

The impact of long-term continuous risk of predation on two species of gerbils

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Abstract: Individuals of *Gerbillus allenbyi* Thomas, 1918 were subjected to artificial illumination in large field enclosures (2-ha sandy-substrate plots in the Negev Desert, Israel). The illumination was similar to that provided by a full moon and was used to mimic the elevated risk of avian predation that accompanies a full moon. We artificially illuminated the enclosures during all hours of darkness for 3 consecutive months. In some cases, we also added individuals of *Gerbillus pyramidum* Geoffroy, 1825 to provide a competitive challenge for the *G. allenbyi*. In the presence of the light source, individuals of *G. allenbyi* shifted their foraging activity to favor experimental areas of darkness. They also foraged less in the open and more beneath bushes. In the absence of the light source, *G. allenbyi* shifted its activity from the subplot with *G. pyramidum* to the subplot without the competitor. However, the competitive effect of the *G. pyramidum* disappeared in plots that were artificially illuminated. These results closely resemble those of earlier experiments during which we increased the apparent risk of predation in brief pulses lasting only 2 h/night.

Résumé : Nous avons exposé des gerbilles (*Gerbillus allenbyi* Thomas, 1918) à un éclairage artificiel dans de grands enclos en nature (des parcelles de 2 ha à substrat sablonneux dans le désert de Néguev, Israël). L'éclairage correspondait à celui de la pleine lune et a servi à évaluer le risque accru de prédation par les oiseaux qui accompagne la pleine lune. Cet éclairage a été maintenu durant toutes les périodes d'obscurité pendant trois mois d'affilée. Dans certains cas, nous avons introduit des individus de *Gerbillus pyramidum* Geoffroy, 1825 pour provoquer un défi de compétition chez *G. allenbyi*. Durant l'éclairage, les individus de *G. allenbyi* déplacent leurs activités de recherche de nourriture vers les zones d'obscurité. Ils recherchent aussi leur nourriture moins dans les zones exposées et plus sous les buissons. En absence d'éclairage, les *G. allenbyi* sont moins actifs dans la partie de la parcelle qui contient *G. pyramidum* et plus actif dans celle où il est absent. Cependant, l'effet de compétition créé par la présence de *G. pyramidum* disparaît dans les parcelles soumises à l'éclairage artificiel. Ces résultats ressemblent beaucoup à ceux que nous avons obtenus dans des expériences antérieures durant lesquelles nous avons augmenté le risque apparent de prédation pour de courtes périodes de seulement 2 h/nuit.

[Traduit par la Rédaction]

Introduction

Potential victims belonging to many animal species should and do modify their behavior in response to variations in predatory risk (e.g., Sih et al. 1982; Lima 1987; Kotler and Holt 1989; Werner and Anholt 1996). Do such modifications depend on the time scale of the risk?

For example, we administered 2-h pulses of predatory risk to a psammophilic gerbil (*Gerbillus allenbyi* Thomas, 1918) in 1-ha field enclosures and measured their response (Abramsky et al. 1997, 2002). Gerbils shifted their foraging to an adjacent risk-free hectare in proportion to the risk intensity. Moreover, in the presence of risk (Abramsky et al. 1998), foraging *G. allenbyi* stopped responding to the pres-

ence of competition from its congener *Gerbillus pyramidum* Geoffroy, 1825.

But gerbils did not need to pay a very high price for avoiding the 2-h predation risk pulses (Abramsky et al. 1996). As soon as we removed the risk, gerbils compensated for their reduced activity by increasing their activity the very night of the pulse. And the presence of extra risk during one night had no influence on the gerbils' activity during the following night. Thus, although our short-pulse experiments lasted several weeks, each night's effect vanished quickly leaving little or no lasting effect on the amount of food that the gerbils collected (Abramsky et al. 1996). Indeed, the risk allocation hypothesis of Lima and Bednekoff (1999) is based on the notion that prey adaptively allocate their foraging efforts, and thus, their exposure to predation risk across high- and low-risk situations (Sih et al. 2000). Namely, under short-term risk of predation the prey may behave in a way that reduces interspecific competition.

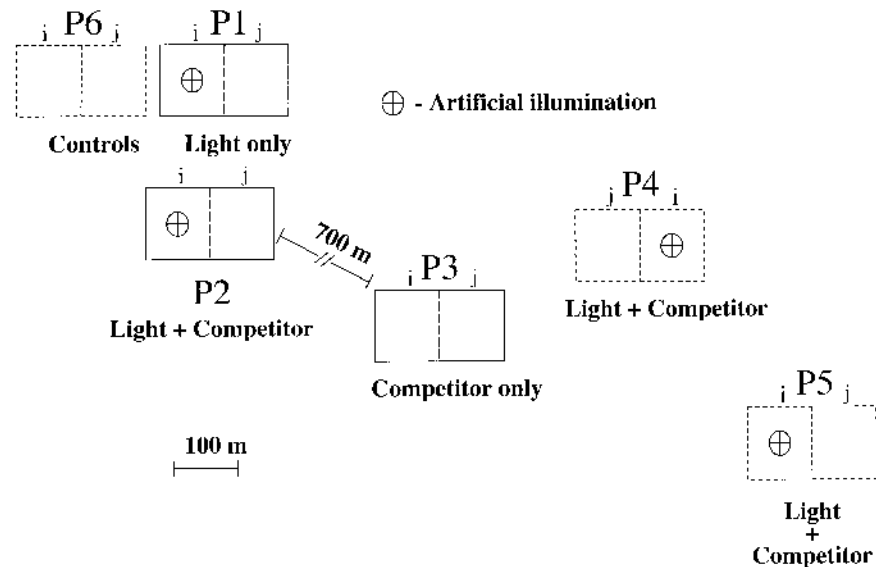
A chronically elevated risk might evoke a different set of behavioral adjustments. If risk were to be sustained over a long time scale, reductions in foraging might lead to significant reductions in the amount of food collected and, thus, to reduced forager fitness. Then foragers would not be able to avoid foraging in the presence of elevated risk. Their responses to short pulses of risk would not accurately reflect those that need to be made to chronic risk.

