. 3d). Although it changed habitat selection behavior little in response to most treatments, its ability to alter behavior as

Fig. 3. Risk and resources combine to affect habitat selection behavior of desert rodents. -- Experimental treatments are ranked according to their expected effect on habitat selection behavior. Treatments which should cause animals to forage more in the open (i.e. S_o) are assigned low rank and those which should draw or force them into bushes are assigned higher rank (see Appendix). A plot of treatment means according to rank against habitat selection values shows negative correlations for the groups listed below. The habitat selection value axis is scaled both in percentages of captures occurring in the open and its angular transformation ($= \arcsin p^{1/2}$). Equations for the lines are derived from distribution-free regression methods and are given in terms of the angular transformation.

- a. All heteromyid rodents.
- b. Dipodomys merriami.
- c. Dipodomys microps.
- d. Dipodomys deserti.
- e. Microdipodops pallidus.
- f. Perognathus longimembris.
- g. Peromyscus maniculatus.



demonstrated by its response to $L + S_b$ is great. The second group consists of D. merriami, D. microps, and M. pallidus, which all showed mild preference for the open and have less steep slopes (Figs. 3c-e). Finally, P. maniculatus was always restricted to bushes and has low intercept and shallow slope (Fig. 3g). P. longimembris has a line much like that of the second group, but there is much more scatter (Fig. 3f). There are three distinct behavioral patterns: animals with great preference for foraging in the open which however have great potential for altering habitat use; animals with slight preference for foraging in the open but with less flexibility; and animals restricted to bush regardless of changes in illumination or resource distributions.

With these basic patterns in mind, I will now examine individual treatment effects for each species.

Effects of Lanterns

The predatory risk hypothesis predicts that foraging is risk-sensitive; animals should avoid areas of increased risk. In the case of the lantern treatment, the increased illumination should make lighted areas in the open more dangerous. Animals should spend more of their foraging time in the safety of bushes and shadows. Since animals must at least traverse open areas while traveling from bush to bush and thus suffer from increased risk, foraging activity should also decrease. Animals should forage elsewhere or should wait for a better time and thus forage less. Such changes should be evident for all species except those showing extreme habitat preferences. In contrast, hypotheses which tie habitat selection behavior solely to

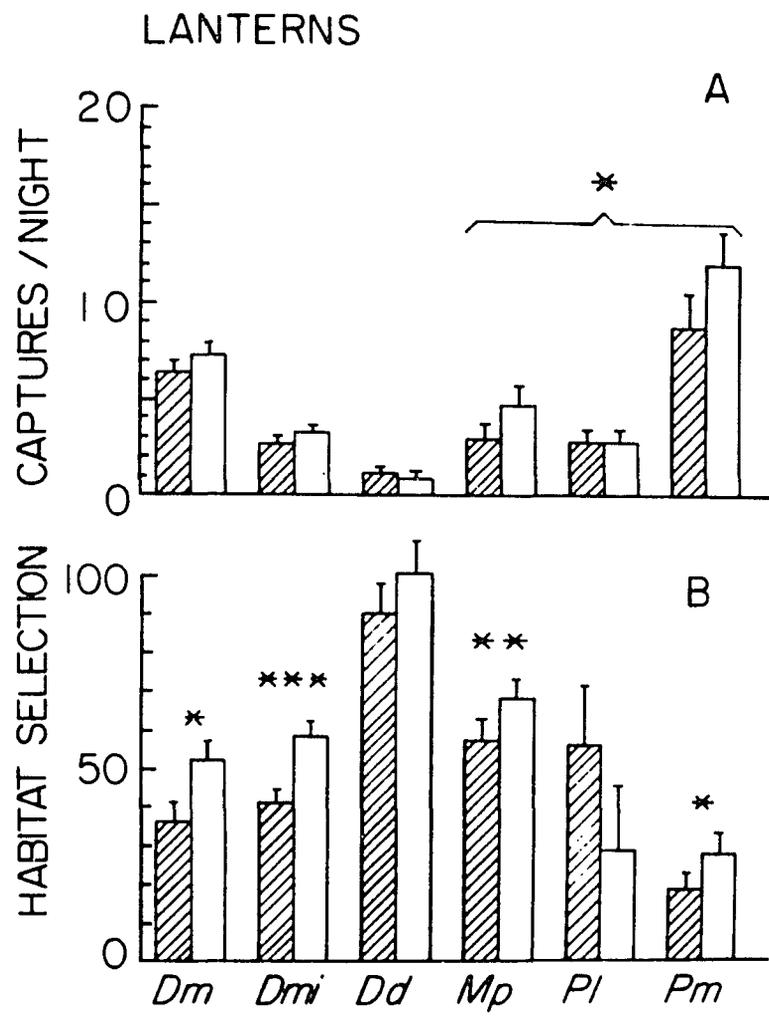
resources, resources distributions, or locomotor abilities (Brown and Lieberman 1973, Reichman and Oberstein 1977, Hutto 1978, Price 1978a) do not predict any changes in foraging behavior in response to increased illumination since the lantern treatment altered none of these factors. What were the responses to lanterns?

The illumination from lanterns caused significant changes in the habitat selection behavior of three species (Fig. 4b). D. merriami ($t = 2.30$, $p < 0.025$), D. microps ($t = 5.78$, $p < 0.001$), and M. pallidus ($t = 2.82$, $p < 0.01$) all reduced foraging in open areas in response to light. The habitat shift seen in D. microps actually involved a switch in habitat preferences; where before more captures occurred in the open, with lanterns more captures occurred under shrubs. D. deserti ($t = 0.54$, $p = 0.40$) and P. maniculatus ($t = 1.77$, $p = 0.055$) showed similar though nonsignificant trends in habitat use. Only P. longimembris showed a surprisingly large, though nonsignificant, shift toward use of open areas.

Increasing the illumination resulted in fewer captures for four species (Fig. 4a), but none of the declines were significant.

When non-Dipodomys species are grouped together, the reduction in foraging activity in response to illumination as measured by nightly capture is significant ($t = 2.02$, $p < 0.05$). Since the number of nightly captures for P. longimembris is identical both with and without lanterns, the results come from the combined effect of lanterns on the foraging activity of M. pallidus and P. maniculatus; activity of these species is reduced 25 to 40 percent by lanterns. Thus, evidence

Fig. 4. Means (and standard errors) of habitat selection value and captures/night for the lantern treatment. -- Open bars represent control data and hatched bars represent experimental data. They show an avoidance of open microhabitat in response to increased illumination. Only P. longimembris increased its use of the open. The habitat selection axis represents the percentage of captures occurring in the open. Dm = D. merriami, Dmi = D. microps, Dd = D. deserti, Mp = M. pallidus, Pl = P. longimembris, and Pm = P. maniculatus, * p < 0.05, ** p < 0.01, *** p < 0.001.



suggests that even though P. maniculatus is restricted to bushes, it may be responsive to changing predatory risk.

Justice (1960), Lockard and Owings (1974a and 1974b; and I (Chapter 1) observed similar reductions in foraging activity and shifts in habitat use for heteromyid rodents in response to natural moonlight.

One sees from these results that, as predicted by the predatory risk hypothesis, foraging is often risk-sensitive; habitat selection behavior is determined in part by predatory risk. Species significantly reduce their use of the open in response to lanterns with the exceptions of D. deserti, P. maniculatus (the species showing the extreme habitat selection preferences), and P. longimembris. I will discuss the foraging behavior of P. longimembris in a later section. Even for D. deserti and P. maniculatus, habitat selection behavior can be understood in terms of predatory risk. D. deserti heavily exploits the open because of its large size (100 g.). Long-eared owls (Asio otus), the most important predator at this site, rarely take prey as large as 100 grams but frequently capture smaller kangaroo rats and other rodents (Marti 1976, Marks and Yensen 1980). Large size apparently reduces the vulnerability of D. deserti to predators (also see below) and allows it to forage safely even under conditions which are too risky for other species. P. maniculatus, in contrast, is probably the most vulnerable. It matches its color background poorly, is the least bipedal, and has the smallest auditory bullae of the species commonly found in this community. It restricts its foraging to the safety of shadows and bushes even under the best of circumstances

and cannot be expected to respond much to increased illumination. Even with its extreme avoidance of the open, P. maniculatus was affected by the lanterns since it apparently reduced foraging activity in response to the light. Risk affects foraging behaviors and contributes greatly toward understanding habitat selection differences among species.

The responses to lanterns seen here are not predicted by the resource hypotheses. Based on these experiments, one sees that hypotheses for explaining habitat selection behavior which fail to include predatory risk are unlikely to be sufficient. What is the role of resources and resource distributions in affecting foraging behavior? To understand this, it is necessary to examine the seed manipulation results.

Effects of Seeds

The two seed enrichment treatments (\underline{S}_b , \underline{S}_o) should have had different effects on habitat selection behavior. Though seed enrichment should normally increase the use of the enriched microhabitat, if P. maniculatus is restricted to foraging in bushes owing to risk, then it should ignore seed enrichments in the open. Kangaroo rats and kangaroo mice, on the other hand, ought to respond to enrichments in the open as well since their anti-predator morphology reduces the cost incurred from exploiting open areas.

