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INTERACTIONS BETWEEN PREDATION RISK AND COMPETITION: A FIELD STUDY OF KANGAROO RATS AND SNAKES[1]

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Abstract. The effects of predation risk from snakes on microhabitat use of kangaroo rats (*Dipodomys deserti* and *D. merriami*) was studied in the Mojave Desert. I concentrated on the effects of the predator on the foraging behavior of the rodents and eliminated effects of prey capture on prey population size. Foraging stations contained three seed trays, one in each of three microhabitats (Open, Bush, Grass). The amount of seed left in each tray after one night of foraging was used to assess the responses to predation risk and other foraging costs; additional data were collected during direct observations and by trapping. To investigate the effect of snakes on foraging and microhabitat use of kangaroo rats I manipulated snake presence at the stations. I studied the interactions between predation risk from snakes and moonlight by conducting experiments near full and new moon nights. Both species of kangaroo rats preferred to forage in the Open and avoided the Bush. This preference is opposite to the preference of the main rodent-eating snake at the study site, the sidewinder (*Crotalus cerastes*), which prefers the Bush over the Open. At stations with snakes, *D. deserti* reduced its foraging and avoided the Bush more than in control plots. However, *D. merriami* foraged more at stations with snakes. *D. merriami* thus foraged at the trays that were avoided by *D. deserti* and it reduced the risk of interference from the dominant *D. deserti*. In contrast to studies by other investigators, moonlight (which is associated with increased risk from owls) did not reduce the foraging or affect the microhabitat use of kangaroo rats in summer; moonlight effect was seen only in the fall, when snakes were not active. Unlike risk from owls, risk from snakes is high under bushes and during dark nights. The activity of rodents in summer is a combined reaction to the different predation risks posed by snakes and by owls.

Key words: Crotalus cerastes; *desert rodents;* Dipodomys deserti; Dipodomys merriami; *field manipulation; foraging behavior; interference competition; microhabitat use; Mojave Desert; moonlight effect; seed tray experiments; snake predation.*

INTRODUCTION

Most of the initial research on interactions between predation and competition has only considered the effects of predators on the number of prey (Holt 1977, Hastings 1978, Vance 1978, Glasser 1979). However, there is a growing interest in effects of predators on the behavior of prey species (Lima and Valone 1986, Schoener 1987). For example, predation risk may affect the time and duration of foraging or it may shift the activity of vulnerable prey species to safe microhabitats (e.g., Brown et al. 1988). Such behavioral effects on prey animals can explain species coexistence as an interaction of both predation and competition (Kotler and Holt 1989).

The understanding of coexistence in animal communities has been greatly enhanced by studies of desert rodent communities (Price and Brown 1983, Kotler and Brown 1988). Despite the fact that predation is often mentioned as one of the likely factors involved in structuring desert rodent communities (Price and Brown 1983, Price 1986, Kotler and Brown 1988, Bowers 1990), few studies have tested this hypothesis. There are two main areas in which studies of the effect of predation are lacking. First, the effect of predation on prey behavior has not been directly studied in the field, presumably because of the difficulty in manipulating predators in the field (Price and Brown 1983, Price 1986). Kotler (1984) attempted to overcome this difficulty by manipulating light in the field, assuming that illumination is correlated with predation risk from visually oriented predators. Other studies were done in artificial arenas, where the density of the predators was much higher than in nature (Brown et al. 1988, Kotler et al. 1988, Longland and Price 1991). Second, studies on behavioral effects of rodent predators have generally focused on owls (e.g., Kotler 1984, Brown et al. 1988, Kotler et al. 1988, Longland and Price 1991) and they rarely consider reptilian and mammalian predators. Effects of mammals on rodent behavior have only been studied once (Dickman 1992, on *Mus domesticus*). Daly et al. (1990) demonstrated the importance of snakes as a cause of mortality of radio-tracked *D. merriami* in the Colorado Desert. However, only few stud-

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ies investigated effects of snakes on rodent behavior: Pierce et al. (1992) studied the differential risk to desert rodents from the Great Basin rattlesnake (*Crotalus viridis lutosus*) in shrub-covered arenas and in arenas without vegetation; Kotler et al. (1992, 1993) exposed, in an enclosure, two species of gerbils to snakes and examined the effects on the gerbils' foraging.

Snake foraging activity is not evenly distributed over space and time (Greene and Santana 1983, Reinert et al. 1984; A. Bouskila, *unpublished data*), suggesting that snakes may affect competitive relations between coexisting rodents by altering the rodents' microhabitat choice. If risk from snakes is involved in the coexistence of rodent species, the species must react differently to this risk. There are two main advantages in using snakes as predators in such a study. First, snakes are relatively easy to manipulate. Second, because snakes rarely capture prey (Mushinsky 1987; A. Bouskila, *unpublished data*), snake predation has small numerical effects on the populations of rodents, allowing the investigator to concentrate on behavioral effects.

In this paper I address the effect of predation risk from snakes on the behavior of two sympatric kangaroo rats. This is the first study, as far as I know, in which predators were manipulated in the field in order to study the effects of a terrestrial predator on prey behavior. Specifically, the study addresses the following questions: Does the presence of snakes affect the foraging and microhabitat use of kangaroo rats? If so, do the species of kangaroo rats differ in their reactions to presence of snakes? And finally, does the risk from snakes interact with moonlight (which is associated with risk from visual predators)?

Methods

Study site

The study site was in the northern part of Kelso Dunes, East Mojave Desert, California (6.5 km southwest of Kelso, 1.6 km south of Kelso Wash). I concentrated my observations and experiments in an area of 1 × 0.8 km, bordered on the southwest by a steep-sloped wash (Cottonwood Wash). The sand is stabilized, except for small patches of shifting sands on top of seven hills. The vegetation is composed of perennial grasses (mainly galleta grass, *Hilaria rigida*) and large (up to 10 m in diameter) creosote bushes (*Larrea tridentata*). The study site was occasionally grazed by cattle. I distinguished between three microhabitats: (1) Bush, under the canopy of creosote bushes and under protruding branches; (2) Grass, under or within 50 cm of a perennial grass; (3) Open, the area devoid of vegetation between bushes and grasses. I determined the proportion of the study site covered by each of the microhabitats in four random transects (mean length, 178.5 m). I measured distances with a measuring wheel (Precimeter model 394, Rolatape Corporation, distributed by Forestry Suppliers, Jackson, Mississippi, USA) to the nearest 10 cm. Bush covered 1.9% of the area, Grass 24.2%, and Open 74%.

Study organisms

The study concentrated on a simple community of two species of kangaroo rats (*Dipodomys deserti* and *D. merriami*), and a common predator, the Mojave Desert sidewinder (*Crotalus cerastes*). All three species are predominantly nocturnal and their distributions overlap in other sandy areas in the Mojave Desert. Although sidewinders may also capture diurnal lizards in the morning or before sunset, these rattlesnakes consume both *D. deserti* and *D. merriami* (Funk 1965, Brown 1970; A. Bouskila, *personal observation*). Other snakes at the site are either diurnal, too scarce, or too small to have an impact on the foraging of kangaroo rats. While there were 3–8 sidewinders active at the study site on any summer night (rainy nights excluded), only three owls were observed flying over the site during summers 1989–1991. Tracks of coyotes (*Canis laterans*) and kit foxes (*Vulpes macrotis*) were infrequently seen at the study site.

