Ann. Zool. Fennici 29:199–206
Helsinki 23 December 1992

ISSN 0003-455X

Predator facilitation: the combined effect of snakes and owls on the foraging behavior of gerbils

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Received 4 March 1992, accepted 6 October 1992

Predator facilitation occurs when prey face two or more predator species and cannot forage and be safe from both types of predators simultaneously: avoiding one predator necessarily leads to increased exposure to the other. Two species of coexisting gerbils (*Gerbillus allenbyi* and *G. pyramidum*) which coexist in sandy habitats in the Negev Desert, Israel may face such conflicting demands from vipers and owls. We tested this by subjecting the gerbils to the presence of snakes and owls in a factorial experiment carried out in a large aviary. We also manipulated illumination and microhabitat, two factors which affect the risk of predation. Gerbils responded to owls by reducing foraging activity, avoiding the open microhabitat, and exploiting resource patches less intensively. Also, *G. pyramidum* showed a significant light × snake × owl interaction indicative of predator facilitation: the gerbils avoided the open entirely when faced with lights and owls, but increased their exposure to owls if vipers were also present. The fangs of the snakes are driving the gerbils into the talons of the owls. Such facilitation may affect the foraging behavior, species interactions, and community structure of the gerbils.

1. Introduction

Natural environments are often rich in predators (e.g. Taylor 1984). As a result, foragers often face the threat of predation from several different types of predators. Tactics that may be effective in reducing mortality from one type of predator may not be effective against another. Indeed, they may even increase the chances of falling victim to other predators (Charnov et al. 1976). Charnov et al. have termed this predator facilitation, i.e., when behavioral responses by a forager to reduce mortality from one predator exposes it to greater mortality from a second predator species. For example, the presence of a predator in one habitat type may cause prey to reduce their use of that habitat and increase their use of another habitat; this increases their exposure to predators in the second habitat (Rahel & Stein 1988). Thus, the presence of a given species of predator in one habitat may shift prey behavior towards another habitat and into the jaws, talons, or fangs of another species of predator. Predator facilitation may have far reaching consequences for predator-prey interactions and community structure.

Owls and snakes present vastly different threats to gerbils which may result in predator facilitation (Kotler et al. 1991, 1993a).

Gerbils are small nocturnal seed-eating rodents commonly found in Old World desert habitats. We have been studying two species, *Gerbillus allenbyi* (Allenby's gerbil, mean mass 25 g), and *G. pyramidum* (the greater Egyptian sand gerbil, mean mass 39.5 g) (Abramsky et al. 1985) (e.g., Kotler 1984, Kotler et al. 1991, 1993, Brown, Kotler, and Mitchell, unpublished data, Kotler al. 1993b). These species live in burrows, have diets composed mostly of seeds (Bar et al. 1985), commonly coexist in the sandy desert habitats throughout Israel. They show strong patterns of habitat selection (Abramsky et al. 1985, Rosenzweig & Abramsky 1985, 1986, Abramsky & Pinshow 1989, Abramsky et al. 1990, Abramsky, et al. 1991) and microhabitat selection (Brown, Kotler, and Mitchell, unpublished data), and compete for seed resources (e.g. Mitchell et al. 1990, Abramsky & Pinshow 1989, Abramsky et al. 1990, 1991).

Owls hunt gerbils in a manner which increases the risk of mortality in the open microhabitat, and gerbils respond to this threat by reducing their use of the open microhabitat and their foraging activity (Kotler et al. 1991). Owls employ both hearing and vision to detect prey and can locate and attack prey several meters away. They hunt from a perch. Shrubs reduce detection of rodents by owls and provide a physical shield against attacks. Prey detection, attack rate and attack success are greater in the open microhabitat (Longland & Price 1991). In fact, in experiments conducted in a large aviary, barn owls (*Tyto alba*) captured significantly more gerbils away from cover (Kotler et al. 1991). Gerbils respond to this threat accordingly. Gerbils in the presence of owls foraged fewer resource patches and quit patches at higher resource levels. Foraging virtually disappeared in the open microhabitat, and overall, they shifted their foraging to the bush microhabitat (Kotler et al. 1991).