As previously noted, with seeds serving both to enrich microhabitats and as bait for traps, the effects of seeds on nightly captures is not so easy to predict. Animals having picked up seeds scattered about for a seed treatment might leave an area before

entering a trap to gather more seeds. The result would then be a decline in number of captures. If animals increased activity and took time to gather seeds scattered on the ground as well as enter traps for seeds, then trapping success could be similar to that observed on control grids. The lack of significant reductions in captures in responses to seeds may mask a true response in foraging activity. Care must be taken in making inferences on the effect of seed enrichments on foraging activity.

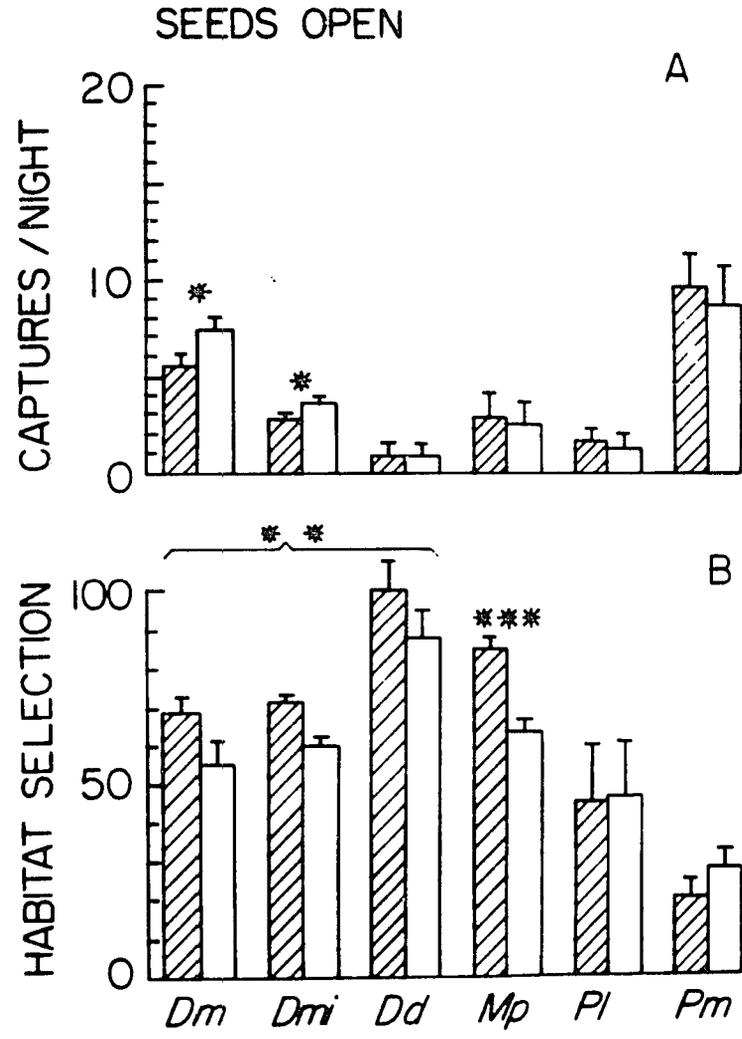
The enrichment of open areas caused significant changes in foraging behavior only of bipedal species (Dipodomys, Microdipodops; Fig. 5b). There were significantly greater proportions of captures in the open for D. merriami, D. microps, and D. deserti as a group ($t = 2.3$, $p < 0.005$) and for M. pallidus ($t = 5.65$, $p < 0.001$; the effects of S_0 on habitat selection were recorded in the open for each species).

At the same time, there were significantly fewer captures per night on the experimental grid for D. merriami ($t = 2.23$, $p < 0.01$) and D. microps ($t = 2.56$, $p < 0.025$; Fig. 5a). This probably reflects the effects of resources on habitat selection since kangaroo rats were likely spending more of their time in the enriched microhabitat gathering seeds rather than entering traps. Though not significant, the captures per night for M. pallidus were greater on the experimental grid than on the control grid during the same period. For similar reasons, in view of the highly significant shift in habitat selection in favor of open areas for M. pallidus, the slight increase may reflect a true increase in foraging activity in response to seeds.

Figure 5. Mean (and standard errors) of habitat selection value and captures/night for the S_0 treatment. -- The data show an increase in the use of the enriched but risky microhabitat by bipedal species only. Quadrupedal species decreased their use of the enriched microhabitat. The habitat selection axis represents the percentage of captures occurring in the open. The abbreviations and open and hatched bars are the same as in Figure 4. * $p < 0.05$, ** $p < 0.01$, and *** $p < 0.001$.

a. Captures/night.

b. Habitat selection.



D. deserti showed no significant responses, and the quadrupedal species P. longimembris and P. maniculatus not only showed no significant responses to seeds, but the trends were in the opposite direction.

The effects of resource enrichments in bush microhabitat were quite different (Fig. 6b). Whereas P. maniculatus showed no response to seeds placed in the open, it showed a significant increase in its already heavy use of the bush microhabitat when seeds were placed under bushes ($t = 2.08$, $p < 0.01$). Because of the enrichment, animals may have stayed in patches longer (Charnov 1976) and so traveled less often through open areas to new bushes, thus increasing the proportion of time spent in the bush microhabitat. Also, the slight increase in captures per night (nonsignificant) may reflect increased foraging activity.

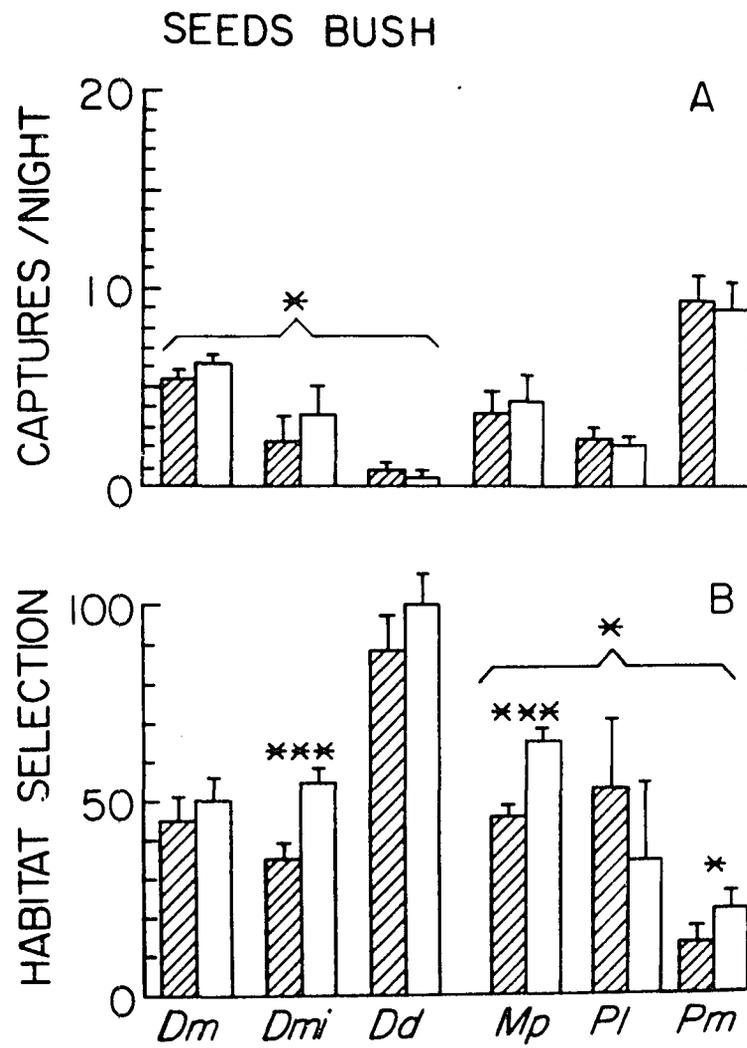
As before, P. longimembris showed no significant responses to the seed addition and even decreased its use of the enriched microhabitat, while M. pallidus ($t = 4.75$, $p < 0.001$) and D. microps ($t = 6.36$, $p < 0.001$) showed significant increases in their use of the enriched microhabitat. In addition, kangaroo rats as a group showed significantly fewer captures for the experimental treatment ($t = 2.03$, $p < 0.05$) (Fig. 6a).

In summary, kangaroo rats and kangaroo mice responded to seed enrichments in both the bush and the open, but deer mice only responded to resource enrichment in the protected microhabitat. Pocket mice showed no significant responses.

Fig. 6. Means (and standard errors) of habitat selection value and captures/night for the S_p treatment. -- They show responses to the resource enrichment: most species increase their use of the enriched microhabitat. The habitat selection axis represents the percentage of captures occurring in the open. The abbreviations and open and hatched bars are the same as in Fig. 4. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

a. Captures/night.

b. Habitat selection.



The complete lack of response to one enrichment by P. maniculatus in contrast to the strong responses to both enrichments by bipedal species indicates that all species do not respond equally to resources and resource distributions. Since vulnerable deer mice traveled through the open on some occasions during the S_0 treatment (as indicated by the small proportion of captures in the open), they had the opportunity to encounter the seeds and to respond to the enrichment. Yet they did not; risk was apparently too great. The kangaroo rats and kangaroo mice, with their morphological equipment for escaping predators, however, responded to seeds in the open. At the same time, they could also exploit seeds in the bush. These results suggest that habitat selection is affected by resources, within bounds set by predatory risk and specific abilities to escape predators. Patterns of seed exploitation are apparently best understood within the context of predatory risk.