During 1990–1991 there was very little activity by the little pocket mouse (*Perognathus longimembris*) and I excluded the data on this species from the analysis. Round-tailed ground squirrels (*Spermophilus tereticaudus*) were often seen at my site, but being strictly diurnal, they did not interfere with the collection of data on the kangaroo rats.

Trapping

To collect basic information on the rodents, I set up a 6 × 4 trap grid in each experimental plot. In summer 1990, I set 96 long folding Sherman traps (model XLK) on 1–5 consecutive nights, in four plots (total of 1152 trap-nights). In summer 1991, I trapped on series of three successive nights; because there were twice as many plots, each plot was sampled every other month (96 traps per night, 1152 trap-nights). I did not trap during nights in which rodent foraging was measured in seed trays. I baited the traps with millet seed around sunset and checked them before sunrise. For each captured rodent I recorded the species, sex, individual mark, body mass (to the nearest gram, on an Ohaus dial spring balance model 8011-M) and the location of capture. On their first capture, rodents were individually marked by a metal ear tag in each ear (Model 1005-1, National Band and Tag Company, Newport, Kentucky, USA); rodents were always released at the location of capture. For many individuals, I had more than one record of body mass. To eliminate dependence between records of body mass, I randomly chose one record for each individual and omitted the others (Blumstein 1992).

Quantifying microhabitat use of the rodents

I refer to microhabitat use as the microhabitat in which foraging takes place, unlike a broader definition

that also includes activities such as social interactions (e.g., Behrends et al. 1986). To quantify microhabitat use of the rodents, I used a slight modification of the Giving-Up Density method (Brown 1988) in seed trays. The theory behind this method is an extension of the marginal value theorem (Charnov 1976) and is based on diminishing returns experienced by a forager in a depleting patch (for details, see Brown 1988). As a forager depletes a patch, it should abandon the patch when the benefits equal the costs. This is true for any forager, regardless of the number of individuals visiting a tray during the night. The quitting harvest rate of the forager is:

$$H = EC + PC + MOC. \quad (1)$$

H is the benefit, and the other components represent the costs: EC is energy cost (metabolic costs while foraging), PC is predation costs, and MOC is missed opportunity costs (the value of alternative activities, such as foraging in other patches, social activities, etc.) (Brown 1988). The benefit and costs are expressed in units of energy rate, using the marginal substitution rate. The marginal substitution rate determines how much of the harvest rate an animal is ready to sacrifice in order to gain the benefits from a nonforaging activity (Caraco 1979). A study involving direct observations of the reaction of rodents to risk from owls in an aviary (Longland and Price 1991) obtained similar results (in terms of risk in microhabitats and moonlight effects) to those from a study that used the Giving-Up Density method (Kotler et al. 1988), supporting the validity of the latter method.

The seed trays in my experiments were reinforced aluminum foil trays (41 × 29 × 6 cm) equipped with metal handles. Each tray contained 4 L of sifted sand (3–4 cm deep). On experimental nights, about half an hour before sunset, a preweighed amount of unhusked millet seeds (3.000 ± 0.004 g) was placed in each seed tray. The seeds were thoroughly mixed with the sand in the trays, and the surface of the sand at and around each tray was smoothed to facilitate identification of the species visiting the tray. Foraging at the trays is not much different from foraging in the sandy substrate surrounding the trays; the main differences are that the trays provide a fixed amount of uniform millet seeds, at a fixed location. The depth from which the kangaroo rats had to dig out the seeds is comparable to the depth at which I observed *D. deserti* caching millet seeds (1.2, 2.8, and 4.2 cm below the surface, measured from the base of the cache) and to the depth at which I found six caches of natural seeds (3–7 cm). On mornings following experimental nights, the trays were sifted, the seeds remaining in each tray were collected into plastic vials, and the species that foraged at each tray were recorded. Tracks of *D. deserti* and *D. merriami* can be easily distinguished by their size; the tracks of the quadrupedal *P. longimembris* have a distinct pattern, and are much smaller than those of the kangaroo rats. In heavily foraged trays, it was easier to identify the tracks approaching the tray than the tracks in the tray. When two species foraged at a tray, I recorded both and analyzed data from these trays separately.

Collected seeds and debris were separated in the laboratory, and mass of remaining seeds were weighed on a precision balance (Fisher Scientific XT-400D, Pittsburgh, Pennsylvania, USA) to the nearest milligram. Because the volume of the sand in the tray was kept constant, and because millet seeds are very uniform in size, total remaining seed mass represents seed density. The density of seeds left in each tray is the Giving-Up Density (GUD) and is considered an indicator of the forager's perception of costs while feeding at the tray (Brown 1988). I used the GUDs to compare the perceived costs for kangaroo rats foraging in presence or absence of snakes and at different microhabitats and moon phases. The GUDs at each microhabitat should not reflect the expectations of the foragers from the habitat, because kangaroo rats seem to estimate food density in a patch at the initiation of foraging, or update the estimate while they forage (Valone and Brown 1989).

Experiments were done on three consecutive nights. In order to test for the effect of moonlight, I chose each series of nights to be either on the three nights preceding full moon, or three nights centered on new moon. Within each of these periods there are minimal differences in the proportion of the night that is moonlit. I cancelled some experimental nights due to thunderstorms or strong winds.

Millet can germinate and produce seeds after summer rains (A. Bouskila, *personal observation*). To prevent this, I exposed the seeds that I took to the field to radiation from a 900 W microwave oven for 4 min. Exposure for 3.5 min was adequate to reduce the percent of germination of seeds in the laboratory from 94 to 0% (A. Bouskila, *personal observation*).

Experimental design

I collected data on the microhabitat use of the kangaroo rats and its relation to presence of snakes in 1990 and 1991. Sidewinders often remain in an area of ≈30 × 30 m for 2–3 nights before moving to another location (A. Bouskila, *unpublished data*). I designed the size of the manipulated plots accordingly, replicating the natural occurrence of snakes at the study area. In 1990 I established four 30 × 60 m plots bordered with aluminum drift-fence, 25 cm high (of which 2–10 cm were forced into the sand). A similar fence divided each plot to two subplots (Fig. 1), which were randomly assigned as treatment (with a snake introduced in each subplot) or control. To avoid potentially adverse effects of enclosures on rodents (Krebs et al. 1969, French et al. 1974), I did not restrict the kangaroo rats in these small plots. I designed the fences to be semipermeable: kangaroo rats readily jumped over the fences and used the openings provided every 15 m (Fig. 1); neverthe-

less, the fences were effective in confining snakes. Sidewinders did not climb the fence, and when they crawled along it, the curvature of the fence near the opening usually prevented them from exiting through the openings. To keep snakes in the treatment subplots the curvature was directed to the center of these subplots; to prevent entrance of snakes to control subplots, the curvature there faced the exterior of the subplot (Fig. 1).

In each subplot I positioned six seed trays, grouped in two stations. Within a station, a tray was placed at each of the three microhabitats, Bush, Open and Grass, forming an equilateral triangle, 3 m on a side (Fig. 1). Laboratory experiments indicated that both *D. deserti* and *D. merriami* detect sidewinder scent (Bouskila 1993). To assure that a rodent foraging in a treatment subplot was aware of the presence of the snake, I applied scent from a sidewinder by gently dragging a snake around each tray and in a line connecting the three trays of each station.