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Fig. 1. Schematic illustration of the study area. Solid rectangles represent the enclosed plots and broken rectangles represent the unenclosed plots. Plots 2 and 3 were separated by 700 m. The scale on the left and the right of the vertically broken line is equal. Each plot is divided into subplots i and j. The location of the plots followed the natural landscape in locations when the proportion of the semi-stabilized dune and stabilized sand were similar.



In the present paper, we report the results of experiments to determine the responses of gerbils to chronic risk and to compare them with their previously described responses to brief pulses. We measured the response of our principal target species, *G. allenbyi*, to the interspecific competition of its congener, *G. pyramidum*, with and without the risk. We observed their activity level, habitat distribution, and micro- and macro-habitat selection in various experimental conditions. Then we used the changes in habitat distribution to estimate the biotic interaction coefficients.

Models of predators interacting with two victim species display a rich variety of dynamic outcomes (e.g., Gilpin 1972; Abrams 1977; Vance 1978; May 1981; Holt 1984). Indeed, many experimental field studies show that predation enhances coexistence in some cases (e.g., Dayton 1973; Paine 1974); however, just as many studies show that predation decreases the number of coexisting species in other cases (e.g., Paine and Vadas 1969; Janzen 1976).

We hypothesized that animals should change their foraging patterns depending on the costs of predation relative to costs of competition to optimize fitness. We predicted that unlike short pulses under conditions of chronic predation risk gerbils would not be able to ignore the cost of competition and, thus, would also respond to the presence of a competitor. As the reader will see below our prediction failed. Not only did many responses stay the same, under certain circumstances, risk actually seemed to change competitors into apparent mutualists. Perhaps the reader will be as surprised as we were by this unexplained result.

Methods

Species

Our experimental system contains two competing species that we have studied intensively for the last 15 years (e.g., Rosenzweig and Abramsky 1997). Both are psammophilic gerbils with mean masses of 24 g (*G. allenbyi*) and 40 g

(*G. pyramidum*). They are nocturnal and feed mostly on seeds (Bar et al. 1984). Both species burrow and prefer semi-stabilized dunes.

Plots

We used six experimental plots: three unenclosed and three enclosed (Fig. 1). Each plot was 100 m × 200 m (2 ha). The plots were at Holot Mashabim Nature Reserve (31°01'N, 34°45'E), 50 km south of Beer-Sheva, in the Negev Desert, Israel. The reserve consists mostly of stabilized sand and semi-stabilized dune habitats.

Each unenclosed plot (plots 4, 5, and 6) was divided into a pair of square, 1-ha subplots (4i and 4j, 5i and 5j, 6i and 6j). Each subplot of a pair had similar proportions of stabilized sand and semi-stabilized dune. In all three plots, gerbils from both species were free to come and go.

Each enclosed plot (enclosures 1, 2, and 3) was surrounded by a fence made from 6 mm mesh hardware cloth that was buried 40 cm below the soil surface and extending 60 cm above ground. A 15 cm wide ribbon of aluminum flashing atop both sides of the fence prevented rodents from climbing over.

We perforated each 100-m length of fence with between four and six portals (19.7 mm diameter). The portals allowed easy passage of individuals of *G. allenbyi*; however, adult individuals of *G. pyramidum* were too large to pass through the portals (Abramsky et al. 1991). Although young *G. pyramidum* were small enough to traverse the portals, the study was conducted during the nonreproductive period when young individuals were absent.

Because our experiments lasted so long, we had to be concerned with the artifact known as pen effects (Krebs et al. 1969). Pen effects are unusual population dynamics observed when small mammals are restricted to experimental enclosures about the size of ours. Often they manifest themselves as population densities that are two, three, or more times as large as those seen in nature. To avoid pen effects,

we simply kept all portals open during all experiments. Therefore, the fences served only to create extreme spatial heterogeneity in the density of *G. pyramidum*.

Using perforated 100-m fences exactly like those that surrounded an enclosure, we divided each enclosure into a pair of square, 1-ha, matched subplots. Each subplot of a pair had similar proportions of stabilized sand and semi-stabilized dune. Previous work with *G. allenbyi* on these subplots showed that the matching was adequate, i.e., in the absence of any experimental treatment, *G. allenbyi* distributed their foraging activity equally between the subplots of each pair (Abramsky et al. 1991, 1996, 1997, 2000, 2002). Evidence of the successful matching comes from this study too, i.e., with no *G. pyramidum* and no experimental treatment, *G. allenbyi* utilized the two subplots of each pair equally (paired *t* test, $t_{[22]} = 0.45$, $p = 0.66$, $n = 23$). Furthermore, in these experiments, *G. allenbyi* could go anywhere (portals were always open), allowing us to see whether they perceived any major differences among the entire set of subplots. They did not. With no *G. pyramidum* present and no experimental treatment, there was no preference in the allocation of *G. allenbyi* activity among all subplots ($F_{[5,44]} = 0.15$, $p = 0.98$). The successful matching of plots and subplots allowed us to perform different treatments in different plots and to compare their results. Allowing individuals of *G. allenbyi* in our experiments to move anywhere (within their home ranges) enabled them to alter their local densities at will. (This aspect of the design is very different from that of the short-term experiments.) In fact, individuals of *G. allenbyi* did change their locations throughout the experiments and the percent similarity in the identity of individuals of *G. allenbyi* between consecutive trapping sessions in the three unenclosed plots was only $32.00 \pm 0.10\%$ (mean \pm SD), which was similar to 32.5% in the three enclosures. Percent similarity in the identity of individuals of *G. allenbyi* between nonconsecutive trappings (every other session) was lower ($18.00 \pm 0.09\%$). During a single session, the percent similarity in the identity of individuals of *G. allenbyi* in adjacent subplots was $6.00 \pm 0.02\%$.