In contrast, snakes appear to hunt in a manner which increases risk in the bush (Kotler et al. 1993, Kotler & Blaustein, unpublished data). Snakes hunt by ambush and employ olfaction, vibrations, and vision to detect prey. This tactic may be more effective in the bush microhabitat. Furthermore, snakes may avoid their own predators by avoiding open areas. Regardless, rodents respond to the presence of snakes as if snakes make the open microhabitat more dangerous.

The presence of both owls and snakes should present gerbils with conflicting demands. They can shift foraging from the open microhabitat (in which owls are most effective) to the bush. They can shift foraging effort from the bush microhabitat (in which snakes are most effective) to the open. Or they can reduce their activity in one or both microhabitats with no compensatory increase in the other microhabitat. However, avoidance of one type of predator must come at the expense of an increase in exposure to the other type or a decrease in the amount of resources harvested. What do gerbils actually do? To answer this, we established populations of two species of gerbils in a large enclosure and manipulated the presence and absence of a snake predator and an owl predator. In addition, we also manipulated the presence and absence of artificial illumination set to produce the light intensity of a full moon; added illumination increases the effectiveness of barn owls preying on gerbils (Kotler et al. 1991). We quantified gerbil foraging effort in manipulated resource patches placed in bush and open microhabitats.

2. Methods

We performed experiments during September and October of 1990 in a large outdoor aviary (measuring 18 × 23 × 5 m) located at the Blaustein Institute for Desert Research, Mitrani Center for Desert Ecology, Sede Boqer Campus of Ben-Gurion University, Israel (30°52′N, 34°47′E; see Kotler et al. 1991 and Kotler et al. 1993a for similar experiments carried out in the same aviary for owls and for snakes as predators on gerbils, respectively). The aviary is divided into two equal-sized halves by a 1 m high rodent- and snake-proof fence. The aviary also contains 13 perches for owls. We simulated a desert environment with 10–15% perennial shrub cover by placing 16 brush piles on each side of the aviary.

In the aviary, we established populations of two species of gerbils, *G. allenbyi* and *G. pyramidum*. On one side, we introduced 12 individuals of *G. allenbyi*, and on the other, we introduced 8 individuals of *G. pyramidum*. These numbers yield approximately equal consumer biomass (corrected for metabolic rate) on each side of the aviary. We marked gerbils with individually numbered ear tags.

We provided food for the gerbils in metal trays (45 × 60 × 2.5 cm) filled with 6 g of millet seed mixed thoroughly into 5 l of sifted sand. Gerbils foraged readily in trays, and their footprints, tail drags, and digs in the sand of the trays made foraged trays easily identifiable. In each half of the aviary, we arrayed 32 trays in 16 pairs (64 seed trays total). We placed one tray of each pair under a brush pile to simulate a resource patch in the bush microhabitat, and we placed the other tray 1 m away in the open microhabitat. The following morning, we recorded which trays had been foraged, sifted the remaining seeds from the sand of each tray, recharged each foraged tray with 6 grams of millet, and later weighed the remaining seeds of a tray.

We used the number of seed trays foraged by gerbils as a measure of foraging activity, and we used the amount of seeds left in a tray as a measure of patch use. Gerbils foraging in seed trays experience diminishing returns, i.e., the number of seeds harvested per second declines with time spent in the seed tray as resources are depleted (Kotler & Brown 1990). For optimal foragers exploiting a patch with diminishing returns, an animal should stay in a resource patch until its harvest rate equals the sum of its energetic costs of foraging, its cost due to the risk of predation, and its missed opportunity costs of not engaging in alternative activities (Brown 1988). We refer to the amount of seeds left in a tray after a night of foraging as the *giving-up density* (GUD; Brown 1988). The GUD is directly related to the harvest rate of the rodent at the time it quit the patch (Brown 1988, Kotler & Brown 1990). As such, it reflects foraging costs; the higher the foraging costs, the higher the GUD. For example, if the risk of predation is high and risk of predation is treated as a foraging cost, we would also expect GUDs to be high.