In 1990 substantial parts of the study site were not visited by kangaroo rats or were visited only for brief periods, and the seeds in many of the 48 trays remained untouched; therefore in 1991 I added four plots for a total of eight plots in that season. In 1991 I modified two other aspects of the experimental design. First, I left all plots unfenced: fencing was not necessary because snakes were placed in cages (30 × 22 × 20 cm) made of 5.5 mm mesh hardware cloth. I observed *D. deserti* near snake cages and because their behavior was similar to that observed in natural encounters between *D. deserti* and sidewinders, I feel confident that a snake in the cage represented a typical ambushing snake. Second, in 1991 I assigned one of three levels of snake treatment to each station in the treatment subplots: in the first treatment (termed Snake 1) I applied the scent from a snake only (by dragging it on, around, and between the seed trays at the station); the intermediate treatment (Snake 2) was similar, but there was also a caged snake at a neighboring station on the same subplot; and in Snake 3, I applied scent and placed a caged snake at the center of a station, equidistant from the trays. Treatments assigned to stations were switched every night.

For several nights prior to an experimental session, I thoroughly searched the site and collected all the active sidewinders on and around the plots, making sure that control subplots had no fresh tracks of snakes at least 48 h before the session. Four of these snakes were then placed in the plots during the experimental session. On the mornings following experiments, I collected the sidewinders from the plots before sunrise, and kept them in individual reptile bags. At the end of a session, I released the snakes at their original site of capture.

In 1991 I switched control subplots to treatment subplots once a month. During all experimental procedures I ensured that the trays in the control subplots were not exposed to scent of snakes. For example, mixing the seeds in the control trays was not done by the same person who placed the snakes in the wire cages in the treatment plots.

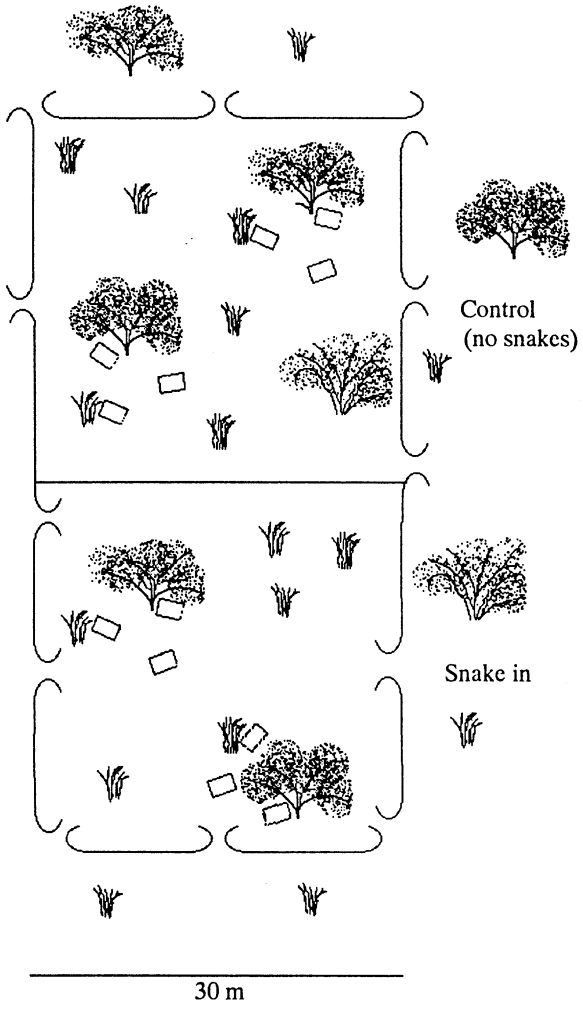


FIG. 1. A typical arrangement of seed trays in stations within a plot. The fences around the plot and between the two subplots were used to manipulate the presence of snakes in 1990, and were removed in 1991.

Despite eliminating snake cues in control subplots, the rodents may not have considered them completely snake free. Rodents may have evolved a perception of snake hazard that is independent of snake presence or odor (Lima and Dill [1990] have raised a similar point). In order to study the microhabitat use of kangaroo rats under absolutely no risk from snakes, I used the same plots and trays to measure the GUDs in November 1991, after sidewinders stopped their activity, but before any natural seeds were added to the system (no annuals germinated during summer or fall 1991). Because the snakes were not active, no treatments were presented and thus all the stations were similar to the

controls in the summer. Two sessions were performed (three nights on new moon and three on full moon).

During summer 1991, I notice a decline in the mean GUD obtained from the plots. To test whether this decline was caused by gradual habituation to the trays and to their location, I established six new stations in September 1991 and I collected GUDs from these stations during three nights of new moon, and three nights of full moon. The stations were widely spaced and far from the experimental plots (100–200 m) to keep them independent of each other and minimize visits by rodents that were already habituated to seed trays. I predicted that if habituation occurs, the GUDs at the new stations would be: (a) higher than the mean GUDs at the established control stations, and (b) similar to the mean GUDs at the beginning of the summer. The GUDs in early June 1991 were more than twice the GUDs in any other period of that year. I excluded the data of early June from my analyses because they reflected the foraging of rodents when annuals were still abundant and foraging at this time was likely to differ from foraging during the rest of the summer.

Direct observations

I supplemented the GUD data with three types of direct observations. (1) Observations on foraging kangaroo rats, at seed trays or near traps, outside the experimental plots (eight nights in total, ≈2 h per night). I used a night vision system (Noctron V, model 9878A) and recorded the behavior on a portable computer (model TRS-80, Tandy Corporation, Fort Worth, Texas, USA), which served as an event recorder. (2) Occasional short observations at dusk, when kangaroo rats started foraging at the seed trays. (3) Observations of natural encounters between rodents and snakes (five encounters in total). These were observed while I was recording the foraging behavior of sidewinders through the night vision system (A. Bouskila, *unpublished data*). All types of observation were infrequent and therefore could not be analyzed statistically, but they provided useful insights, especially on the foraging behavior of *D. deserti*. *D. merriami* was rarely seen during direct observations.

Statistical analysis

I analyzed the GUDs from 1991 with repeated measures Analysis of Variance (O'Brien and Kaiser 1985, von Ende 1993). This analysis is most appropriate when measurements are taken from the same experimental units, either over time or over different treatments (O'Brien and Kaiser 1985). Repeated measures ANOVA blocks by the experimental unit, therefore removing the variation due to differences between experimental units from the error term; this requires a smaller number of experimental units compared to the numbers needed in a regular ANOVA (Stevens 1986, von Ende 1993). In my analysis, the eight plots represent the experimental units. The repeated factors (within-subject effects, von Ende 1993) included treatment, moon phase, and microhabitat. Season or month were included in some of the analyses as additional repeated factors. Although species are commonly used as grouping factors (between-subject effects), my analysis required treating species as a repeated factor: both species were recorded in each experimental unit, and by treating them as a repeated factor, the dependence between them is taken into account. Although on occasions the multivariate approach may have lower power compared to the univariate approach (Koch et al. 1980, von Ende 1993), its use is recommended because it requires fewer assumptions (O'Brien and Kaiser 1985, von Ende 1993). Multivariate repeated-measures ANOVA is sensitive only to the assumption of independence of experimental units (O'Brien and Kaiser 1985). The spacing of the plots (100-300 m) minimized the chance that the same rodent used more than one plot, and thus this assumption is plausible (see *Results: Trapping* below). When I tested specific hypotheses by comparing means in contrasts, I employed the sequential Bonferroni correction for multiple comparisons (Rice 1989) with an overall α of 0.05.

