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Predator – prey relationships: rodent – snail interactions in the Central Negev Desert of Israel

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We investigated the effects of increasing rodent (*Acomys cahirinus* and *Gerbillus dasyurus*) predation efficiency on their population density and the population of their prey, the desert snail (*Trochoidae seetzenii*). The study was carried out on a rocky hillslope in the Central Negev Desert, Israel.
Rodent predation on snails is limited by the number of shelters for rodents in the area. In most natural conditions, more shelters are found on the upper than on the lower slope. We introduced artificial shelters along the slope. We then censused the number of rodents, snails, and of eaten snails for five years. In the presence of artificial shelters the predation efficiency of rodents (number of snail eaten per rodent) increased. The number of rodents also increased and the number of snails decreased on the experimental plots relative to control plots.
We suggest that the persistence of the snail-rodent system is due to spatial variation in the relative importance of direct prey-predator relations and the indirect effects of snail immigration to the slope and presence of protective shelters for the rodents.
Our study supports recent work indicating that in a prey-predator system, in addition to direct predation, the heterogeneity of the environment and predation risk while foraging, affect both the behavior and the density of the predator and the prey.

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Most ecologists agree that predation has an important direct effects on prey density (e.g., Connell 1975) and indirect effects on prey behavior, morphology, physiology, chemistry, and life history (e.g. Werner et al. 1983, Sih et al. 1985, Kerfoot and Sih 1987, Miller and Kerfoot 1987, Mittelbach and Chesson 1987, Kotler and Holt 1989).

Theoretically, the dynamics of predator prey systems can be described by isoclines plotted on a state space of population densities (Rosenzweig and MacArthur 1963). The prey isocline has a hump while the predator isocline is often assumed to be vertical or with a positive slope (Rosenzweig 1969, Begon et al. 1986). Stability analysis of such isocline graphs shows that on the right of the hump the system tends to stabilize while on the left it tends to destabilize. The efficiency of the preda-

tors in transferring the prey into its own biomass determines the location of the predator isocline. One of the predictions of the theory is that, in general, the system should become less stable when the efficiency of the predators increases.

We conducted a five year study in which we artificially increased the efficiency of a predator (rodents) by providing artificial shelters for them without changing prey (snails) conditions. Our long term experiment is based on a one year study of snail-rodent interactions (Abramsky et al. 1990). The one year study suggested that predation pressure by rodents is important in explaining the density distribution pattern of the snails in the area. The existence of shelters is probably crucial for the rodents by providing protection against their own predators. In the present study we test the hy-

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pothesis that artificial shelters for rodents increase their efficiency as snail predators resulting in higher rodent and lower snail densities.

The rodent-snail system

Several species of rodents (*Gerbillus dasyurus*, *Acomys cahirinus*, *A. russatus*, *Eliomys melanurus*, *Sekeetamys calurus*, and *Meriones crassus*) that prey on snails inhabit the rocky Central Negev Desert. The actual feeding occurs only after the rodents have carried the snails to specific sites termed feeding tables. Feeding tables are typically found under a rock or a shrub (Abramsky et al. 1990). The cracked shells in the feeding tables, persist for a long time (many years) carrying diagnostic marks as evidence of predation by the rodents (Yom Tov 1970). The most common predators on these rodents are owls, foxes, hyenas, and snakes.

The snail *Trochoidae seetzenii* is the most common snail species found in the Negev desert. It is distributed throughout the Negev Desert and into the Judean Desert. Its center of distribution is located near the Sede-Boqer area where its densities are highest (as many as 60 snails m^{-2}, Genot-Lahav 1986).

In summer, most individuals of *T. seetzenii* are found attached to shrubs. In winter, after the rains, the snails feed on the shrubs and descend to the ground to copulate and lay eggs. Between rainy days, when the ground surface is dry, the snails climb back onto the shrubs. The adult snails are conspicuous and thus always exposed to predation (Shachak et al. 1981). Most of the rodent predation on snails occur in the summer when all snails are attached to shrubs (Abramsky et al. 1990).