These results agree with with the work of Hay and Fuller (1980). They demonstrated that seed preferences of desert rodents are risk-sensitive. Having measured seed preferences in the laboratory for two heteromyid species (D. merriami and Perognathus fallax), they found that the preferences were maintained in the field. Furthermore, the selectivity was three times more pronounced when trials were run 1-2 meters from cover than when run under shrub canopies. Animals foraged less in the risky open areas, but concentrated more of that foraging on preferred seed types.

Both risk and resources affect foraging behavior in predictable ways. Which, then, is of greater importance in determining habitat use for each species?

Combined Treatments

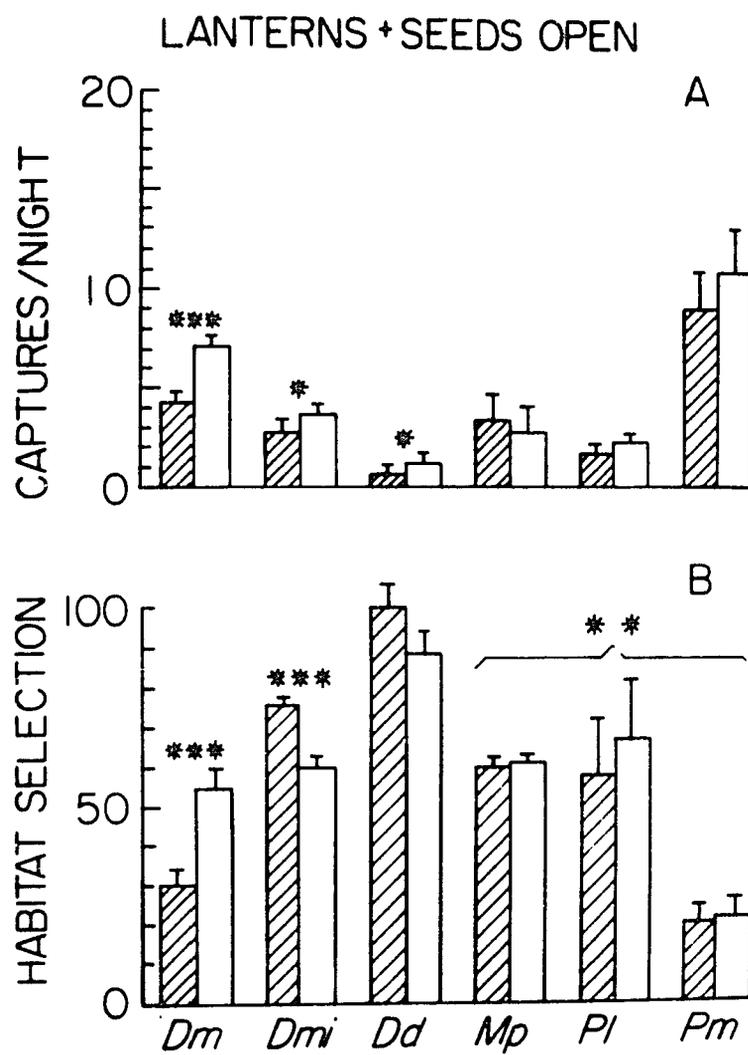
The importance of resources relative to risk can be examined for each species using the results of the combined treatments of lanterns and seeds. Often, the single factors alone had opposite effects on foraging behavior. Lanterns caused fewer captures in the open, but seeds in the open led to a greater proportion of captures occurring in the open. When the factors are combined in one treatment, S_o may swamp out the effects of L if resources are more important than risk and vice versa. Since the manipulations correspond to conditions normally encountered in nature, factors in combination may indicate which factor is of greater importance.

Significant shifts into bushes in response to $L + S_o$ (Fig. 7b) show that lanterns were more important for D. merriami ($t = 3.67$, $p < 0.001$) and the grouped non-Dipodomys ($t = 2.82$, $t < 0.01$). Meanwhile, the seed addition had a greater effect on the foraging behavior of D. microps as indicated by the significant shift more into the open ($t = 4.97$, $p < 0.001$). The treatments appeared to have equal effect on M. pallidus since $L + S_o$ did not significantly alter habitat use compared to controls.

As is best illustrated by the case of M. pallidus, species combine assessments of risk and resources in order to make foraging decisions. This was true for other species as well although one factor

Fig. 7. Means (and standard errors) of habitat selection value and captures/night for the $L + S_0$ treatment. — They show that resources are more important than risk for D. microps and perhaps D. deserti, but that risk is more important for D. merriami. The habitat selection axis represents the percentages of captures occurring in the open. The abbreviations and open and hatched bars are the same as in Figure 4. * $p < 0.05$, ** $p < 0.01$, and *** $p < 0.001$.

- a. Habitat selection.
- b. Captures per night.



or the other would take on greater importance. Seeds would take on greater importance for large species, particularly D. microps, and risk would do so for smaller species including D. merriami along with the non-Dipodomys.

$\underline{L} + \underline{S}_0$ should have decreased nightly captures in comparison to controls for all species, particularly D. merriami and D. microps. In fact, D. merriami ($t = 4.23$, $p < 0.001$), D. deserti ($t = 2.09$, $p < 0.05$) all showed significant reductions in nightly captures (Figure 7a). Only M. pallidus showed an increase (nonsignificant).

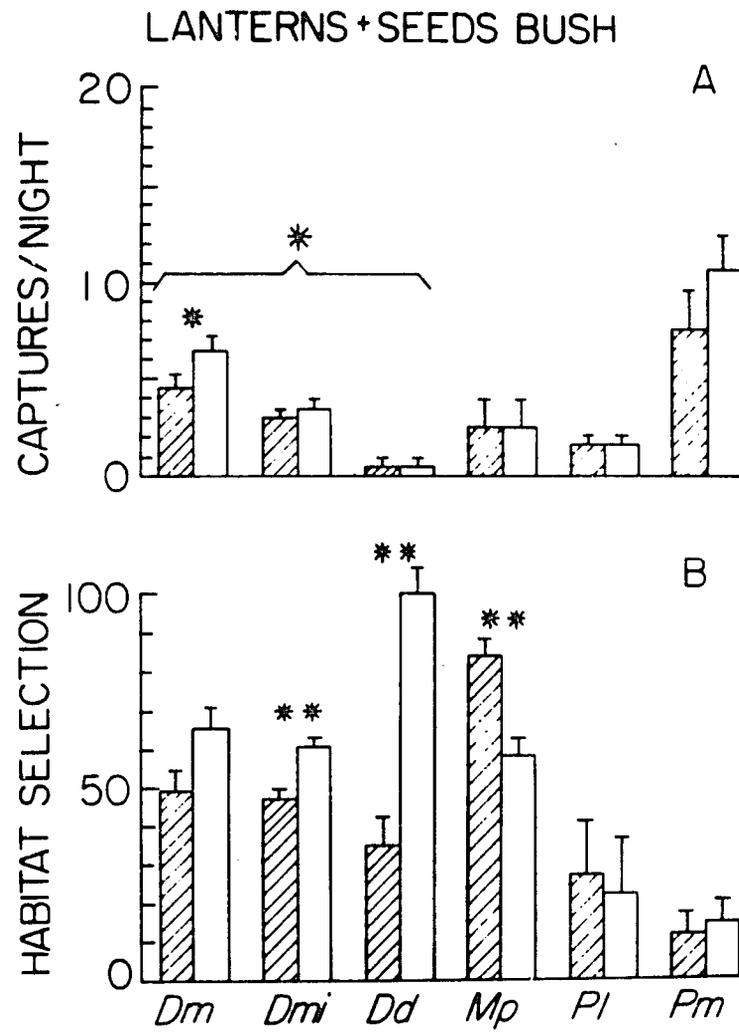
Since both \underline{S}_b and \underline{L} should lead to a greater proportion of captures occurring in bushes, the treatments in combination $\underline{L} + \underline{S}_b$ should cause an even greater use of the bush. Both should also reduce nightly captures.