We emphasize that seed trays measure the GUD of only the most efficient (highest ratio of harvest rate to foraging costs at low seed density) forager to visit the tray; other less efficient foragers will not find a profitable foraging opportunity in a tray previously foraged by a more efficient individual. That a seed tray measures the GUD of only one individual is true regardless of the number of individuals which have visited the tray in a night (Brown 1988).

On successive experimental nights, we manipulated the presence and absence of snakes, owls, and illumination. For snakes, we used the greater sand viper, *Cerastes cerastes*. In Israel, this snake inhabits sandy, arid habitats. It is largely nocturnal, eats mostly rodents, and kills its prey by envenomation (Alon 1984). On nights calling for the presence of snakes, we placed one snake on each side of the aviary prior to sunset and removed them the next morning.

For owl predators, we used eagle owls, *Bubo bubo*. We chose this species because it can prey on both gerbils and snakes. We placed two owls in the aviary for nights calling for the presence of owls. We used the same two owls throughout the experiment since no additional animals were available. Following a night with owls, we recaptured owls and removed them from the aviary.

When we obtained evidence of successful predation events from recovered spit pellets or feces, we added new rodents to the aviary to replaced captured gerbils. This kept gerbil numbers in the aviary constant from night to night.

For illumination, we used a set of six electric lights controlled by rheostat. One light was located at each corner of the aviary, with two others located on the sides half way along the long axis of the aviary. On experimental nights with illumination present, we set the rheostat to provide light intensity equivalent to that of a full moon.

We performed 29 nights of experimentation; on each night we ran one of the 8 different combinations of the experimental factors of presence or absence of vipers, owls, and added illumination. In total, we obtained 29 nights of data for *G.*

allenbyi and 27 nights for *G. pyramidum*. The nightly order of treatments was randomized subject to the constraint that nights near full moon (one night on either side) received illumination present.

The data analysis consisted of two parts. First, we considered how the experimental factors of vipers, owls, illumination, and microhabitat affected the number of seed trays visited and foraged by gerbils. This aspect of foraging activity reflects the number of acceptable seed trays in which the initial harvest rate exceeds perceived foraging costs. These data measure the gerbils' selection of foraging patches as a function of experimental treatments. We analyzed these data using ANOVA, with the proportion of trays foraged per night (the total number of potential forages each night was always the same) by a species in a particular microhabitat (arcsine transformed) as the dependent variable.

Next, we considered how vipers, owls, illumination, and microhabitat affected patch use as measured by the giving-up density (GUD) of seeds left behind by gerbils in seed trays. These data measure the gerbils' perception of foraging costs among different patches and microhabitats. A higher GUD indicates higher foraging costs (Brown 1988). We analyzed these data using a four-way ANOVA. For each combination of species, microhabitat, and night, (there is only one combination of vipers, owls, and illumination per night) we calculated the mean of the log-transformed GUDs; the mean GUDs provided the dependent variable for the ANOVA.

Of particular interest in both analyses are significant interactions involving snakes and owls. These may be indicative of gerbils increasing their use of one microhabitat because of the presence of the other predator in the other microhabitat.