In most of the hills of the Central Negev, *T. seetzenii* exhibits a repeated spatial pattern of abundance. The highest densities of the snails are found in wadi beds with gradually decreasing density uphill along the slopes. Only a few snails occur at the top of the hills. Most feeding tables and the highest density of eaten snails are found in the upper parts of the slopes, where natural shelters for the rodents are common (Abramsky et al. 1990).

Five additional species of snails (*Sphincterochila zonata*, *S. prophaterum*, *Euchondrus desertorum*, *E. albulus*, and *Xeropicta vestalis*) are common in the rocky Central Negev. However, they are relatively rare in our study area (Yom Tov 1970, Abramsky et al. 1990) and occur very infrequently in feeding tables.

Additional aspects of the natural history and ecology of *T. seetzenii* were studied by Yom Tov (1970, 1971, 1972). Schmidt-Nielsen et al. (1971) studied its physiology, and Genot-Lahav (1986) studied its taxonomy and geographical distribution.

Methods

Study site

The study was conducted on a hillslope located about 40 km south of Beer Sheva (Site A in Abramsky et al. 1990). On south facing slopes in this area, there are cliffs and boulders that can provide many natural shelters for the rodents. North facing slopes are more moderate and are covered with small stones. Very few natural shelters for rodents are available. Therefore we selected a north facing slope for introducing artificial shelters.

Two experimental and two control plots, each 30 × 60 m in size, were constructed on the slope. On each of the 2 experimental plots, 40 shelters were constructed in a 4 by 10 grid with 7 m separating the artificial shelters. Each shelter consisted of a heavy cardboard cylinder 40 cm long and 15 cm in diameter, with several stones piled on the cylinder for camouflage. Snails and rodents were censused on the plots for 2 months before the construction of the shelters. During the first year of the experiment (July 1985–1986), the numbers of eaten snails in each of the artificial shelters and the number of snails and rodents were censused every two months. After July 1986, we censused the plots only once or twice every year.

Sampling techniques

Each plot was trapped for rodents for 5 consecutive nights using 40 Sherman live folding traps arranged in a 5 by 8 grid. Traps were placed ten meters apart. Traps were set in late afternoons, baited with a mixture of seeds and checked in the early mornings. Captured individuals were identified to species, marked by toe clipping and their location of capture noted. Number of snails in the plots were counted in a grid of 2 × 2 m squares that covered the entire area of experimental and control plots. The content of artificial feeding tables was collected every sampling period, brought to the laboratory, and counted. The content of natural feeding tables was collected only during the last two years of the research. Collecting eaten snails from artificial and natural feeding tables allowed us to obtain an unbiased estimate of predation rate on both the control and experimental plots. This is because cracked shells stay intact for many years and are not influenced by weathering or other factors during our relatively short (five yr) period. Furthermore, since our study site had no natural crevices we were able to find all natural feeding tables and eaten snails in the area. For more information regarding the study area, organisms, and sampling technique see Abramsky et al. (1990).
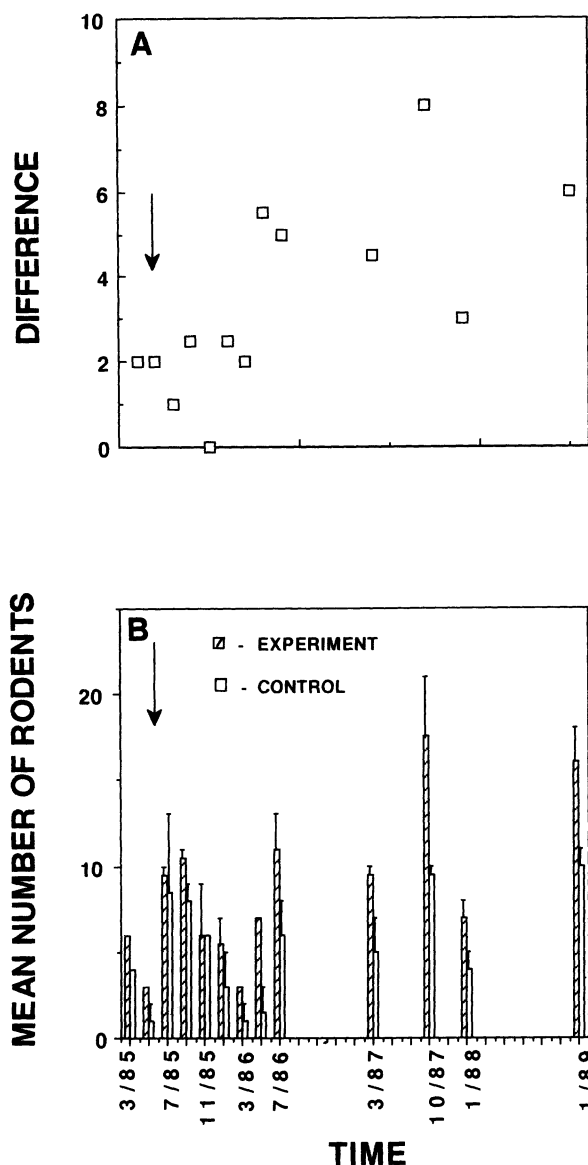
Fig. 1. Mean number (±SE) of rodents/plot found in the experimental and control plots during the study period (B) and the difference between mean rodent densities in the experimental and control plots (A). The arrow represents the time when artificial shelters were constructed.