Some of the responses to $\underline{L} + \underline{S}_b$ were quite surprising (Fig. 8). Though they were mostly in the predicted direction (fewer total captures, more captures in the bush), the responses themselves were often nonsignificant or of a lesser magnitude than for either of the corresponding single-factor treatments (\underline{L} or \underline{S}_b). Three species showed shifts of lesser magnitudes. The habitat use of D. microps significantly changed in response to the combined treatment ($t = 3.72$, $p < 0.001$), but the magnitude of the response was smaller than for each factor by itself. D. merriami showed a significant habitat shift during the \underline{L} treatment, but showed a significant reduction in total captures only during the combined treatment ($t = 2.58$, $p < 0.02$). P. maniculatus foraged significantly more in bushes during the \underline{S}_b

Fig. 8. Means (and standard errors) of habitat selection value and captures/night for the L + S₀ treatment. -- They show surprisingly unspectacular results except in the case of D. *desserti*. There, the combined factors cause a shift in habitat selection far stronger than did either factor by itself. The habitat selection axis represents the percentage of captures occurring in the open. The abbreviations and open hatched bars are the same as in Fig. 4. *p < 0.05; ** p < 0.01; and *** p < 0001.

a. Habitat selection.

b. Captures/night.



treatment but the shift was not significant for the $L + S_b$ treatment. M. pallidus used the bush significantly more during the L treatment and the S_b treatment, but foraged significantly more in the open during the combined treatment ($t = 6.68$, $p < 0.001$). Some responded as predicted. Kangaroo rats as a group responded to the combined factors as if the effects of the single factors were additive and showed a significant reduction in average nightly captures ($t = 2.41$, $p < 0.025$). Also, though D. deserti showed modest nonsignificant habitat shifts in response to the single factors, when both factors were combined the shift was quite pronounced and significant ($t = 3.74$, $p < 0.025$). This and the significant decrease in nightly captures for the $L + S_o$ treatment indicates that seeds may have most affected the foraging behavior of D. deserti. The abandonment of the bush by M. pallidus in response to $L + S_b$ (noted above) may be a response to interference or some other form of competition from both D. microps and D. deserti (the two largest kangaroo rats), both of which significantly increased their use of bushes during the treatment (see below).

General Discussion

Foraging behavior in desert rodents responds to both predatory risk and resources. The graphs presented in Figure 3 illustrate this point well. While species differ in mean microhabitat use, they use assessments of both risk and resources to make foraging decisions; microhabitat selection is flexible, and the need to respond to both risk and resource variation contributes to the flexibility. This is important owing to the role of differential habitat use among species

important owing to the role of differential habitat use among species in promoting species coexistence (Rosenzweig and Winakur 1969, Brown and Lieberman 1973, Rosenzweig 1973, Rosenzweig et al. 1975, Schroder and Rosenzweig 1975, Reichman 1975, M'Closkey 1978, Price 1978b, Whitford et al. 1978, Lemen and Rosenzweig 1978, Wondolleck 1978).

Combining Risk and Resources

Many optimal foraging theories assume that animals can combine qualitatively dissimilar factors together into a common currency in order to make foraging choices (e.g. Pearson 1975, Pulliam 1975, Belovsky 1978). This study demonstrates that animals do in fact do this. The experimental factors of seed enrichments and increased illumination both caused changes in foraging behavior. Furthermore, an examination of Fig. 1a shows that for the grouped heteromyid rodents the habitat selection value for $L + S_0$ is intermediate to the values for S_0 and for L , a result expected if habitat selection behavior is the result of combining the effects of risk and resources. This is also the case for M. pallidus considered alone. Similar sensitivity to predatory risk and resources has been demonstrated for many animals including yellow-eyed juncos (Caraco et al. 1980), notonectids (Sih 1981), sparrows (Pulliam and Mills 1977), and crayfish (Stein 1977). For P. maniculatus, the role of risk in restricting foraging to bushes and the significant effect of S_b on habitat selection show that here, too, both risk and assessment of resources combine to affect foraging behavior.

In a different experiment, I have directly demonstrated that the resource harvesting rates for desert rodents are reduced by increased predatory risk (Chapter 3).

The experiments presented here show that this is a result of avoidance or of decreased activity in the risky patch. This suggests that risk and resources can be combined because they each affect harvesting rates. The realized harvest rate of an animal in a patch will be a function of not only resource density and the ability of the animal to gather seeds but of its ability (and hence "willingness") to safely expose itself to predators. If animals rank patches according to realized harvesting rates, then, as risk increases and harvesting rates decline, so does patch quality. Animals which rank patches according to harvesting rates and exploit them accordingly use both assessments of risk and resources in making foraging decisions.

The experimental results, for kangaroo rats, indicate that how risk and resources are combined in making foraging decisions may depend on body size. D. merriami (42 g.) was affected by both the L and the S₀ treatments and the effect of L + S₀ was similar to the response to L. For D. microps (65 g.), habitat selection behavior was similar for S₀ and for L + S₀, so seeds were more important than risk in determining habitat selection. For D. deserti (100 g.), the results indicate a slight effect of seeds. As body size increases, risk apparently becomes progressively less and less important in affecting habitat selection. The difficulty which larger animals may experience while moving in bushes may also contribute to this. The pattern also

supports the notion that among kangaroo rats the ability to escape predation is associated with body size.

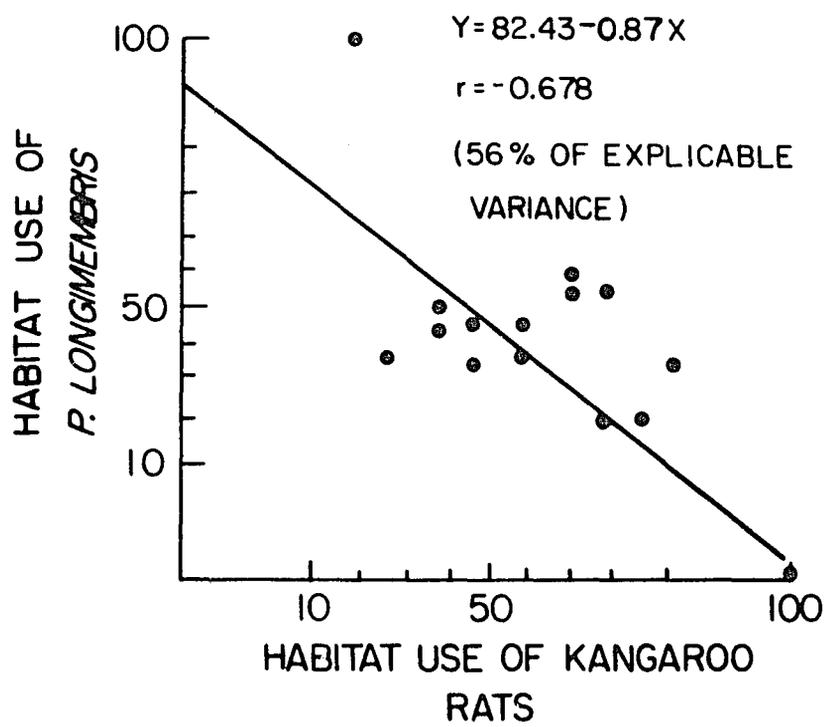
Those parts of a kangaroo rat's morphology which help it to detect and avoid predators include inflated auditory bullae and dorsally placed eyes to detect predators, and long legs to aid in escape from attacks (Bartholomew and Caswell, 1951, Webster 1962, Eisenberg 1963). The bipedality allows animals to jump out of harm's way and to make dramatic changes in directions while fleeing at great speeds. Abilities to detect predators are more tied to bullar inflation than to body size (Webster and Strother 1971), and as a result, there is a significant positive correlation for the species in this community between use of the open microhabitat and bullar volume (Fig. 10a). Aside from larger animals having larger auditory bullae, large size also aids escape. Large animals can jump higher to avoid attacks, run faster to reach safety of a burrow or bush, and dodge more effectively. In addition, large size renders animals harder to capture for some owls (Marti 1976, Mark and Yensen 1980). Among the kangaroo rats at Tonopah Junction, D. merriami and D. microps possess auditory bullae of similar volume despite the larger body size of D. microps. The experiments show that D. merriami is more responsive to changes in predatory risk than to changes in resources, and D. microps is more responsive to resource manipulations. While both species presumably have similar abilities to detect predators, the large size of D. microps apparently renders it superior in escaping once an attacking predator has been detected. Size reduces the impact of risk on foraging behavior to the point where the largest kangaroo rat in the

community, D. deserti, may not alter foraging behavior at all in response to changing predator risk. Hence, the larger the kangaroo rat, the better it is at escaping and the better it is at exploiting open areas,

Habitat Selection in Perognathus longimembris

Throughout the experiments, P. longimembris failed to respond as predicted. Although in no case did it respond significantly to an experimental factor, the sign of the trends was often in the opposite direction, suggesting that some pattern is present. P. longimembris was captured more times in the open than in bushes during the lantern treatment and during the treatment when seeds were added to bushes, and was captured fewer times in the open when seeds were placed in the open. Since recent work by Frye (1983) shows that kangaroo rats can aggressively displace smaller species from preferred habitats. If such is the case here, pocket mice should avoid areas with high densities of kangaroo rats. I have tested the hypothesis that there is an inverse relationship between habitat use of P. longimembris and by the kangaroo rats as a group on a nightly basis (Fig. 9). Due to occasional low captures per night for P. longimembris, I grouped nights together over intervals of 5 for the habitat selection value axis of the kangaroo rats. This yielded more accurate estimates of pocket mouse behavior in response to a given behavior of kangaroo rats. Linear regression shows a significant negative correlation ($r = 0.678$, $p < 0.01$). The regression equation for the ungrouped data is nearly identical ($y =$

Fig. 9. The presence of kangaroo rats in a microhabitat causes a decrease in the use of that habitat by P. longimembris. There is a strong negative correlation between habitat use of kangaroo rats and P. longimembris on a nightly basis. With kangaroo rats responding to the experimental treatments, P. longimembris apparently is forced to exploit risk microhabitats or those lacking resource enrichments. The two axes are market in percentage of captures occurring in the the open, but the spacing reflect the angular transformation. The regression equation is in terms of the transformed data.