Experimental risk

In previous experiments, risk was either artificial illumination or overflights of a subplot by trained barn owls, *Tyto alba* (Scopoli, 1769). But risk pulses lasted only 2 h/night. To impose a chronic risk of predation, or at least the perception of a chronic risk on the part of the gerbils, it is not practical to fly trained owls constantly over the experimental areas. One must employ the surrogate variable (artificial illumination).

Artificial illumination is quite effective. Moonlight should help nocturnal predators such as owls to detect and catch their prey (e.g., Lockard and Owings 1974; Clarke 1983; Kotler 1984; Longland and Price 1991). Thus, moonlit nights should be perceived as a higher risk by victim species such as gerbils. Lockard and Owings (1974), Clarke (1983), and Price et al. (1984) showed that moonlit nights could be regarded as nights with increased risk of predation. Nocturnal desert rodents drastically reduce their activity during moonlit nights in a way that is similar to their response to the presence of predators (Daly et al. 1992). And artificial illumination produces a similar reduction in activity (e.g.,

Lockard and Owings 1974; Kaufman and Kaufman 1982; Kotler 1984; Price et al. 1984; Kotler et al. 1993). Moreover, the energetic costs to gerbils generated by owl flights is comparable to the costs imposed by simulated full moonlight (Abramsky et al. 2002).

Relying on this information, we used artificial full moonlight to simulate a chronic risk of predation that lasts for several months. The artificial illumination was present during all hours of darkness of each night.

We set up a 6 m tall pole in the middle of subplots 1i, 2i, 4i, and 5i. At its top, we placed a 15-W neon light. Each light had a hood that limited the light to a radius of about 45 m. A small generator (450 W) no closer than 900 m to any plot provided energy for the lights. Using a Luna Pro light meter, we determined that the intensity of the artificial light was 7 lx at 0 m from a pole and 0.17 lx at 40 m. The intensity of the full moon in August was 4 lx. We operated the generator and the lights every night except during the 4 nights/month nearest to the full moon. The adjacent subplots of each treatment (1j, 2j, 4j, and 5j) served as controls. In subplots 3i and 3j, we measured interspecific competition in the absence of simulated moonlight. Light intensity in the control subplots was the natural moonlight.

Treatments

The unenclosed plots 4 and 5 was artificially illuminated and contained natural densities of gerbils. Enclosure 1 was also illuminated and contained *G. allenbyi*, but *G. pyramidum* were excluded. Enclosure 2 was illuminated and contained both *G. pyramidum* and *G. allenbyi*. Enclosure 3 had both gerbil species but was not artificially illuminated. Plot 6 was a control that contained natural densities of gerbils.

All enclosed and unenclosed plots had variations in microhabitat. Light changed in intensity from the centre of the subplot outward. Nevertheless, we treated the data of the subplots as if each one were homogeneous. We did it for all treatment plots and all controls. This should introduce no error, as we did the same thing in the earlier 2-h pulsed experiment (Abramsky et al. 2002).

Except for plots 4 and 5, the experiments were not replicated spatially. This kind of design is entirely appropriate when working with systems such as ours where treatments are very costly (Hurlbert 1984). In addition, although there was no spatial replication, there was temporal replication.

Protocol

We began by removing all *G. pyramidum* from all subplots of all enclosures. Next, for 4 months prior to the initiation of the treatments, we followed the activity of *G. allenbyi* in all subplots of all enclosures. Then we added four *G. pyramidum* to subplots 2i and 3i and began the simulated full moonlight treatment in subplots 1i, 2i, 4i, and 5i.

In the middle of the experiment, we removed *G. pyramidum* from subplot 2i and introduced them to subplot 2j. Thus, in the second enclosure, competition and predation risk worked in tandem in 2i during the first half of the experiment but were instituted in opposite subplots during the second half of the experiment. In several cases the removal of *G. pyramidum* was not 100% and *G. pyramidum* occurred in both subplots. But the activity of *G. pyramidum* in the in-

tended subplot was always higher than in the adjacent subplot.

Time frame

We conducted the experiments during the fall of 1999, and between July and December 2000. As a result of a severe drought, *G. pyramidum* was almost extinct at Holot Mashabim from December 1999 to June 2000 and the population of *G. allenbyi* was extremely low. Thus, we did not perform treatments during that period. Effectively, this divided our experiments into halves: October–December 1999 and July–December 2000. New individuals of *G. pyramidum* were introduced to the appropriate enclosed plots in July 2000.

Gerbil activity densities

We measured foraging activity by counting gerbil tracks left in 0.4 m × 0.4 m sand-tracking stations. Sampling the number of tracks in the sand did not interfere with the rodents' natural behavior. Each 1-ha subplot had 40 sand-tracking plots arranged in 20 stations. Ten stations were located in semi-stabilized dune and 10 in stabilized sand. At each station, one tracking plot was placed under a shrub and one in the open. We smoothed the stations at dusk and read them at dawn.