Results and discussion

The response of the rodents

Two species of rodents were captured during the study (*Gerbillus dasyurus* and *Acomys cahirinus*). Since we don't know of differences between the feeding rates of the two rodent species we combined their densities in each plot. However, both species exibited similar pattern of changes in density. Fig. 1 shows the mean densities/plot of the rodents and the difference in mean den-

sities in control and experimental plots. Although the rodent densities varied significantly on all plots during the study (time effect in Repeated Measures Anova; $F=69.2$, $p=0.001$), number of rodents was significantly higher on the experimental plots relative to their density on the control plots ($F= 10.15$, $p < 0.05$). Furthermore, the fact that the treatment × time interaction was also significant (Repeated Measures Anova; $F=9.05$, $p=0.0008$) suggests that the difference between the experimental and control plots changed with time. Throughout the experiment, even before the manipulation, more rodents were trapped on the experimental plots than on the control plots (Fig. 1B). The difference between mean rodent densities on the experimental and control plots increased from 2 individuals during the first year of the study to about 6 individuals during later parts of the study (Fig. 1A). The increase in the difference of rodent densities between experimental and control plots occurred rather rapidly, after one year, and fluctuated at a density difference of about 6 individuals.

The difference in rodent density on the control and experimental plots could, theoretically, be the result of a proportional increase of the density of the rodents on all plots, rather than a density response to the existence of the shelters. However, the increase in the density of the rodents on the experimental plots (density of rodents = $4.3 + 0.25$ time; $r=0.60$, $p=0.03$) was significant, while on the control plots it was not (density of the rodents = $3.4 + 0.11$ time; $r=0.36$, $p=0.23$). Furthermore, the slope of the regression line for the experimental plots is significantly ($p<0.01$) steeper than that for the control plots.

The significant increase in number of individuals on the experimental plots suggests that shelters for the rodents are crucial in limiting their density even when
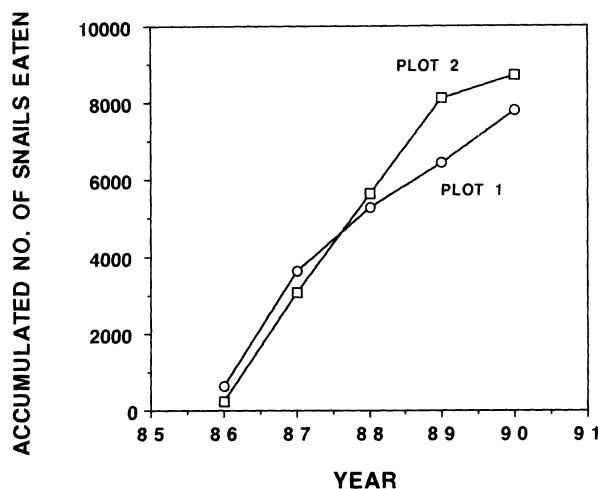