$-0.87X + 82.22$, $r = -.343$, $p = 0.001$) to the equation for the grouped data, indicating that the result is robust to the data transformation.

Because of discreteness in the response variable, habitat use by kangaroo rats actually accounts for 56% of the explicable variance in habitat use by P. longimembris. For example, on one grid there were 5 captures of P. longimembris when the habitat selection value for the kangaroo rats was 57.50 (71.15% of captures in the open). For five captures, the possible values of habitat selection are 0, 26.57 (1/5), 39.23 (2/5), 50.77 (3/5), 63.43 (4/5), and 90 (5/5). The regression predicts a value of 32.42. The actual measured value was 26.57, which happens to be the closest possible value to the regression line. The difference between the closest possible value and the predicted value is 5.85. This part of the regression variance therefore could not have been explained.

The relationship has several possible causes. As already noted, kangaroo rats may be actively excluding the pocket mice from preferred microhabitats (or the pocket mice may be avoiding the kangaroo rats). Another possibility is that kangaroo rats are getting to the preferred microhabitat more quickly to gather seeds or to enter traps. Similarly, trap competition may exist even without high trapping success due to animals avoiding traps in one microhabitat at a station when a kangaroo rat has already been captured there. Captured animals make noise by hopping around in traps, and noise such as drumming of hind feet is an important means of communication in desert rodents. Drumming is believed to be important in agonistic behavior.

The end result is that capturing a kangaroo rat may actually prolong the time which kangaroo rats exclude others from an area.

Evaluation of the hypothesis that captures of P. longimembris are negatively affected by previously captured kangaroo rats is inconclusive. I have used two methods. In the first, I examined how trap success of P. longimembris in the two microhabitats is affected by capture of a kangaroo rat that same night somewhere at the station. I evaluated data using only stations where both species had been captured during the same experiment, and I assumed that P. longimembris individuals were the last animals caught each night. I then compared capture success of P. longimembris in the bush and in the open at stations without kangaroo rat captures on a given night to capture rates at stations where kangaroo rats had been caught in the bush and to rates at stations where kangaroo rats had been caught in the traps in the open. The trap competition hypothesis predicts that the capture of a kangaroo rat in a microhabitat will reduce the chances of capturing a P. longimembris in the same microhabitat at that station while increasing the chances in the other microhabitat. The results appear in Table 10. The only significant effect comes from an increase in captures of P. longimembris in bushes when a kangaroo rat is captured in the open. In fact, there is an overall effect of the presence of kangaroo rats on habitat-specific capture frequencies of P. longimembris ($\chi^2 = 13.2$, $p < 0.001$) which is largely due to the capture frequency of P. longimembris in bushes given that a kangaroo rat has been captured in the open. However, capturing a kangaroo rat in the open does not affect capture rates of pocket mice in the open. Also,

Table 10. Habitat-specific capture rates for Perognathus longimembris. -- The capture frequency of P. longimembris was significantly affected by the capture of kangaroo rats at stations which caught pocket mice, but only for P. longimembris captured in bushes when kangaroo rats were caught in the open. Here, capture of kangaroo rats in the open increased the capture frequency of pocket mice in bushes.

Kangaroo Rats	<u>Perognathus longimembris</u>			
	<u>Bush</u>		<u>Bush</u>	
	Capture Frequency	Z	Capture Frequency	Z
None	.331		.264	
Bush	.333	.017	.371	1.27
Open	.559	2.26*	.136	1.30

* $p < 0.05$.

capturing a kangaroo rat in the bush does not affect the probability of capturing a P. longimembris in the bush and has a nonsignificant effect on the capture frequencies in the open. The microhabitat-specific results suggest that it is not the mere negative effect of the presence of a kangaroo rat in a trap which is affecting P. longimembris trapability.

I also analyzed the data using a simulated regression. I asked what the regression between habitat selection of the kangaroo rats and habitat selection of P. longimembris would be if P. longimembris was responding only to the presence of kangaroo rats. Once I obtained the simulated regression, I compared it with the regression obtained from data. Based on actual capture success of P. longimembris and kangaroo rats at stations, I simulated P. longimembris trap success in microhabitats as follows. First, I assumed that kangaroo rats which were captured in the preferred microhabitat were captured first in any given night, after which I assumed that the pocket mice were caught, followed by the remaining animals. If a kangaroo rat was caught in the preferred microhabitat then all the pocket mice caught at that station that night were assumed to be caught in the non-preferred microhabitat. Where no kangaroo rats were caught, P. longimembris individuals were either assigned to a microhabitat at random based on the overall 60% preference for the bush, or assigned to the preferred microhabitat.

The following regression lines were obtained. For P. longimembris assigned at random to microhabitats in the absence of kangaroo rats, $Y = 23.63 + .220x$. This line differs significantly in slope from the regression line actually obtained from data ($t = 2.312$,

$p < 0.05$). One would expect no significant differences if trapping success on P. longimembris was solely a function of capture success of kangaroo rats. For P. longimembris assigned to the preferred microhabitat at stations where no kangaroo rats were caught, $y = 51.705 - .69X$. While this line does not differ in slope from the actual line ($t = 0.329$, $p > 0.05$), it does in intercept ($t = 4.303$, $p \ll 0.001$). Therefore, while trap competition due to noise made by a captured animal apparently does not contribute to the intercept, it may contribute to the slope of the relationship.

Regardless of the mechanism, the presence of kangaroo rats in a microhabitat reduces its exploitation by P. longimembris, resulting in increased exposure to predators or lack of access to enriched resources for the pocket mice.

This increased exposure to predators is in striking contrast to the behavior of P. longimembris in response to similar experiments conducted in 1980 (Chapter 1). In that year, P. longimembris was restricted more to bushes ($t = 16.21$, $p \ll 0.001$). While 39.3% of all captures of P. longimembris occurred in the open in 1981, only 16.43% occurred in the open in 1980. Why did P. longimembris forage more extensively in bushes in 1980?

The rodent community in 1980 had a different composition. Though P. maniculatus, which also mostly forages under shrubs, was the most abundant species in 1981, it was entirely absent in 1980, so the safety and resources of the bushes were more readily available to P. longimembris that year. In 1981, resources under bushes were exploited by a large number of P. maniculatus, and the likely decrease in

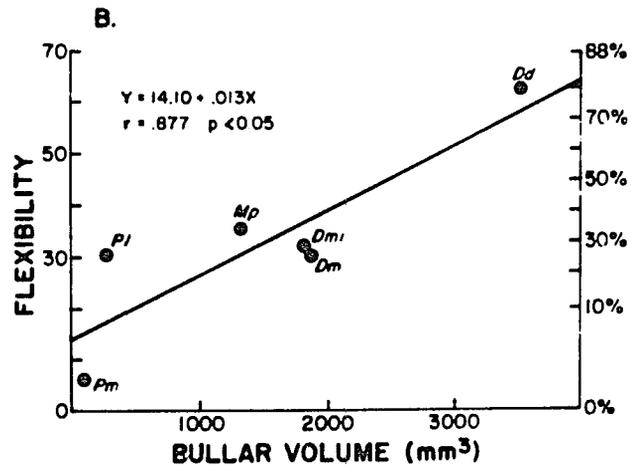
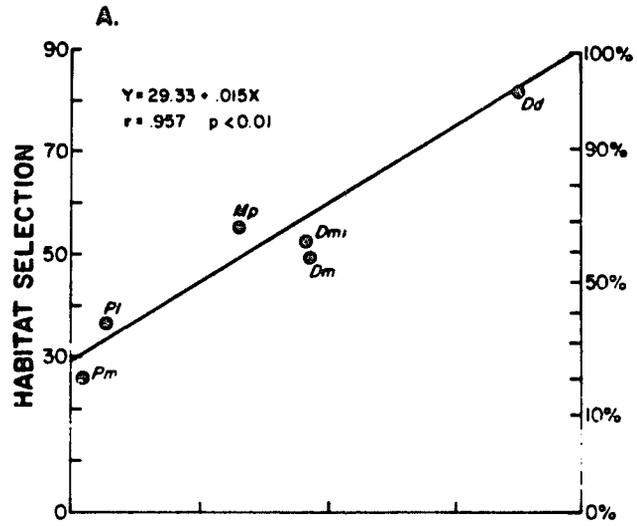
resource density there may have caused pocket mice to look elsewhere for food. The interaction between the two species was unlikely to have been interference since the correlation of habitat use between the two from night to night was weak and insignificant ($r = -0.23$, $p = 0.591$). P. longimembris did not avoid areas where there were concentrations of P. maniculatus. Possibly, also the presence of P. maniculatus relieved some of the predation load on P. longimembris, thus decreasing the risk of foraging in the open. Though deer mice venture infrequently into the open, they were overrepresented in the diet of resident long-eared owls (Asio otus) on the study site (unpublished data). If owls were spending most of their time catching deer mice, pocket mice would have been free to go where they pleased.

In 1981, P. longimembris must have been squeezed from both sides. It was outcompeted under bushes by deer mice and excluded from preferred areas by kangaroo rats.