We distinguished the tracks of *G. pyramidum* and *G. allenbyi* by amputating outside left (*G. pyramidum*) or right (*G. allenbyi*) hind-limb toes. We distinguished individuals by forelimb toe amputation.

The score given to a tracking plot depended on footprint coverage and ranged from the following: 0 (no tracks), 1 (1/4 track coverage), 2 (1/2 track coverage), 3 (3/4 track coverage), and 4 (full track coverage). We obtained our measures of foraging activity by summing the activity-density score in all 40 stations of a subplot. AGA is the activity density of *G. allenbyi* and AGP is the activity density of *G. pyramidum*.

Activity of the rodents should be, and is, significantly correlated with density (Abramsky et al. 1990, 1991, 1997; Mitchell et al. 1990). This remained true in the current experiments: $AGA = 36.35 + 0.83GA$ ($r = 0.43$, $p = 0.01$, $n = 35$) where GA is the density of *G. allenbyi*. Furthermore, Abramsky et al. (1990, 1991), Ziv et al. (1993), and Mitchell et al. (1990) showed that activity data can better assess interactions between gerbils than numbers of gerbils obtained from trapping. Thus, we continue to use AGA and AGP as surrogate variables for actual population densities in our studies.

We measured the activity densities of the gerbils for 1–2 nights every month. In addition, we trapped gerbils on the plots for 1–3 nights every 2nd month. Both activities were done in the enclosed and unenclosed plots. We collected all data during phases of the moon with little or no moonlight.

Statistical analysis

We used standard multiple regressions, ANOVA, ANCOVA, and Student's and paired *t* tests. The α level was set at 0.05. All proportional data were arcsine transformed for the statistical tests.

Species respond to spatial heterogeneity continuously rather than categorically, i.e., when faced with a variety of

habitat types, all individuals of a species do not respond by moving to the best one. Instead they adjust their spatial distributions, creating inequalities in their density that compensate for the inequalities among habitats (Fretwell and Lucas 1970; Fretwell 1972).

Our method of estimating interactions in the field depends on such density adjustments. It also assumes that the animals doing the adjusting are doing so appropriately, i.e., achieving distributions that approximate an evolutionary stable strategy (ESS). This allows us to measure competitor–competitor isoclines (or at least the perception of these isoclines by foragers). We describe the method elsewhere (Abramsky et al. 1991; Rosenzweig and Abramsky 1997) and in Appendix A.

We could not use the method of Abramsky et al. (1997) to compare the responses of *G. allenbyi* to predation threats in the present study with the responses from the earlier study. This is because in the present study the full moonlight treatment is a categorical variable (i.e., it is either present or absent), whereas the experimental threat is a continuous variable in the earlier study (Abramsky et al. 1997); we used various numbers of trained owl flights during different experiments. Thus, we replaced the earlier method with an index that measures the response of the target species (*G. allenbyi*) to artificial illumination.

We define the response index to be $(AGA_i - AGA_j) / (AGA_i + AGA_j)$ for the following reasons. The response to a predation threat should be negative, i.e., *G. allenbyi* should spend more time foraging in dark subplots (*j*) than in their artificially illuminated twins (*i*). The index thus begins with the term $AGA_i - AGA_j$. But this term has a bias. Its minimum equals $-(AGA_i + AGA_j)$, which would occur if all foraging were to take place in the dark subplot. Dividing the first term by $AGA_i + AGA_j$ yields an index that is a negative proportion of the maximum response. For example, the result from one trial is as follows: if $AGA_i = 33.5$ and $AGA_j = 63.0$, then the difference is -29.5 and the response index is -0.306 .

In summary, the response index can vary between 0 and -1 . And a large negative value of the index indicates a large response to illumination, whereas a small negative value indicates a small response.