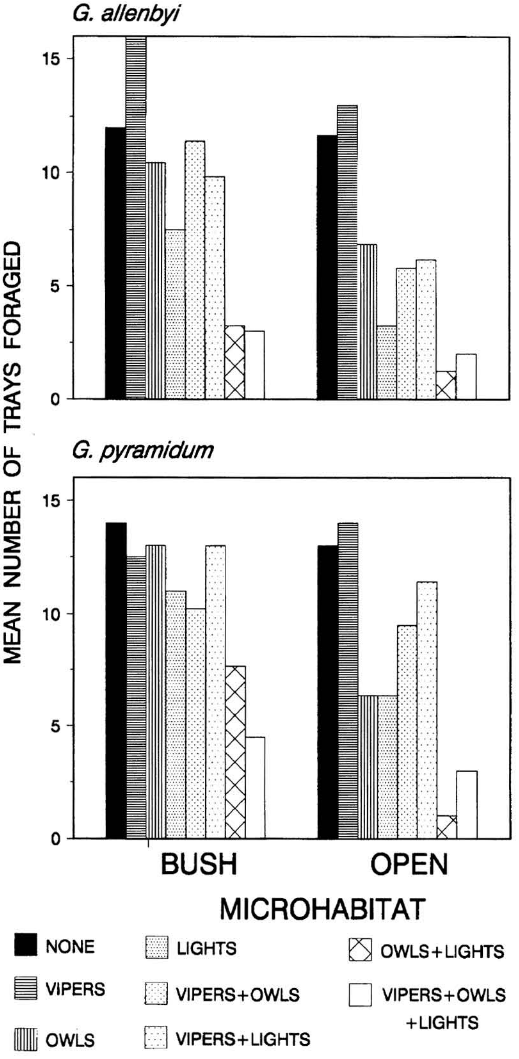

Fig. 1. Effects of the presence of owls, vipers and added illumination on the mean number of seed trays foraged per night for *Gerbillus allenbyi* and *G. pyramidum* in the bush and open microhabitats.

3. Results

We first consider the effect of the experimental factors of vipers (presence or absence), owls (presence or absence), illumination (presence or absence), and microhabitat (bush or open) on gerbil foraging activity as measured by the presence or absence of foraging in seed trays (Fig. 1). We used the proportion of seed trays foraged each night (arcsine transformed) as the dependent variable and performed separate analyses for each species. This analysis reveals that predatory risk affects foraging activity in both species. For both species, animals foraged fewer trays in response to the presence of owls (for *G. allenbyi*, $F = 12.28$, $df = 1,46$, $P = 0.001$; for *G. pyramidum*, $F = 18.985$, $df = 1,38$, $P < 0.001$) and added illumination (for *G. allenbyi*, $F = 23.036$, $df = 1,46$,