Community Structure of the Desert Rodents of Tonopah Junction

In addition to demonstrating that changes in habitat-specific mortality risk cause predictable changes in habitat utilization of several species of desert rodents, these experiments support the hypothesis that habitat-specific differences in risk allow habitat partitioning according to morphological anti-predator specialization. The auditory bullar volume of species is strongly and positively correlated with use of open microhabitat in the absence of experimental manipulations (Fig. 10a). Flexibility of foraging behavior as measured

Fig. 10. Habit selection behavior in desert rodents is dependent on morphology. -- Animals with greater bullar volume have (a) greater preference for the open; and (b) greater behavioral flexibility (greatest difference between experimental treatment means) in response to changes in risk and resources. The abbreviations are the same as in Figure 4. The dependent axes are scaled both in percentage of captures in the open and its angular transformation.



treatments is also significantly correlated with bullar volume (Fig. 10b). Animals with large bullae show a greater preference for the open and have greater behavioral flexibility than animals with smaller bullae. Since animals with larger bullae can better detect predators (Webster and Strother 1972), exploitation of the open microhabitat is directly related to the ability to avoid predators. Habitat-specific risk allows habitat segregation according to morphologies. The relationship also suggests that as more and more open area is found at a site, animals with larger and larger bullae can be added to the rodent community. Hence, community structure can be directly related to predatory risk.

Bullar volume is a complex variable which includes body size as well as relative bullar inflation. While bullar inflation reflects anti-predator morphology only, body size is also involved in considerations regarding mobility and ability to use distant patches (Reichman and Oberstein 1977, Price 1978a, Hutto 1978, Hutto 1978, Thompson 1982a). While habitat selection differences among species which affect coexistence and community structure are related to adaptations to reduce predatory risk, they may also reflect the competitive structure of these communities.

Although community composition at Tonoaph Junction changed between the years, there seems to have been a consistent pattern of microhabitat use: one species which forages mainly under bushes, four "kangaroo rats," which forage to varying degrees in the open, and one species which forages away from the nightly action. In 1980, P. longimembris foraged mostly in bushes regardless of manipulations of

illumination and resources; in 1981, the same role was filled by P. maniculatus. In 1981, M. pallidus behaved much like a kangaroo rat; in 1980, it was odd man out much like P. longimembris in the following year. For example, in 1980 M. pallidus avoided open areas during a treatment designed to reduce risk in the open ($t = 2.30$, $p < 0.05$). While M. pallidus was behaving so oddly, D. merriami was very common along with D. microps, D. ordii, and D. deserti. In 1981, the kangaroo rats were less abundant, and D. ordii was nearly absent. At this time, M. pallidus behaved more like a kangaroo rat (although when the L + S_b treatment pulled D. deserti into bushes, M. pallidus foraged more in the open, much as in 1980). Even with a different species composition, the community was organized similarly in both years.

That there are four kangaroo rat strategists but only one bush competitor may be due to the competitive abilities of species aside from abilities to escape predators and to interfere with others. Rosenzweig and Sterner (1970) demonstrated that rodents of smaller body size always derive more net energy from each seed consumed. In addition, they require far fewer seeds and a smaller home range in which to meet their daily requirements. From an energetic point of view, they have inherent advantages as competitors. Since predatory risk under shrubs is low and interference there difficult, animals which are restricted to the safe microhabitat can maximize energy intake while under bushes rather than minimize exposure time and foraging time and should evolve to be the best energetic competitor possible.

Such a strategy can also serve to minimize the necessity of crossing open, risky areas in order to travel to new patches (Thompson 1982). The result is that a single species of small body size exploits areas under bushes. In this community, the bush competitor weighs only 7 grams (P. longimembris) and under certain circumstances is replaced by a prolific breeder weighing 17 grams (P. maniculatus). In contrast, the kangaroo rats which specialize in predator avoidance in open microhabitats where large size is an advantage weigh from 40 to 100 grams and so have much higher metabolic requirements and foraging costs. Were it not for the effects of predatory risk and interference, the only advantage that kangaroo rats would have would be shorter traveling times while moving between patches and perhaps a higher harvesting rate (Hutto 1978; but not enough to compensate for higher metabolic costs). If not for predatory risk, the small deer mice and pocket mice would probably outcompete the larger species everywhere.

Why are there so many coexisting kangaroo rats? To begin with, the coexistence of the four kangaroo rat strategists is made easier by the large component of vegetation in the diet of D. microps (Kenagy 1973b). The remaining kangaroo rats differ in habitat selection: animals with larger bullae forage more in the open, owing to their greater ability to detect predators and escape. Interference competition may also promote the coexistence of kangaroo rats of different body sizes (Frye 1983). In addition, smaller kangaroo rats have an energetic advantage over larger kangaroo rats similar to the advantage deer mice and pocket mice enjoy over kangaroo rats. As such,

they should be able to exploit certain patches or combinations of microhabitats which are unprofitable for larger species (Frye 1983).

It seems that the evolution of kangaroo rats and their presence in the community is owed to the presence of predators. With harvesting rates lower in risky habitats due to predatory risk (Chapter 3) and an energetically efficient competitor exploiting seeds under the safe haven of shrubs, resources in the open should be underexploited and relatively abundant. Natural selection should favor the evolution of species which specialize in exploiting the risky environment (Rosenzweig 1978). This is apparently what has happened.

For any group of competing species which make foraging decisions regarding habitat use where risk differs among habitats or microhabitats, predation may influence community structure by selecting for anti-predator specialists.

In contrast to the community described in this paper, other rodent communities may have many more quadrupedal species than bipedal species. For example, in semi-arid grasslands in Arizona there may be only one common kangaroo rat occurring with three common Perognathus species (e.g. Wondolleck 1978). At these sites, open areas are much smaller than on Great Basin sand dunes and may be filled or surrounded with clumps of grass and small shrubs. Also, the plants themselves are much more diverse in size, species richness and foliage-height diversity and perennial cover is greater. In light of Rosenzweig's (1973) findings that P. penicillatus can exploit open area less than 4 meters in radius but is excluded from areas greater than 8 meters in radius, it seems likely that there are more areas that bush mice can

exploit in semi-arid grasslands. The anti-predator adaptations of kangaroo rats would be less of an advantage since they would open up fewer unerexploited resources to species foraging in open areas. The high foliage-height diversity is associated with the coexistence of several bush species (Rosenzweig and Winakur 1969) which may exploit different foliage heights (Rosenzweig et al. 1975) or may specialize on certain patch types within the rich array of microhabitats (Price 1978b). In addition, with kangaroo rats reduced in importance, some bush mice would be at an advantage if they could aggressively exclude others from preferred patch types, which should favor some of the larger pocket mouse species (e.g. Perognathus baileyi and P. hispidus). Thus the role of habitat usurper may be taken over by pocket mouse species. Otherwise, the high species diversity of pocket mice is determined by differential habitat use. In short, the relative abundance and species richness of a heteromyid genus in a desert community seems to depend on the abundance of its preferred microhabitat.

If species coexistence is shaped by predatory risk, then changes in risk should change community structure. Experiments by various investigators have changed the physical structure of the environment and observed changes in the composition or relative abundance of species which seem to be related to changes in risk (Rosenzweig 1973, Whitford et al. 1978, Thompson 1982b). Rosenzweig (1973) experimentally altered vegetation densities in a community containing D. merriami and Perognathus penicillatus. Removing vegetation eliminated P. penicillatus from the plots providing the size

of the open area was greater than 8 meters in radius. The same treatment favored D. merriami. Augmenting vegetation on plots increase P. penicillatus densities at the expense of the kangaroo rats. Whitford et al. (1978) obtained similar results between D. ordii and D. merriami by using a defoliant to alter vegetation structure. These experiments altered risk by augmenting or eliminating cover, and resulted in changes in species densities. Thompson (1982b) changed habitat structure by erecting shelters in open areas. This reduced effective inter-plant distance without substantially increasing vegetation cover, because animals could move with less exposure from plant to plant. Species diversity increased on the plot as two new species which were previously absent were now able to enter the community. Abramsky (1978) also observed new species entering the community in response to an experimental manipulation. Rather than changing vegetation structure, Abramsky added seeds to short grass prairie habitat. In response to the enrichment, D. ordii entered the community and reached high density. The response may have been due to a change in the risk and reward schedule which now allowed D. ordii individuals to gather more resources with the same expenditure of risk (Abramsky, personal communication, 1982).

Foraging decisions are affected by food resource availability and predatory risk as well as by morphology. Hence, the extent to which predation affects species interactions will depend upon the extent to which predatory risk affects decisions regarding diet and habitat use by individuals of different species and whether there are trade-offs between competitive ability and predator avoidance or

predator avoidance in one habitat over another. While either predation or competition may be of greater importance in shaping the structure of one community or another, both factors affect foraging decisions of individuals, and so both are inextricably linked in shaping species interactions and community structure.