Results

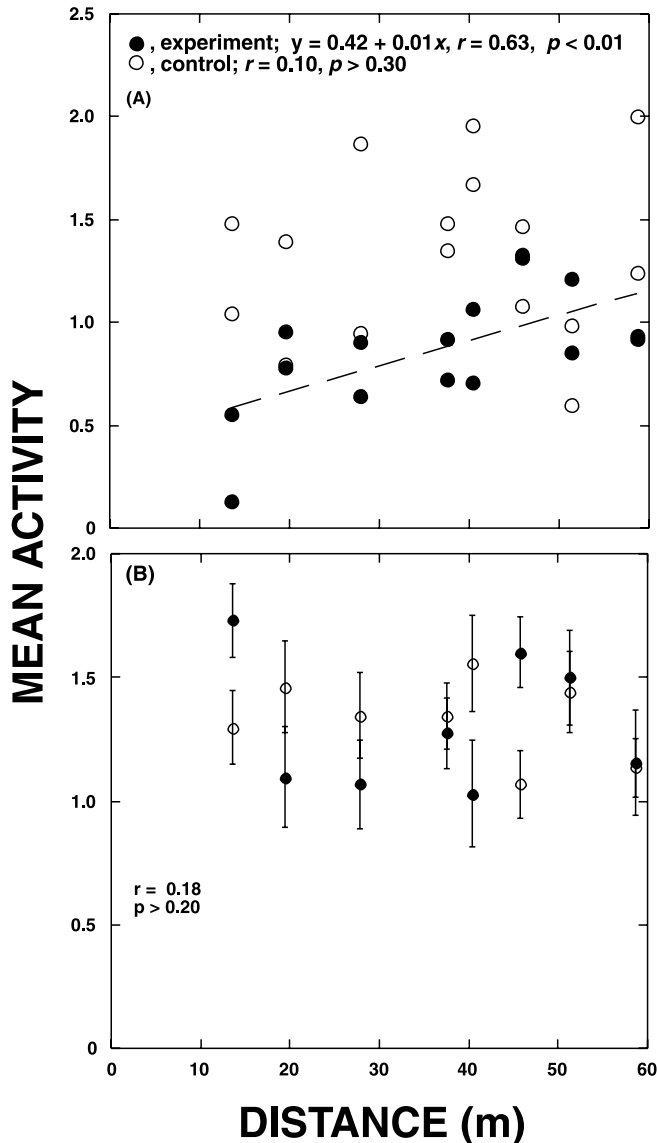
Activity and distance from light

In all plots with artificial illumination, gerbil activity increased significantly as a function of the distance from the centre of the subplots where the light pole was located out to about 45 m, which was as far as the simulated moonlight traveled. This was true in the unenclosed subplots 4i and 5i and in enclosures 1i and 2i, one of which also had the competitor *G. pyramidum* (Figs. 2A, 3A, and 3B).

In contrast, subplots without artificial illumination usually did not show the trend. Whether unenclosed (4j, 5j, 6i, and 6j) or enclosed (1j, 2j, 3i, and 3j), AGA did not vary with distance from the centre (Figs. 2B and 3C).

To test whether the gerbil response to illumination changed during the experiments, we divided the data of plots 4 and 5 between the first and second halves of the experiment. The response of the gerbils to artificial illumination did not change (ANCOVA, $F_{[1,152]} = 0.36$, $p = 0.61$). This re-

Fig. 2. (A) Activity increased significantly as a function of distance from the centre of the unenclosed, experimentally illuminated subplots (4i and 5i) but not on their control, unilluminated, twin subplots (4j and 5j). (B). It also did not change on either of the twin unenclosed, unilluminated, control subplots (6i and 6j). The figure shows the combined data for subplots 4i and 5i and for 4j and 5j, but similar trends exist in each separate subplot.

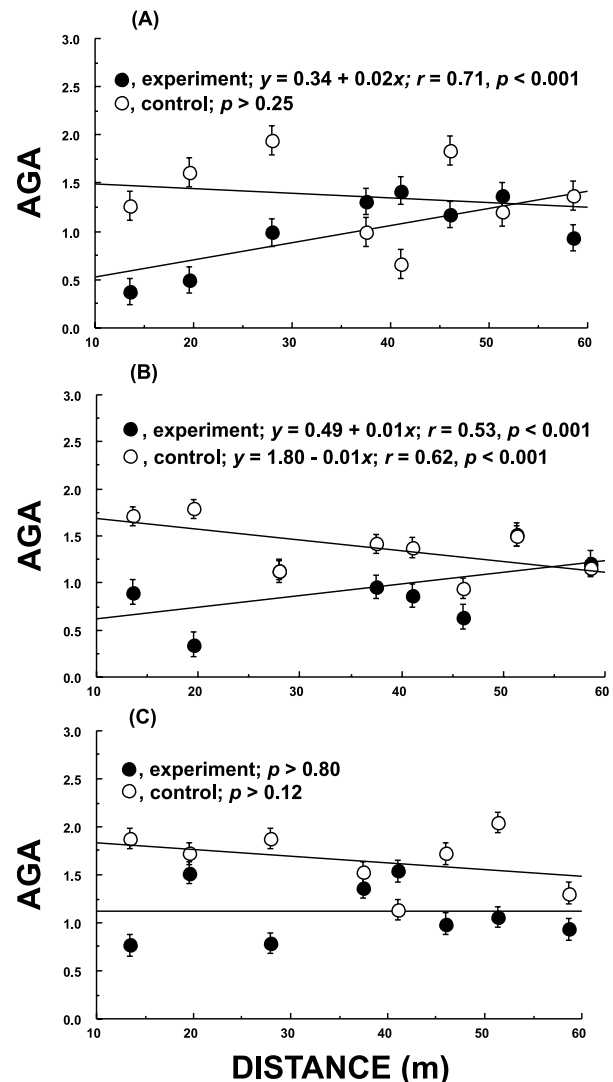


sult confirmed earlier results in which the effect of time on the magnitude of the interaction coefficients was tested (Abramsky et al. 1991).

Effect of illumination on gerbil numbers and subplot preferences

Our treatments did not influence the densities of either gerbil species as seen from the unenclosed plots 4 and 5 (Fig. 4). The ANOVA showed that the numbers of *G. allenbyi* in illuminated i subplots did not differ from the numbers in j subplots that were not illuminated ($F_{[1,16]} = 1.19$, $p = 0.29$). The numbers of *G. pyramidum* yielded the same insignificant difference ($F_{[1,16]} = 0.65$, $p = 0.43$). There was also no treatment \times month effect on gerbil density