Fig. 2. Accumulated number of snails eaten found in artificial shelters in each of the two experimental plots. During the last four years of the study eaten snails were collected in the autumn. For 1986, we summed the number of eaten snails that were collected every two months.
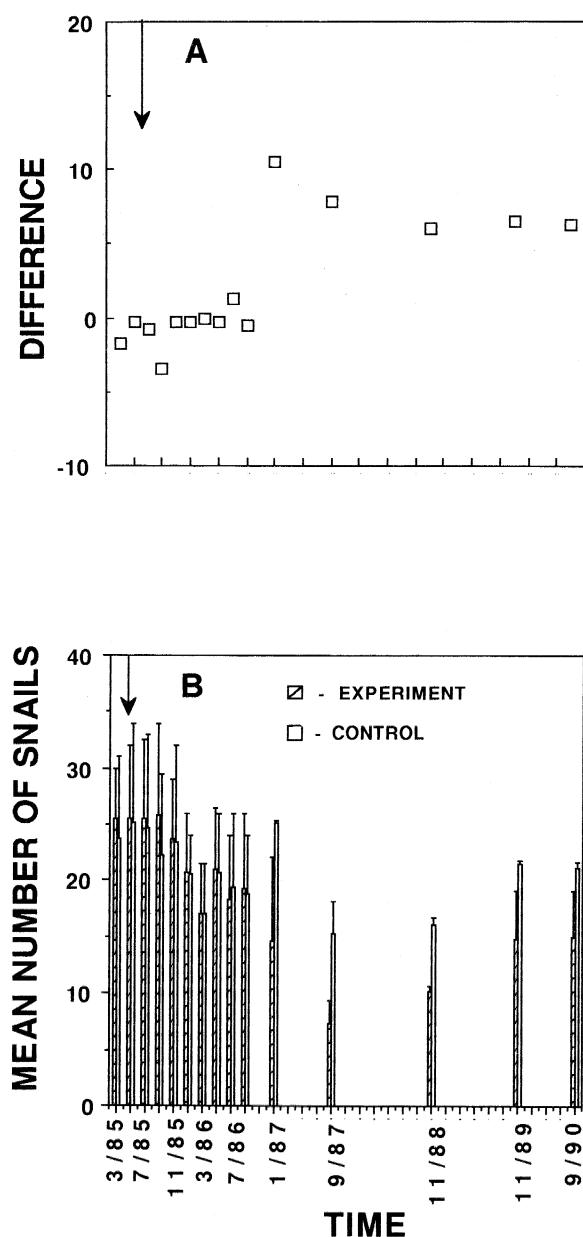
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Fig. 3. Mean number (±SE) of snails/4m² found in the experimental and control plots during the study (B) and the difference between mean snail densities in the experimental and control plots (A). The arrow represents the time when artificial shelters were constructed.

food is available. Shelters can provide protection from predators and from heat stress during summer days.

The impact of rodents on snail density

During the experiment a total of 16 505 cracked shells were collected in the artificial feeding tables (Fig. 2).