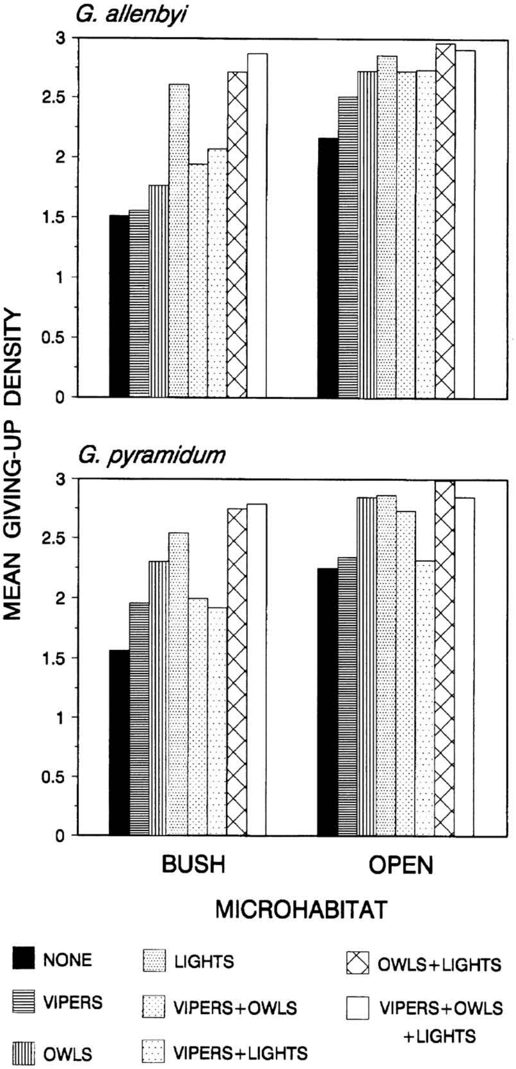

Fig. 2. Effects of the presence of owls, vipers and added illumination on the mean giving-up density per night for *Gerbillus allenbyi* and *G. pyramidum* in the bush and open microhabitats.

$P < 0.001$; for *G. pyramidum*, $F = 13.182$, $df = 1{,}38$, $P = 0.001$). Also, animals overall foraged fewer trays in the open microhabitat (for *G. allenbyi*, $F = 5.288$, $df = 1{,}46$, $P = 0.026$; for *G. pyramidum*, $F = 5.996$, $df = 1{,}38$, $P = 0.019$). We found no significant interactions. For the density of predators used in these experiments, gerbils apparently perceived higher predatory risk from owls than from snakes; animals responded significantly to owls, but not to snakes, and the avoidance of the open microhabitat is in concordance with how gerbils respond in experiments where we used owls as predators (Kotler et al. 1991) rather than snakes (Kotler et al. 1993a).

We obtained similar results regarding the intensity of patch use. We used average daily GUDs (log transformed) as a measure of patch use. For *G. allenbyi*, GUDs were significantly higher when owls were present ($F = 4.346$, $df = 1{,}49$, $P = 0.046$), with added illumination ($F = 16.885$, $df = 1{,}49$, $P < 0.001$), and in the open microhabitat ($F = 25.744$, $df = 1{,}49$, $P < 0.001$; Fig 2). The effect of microhabitat was especially pronounced with added illumination (microhabitat × lights interaction, $F = 8.376$, $df = 1{,}49$, $P = 0.006$); no other interactions were significant. These results further suggest that *G. allenbyi* treats the risk of predation as a foraging cost and that owls are of greater concern than snakes. For *G. pyramidum*, we also measured higher GUDs in response to the presence of owls ($F = 10.774$, $df = 1{,}41$, $P = 0.002$), with added illumination ($F = 9.185$, $df = 1{,}41$, $P = 0.004$), and in the open microhabitat ($F = 13.646$, $df = 1{,}41$, $P = 0.001$; Fig. 2). Likewise, *G. pyramidum* treats predatory risk as a foraging cost and responds more strongly to owls than to snakes. Most interesting is the significant interaction of vipers, owls, and lights ($F = 4.236$, $df = 1{,}41$, $P = 0.046$). When owls and light are present, gerbils avoid the open microhabitat almost entirely. This is appropriate behavior since owls are more effective in capturing prey in the open and are especially effective in capturing prey when illumination is added (Kotler et al. 1991). When snakes are also present, however, the use of the bush microhabitat drops and use of the open increases. Gerbils are apparently being forced into the open microhabitat and to increase their exposure to owls due to the added danger of snakes in the bush microhabitat.

4. Discussion

Our previous experiments provided the basis for predicting predator facilitation between snakes and owls preying on gerbils (Kotler et al 1991, 1993a). We demonstrated in those experiments that gerbils respond to snakes and to owls in qualitatively different manners. In particular, gerbils avoided the open microhabitat in response to owls and avoided the bush microhabitat in response to snakes. If those responses are appropriate with regards to microhabitat specific predatory risk (in fact, rates of predation by owls on gerbils are higher away from cover, Kotler et al. 1991), then gerbils facing snakes and owls may contend with conflicting demands: they cannot forage and be safe from both types of predators simultaneously. If so, then when faced with a second type of predator, gerbils may increase their exposure to the first in order to be safer from the new threat. To test this, we subjected gerbils to the presence of both snakes and owls.