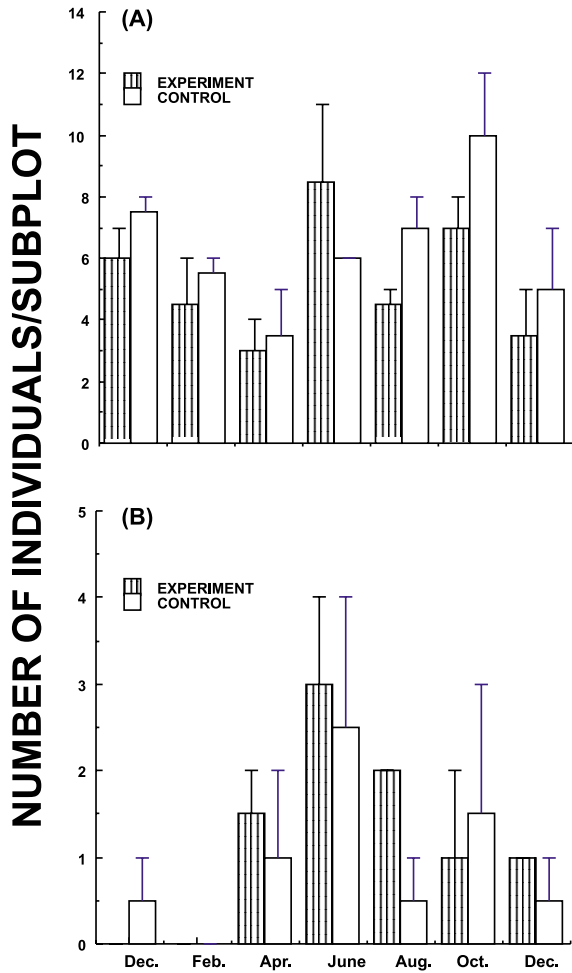
Fig. 3. Activity of *Gerbillus allenbyi* (AGA; mean \pm 1 SE) increased as a function of distance from the centre of the enclosed (subplots 1i and 2i), illuminated subplots (● in A and B). It neither changed on the enclosed (subplots 1j and 2j), unilluminated subplots (○ in A and B) nor on the unilluminated subplot (3i) that had *Gerbillus pyramidum* (● in C) or its (3j) twin subplot (without *G. pyramidum*; ○ in C). In A and B, the AGA regression lines intersect at <55 m, indicating that the impact of the light treatment vanished beyond this distance. In C, as expected, AGA was larger in the twin subplot without *G. pyramidum*.



(*G. allenbyi*: $F_{[5,16]} = 0.69$, $p = 0.63$; *G. pyramidum*: $F_{[5,16]} = 0.43$, $p = 0.82$).

Despite the lack of effect on densities, illumination did affect the way individuals of *G. allenbyi* used the subplots. Before they were illuminated, about half of *G. allenbyi* activity was recorded in the i subplots (0.52 ± 0.07). This proportion declined significantly (to 0.37 ± 0.11) after the moonlight treatment was initiated (Student's *t* test, $t_{[42]} = 4.43$, $p < 0.0001$). But individuals of *G. pyramidum* showed no such change. Before illumination began, 0.61 ± 0.20 of their activity was in i subplots; afterwards, 0.69 ± 0.24 was in i subplots. This increase of 8% was not significant (Student's *t* test, $t_{[30]} = 0.92$, $p = 0.36$), although both propor-

Fig. 4. Density (mean \pm SE) of *G. allenbyi* (A) and *G. pyramidum* (B) in the experimental (4i and 5i) and control (4j and 5j) subplots of the two pairs of the unenclosed plots.



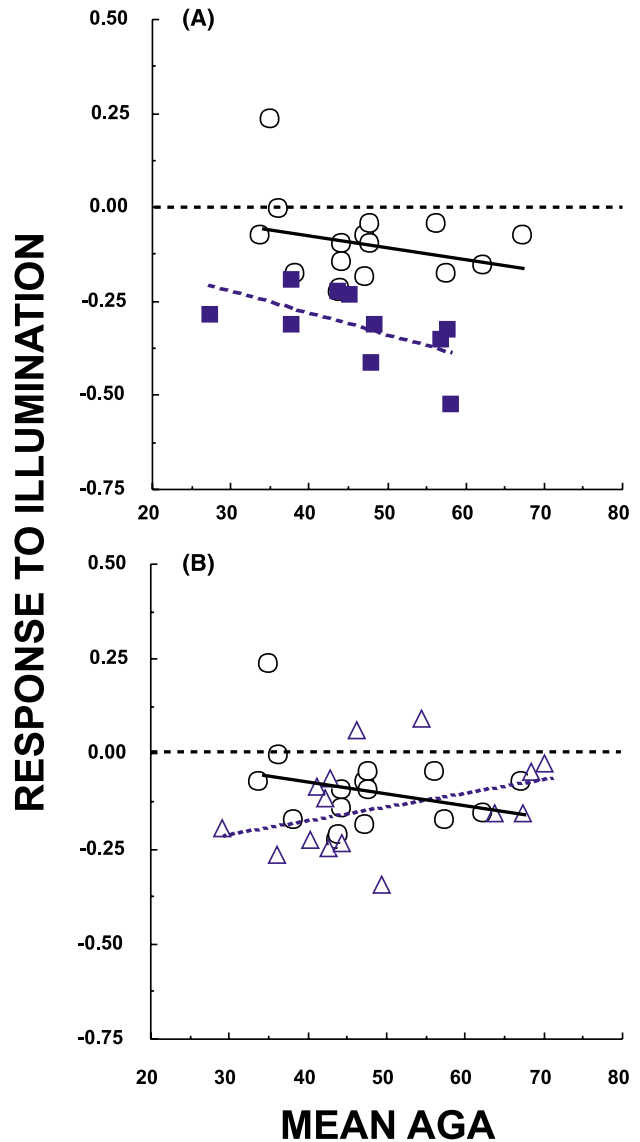
tions were significantly larger than those of *G. allenbyi* (paired *t* test, $t_{22} = 6.6, p < 0.0001$). Thus, *G. allenbyi* responded to illumination by moving about 15% of its activity from illuminated to unilluminated subplots, whereas *G. pyramidum* did not show a significant change in its preference for the i subplots.

We obtained the same result for *G. allenbyi* in enclosure 1, which had no *G. pyramidum*. In the illuminated subplot 1i, AGA was significantly lower than that on the adjacent, unilluminated subplot j (paired *t* test, $t_{35} = 6.12, p < 0.0001$). *Gerbillus allenbyi* always biased its activity toward the subplot j (16 cases; Fig. 5, ○). This bias was significant (paired *t* test, $t_{15} = 4.0, p < 0.001$). Abramsky et al. (1997, 1998) obtained a similar result in enclosures from which *G. pyramidum* was excluded.