The heavy predation of snails started one year after the initiation of the study. This agrees with the one-year lag in the density response of the rodents to the manipulation. In the natural feeding tables a total of 2850 and 1202 snails were found during the study in the control and the experimental plots, respectively. Predation of snails on the experimental plots (1202 + 16 404 = 17 707) exceeded that on the control plots (2850) by 14 857 snails. Although snail densities significantly decreased (Fig. 3B) on all plots between 1985 and 1990 (time factor in Repeated Measures Anova; F = 14.8, p = 0.0001), the predation on snails significantly reduced (F= 49.8, P < 0.02) their mean density on the experimental relative to the control plots (Fig. 3B). Also, the significant treatment × time interaction (Repeated Measures Anova; F=4.96, p=0.0002) suggested that the difference between the experimental and control plots changed over time. There was no difference between mean snail density in the experimental and control plots in the first year. The difference increased to about 1.25 snails m^{-2} after about two years and then seemed to level off till the end of the study (Fig. 3A). Although natural population of snails fluctuated (Fig. 3B), snail density in the experimental plots was still high and the difference between experimental and control plots (Fig. 3A) appeared to level off. Note that the difference between experimental and control plots stayed relatively constant despite large changes in absolute densities.

The efficiency of the rodents

The density of the rodents on the experimental plots (17.2 ±2.46, mean ± SE) was significantly higher (p < 0.05) than the density on the control plots (10.4 ± 1.75). In addition, the mean predation efficiency of the rodents on the experimental plots (1030 snails eaten rodent⁻¹) was much higher than on the control plots (274 snails eaten rodent⁻¹). In the presence of shelters the rodents better utilized the high snail density in the lower parts of the slope (y = 3702 + 17.2 [distance from hilltop], r=0.96, p<0.04) although high predation was evident on the entire slope. 3700, 4176, 4311, and 4517 cracked shells were found at distances of 5, 20, 35, and 50m, respectively, from the hilltop toward the wadi. In natural areas most of the shelters are found in the upper part of the slope and most snail predation occurs there (Abramsky et al. 1990).

The increased efficiency of the rodents may lead to larger fluctuations in densities of predator and prey as predicted by some models (Rosenzweig and MacArthur 1963). We measured fluctuations in density using the coefficient of variation (CV) as an index of variability. There were no significant differences (p = 0.20) between the CVs of snail densities on the experimental plots (0.31) and on the control plots (0.15). For the rodents, as well, the difference was not significant (p>

0.50). CV was 0.60 for the control and 0.52 for the experimental plots. However, with only two replicates the power of the test is low.

General discussion

One may expect that in a system where a rodent predator feeds on unprotected snails, the prey have a high risk to become extinct. This is especially true in our desert system, since the snail is not only a source for energy and protein but also a water source. However, *Trochoidae seetzenii* is not on the verge of extinction in the Negev Desert. In natural areas of the Central Negev, the snail is very common not only in wadi washes, where the rodents are scarce, but also on the hills where the rodents reside.

We will try to address the question why the snails do not become extinct in our manipulated area. We analyze our results in relation to direct and indirect effects in a predator-prey system (Rosenzweig and MacArthur 1963, Abrams 1984, 1987, Holt 1984, 1985, Roughgarden 1986, Schoener 1986, Kerfoot and Sih 1987).

In the first two years of the study (1985–1987) the decrease in snail population densities was larger than the observed predation. This indicates either emigration to the wadis or mortality, or both. In the last three years (1987–1990), snail densities increased despite the heavy predation by the rodents. The increase in density could have been the result of higher reproduction rates or immigration from the wadis, or both. Hermony et al. (1992) showed that reproduction in *T. seetzenii* is density dependent. Thus, in the low snail density of the experimental plots, higher reproduction is expected relative to the control plots. In addition, high immigration of snails onto the experimental plots might also be important. Indeed, Hermony et al. (1992), in an experimental study on habitat distribution of *T. seetzenii*, showed that at the onset of the rainy season snails move from the high wadi density to the slope to lay eggs. If this is also true in the present study then indirect factors also influence the rodent-snail relationship. This is because the density and reproduction on the slope might be dependent on immigration from the wadi where predation is negligible. This may imply that the wadi bed is the source habitat of the snails while the slopes are the sinks (source and sink are defined as in Pulliam 1988). The idea underlying this possibility is that excess snails produced in the wadi invade the slopes where reproduction is lower than mortality. If the slopes are the sinks of the wadi populations, then the direct effect of predation on extinction might be true. However, the effect is counterbalanced by immigration from the wadi. In fact, in an area where shelters were constructed 33 years ago and very little immigration is possible due to barriers between the wadi and the slope (see Keidar plots in

Abramsky et al. 1990) the snail population is almost extinct on the slope.