As in previous experiments, gerbils responded to the presence of owls by reducing their foraging activity (visiting fewer resource patches), quitting resource patches at a higher harvest rate (higher GUD, Kotler & Brown 1990), and reducing their use of the open microhabitat (Kotler et al. 1991). These results demonstrate that gerbils respond to owls, treat predatory risk from owls as a cost of foraging (higher GUDs in response to the presence of owls), and perceive owls to be a greater threat in the open microhabitat than the bush. These results also show consistency with results from our past experiments.

In contrast to our previous experiments (Kotler et al. 1993a, Kotler, Dednam, and Blaustein, unpublished data), the gerbils did not respond to the presence of snakes. In previous experiments with vipers, gerbils quit resource patches at higher harvest rates (GUDs), had higher GUDs in the open microhabitat, and foraged more patches in the open microhabitat in response to vipers; in those experiments, responses of *G. pyramidum* to snakes were stronger than those of *G. allenbyi*. One possible explanation of why gerbils did not respond to snakes alone in the current experiments is that gerbils do not perceive snakes to be a threat. But we have previously shown otherwise. Another explanation is that gerbils perceive owls to be a greater threat than snakes, and this swamps out the snake effect. In previous experiments involving snakes, we only used snakes, while here we used owls and snakes. We have demonstrated elsewhere that the response of gerbils to owls can linger for several days after they are no longer exposed to owls (Kotler 1992). This suggests that in the current experiment, gerbils always had some perceived risk of predation from owls even on night without owls. This may have masked the response to snakes.

Our results provide experimental evidence of predator facilitation in the aviary. The presence of illumination and owls causes *G. pyramidum* to use resource patches less intensively and to eliminate its foraging in the open microhabitat; the addition of snakes, too, lead gerbils to increase their intensity of patch use in the open. This increases the exposure of gerbils to owl predation. The fangs of the vipers are driving the gerbils into the talons of the owls.

Should a similar phenomenon occur in nature, then the composition of the predator community may affect many aspects of gerbil ecology including microhabitat selection, habitat selection, and even species coexistence.

In areas where snakes are the major rodent predators, we might expect rodents to prefer resource patches in the open, but to prefer the bush microhabitat where owls and other visually aided, pursuing predators are dominant. In areas where both types of predators are important, microhabitat selection should be less pronounced and change seasonally with predator activity. Precisely this occurs in a species of pocket mouse (*Perognathus amplus*), kangaroo rat (*Dipodomys merriami*), and ground squirrel (*Spermophilus tereticaudus*) at a Sonoran Desert site (Brown 1989). In regards to habitat selection, Rosenzweig & Abramsky (1986) have suggested that both *G. allenbyi* and *G. pyramidum* prefer the semi-stabilized sand dune habitat, but differ in their secondary preferences. *G. pyramidum* has a secondary preference of open sand dunes, and *G. allenbyi* has a secondary preference of stabilized sand field. We have suggested that this difference is due to the better ability of *G pyramidum* to avoid owl predation (Kotler et al. 1991). Snakes may also contribute to this since previous results suggest that *G. pyramidum* is also better at detecting snake predators (Kotler et al. 1993a; Kotler and Blaustein, unpublished data). Finally, predator composition may affect prey community structure. Abramsky (1988) has suggested that species diversity in gerbils is affected by the openness of the environment and resource availability. Sites with intermediate productivity have the highest rodent species diversity. Abramsky suggested that this is due to the mix of high microhabitat diversity, moderate risk of predation from owls due to protection offered by perennial plants, and moderate availability of food. High rodent species diversity may also be explained by intermediate amounts of perennial cover offering the best combination of protection from the duel threat of snakes and owls.