Enclosure 3 had *G. pyramidum* but had no artificial illumination. In it, *G. allenbyi* acted as if *G. pyramidum* was a competitor (Fig. 6, ○). In 19 out of 20 cases, AGA in the subplot without *G. pyramidum* was higher than AGA in the subplot with *G. pyramidum* (paired *t* test, $t_{20} = 4.7, p < 0.0001$). The relationship was quantitatively expressed as $AGA = 65.9 - 0.73AGP$ ($r = -0.36, p = 0.03, n = 27$).

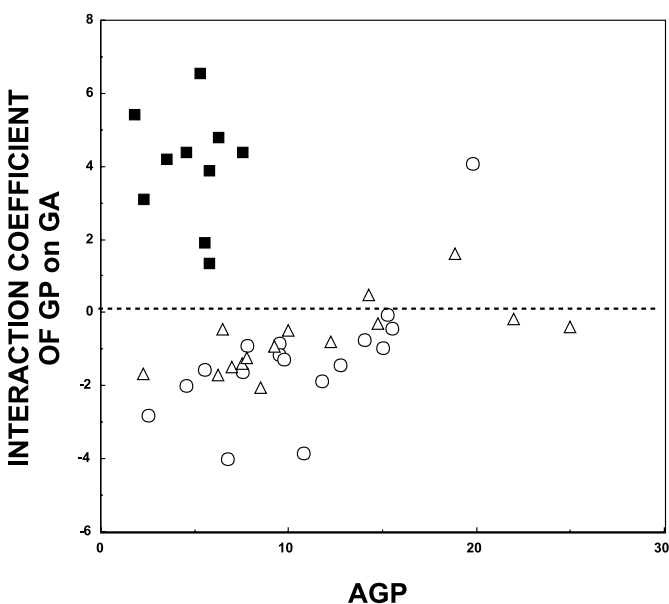
One reason for the low *r* value of the latter relationship is that the strength of interspecific competition varies depend-

Fig. 5. Responses of *G. allenbyi* to the treat of predation in the absence of *G. pyramidum* (plot 1) compared with responses in its presence (plot 2). The more negative the response, the stronger the perceived predation cost. The apparent predation coefficients of simulated moonlight on *G. allenbyi* do not vary with AGA, but this may be a type II error; therefore, we graph the result against AGA anyhow. (A) When *G. pyramidum* was added to the subplot (2j) opposite the light source, *G. allenbyi* avoided the illuminated subplot (2i) strongly. These responses by *G. allenbyi* suggest that *G. pyramidum* becomes a mutualist in unilluminated plots opposite illuminated ones. (B) However, *G. allenbyi* did not respond to the addition of *G. pyramidum* when *G. pyramidum* was added to the to the same subplot (2i) as the illumination. Competition between *G. pyramidum* and *G. allenbyi* was neutralized by the threat of predation. ○, illumination only; △, *G. pyramidum* and illumination in the same subplots; ■, *G. pyramidum* and illumination in opposite subplots.



ing upon population sizes as predicted by the isoleg theory (Rosenzweig 1981). We used the method described in Appendix A to quantify this dependence, which is as follows

Fig. 6. The interaction coefficients of *G. pyramidum* (GP) on *G. allenbyi* (GA) as a function of different values of mean activity of GP (AGP) in plots 2 and 3. The more negative the coefficient from the reference line at zero, the stronger the competition. Refer to the appendix for an explanation of how the interaction coefficients were estimated. Plot 3 (no illumination; ○): $y = -4.1 + 0.27x$, $r = 0.70$, $p < 0.01$. The decline in the interaction coefficient as AGP grows (over this range of AGP values) was theoretically predicted and was observed previously (Abramsky et al. 1991, 1994). Plot 2 (trials with GP and illumination in the same subplot; ▲): $y = -1.9 + 0.10x$, $r = 0.67$, $p < 0.01$. There was no significant difference between responses to this treatment (▲) and those of the former treatment (○). Plot 2 (trials with GP and illumination in opposite subplots; ■): $r = 0.13$, $p > 0.30$. The response of *G. allenbyi* to *G. pyramidum* has shifted significantly and has become positive, suggesting that *G. pyramidum* acts as a mutualist.



(Fig. 6): $\alpha_{a,p} = -4.07 + 0.27 \text{ AGP}$ where a is *G. allenbyi* and p is *G. pyramidum*.

This equation gives the slopes of the isoclines as functions of AGP. Hence, its solution is the set of isocline equations themselves: $\text{AGA} = -4.07\text{AGP} + 0.27\text{AGP}^2/2 + C$ where C is the constant of integration that determines which isocline the equation describes.

During the experiment, the average values of AGA and AGP were 59 and 10, respectively. Substituting these into the isocline equation yields the value of the constant for the isocline passing through the point (59,10). Its equation is $\text{AGA} = 86.2 - 4.07\text{AGP} + 0.27\text{AGP}^2/2$.

Combination treatments

Enclosure 2 had both artificial illumination and competition from *G. pyramidum*. Regardless of the presence of *G. pyramidum*, *G. allenbyi* biased its activity in favor of the dark subplot except in two trials (one in the presence of *G. pyramidum*, one in the absence of *G. pyramidum*). Using a dummy variable for simulated moonlight (MnLit), the relationship was $\text{AGA} = 57.1 - 17.3\text{MnLit}$ where MnLit was equal to 1 or 0 ($r = 0.51$, $p < 10^{-4}$).