The results of the present study show that where artificial shelters were built along the entire slope the efficiency and density of the rodents increased. The rodents significantly reduced the snail densities, relative to the control plots. In natural areas, shelters occur mostly in the upper parts of the slope. The distribution of the snails along the slope can be explained as the results of scale-dependent, direct and indirect prey predator interactions. On a small scale, in patches with high number of shelters for the rodents, such as the upper rocky parts of the slope, the predation efficiency of the rodents is high. In addition, it is a long distance (50–60 m) for a snail to travel from the wadi to the upper rocky parts of the slope. Thus, immigration from the wadi to the upper slope is expected to be negligible. Under these conditions we assume that in the upper slope, snails almost become extinct as a result of direct prey-predator relationships. Indeed, this is the case in most of the watersheds in the central Negev. On a larger spatial scale, as one moves along the slope from the upper rocky parts to the wadi, two indirect factors, i.e., number of shelters and intensity of immigration rate, may also affect the rodent-snail relationship. The number of shelters decrease due to the change of the geomorphological structure along the slope (Yair and Shachak 1987). This decreases the efficiency of the rodents as snail predators in the lower relative to the upper slope. In addition, the short distance between the wadi, with negligible predation load, to the lower slope, enables high immigration of snails (Hermony et al. 1991) into this area. These two indirect effects seem to counterbalance the direct predation of snails and stabilize the system. The differences between the upper and lower slope create a gradient of snail-rodent interactions along the slope. The relative effect of the direct relationship increases and the effects of indirect relationships decrease from lower to upper slope.

Why does the efficiency of the rodents as snail predators increase in areas where shelters occur? Although we have no data to support our suggestion, we think that the activity of the rodents is limited by their predators to areas where safe sites occur. The artificial shelters reduced the risk of predation for the rodents on the entire slope and enabled the rodents to take advantage of the higher snail densities in the lower parts of the slope. This, in turn, resulted in increased rodent density and efficiency.

In conclusion, our study supports recent work indicating that in a prey-predator system, in addition to direct predation, the heterogeneity of the environment and predation risks while foraging, affect the behavior and the density of both prey and predator (Rosenzweig 1974, Kotler 1984a, b, Brown 1988, Kotler and Holt 1989).

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References

Abrams, P.A. 1984. Foraging time optimization and interactions in food webs. – Am. Nat. 124: 80–96.
– 1987. Indirect interactions between species that share a predator: varieties of indirect effects. – In: Kerfoot W. C. and Sih, A., (eds), Predation: direct and indirect impacts on aquatic communities. Univ. Press of New England, Hanover, NH, pp. 38–56.
Abramsky, Z., Alfia, H., Schachak, M. and Brand, S. 1990. Predation by rodents and the distribution and abundance of the snail *Trochoidea seetzenii* in the Central Negev Desert of Israel. – Oikos 59: 225–234.
Begon, M., Harper, J. L. and Townsend C. R. 1986. Ecology. – Sinauer, Sunderland, MA.
Brown, J.S. 1988. Patch use as an indicator of habitat preference, predation risk, and competition. – Behav. Ecol. Sociobiol. 22: 37–48.
Connell, J.H. 1975. Some mechanisms producing structure in natural communities: a model and evidence from field experiments. – In: Cody, M. L. and Diamond, J. M., (eds), Ecology and evolution of communities. Harvard Univ. Press, Cambridge, MA, pp. 460–490.
Genot-Lahav, S. 1986. Morphological variation in a desert snail. – M.Sc. thesis, Ben Gurion Univ. (in Hebrew).
Hermony, I., Shachak, M. and Abramsky, Z. 1992. Habitat selection in the desert snail *Trochoidea seetzenii*. – Oikos, in press.
Holt, R. D. 1984. Spatial heterogeneity, indirect interactions, and the coexistence of prey species. – Am. Nat. 124: 377–406.
– 1985. Density independent mortality, non-linear competitive interactions, and species coexistence. – J. Theor. Biol. 116: 479–493.
Kerfoot, W. C. and Sih, A. (eds). 1987. Predation: direct and indirect impacts on aquatic communities. – Univ. Press of New England, Hanover, NH.
Kotler, B. P. 1984a. Harvesting rates and predatory risk in desert rodents: A comparison of two communities on different continents. – J. Mammal. 65: 91–96.
– 1984b. Risk of predation and the structure of desert rodent communities. – Ecology 65: 689–701.
– and Holt, R. D. 1989. Predation and competition: The interaction of two types of species interactions. – Oikos 54: 256–260.