Counting only nights in which GUD could be recorded and excluding stations visited by *P. longimembris* or those not visited at all, my data set included 204 GUDs in summer 1990, 1572 GUDs in summer 1991, and 573 GUDs in November 1991. The data from seed trays in 1990 were fewer due to low densities of rodents and bad weather. GUDs collected at stations from a given plot, which were visited by the same species and had the same treatment and moonphase, were averaged to avoid pseudoreplication (Hurlbert 1984). This also prevented an unbalanced design in 1991. However, because data were missing too often in 1990 and because most GUDs in that year were obtained from fewer plots, I could not analyze the 1990 data with the appropriate repeated-measures analysis. Therefore I only mention the trends seen in 1990 and briefly compare them to the results from the 1991 data.

RESULTS

Trapping

Trapping success differed between years: in 1990, rodents were caught in only 0–3% of the 96 traps set per night, but in 1991 the range was 20–52%. I caught a total of 7 and 120 individual kangaroo rats in 1990 and 1991, respectively (Table 1). *P. longimembris* was only captured twice. Although the data from 1990 are not sufficient for a statistical analysis, clearly the density of rodents must have been much lower during this year compared to 1991. This was confirmed by the fact that in 1990 large parts of the field site, including some of the plots, had no rodent tracks for long periods of time. During all experimental nights in 1990, at least half of the stations had no rodent footprints in their vicinity.

TABLE 1. Summary of rodent trapping in the experimental plots.

D. deserti	1990	1991
Total no. of captures	5	302
No. of individuals	3	84
No. of females	2	48
No. of males	1	36
Mean mass of females (g)	100.5	83.1
Mean mass of males (g)	132	96.7
D. merriami	1990	1991
Total no. of captures	7	62
No. of individuals	4	34
No. of females	3	21
No. of males	1	13
Mean mass of females (g)	32.6	34.4
Mean mass of males (g)	42	37.3

In 1991, *D. merriami* were recaptured less often than *D. deserti* (Table 1; 1.8 and 3.6 captures per individual, respectively). The mean ratio between the species trapped on any given night in summer 1991 was 1:4.5 and was not significantly different between nights (*G* test for homogeneity [Sokal and Rohlf 1981], $G = 12.33$, df = 9, $P > 0.10$). The ratio on one night of trapping in November 1991 was similar, 1:5 (*G* test for goodness of fit, $G = 0.035$, df = 11, $P > 0.99$). Mean body mass of *D. deserti* was 88.7 g, and of *D. merriami* was 35.4 g (see Table 1 for a breakdown to sexes and years). The data in 1991 include juveniles that were captured mainly in June (*D. deserti*) and in July–August (*D. merriami*).

In 1990, all recaptures were in the original plot of capture. Recaptures in 1991 showed that individual rodents tended to remain in the same plots, although the trapping location within a plot varied and indicated extensive overlap in home ranges. Of the 120 rodents caught in 1991, only 13 (all *D. deserti*) were recaptured in another plot; nine of these shifts occurred between trapping sessions (i.e., at least 1 mo apart). I thus considered the mean GUDs obtained from different plots independent for the statistical analyses.

Rodent species at seed trays

In summer 1991, there were two main patterns of rodents' visits at stations: at most stations, only *D. deserti* collected seeds, and at others, both *D. deserti* and *D. merriami* foraged. No station was visited exclusively by *D. merriami.* A contingency table analysis (Zar 1984) revealed that the occurrence of stations foraged exclusively by *D. deserti* depends on both moonphase and month (Fig. 2, $\chi^2 = 90.8$, df = 9, $P < 0.001$). During summer months, 78.4% of the stations were visited exclusively by *D. deserti,* and only 21.6% by both *D. deserti* and *D. merriami.* However, in November, the proportion of stations at which both species foraged increased to 40.2%. This seasonal change was probably not caused by changes in relative population densities or in activity levels of *D. deserti* and *D. merriami,* because as mentioned above, the ratio between the numbers of *D. deserti* and *D. merriami* trapped per night in November was similar to the ratio in summer.

In 1990, 52 stations were visited exclusively by *D. deserti,* 21 exclusively by *D. merriami,* and only 3 by both species (*G* test of independence with Williams' correction [Sokal and Rohlf 1981], $G = 3.91$, df = 1, $P < 0.05$]. Dice's coefficient of interspecific association ([Dice 1945], one of the coefficients recommended by Hubalek [1982]) is 0.0076, indicating that the two species foraged at the same stations less than expected if their visits were independent. In 1991 all the stations were visited by *D. deserti,* precluding the computation of the coefficient.

Seasonal trends

The amount of seeds left in the trays (GUD) decreased during the course of the season ($F_{3,7} = 48.726$, $P = 0.0001$). GUDs were highest in early June (1.061 g) and then declined sharply by July; this decline reached an asymptote in September. Data from 1990 did not show a similar trend (Fig. 3a, b).

The new stations that were established in September 1991 to test if the seasonal decline was caused by habituation were visited almost exclusively by *D. deserti.* A few cases in which both species foraged at the same trays were excluded from the analysis. The mean GUD for *D. deserti* at these stations was 0.196 g, not significantly different from the mean GUD at the same time at previously established stations (0.157 g, $F_{1,12} = 2.808$, $P = 0.12$). However, the mean GUD at new stations was significantly lower than the mean GUD in June (0.805 g, $F_{1,12} = 48.523$, $P = 0.0001$).

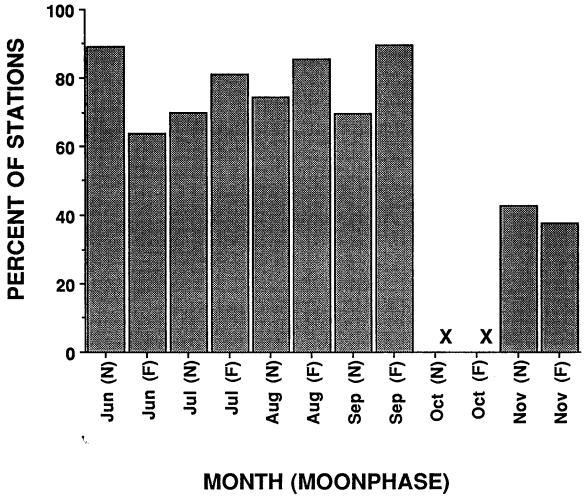


FIG. 2. The proportion of stations that were visited by *D. deserti* only, in 1991. The rest of the trays were visited by both *D. deserti* and *D. merriami.* On periods marked with × no data was available. N = new moon, F = full moon.