Risk and the Community Structure of Animals

Predation structures communities of mobile, foraging prey by reducing competitive interactions among species over evolutionary time. If two adjacent or interspersed habitats occupied by a single species differ in predatory risk, the riskier habitat should contain relatively abundant and underexploited resources. Under such conditions, natural selection could favor the evolution of a second species or species group which specialize in exploiting the risky environment (Rosenzweig 1978). As the newly evolving anti-predator specialist gains access to the underexploited habitats, at the same time it alleviates competition with species still restricted to the safe habitat. This assumes that there is a trade-off between anti-predator adaptations and exploitative abilities (e.g. mediated through body size). As overlap in habitat use declines, competitive interactions among species are reduced. This allows for the coexistence of more species because of finer habitat partitioning (Vandermeer 1970), and species diversity increases.

Predation structures communities of sessile prey over ecological time by means of a different mechanism (e.g. Harper 1969, for plants; Paine 1966, 1971, Lubchenco 1978, Menge and Lubchenco 1981 for intertidal organisms). There, the community effects of predation

are mediated through changes in prey densities within habitats. Because prey communities are spatially structured, if predators selectively remove dominant competitors space is made available for competitively inferior species. Predation increases within-habitat species diversity by selectively reducing prey densities. A spatial gradient in predation pressure can also lead to between-habitat partitioning.

Though the mechanisms differ, predation affects both sessile and mobile organisms and can help promote high species diversity.

CHAPTER 3

HARVESTING RATES AND RISK-SENSITIVE FORAGING IN DESERT RODENTS: A COMPARISON OF CONVERGENT COMMUNITIES

In recent years both theoretical and empirical studies have appeared which concern themselves with the effects of predatory risk on foraging behavior. For example, Caraco et al. (1980) have shown that flock size and scanning rate in yellow-eyed juncos (Junco phaeonotus) change dramatically in the presence of a predator. Sih (1981) has demonstrated that young notonectids (Notonecta hoffmannii) choose to forage in areas which are free of cannibalistic adults even if the safe area is relatively resource-poor. In addition, Pearson (1976) and Rosenzweig (1974) have demonstrated theoretically that predatory risk should affect such foraging behavior as patch choice and activity.

The most desert-adapted of the rodents of North America belong to the family Heteromyidae. Their adaptations include elongated hind legs for bipedal locomotion (Eisenberg 1963) and inflated auditory bullae (Webster 1962). These adaptations are important anti-predator defenses. The heteromyid rodents are strongly convergent morphologically with their Old World counterparts (Mares 1980). Morphological similarities include elongated hind legs for saltatorial locomotion and inflated auditory bullae. These characteristics are associated with the exploitation of risky microhabitats in heteromyid rodents of North America (Chapter 2). Like desert rodents of North

America, Old World desert rodents are diverse and abundant. Brown, Reichman and Davidson (1979) suggest that community structure and behavior of North American and Old World desert rodents should be convergent as well.

Biologists have looked for convergence between organisms from areas with similar climates on different continents. They have compared species morphologies and community organization with the intent of demonstrating and deciphering general principles of natural selection (e.g. Sage 1970, Lein 1972, Karr and James 1975, Fuentes 1976, Mares 1976, Cody and Mooney 1978). An assumption often made in these investigations is that similar climatic conditions will yield similar selective pressures (e.g. physiological requirements, resource availability, and competition) which result in the evolution of similar morphologies and even community structure. That is to say, natural selection leads to the same, best solution. Rarely have these studies identified the selective pressures and made predictions regarding how they may affect characters such as behavior and morphology, nor have attempts been made to elucidate the factors promoting species coexistence.

Here, I examine how predation might influence one aspect of foraging behavior and thereby how it may influence community structure in desert rodent communities on two different continents.

Methods

Study Sites

The North American study was conducted on Great Basin Desert sand dunes located at Tonopah Junction, 12 km south of Mina, Nevada, U.S.A. at an elevation of 1346 m and latitude 38.2° N. The sand dunes are derived from sedimentary deposits laid down in Pleistocene lakes (Brown 1973). Precipitation averages 114 mm per year with no pronounced rainy season. The dominant vegetation is greasewood (Sarcobatus vermiculatus) along with four-winged salt bush (Atriplex canescens). The rodent species present during the study include Merriam's kangaroo rat (Dipodomys merriami), Ord's kangaroo rat (D. ordii), Great Basin kangaroo rat (D. microps), desert kangaroo rat (D. deserti), pallid kangaroo mouse (Microdipodops pallidus), small pocket mouse (Perognathus longimembris), and white-footed deer mouse (Peromyscus maniculatus).

The Old World study was conducted in the Negev Desert on the sand dunes of Mishor Rotem, located 12 km south of Dimona, Israel at an elevation of 380 meters and at latitude 31.14° N. There, the sand dunes are derived from local weathering of sandstone. Annual mean precipitation is 101 mm, most of which occurs between November and April. The dominant vegetation consists of Retama raetam and Calligonum comosum (Abramsky, manuscript). The rodent community consists of the pigmy gerbil (Gerbillus henleyi), Allenby's gerbil (G. allenbyi), greater Egyptian gerbil (G. pyramidum), and gentle jird (Meriones crassus).

Experiments

I conducted experiments at Tonopah Junction in July 1980 and June and July of 1981 and at Mishor Rotem in June of 1982. The experiments were designed to test whether changes in perceived risk of predation affects the level of foraging activity for the respective communities of desert rodents.

I manipulated predatory risk by simulating moonlight with a camp lantern. Animals foraging in light will cast shadows, and the contrast should be more easily spotted by predators. Also, important rodent predators such as owls have been shown to be much more dangerous when light is present (Dice 1945, 1947). Hence, altering levels of illumination is tantamount to altering predatory risk.

At the Tonopah Junction site, thirty feeding trays filled with 30 g of mixed bird seed were placed out on consecutive nights under levels of either low or relatively high illumination. The 30 trays were arranged in a 5 by 6 grid with trays separated by 5 meters. I conducted four trials and randomized the order of treatments within each trial. The low-illumination treatment was run during moonless nighttime hours, and the high illumination treatment was run during "moonlit" hours. "Moonlight" was supplied artificially with a camp lantern which was situated 8 meters off the grid. Trays were checked every ten minutes, and the length of time it took until a tray was completely emptied of seeds was recorded for each tray. Since the same grid was used for both treatments, I was able to test for treatment effects using paired observations of the same tray.

The experiment at Mishor Rotem had a slightly different design which allowed me to test whether illumination intensity affects foraging activity. Instead of a grid pattern, 30 feeding trays with 14 grams of seeds were placed in 4 concentric circles surrounding the lantern. The radius of the first circle was 5 meters; the others were at 5-meter intervals greater than that. Trays were placed at a constant distance along the circles; therefore the first circle contained 3 trays, the second had 6, the third had 9, and the fourth had 12. In addition, there was a control plot with a similar layout. Seed removal was measured by checking trays every half hour, collecting the remaining seeds at trays at which seed removal had occurred, and weighing the remainder. Each time seed remainders were collected, the time and station were recorded and another 14 grams of seeds were left in the tray. The trials on both plots were run simultaneously.

In both experiments, the light supplied by lanterns approximated natural light intensities from moonlight (Chapter 2).

Results

At the North American site, in every trial the mean time to emptying of a tray was greater for the "moonlight" treatment (Table 1). It varied from 54.57 minutes to 130.67 minutes whereas the mean time to emptying varied from 43.67 minutes to 84.33 minutes for the moonless treatment. Owing to departures of the data from normality (g_2 as much as -2.52), I used the sign test to analyze the data. In all four trials, the rate of seed harvesting by North American desert rodents

was decreased significantly (Table 11) by illumination and therefore apparently by perceived risk of predation.

There were also significant treatment effects at Mishor Rotem, although the mean harvesting rates over the entire grid did not differ significantly. Harvesting rates nearer to the light source were much lower than under control conditions, but as distance from the plot center increased and light intensities dropped, the rates on the two plots became very similar (Figure 11a). The regression line of the natural logarithm of harvesting rate versus distance from plot center has a significantly lower y-intercept than for the control ($t = 2.212$, $p < 0.05$). It also has a significantly steeper slope ($t = 9.94$, $p < 0.001$).

Variance in harvesting rates differed greatly between the treatments. The variance among trays in seed removal increased significantly with distance from the plot center for the control treatment ($r = 0.98$, $p < 0.05$). However, the variance on the inner circles for the experimental treatment was far lower than on the control. At the same time, it was far higher on the outer circles. Hence, the increase in variance with distance (slope) is significantly greater for the experimental treatment ($t = 29.11$, $p \ll 0.001$, Figure 11b).

Further evidence suggests that risk also affects resource harvesting rates in sand dune communities in the Negev. The concentric circles experiment was conducted there in April 1982 as well. However, cold nighttime temperatures kept foraging rates low, so instead of

Table 11. The rate of harvesting of resources at Tonopah Junction is decreased by illumination. -- The mean time to emptying of feeding trays along with standard error of the mean appear in this table. Also appearing are pairwise comparisons between trans under light and dark conditions.