The conflicting demands placed on prey individuals when faced with multiple predator species influence foraging behavior, species interactions and community structure of other species, as has been illustrated in many examples. Mosquito larvae may have to choose between the risk of notonectid predation at the pond's surface (Cockrell 1984) and odonate predation at the pond's bottom (Blaustein, Nagar, and Margalit, unpublished data). The small johnny darter fish, *Etheostoma nigrum*, leaves hiding places under rocks due to predatory risk there from the crayfish, *Orconectes rusticus*, and by so doing, increases its exposure to small mouth bass, *Micropterus dolomieui*, in the open (Rahel & Stein 1988). Larval amphibians have to contend with both invertebrate (Skelley & Werner 1990), and vertebrate (Petranka et al. 1987) predators, which may influence foraging behavior and the organization of larval amphibian communities (Morin 1986). Diverse predators may influence habitat selection and promote the coexistence of *Daphnia pulicaria* and *D. galeata* (Leibold 1989). Finally, in the Sonoran Desert rodent example previously cited, seasonal changes in the abundance and activity of owls, diurnal raptors, and rattlesnakes contribute to species coexistence of a species of *Perognathus amplus*, *Dipodomys merriami* and *Spermophilus tereticaudus* (Brown 1989).

As in our previous aviary experiments, the artificial setting of the experiments may confound and compromise our experimental results and limit their application to field situations. Complications include the high densities of rodents, owls, and snakes, the use of brush piles to mimic shrubs, and the use of millet within trays as a seed resource for gerbils. Despite these unrealistic features of the experiments, we are confident in the realism of the results.

Gerbils acclimated right away to the experimental conditions. They occupied existing burrows or dug their own, they foraged in seed trays, and avoided predators. In regards to gerbil foraging behavior in seed trays, we have extensive experimental evidence showing that gerbils use these trays in a manner consistent with cost-benefit considerations and fitness maximization (e.g., Brown 1988, Kotler et al. 1991, Mitchell, Brown, and Kotler, unpublished data). Also, rodents responded appropriately to the experimental treatments: gerbils reduced their foraging activity under conditions which actually were more dangerous (e.g., the presence of predators) and avoided the open microhabitat (the microhabitat rendered most dangerous by owls; Kotler et al. 1991) when owls were present. Finally, the reaction of gerbils to the experimental factors in the aviary parallel their reaction to similar experiments in the field: gerbils reduce their foraging activity in response to added illumination (e.g. Kotler 1984) and the presence of owls (Vaginsky, unpublished data). These facts suggest that the aviary was a realistic abstraction of the field and that the results from these aviary experiments are qualitatively applicable to field situations.

In summary, the aviary experiments presented here demonstrated that owl and snake predation strongly influences the foraging decisions of two gerbil species. In response to the presence of predators, gerbils reduced foraging activity, altered their use of microhabitat, and left food patches at a higher harvest rate. Overall, the duel threat of snakes and owls presented the gerbils with conflicting demands where they could not forage for seed resources and remain safe from both predators simultaneously. *G. pyramidum* in particular responded to the threat of snakes in a manner which increased its exposure to owls. Thus, predator facilitation between snakes and owls preying on gerbils is occurring in the aviary. This may have implications for rodent foraging behavior, species interactions and community structure in the field.

Acknowledgements. We thank A. Subach for assistance in capturing snakes and gerbils used in the experiments. H. Dednam and C. Shochet assisted with the experiments. We also thank Z. Abramsky, A. Bouskila, O. Hasson, W. A. Mitchell, and M. L. Rosenzweig for valuable discussion.

We give special thanks to A. Bouskila for helping make this project possible. BPK is a Bat-Sheva de Rothschild fellow. This work was supported by the Israel Academy of Sciences and Humanities (Basic research grant 524/88). This is publication 153 of the Mitrani Center for Desert Ecology.

References

Abramsky, Z. 1988: The role of habitat and productivity in structuring desert rodent communities. — Oikos 52:107–114.