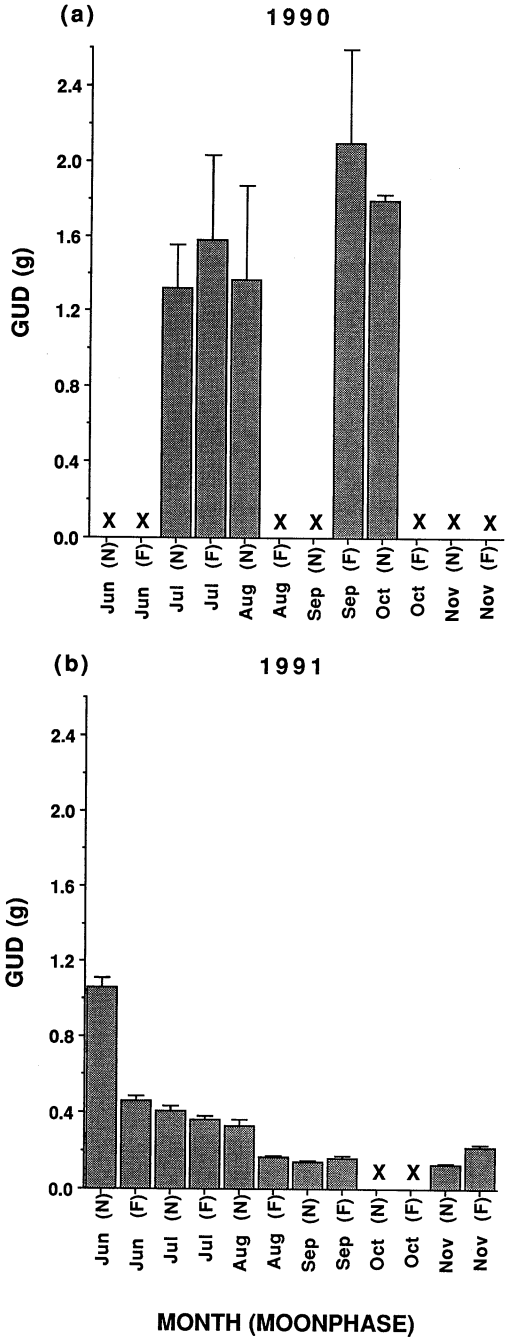


FIG. 3. Seasonal trends in the GUDs (Giving-Up Densities) in control stations (a) in 1990, (b) in 1991 (both species of kangaroo rats pooled). On periods marked with × no data was available. Vertical bars represent 1 SE. N = new moon, F = full moon.

Comparison of GUDs from the two species

In summer 1991, there was no significant difference in GUD between the trays in which only *D. deserti* foraged and the trays in which both species foraged ($F_{1,7}$ = 0.034, P = 0.858). The mean GUD over all

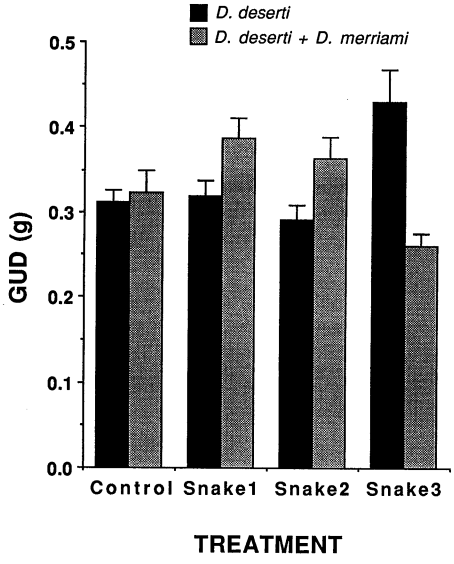


FIG. 4. GUDs under different treatments in summer 1991. Control = no cues of snakes; Snake 1 = only scent of snake in the station; Snake 2 = scent of snake in the station, and a snake in an adjacent station; Snake 3 = snake and scent of snake in the station. The significance level of the interaction treatment by species was P = 0.004. Vertical bars represent 1 SE.

treatments was 0.335 g. However, during fall 1991, trays at which both species foraged had lower GUDs compared to trays where only *D. deserti* foraged ($F_{1,7}$ = 6.148, P = 0.042). This suggests that under the conditions of fall 1991, *D. merriami* foraged more intensively than *D. deserti.*

Effects of snakes on GUDs and microhabitat use

The effect of treatment interacted significantly with the effect of species visiting the station ($F_{3,21}$ = 5.985, P = 0.004, Fig. 4). Where *D. deserti* foraged alone, it left higher GUDs in presence of a snake (Snake 3 treatment), than at control stations or at Snake 1 and Snake 2 stations. However, at stations where *D. merriami* had also foraged, the lowest GUDs were left in presence of snakes (Fig. 4).

In 1991 the scent of a snake was not sufficient to reduce foraging in *D. deserti*: neither Snake 1 nor Snake 2 treatments caused a higher GUD. In 1990, however, there was a trend for higher GUDs for both kangaroo rats in the snake treatment (which was quite similar to the Snake 2 treatment of 1991). In presence of snake scent, *D. deserti* and *D. merriami* left an average of 1.91 and 1.841 g, respectively, but in control trays, they left only 1.603 and 1.566 g.

In the summer, when all treatments and both species are included, kangaroo rats preferred to forage in the Open and avoid the Bush ($F_{2,14}$ = 7.072, P = 0.008). The amount of seed left in the Grass was intermediate between the Open and the Bush. GUDs at the three

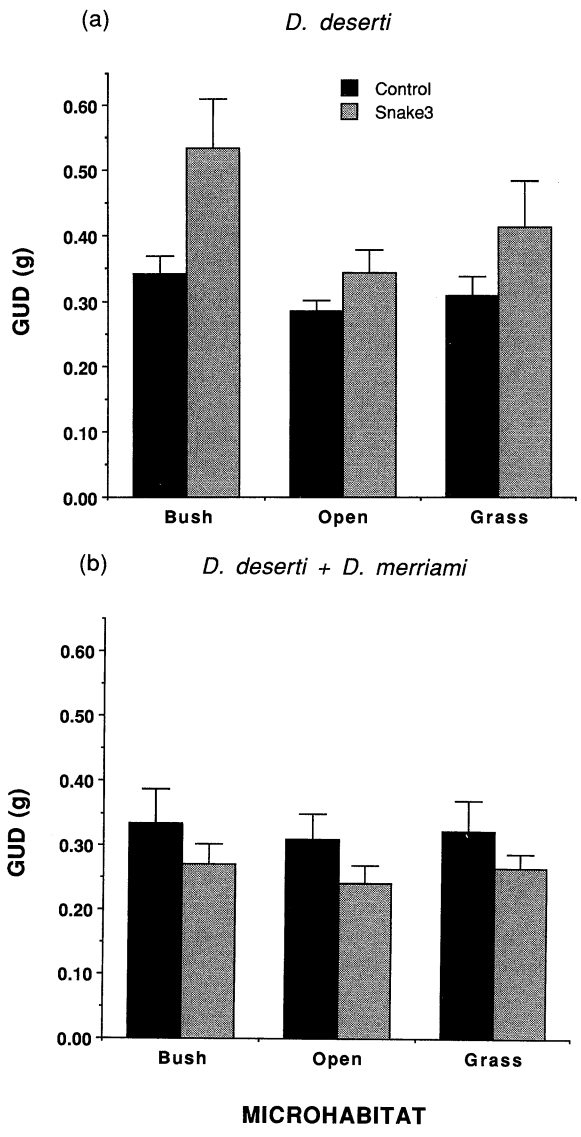


FIG. 5. GUDs in microhabitats: a comparison between control and treatment Snake 3 (summer 1991). Stations visited (a) only by *D. deserti,* (b) by both species. Only in trays that were foraged exclusively by *D. deserti* was the avoidance of the Bush stronger in presence of snakes. Vertical bars represent 1 SE.

microhabitats are shown in Fig. 5, for control and for treatment Snake 3. There was a significant interaction between treatment and microhabitat ($F_{6,42} = 2.789$, $P = 0.022$). The hypothesis that in presence of snakes kangaroo rats leave more seed near bushes was tested for each species separately, contrasting Bush with the other microhabitats in control stations and under treatment Snake 3. Only *D. deserti* significantly avoided the Bush in presence of snakes ($F_{1,42} = 37.224$, $P < 0.05$); microhabitat preference at the stations visited by both species was not affected by snake presence (Fig. 5). In 1990, both species tended to avoid bushes in the snake treatment more than in control stations, even though the snake treatment then was only equivalent to Snake 2 of 1991.