Miller, T. E. and Kerfoot, W. C. 1987. Redefining indirect effects – In: Kerfoot W. C. and Sih, A. (eds), Predation: direct and indirect impacts on aquatic communities. Univ. Press of New England, Hanover, NH, pp. 33–37.
Mittlebach, G. H. and Chesson, P. L. 1987. Predation risk: indirect effects on fish populations. – In: Kerfoot, W. C. and Sih, A. (eds), Predation: direct and indirect impacts on aquatic communities, Univ. Press of New England, Hanover, NH, pp. 315–332.
Pulliam, H. R. 1988. Sources, sinks, and population regulation. – Am. Nat. 132: 652–661.
Rosenzweig, M.L. 1969. Why the prey curve has a hump. – Am. Nat. 103: 81–87.
– 1974. On the optimal above ground activity of Bannertail Kangaroo rats. – J. Mammal. 55: 193–199.
– and MacArthur, R. H. 1963. Graphical representation and stability conditions of predator prey interactions. – Am. Nat. 97: 209–223.
Roughgarden, J. 1986. A comparison of food-limited and space-limited animal competition communities. – In: Diamond, J. and Case, T. J. (eds), Community ecology. Harper and Row, New York, pp. 492–516.
Schmidt Nielsen, K., Taylor, C. R. and Shkolnik, A. 1971. Desert snails: Problems of heat, water and food. – J. Exp. Biol. 55: 385–398.
Schoener, T. W. 1986. Patterns in terrestrial vertebrate versus arthropod communities : do systematic differences in regularity exist? – In: Diamond, J. and Case, T. J. (eds), Community ecology. Harper and Row, New York, pp. 556–586.
Shachak, M., Safriel, U.N. and Hunum, R. 1981. An exceptional event of predation on desert snails by migratory thrushes in the Negev Desert, Israel. – Ecology 62: 1441–1449.
Sih, A., Crowley, P., McPeek, M., Petranka, J. and Srohmeier, K. 1985. Predation, competition and prey communities: a review of field experiments. – Annu. Rev. Ecol. Syst. 16: 269–311.
Werner, E. E., Gilliam, J. F., Hall, D. J. and Mittlebach, G. G. 1983. An experimental test of the effects of predation risk on habitat use in fish. – Ecology 64: 1540–1548.
Yair, I. and Shachak, M. 1987. Studies in watershed ecology. – In: Berkofsky, L. and Wurtele, M. G. (eds), Progress desert research. Rowman & Littlefield, Totawa, NJ, pp. 145–193.
Yom Tov, Y. 1970. The effects of predation on population densities of some desert snails. – Ecology 51: 907–911.
– 1971. The biology of the desert snails *Trochoidea seetzenii* and *Sphincterochila boissieri*. – Isr. J. Zool. 20: 213–248.
– 1972. Field experiments on the effect of population density and slope direction on the reproduction of the desert snail *Trochoidea seetzenii*. – J. Anim. Ecol. 41: 17–22.