Abramsky, Z., Brand, S. & Rosenzweig, M. L. 1985: Geographical ecology of gerbilline rodents in sand dune habitats of Israel. — J. Biogeogr. 12:363–372.

Abramsky, Z. & Pinshow, B. 1989: Changes in foraging effort in two gerbil species correlate with habitat type and intra- and interspecific activity. — Oikos 56:43–53.

Abramsky, Z., Rosenzweig, M. L., Pinshow, B. P., Brown, J. S., Kotler, B. P. & Mitchell, W. A. 1990: Habitat selection: An experimental field test with two gerbil species. — Ecology 71:2358–2357.

Alon, E. 1984: Reptiles and amphibians. — Animals and plants of the land of Israel. 5. Yoav Graphics, Ramat Gan, Israel.

Bar, Y., Abramsky, Z. & Gutterman, Y. 1984: Diet of gerbilline rodents in the Israeli desert. — J. Arid. Environ. 7:371–376.

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

— 1989: Desert rodent community structure: a test of four mechanisms of coexistence. — Ecol. Monogr. 59:1–20.

Charnov, E. L., Orians, G. H. & Hyatt, K. 1976: Ecological implications of resource depression. — Amer. Natur. 110:247–259.

Cockrell, B. J. 1984: Effects of water depth on choice of spatially separated prey by Notonecta glauca L. — Oecologia 62:256–261.

Kotler, B. P. 1984: Harvesting rates and predatory risk in desert rodents: a comparison of two communities on different continents. — J. Mammal. 65:91–96.

— 1992: Behavioral resource depression and decaying perceived risk of predation in two species of coexisting gerbils. — Behav. Ecol. Sociobiol. 30:239–244.

Kotler, B. P. & Brown, J. S. 1990: Harvest rates of two species of gerbilline rodents. — J. Mammal. 71:591–596.

Kotler, B. P., Brown, J. S. & Hasson, O. 1991: Owl predation on gerbils: the role of body size, illumination, and habitat structure on rates of predation. — Ecology 72:2249–2260.

Kotler, B. P., Brown, J. S., Slotow, R., Goodfriend, W. & Strauss, M. 1993a. The influence of snakes on the foraging behavior of gerbils. — Oikos, in press.

Kotler, B. P., Brown, J. S. & Subach, A. 1993b: Mechanisms of coexistence of optimal foragers: temporal partitioning by two species of sand dune gerbils. — Oikos, in press.

Leibold, M. A. 1989: Resource edibility and the effects of predators and productivity on the outcome of trophic interactions. — Amer. Natur. 134:922–949.

Longland, W. & Price, M. V. 1991: Direct observations of owls and heteromyid rodents: can predation risk explain microhabitat use? — Ecology 72:2261–2273.

Mitchell, W. A., Abramsky, Z., Kotler, B., Pinshow, J. & Brown, J. S. 1990: The effect of competition on foraging activity in desert rodents: theory and experiments. — Ecology 71:844–854.

Morin, P. J. 1986: Interactions between intraspecific competition and predation in an amphibian predator-prey system. — Ecology 67:713–720.

Petranka, J. W., Kats, L. B. & Sih, A. 1987: Predator-prey interactions among fish and larval amphibians: use of chemical cues to detect predatory fish. — Anim. Behav. 35:420–425.

Rahel, F. J. & Stein, R. A. 1988: Complex predator-prey interactions and predator intimidation among crayfish, piscivorous fish, and small benthic fish. — Oecologia 75:94–98.

Rosenzweig, M. L. & Abramsky, Z. 1985: Detecting density-dependent habitat selection. — Amer. Natur. 126:400–417.

— 1986: Centrifugal community structure. — Oikos 46:339–348.

Skelly, D. K. & Werner, E. E. 1990: Behavioral and life-historical responses of larval American toads to an odonate predator. — Ecology 71:2313–2322.

Taylor, R. T. 1984: Predation. — Chapman and Hall, New York and London. 166 pp.