Microhabitat preferences of kangaroo rats in the fall, when snakes are absent, differed significantly from the preferences at control stations in summer ($F_{2,14} = 5.075$, $P = 0.022$). Bush was significantly avoided in summer ($F_{1,14} = 6.349$, $P < 0.05$), but not in the fall (Fig. 6).

Moonphase effect

In summer, moonphase did not have a significant effect on GUDs (rodents left 0.353 g and 0.318 g, on full moon and on new moon nights, respectively; $F_{1,7} = 2.231$, $P = 0.179$). The interactions between moonphase and each of the other factors (species, microhabitat, and treatment) were not significant either. In 1990, mean GUD on full moon nights tended to be lower than on new moon nights (1.543 and 1.971 g, respectively).

The effect of moonphase on the average GUD was different between seasons (Fig. 7, $F_{1,7} = 10.403$, $P = 0.014$): during the summer, there was only a small difference between full moon and new moon; in the fall, when snakes are not active, more seeds were left in full moon than in new moon. In an analysis of the data from the fall, GUDs were higher during full moon than during new moon ($F_{1,7} = 58.731$, $P = 0.0001$). Microhabitat preferences in the fall were different between moon phases ($F_{2,14} = 4.972$, $P = 0.023$). On new moon nights, the GUDs were equal at all microhabitats, but on full moon nights, kangaroo rats significantly preferred the Bush over the two other microhabitats (Fig. 8, $F_{1,14} = 19.233$, $P < 0.05$).

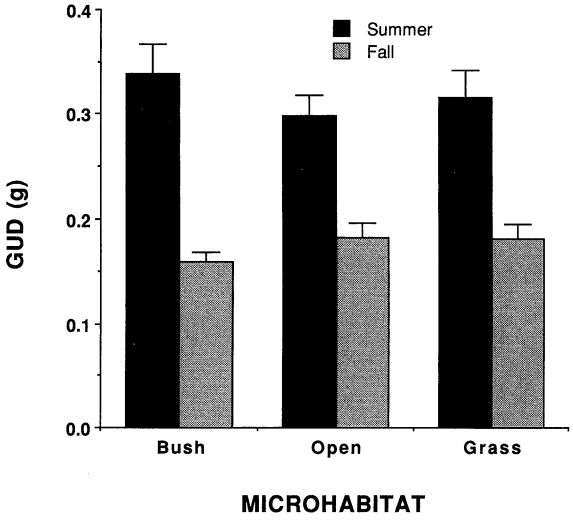


FIG. 6. GUDs in microhabitats: a comparison between seasons (1991). The Bush was avoided only in summer. The significance level of the interaction term season by microhabitat was $P = 0.022$. Vertical bars represent 1 SE.

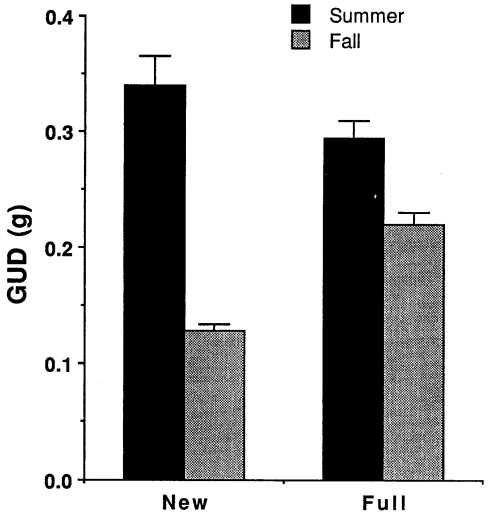


FIG. 7. GUDs at different moon phases: a comparison between seasons (1991). In the fall, more seeds were left on full moon, but in the summer there was only a slight difference, in the opposite direction. The significance level of the interaction term season by moonphase was $P = 0.014$. Vertical bars represent 1 SE.

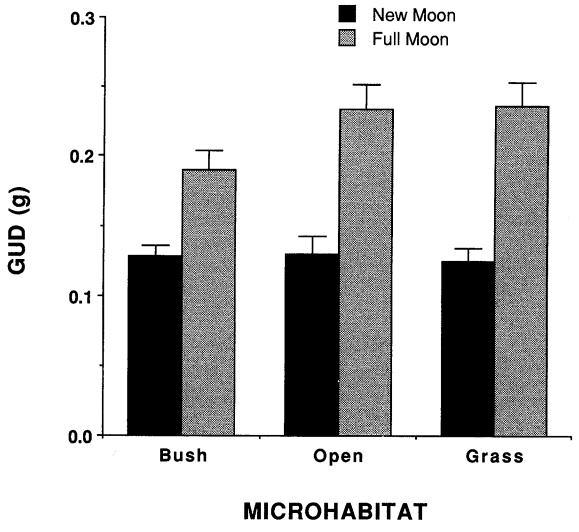


FIG. 8. GUDs in the fall: interaction between moonphase and microhabitat ($P = 0.023$). The Bush is significantly preferred only on full moon. Vertical bars represent 1 SE.

Evidence from predatory events

Table 2 summarizes the records of predatory events in which snakes successfully captured a rodent. In all six cases the snake was found a few hours after ingesting the rodent. The site of capture was identified from tracks on the sand, and its microhabitat was recorded. The species ingested was identified by palpation, by the size of the rodent, and in two cases where the tracks of the rodent could not be mistaken, by footprints at the site of capture.

Both *D. merriami* and *D. deserti* were captured by sidewinders, but the proportion of *D. merriami* (0.67, Table 2) was higher than the proportion of individuals from this species trapped at the field site (0.29, Table 1; $Z = 1.962$, $P < 0.05$, two-tailed test for comparing proportions [Zar 1984]). Three of the six rodents were captured under bushes, only two were captured in the Open, and one in the Grass. All the known cases of snake predation occurred on new moon nights.

DISCUSSION

Characteristics of predation risk from snakes

The effects of predators on the behavior of rodents most often have been studied in relation to owl predation (e.g., Kotler 1984, Brown et al. 1988). However, for several reasons, predation risk from snakes may impose different constraints on the behavior of rodents. Because snakes are poikilotherms, they are strongly affected by seasonality: sidewinders at my study site are not active between October and May, creating a period of five snake-free months. Resident owls, in contrast, pose a risk to rodents throughout the year. Another aspect of snake predation is that, unlike owls, snakes are not affected by moonlight. Illumination increases the success of owls in capturing rodents (Clarke 1983, Kotler et al. 1988, 1991). Because snakes locate prey with senses other than vision (vibrations, chemoreception, and for some species, also thermoreception; Cock Buning 1983) illumination probably does not increase the number of rodents captured by snakes. On the contrary, rodents are more likely to visually detect snakes at high levels of illumination, reducing the capture rate of snakes on illuminated nights. The predatory events in the present study (Table 2) were recorded over three summers, with equal efforts on full and new moon periods. That all the events occurred on new moon nights supports the hypothesis that rodents are more vulnerable to snakes on dark nights. Additional support is provided by observations of nonfatal encounters between *D. deserti* and snakes in the field: all five cases that I recorded occurred on full moon. Finally, the effects of microhabitat on predation risk from snakes and owls differ: owls mainly impose pre-

TABLE 2. Records of rodents killed by sidewinders.