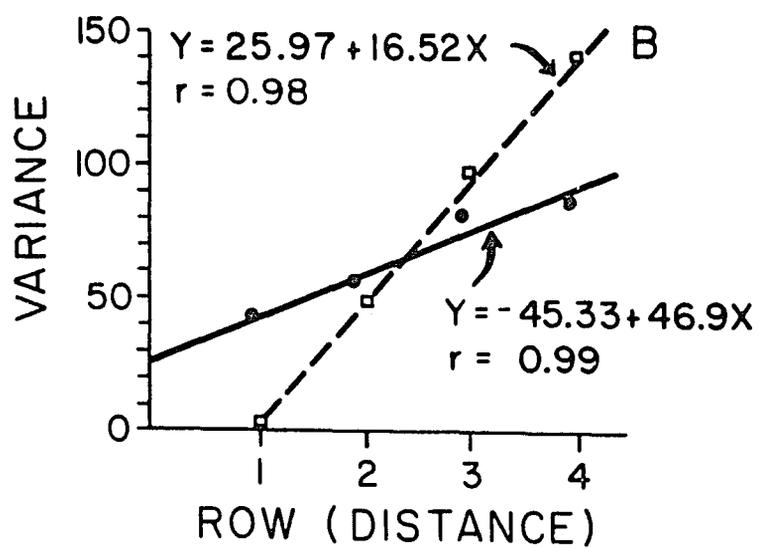
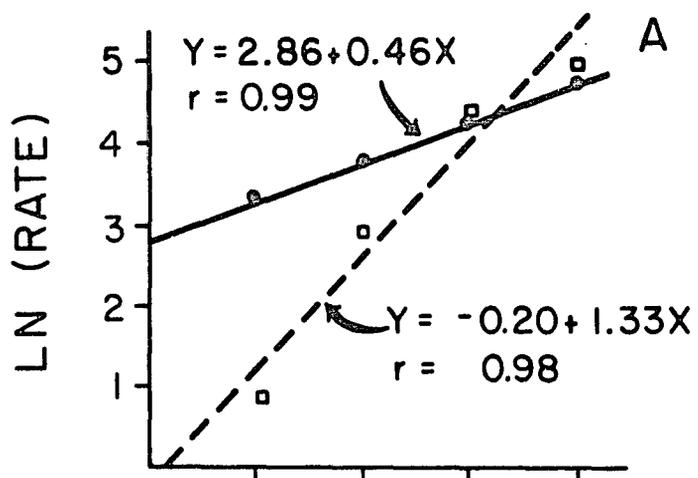
Dates of Trial	Mean with Lantern (minutes)	Mean Without Lantern (minutes)	Comparisons ¹			Significance
			-	+	0	
8, 15 July 1980	54.66 (3.67)	43.66 (5.31)	4	18	8	p < 0.005
27, 28, June 1981	100.33 (8.18)	84.3 (7.32)	9	20	1	p < 0.05
29, 30 June 1981	92.00 (8.17)	78.33 (7.66)	9	19	2	p < 0.05
2, 3 July 1981	130.67 (9.93)	73.00 (5.15)	2	24	4	p < 0.005

1. "+" Indicates that the tray was emptied in more time when the lantern was present.
 "-" Indicates that it was emptied in less time.
 "0" Indicates a tie.
2. Sign test.

Figure 11. Predatory risk affects foraging behavior for animals at Mishor Rotem.

a. Harvesting rates.

- b. Variance in harvesting rates among trays in a row increases with distance from plot center, but harvesting rates and variance on inner circles are lower for experimental treatment. Open boxes represent experimental data, and filled circles represent control data. "Row" refers to circle and represents increasing distance (by 5 meters for each circle) from plot center. Feeding rates are plotted in terms of grams of seeds removed per tray per minute.



recording rates of seed removal, I took advantage of the rodents' habit of emptying a tray completely of seeds once it had been discovered. I thus allowed the experiment to run all night long and counted the empty trays in the morning. I then compared the number of empty trays on the two plots on a circle-by-circle basis (Table 12). By paired t-test, there was significantly greater seed removal on the control plot ($t = 2.21, p < 0.05$).

General Discussion

These experiments suggest that perceived predatory risk affects the foraging behavior of desert rodents. Harvesting rates dropped in response to increased illumination, so as risk increased animals foraged less or foraged elsewhere.

Other experiments and observations also support this conclusion. At Tonopah Junction, pocket mice, deer mice and kangaroo mice show significant declines in foraging activity in the face of increased risk (Chapters 1 and 2). Also, North American rodents are less active in periods of full moon (Justice 1960, Lockard and Owings 1974b) when the act of simply crossing an open area may prove to be a risky venture. Furthermore, animals are more active in shadows around bushes than in open areas (Lockard and Owings 1974a). Finally, in the Negev Desert the foraging activity of all species, as indicated by animal tracks, declines greatly and shifts to bushes in response to moonlight (Orr, personal communication, 1983). Hence, animals in both communities avoid risky patches in space and time.

Table 12. There are significant differences between experimental and control plots at Mishor Rotem in the amount of seed removal by rodents. -- Number of trays emptied of seeds on each circle on the experimental and control plots is given. A comparison of number of trays emptied per circle shows significant differences between control and experimental plots with seed removal being greater on the control plot (paired t, $t = 2.21$, $p < 0.05$). Circle 1 is closest to the plot center, and circle 4 is furthest away.

Trays Emptied			
Circle	Experimental	Control	d_i
1	0	2	2
2	1	3	2
3	5	8	3
4	6	6	0

Observed variance in harvesting rates can also be understood as a response to predatory risk. As distance from the light source increased so did the variance in illumination. This is a consequence of using a point source of light, because the further a feeding station is from the point source, the more likely the light will be intercepted somewhere along the way to the shrub, thus casting a shadow. Hence, stations close to the lantern were uniformly well illuminated, foraging rates were low there, and the variance in foraging rates was low. Further from the lantern, light intensities were lower and foraging rates increased; also, some trays were in shadow while others were in light. It seems that rodents on the outer circles were concentrating foraging activity on trays in shadows while avoiding stations in the light. Similar behavior has been observed for North American desert rodents (Chapter 2).

Optimal foraging theory predicts that animals should preferentially exploit patches according to patch-specific harvesting rates (e.g. MacArthur and Pianka 1966, Schoener 1971, Charnov 1976), but predatory risk through its effect on harvesting rates should also affect habitat use. As has been demonstrated here, increased predatory risk in a microhabitat leads to a decline in harvesting rates. Animals forage less, spend more of their limited foraging time in safer microhabitats and perhaps spend more of their active time watching for predators (Caraco 1979). Similarly, if risk differs between two microhabitats then harvesting rates should be higher in the safer microhabitat, providing that the resource levels are comparable. Animals should select the safer microhabitat. Indeed, at Tonopah

Junction when risk was manipulated in a habitat-specific manner, animals increased foraging activity in the safer microhabitat (Chapters 1 and 2). Similarly, at Mishor Rotem harvesting rates were higher further from the light source, where risk was presumably lower. Animals at both sites selected low-risk areas. Hence, habitat selection as well as foraging activity is affected by predatory risk.

If predatory risk differs among habitats or microhabitats, then risk may be an axis along which habitat partitioning may occur. This is especially important since habitat selection differences among coexisting species help promote coexistence in both these communities (Brown and Lieberman 1973, Abramsky, personal communication, 1982). At Tonopah Junction, the coexisting species differ strikingly in their morphological and behavioral anti-predator adaptations (e.g. inflated bullae and bipedal locomotion). Furthermore, the preference to forage in the open, riskier microhabitat for a species is significantly correlated with its degree of morphological anti-predator specialization as measured by bullar volume (Chapter 2, Figure 8a). Hence, anti-predator specialization allows habitat specialization in this community. Similarly, in the Negev the preference for open habitats seems to be associated with the ability to avoid predation (personal observation). For example, the gerbil species which specializes in exploiting the most open habitat is also the most fleet afoot. In North America, the foraging behavior of animals is affected by predatory risk and predation helps shape habitat selection patterns and community structure. In Israel, predatory risk also affects

foraging decisions, and there is a reason to think that predation also contributes to shaping community structure.

In summary, the New World assemblage at Tonopah Junction is convergent with the Old World community at Mishor Rotem in that predatory risk affects foraging behavior of animals similarly in both locations, and may well structure both communities in similar ways by promoting habitat selection differences among species.

APPENDIX

To illustrate better the role that both predatory risk and resources play in determining habitat selection behavior of various species, I plotted mean habitat selection for a treatment against a ranking of the treatments. Treatments were ranked according to their expected effect on habitat selection. \underline{S}_0 is the only treatment which clearly should draw animals onto the open. It was assigned a rank of 1. In contrast, both the \underline{L} and the \underline{S}_b treatments should force animals to forage more under the cover of bushes; the treatments were assigned a rank of 3. $\underline{L} + \underline{S}_0$ consists of a factor which draws animals into the open and one which forces them into bushes. It should have an intermediate effect on habitat selection. It was given a rank of 2. The \underline{C} control which consists of no factor should have an "effect" which is intermediate to \underline{S}_0 on one hand and \underline{S}_b or \underline{L} on the other. Like $\underline{L} + \underline{S}_0$, it was given a rank of 2. Since both \underline{L} and \underline{S}_b should have caused animals to forage more in bushes, the combined $\underline{L} + \underline{S}_b$ treatment should have an even stronger effect. It should be placed to the right of all the treatments and was given a rank of 4. The rankings were the same for each species.

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