Date	Moon-phase	Species consumed	Habitat
28 July 1989	new	*D. merriami*	Bush
7 June 1991	new	*D. merriami*	Grass
6 August 1991	new	*D. merriami*	Bush
6 August 1991	new	*D. deserti*	Bush
11 August 1991	new	*D. merriami*	Open
7 September 1991	new	*D. deserti*	Open

dation risk for rodents in the open (Kotler et al. 1988, Longland and Price 1991); snakes, however, impose a higher risk in the bush. One indication of greater risk from snakes in the bush is the relatively higher abundance of ambush sites of sidewinders in this microhabitat: of 173 ambush sites found at 1990–1991, 17.3% were in the bush, a microhabitat that covers only 1.9% of the area ($\chi^2 = 41.7$, df = 2, $P < 0.0001$, Bouskila 1993). It is not clear if snakes prefer ambushing in the bush regardless of the distribution of the prey. If the rodents and snakes respond to each other's behavior when choosing microhabitats for foraging, the preference of the snakes may be a result of a game between the two species. A game theoretic model (Bouskila 1993) showed that potential reasons for the distribution of the sidewinders include (a) interactions with risk from owls to rodents in the open, and (b) higher success to snakes ambushing for rodents in the bush (e.g., due to better camouflage). In addition, snakes may be less exposed to their own predators in the bush, but the importance of this factor has not been established yet.

Sidewinders captured kangaroo rats under bushes on three out of six occasions (Table 2). The small sample precludes a test for statistical significance, but considering that the Bush microhabitat covers only 1.9% of the study site, and that kangaroo rats avoid the bush during summer, it seems that relatively more rodents are captured under bushes compared to those in the Open or the Grass. This conclusion differs from the conclusions of Pierce et al. (1992) who compared the success of another rattlesnake (*Crotalus viridis lutosus*) in arenas with or without vegetation. Pierce et al. (1992) found no difference among the two types of arenas, but as they pointed out, the rodents in their experiments were often aware of the introduction of the snake to the arena. Rodents in the field are not likely to know the location of ambushing snakes in their entire home range, and the difficulty in detecting a snake in the Bush may be critical. Of five recorded cases of rodents detecting snakes, one occurred under a bush and four in the Open, supporting the hypothesis that snakes are less detectable under bushes.

Rodents attempting to avoid both owls and snakes may face conflicting demands: the Bush, which is safe from owls (Longland and Price 1991) poses the highest risk from snakes. Similarly, on dark nights, when the risk from owls is low (Kotler et al. 1988), snakes have a greater success capturing rodents. The extent to which the behavior of rodents is directed to minimize the risk from snakes or from owls should be determined by the relative importance of snakes and owls at each location. Predation risk from mammals and its interactions with risks from owls and snakes still need to be studied.

Effect of snakes

The presence of snakes may affect foraging in two ways: (a) rodents may reduce their foraging at stations in which cues for snakes are present, and this will be manifested by higher GUDs at those stations; (b) in the presence of snakes, rodents may shift microhabitat preferences within a station, so that more seeds are left at the risky microhabitats. In this case, we should expect higher GUDs in the trays under bushes.

The manipulations of snakes in my study demonstrated that sidewinders induce both effects on the foraging of kangaroo rats. *D. deserti* reacted to presence of snakes by (a) collecting fewer seeds in all three microhabitats and (b) avoiding the Bush more than Open or Grass. Because the snakes were placed at the center of the stations, at equal distances from all microhabitats, this indicates that *D. deserti* associated the Bush with higher risk from snakes. This is the first demonstration that rodents in the field modify their foraging behavior in the presence of snakes. Experiments in an enclosure, with other rodents, support the findings of the present study. Kotler et al. (1993) exposed two species of gerbils (*Gerbillus allenbyi* and *G. pyramidum*) to a colubrid snake (*Spalerosophis diadema*) and found that the gerbils reduced their foraging in response to the presence of the snakes.

Avoidance of bushes by both kangaroo rats was evident over all treatments, including control stations. However, kangaroo rats did not avoid the Bush in November, when snakes were not active; this supports the hypothesis that a general perception of high risk from snake predation under bushes is triggered only during the activity season of the snakes. In summer, the rodents may be using a rule of thumb for risk assessment, i.e., all bushes are risky. Rodents following such a rule are likely to leave unexploited seeds under bushes that have no snakes, because collecting more precise information on the location of snakes may be too costly in terms of time and risk of predation (Bouskila and Blumstein 1992).

These results have important implications for microhabitat selection in desert rodents. Kangaroo rats prefer the open over the bush; this preference has been demonstrated in many studies and has been tied to the bipedal morphology of kangaroo rats (e.g., Brown and Lieberman 1973, Lemen and Rosenzweig 1978, Price and Brown 1983). Various mechanisms have been suggested to account for this preference. These mechanisms include better exploitation of fine soil texture in the open (Price and Waser 1985, Price and Podolsky 1989), higher efficiency when foraging on seed clumps in the open (Reichman and Oberstein 1977, Price 1978*b*), and greater ability to evade avian predators (which, in turn, causes the trade-off between risk and unexploited seeds in the open; Kotler 1984, Brown et al. 1988, Longland and Price 1991). Although risk from snakes cannot be the sole cause for the preference of kangaroo rats for the open, considering the risk from snakes in communities where snakes are present may be helpful. For instance, Price (1978*a*) and Brown (1989) showed that *D. merriami* preferred the open in

summer, but shifted toward bushes in winter. These results are compatible with the distribution of risk from snakes, as shown in this study: when snakes are active, the risk is higher under bushes, and kangaroo rats avoid the bushes; when snakes are inactive, kangaroo rats should shift toward the bush.

The reaction of prey animals to predation risk has been shown to depend on prey hunger state or on food level in the hoards of prey (e.g., Godin and Sproul 1988, Bouskila 1993) and this agrees with theoretical models (Mangel and Clark 1988, Bouskila 1993). When rodents are less stressed for food than in 1991 (see *Differences between years* below), I expect to find a stronger avoidance of snakes compared to my findings in that year. The data from 1990 cannot be used quantitatively to test this expectation, but the trends are in the right direction.

Differences between the species of kangaroo rats

When *D. merriami* and *D. deserti* foraged individually in the laboratory, they did not differ in their respective GUDs (Bouskila 1993). Because *D. merriami* foraged in 1991 only at stations that were also visited by *D. deserti,* I draw conclusions about *D. merriami* indirectly, by comparing the GUDs in trays that were visited by both species to GUDs in trays that were visited only by *D. deserti.* This comparison is limited to cases in which the GUD left by two species is lower than the GUD in trays foraged only by *D. deserti.* When two species visit a tray, the remaining seeds represent the species that has the lowest GUD, regardless of who was the last visitor at the tray.

The results from summer 1991 indicate that while *D. deserti* reduced its foraging in presence of snakes (especially under bushes), *D. merriami* may have foraged more at those stations and trays. The mean body mass of *D. deserti* at my field site was 2.5 times the mass of *D. merriami.* I did not observe any encounter between the two species, but in a study of the same species in Kelso Dunes, Congdon (1974) found that *D. deserti* was dominant over *D. merriami,* and the latter always avoided encounters with *D. deserti.* It seems plausible that in my study too *D. merriami* avoided encounters with *D. deserti,* especially near the relatively rich food patches in the seed trays, where *D. deserti* often showed aggression towards conspecifics. By foraging at the stations and trays that *D. deserti* avoided, *D. merriami* individuals were able to collect more seeds with smaller risk of interference from the dominant *D. deserti.* The dominant species primarily responds to the distribution of risk from the predator, while the subordinate species appears to respond to both the risk of predation and the risk of interference from the dominant competitor. Although the risk from a snake is likely to be lethal to *D. merriami* more often than an encounter with *D. deserti,* the chances of interference from the abundant *D. deserti* may have been high enough to be traded off against the risk from snakes.

In order to incorporate interference competition (Kaufmann 1983) from a dominant competitor into the concept of GUD, I suggest adding interference cost (IC) to Eq. 1:

$$H = EC + PC + MOC + IC. \quad (2)$$

This cost may be negligible for the dominant species, but it may be substantial for subordinate species. Subordinate individuals of the dominant species may also suffer from a cost of interference, if they are subject to attacks by dominant conspecifics. Where *D. merriami* is the largest rodent (e.g., Price 1978*a,* Brown 1989) I expect it to avoid patches with high predation risk, because at such sites, the main consideration should be the distribution of the predators rather than the cost of interference.

The present study found predator-related differences in the exploitation of microhabitats between two species of kangaroo rats. This effect of the snakes may be important to the community structure even if the predator consumes only few prey, as suggested by Kohler and McPeek (1989) for an aquatic system.

Moonphase effect

Two types of moonlight avoidance have been demonstrated among rodents: less activity on full moon nights (Kaufman and Kaufman 1982, Bowers 1988, Kotler et al. 1988, Wolfe and Summerlin 1989, Daly et al. 1992), and stronger preference for bushes on illuminated nights (Kaufman and Kaufman 1982, Price et al. 1984, Kotler et al. 1988, Wolfe and Summerlin 1989). My data from the summer showed neither of the types of moonlight avoidance. However, the results from the fall, when snakes are not active, may assist in understanding the results from the summer. In the fall kangaroo rats left more seed on full moon than on new moon nights; on full moon nights they also preferred the Bush over the Open and the Grass. Several factors were likely to differ in the fall from the summer: ambient temperatures were lower, the nights were longer, natural food supply was probably lower, and there was no risk from snakes. However, neither of the first three factors can explain the differences between fall and summer in microhabitat preferences and in the reaction to moonlight. Considering the unique characteristics of risk from snakes, these differences suggest that the avoidance of snakes during the summer is responsible for the lack of moonlight avoidance by kangaroo rats. Lower risk from snakes on full moon nights may be balancing off the increased risk from visual predators on such nights. In addition, increased risk from sidewinders under bushes reduces the advantage of the Bush as a shelter from owl predation on moonlit nights.

Another factor that may have contributed to the lack of moonlight avoidance by rodents during the summer

is the reaction of snakes to moonlight: sidewinders always preferred the Bush for ambush, but on full moon nights the preference was stronger (Bouskila 1993). This behavior of the snakes may have inhibited the expected shift of rodents into the Bush on full moon nights, and is predicted by a game theoretic model for snakes and rodents (Bouskila 1993).

Several studies did not find inhibition of activity by moonlight (see references in Wolfe and Summerlin 1989). Wolfe and Summerlin claim that moonlight avoidance is very general and suggest that studies that did not find an effect of moonlight were not properly designed. However, interactions between predation risk from both owls and snakes could explain some of the exceptions. The possibility of inadequate design can be refuted in Lockard and Owings (1974) and in the present study, because in both studies, the same designs that demonstrated moonlight avoidance in one season did not show moonlight avoidance in another. Many of the studies that were able to demonstrate an effect of moonlight were done in winter (Lockard and Owings 1974, Price et al. 1984, Daly et al. 1992) or in areas that are too cold for intensive activity of nocturnal snakes (e.g., Kotler 1984). The structure of the habitat may also have an effect on the relative importance of risk from owls and from snakes. In large parts of the Kelso Dunes (including my study site), there are very few perches for owls; this may limit visits of owls in such areas, contributing to the relative importance of risk from snakes.

Differences between years

There are several indications that rodents were stressed for food in summer 1991. First, the decline of GUDs throughout summer 1991 was not observed in the previous summer. The hypothesis of gradual habituation to the trays was not supported because there was no evidence that established stations have lower GUDs compared to new stations. The GUDs declined probably because the reservoir of natural seeds in the dunes had been depleted during the summer and the rodents were increasingly stressed for food. The low GUDs in control trays in 1991 (5 times lower than in the control trays in 1990) may also indicate a difference between 1990 and 1991 in the per capita amount of natural seeds available to the rodents. Second, *D. deserti* were reluctant to enter the traps in 1990 and preferred to forage for natural seeds in the vicinity (A. Bouskila, *personal observations*). In contrast, I observed in 1991 (starting from the first trapping night) rodents entering traps soon after the traps were opened. Third, rodent home ranges overlapped extensively in 1991 but not in 1990 (based on trapping). Additionally, only in 1990 did I observe two or three different rodents foraging simultaneously at a station. Fourth, aggression between *D. deserti* over seed trays was common in 1991 (A. Bouskila, *personal observation*), and was never seen in 1990.

The increase in rodent populations between summers 1990 and 1991 is likely to have been caused by differences in rainfall between these years (Beatley 1969, 1974). In the period July 1990–April 1991 Kelso received 207.9 mm of rain, ≈4 times the amount of rain from a comparable period in the previous year (S. Secor, *personal communication*). Nevertheless, relative to the number of rodents, the seed bank at Kelso Dunes must have been smaller in 1991 compared to 1990. Moreover, the rodents in 1991 seemed increasingly stressed for food from June through September (Fig. 3b). When referring to "stress for food" I do not mean that rodents were necessarily hungry; if rodents fail to collect enough seed in their hoards, they may react like hungry rodents. Laboratory experiments indicated that kangaroo rats with few seeds at their caches took higher risks when foraging, as would have been expected from hungry animals (Bouskila 1993). Because food supply in nature fluctuates between years, the reactions of kangaroo rats to predators in the field may vary too. These conclusions have important implications on the interpretation of the results from 1991, because in such a year, with low per capita food supply, we would expect to find a reduced reaction of rodents to predation risk.

Conclusions

Snakes had an effect on the foraging of rodents in the Mojave Desert, and the intensity of the effect may vary between years (stronger reaction is expected in years with weak competition between rodents over food). The two kangaroo rats differ in their reaction to snakes, and these reactions may also depend on the intensity of competition: when competition is intense, the subordinate species trades off risk from snakes with interference from the dominant species. When competition is weak, both species may similarly avoid the risk from snakes. The interaction between risk from snakes and risk from owls in the summer may explain the lack of moonlight effect in this, and in other studies. In contrast to risk from owls, risk from snakes is high under bushes and during new moon nights.

It is difficult to separate the reactions of rodents to various predators or to separate the effects of predator avoidance and interference competition. The expression of each one may be affected by the others, and together they influence the coexistence of species. Focusing on one component only (one type of predator, or only on competition) may provide a good description for some situations, but may prove to be incomplete in many others. The present study was carried out in a simple community of rodents and snakes; in communities that include more than two species of rodents and one nocturnal rodent-eating snake, the relationship between the effects of various predators and the interaction with competition are likely to be even more complex.

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