Adding the activity of *G. pyramidum* (AGP) failed to improve the regression significantly ($p_{\text{AGP}} > 0.32$). Hence, when the simulated full moonlight treatment was present, *G. pyramidum* had no effect on the foraging of *G. allenbyi*. As in the earlier results from the pulsed risk experiments (Abramsky et al. 1998), it would seem that the threat of predation had neutralized the effect of interspecific competition. However, we did detect an unexpected interaction when we looked at the illumination responses of *G. allenbyi*.

Because *G. pyramidum* is a competitor whose activity is known to reduce AGA, we expected that AGP would act in much the same way as illumination. Thus, we expected that adding *G. pyramidum* to the illuminated side would further depress AGA on that side, whereas adding them to the dark side would reduce the depression of AGA on the illuminated side. However, the results contradicted that hypothesis.

First, using an ANCOVA ($F_{[1,35]} = 0.99$, $p = 0.32$), we determined that the response of AGA to illumination did not depend significantly on the value of AGA itself in enclosures 1 or 2. Then with an ANOVA ($F_{[2,37]} = 12.5$, $p = 0.0001$), we saw that it did depend on whether *G. pyramidum* was present and, if present, on whether *G. pyramidum* was on the illuminated or unilluminated side of the enclosure. Figure 5 compares the responses from enclosure 1 (no *G. pyramidum*) to those of enclosure 2 (with *G. pyramidum*).

Figure 5A compares the responses of enclosure 1 (illumination only) to those of enclosure 2 (*G. pyramidum* in the unilluminated subplot). If *G. pyramidum* is a competitor in enclosure 2 than the response of *G. allenbyi* to illumination in enclosure 2 should be weaker than in enclosure 1. The response values from enclosure 1 would have to lie below those of enclosure 2. But instead, they were significantly higher (Student's t test, $t_{[24]} = 5.18$, $p < 0.0001$).

Mutualism can be defined as positive feedback between populations (e.g., Holland et al. 2002). A mutualist added to a habitat therefore increases the value of the habitat for the other species. *Gerbillus allenbyi* behaved as if *G. pyramidum* added value to the habitat when light was present in the neighboring hectare. Thus, the behavior of *G. allenbyi* was what one expected if *G. pyramidum* were a mutualist rather than a competitor.

Figure 5B compares the responses of enclosure 1 to those of enclosure 2 with *G. pyramidum* in the illuminated subplot. Our hypothesis now predicted that the response values from enclosure 1 would lie above those of enclosure 2. But they were not significantly different (Student's t test, $t_{[28]} = 1.63$, $p > 0.11$). Thus, in the data from Fig. 5B, *G. pyramidum* appears to have had no interaction with *G. allenbyi*; the threat of predation overwhelmed it. (There is a possibility of a type II error here because the depressions over very low AGA values may have followed the hypothesis, but we may not have had enough data to show it.)

We used the technique described in Appendix A to calculate the interaction coefficients of *G. pyramidum* on *G. allenbyi* without illumination, with illumination + the competitor on the same or opposite side (Fig. 6). Using ANCOVA, we established that the competition coefficient did not depend on the value of AGP ($F_{[1,36]} = 1.18$, $p = 0.29$), but it did depend on the treatment ($F_{[2,36]} = 19.6$, $p = 0.000$).

Figure 6 compares the responses of enclosure 3 (○) to those of enclosure 2 with *G. pyramidum* in the unilluminated subplot (■). Our prediction was that competition from *G. pyramidum* will reduce the effect of predation (competition and predation are working in opposite directions). In fact, *G. allenbyi* behaved as a mutualist, ignoring all possible effects from *G. pyramidum*. Similar results were reported by Abramsky et al. (1998).

Figure 6 also compares the responses of enclosure 3 (○) to those of enclosure 2 with *G. pyramidum* in the illuminated subplot (▲). Our hypothesis predicted that the competition coefficients from enclosure 2 would be higher and thus lie below those of enclosure 3 (competition and predation working in the same direction). This was not the case and the two sets of coefficients were not significantly different (Bonferroni's post hoc test, $p = 0.114$). The lack of noticeable competitive effect was also found in our earlier 2-h pulses of predatory risk (Abramsky et al. 1998).

In any case, the presence of simulated moonlight not only neutralized the competitive influence of *G. pyramidum*, it somehow turned *G. pyramidum* into a mutualist in one experiment.

Microhabitat selection

The proportion of activity of *G. allenbyi* in the bush microhabitat of the simulated moonlight subplot i of enclosure 1 (0.62 ± 0.03 , mean \pm SE) was significantly higher than that in the adjacent subplot j without illumination (0.45 ± 0.05) (paired t test, $t_{[12]} = 4.47$, $p = 0.001$). In enclosure 3, the presence of the competitor, *G. pyramidum*, did not cause such a shift in microhabitat use (paired t test, $t_{[12]} = 1.15$, $p = 0.27$). The proportion of activity in subplot 3i was 0.46 ± 0.04 , whereas the proportion of activity in subplot 3j was 0.49 ± 0.07 .

The combined treatment (enclosure 2) showed that the microhabitat choice of *G. pyramidum* also depended on simulated moonlight. In subplot 2i, the proportion of their activity under a bush (0.512 ± 0.03) was significantly larger than when they were in subplot 2j (0.27 ± 0.03) (Student's t test, $t_{[21]} = 4.24$, $p < 0.0001$).

Discussion

We used the indirect cue (Thorson et al. 1998) of artificial moonlight to increase the perceived risk of predation by the nocturnal, psammophilic gerbil *G. allenbyi*. We maintained the treatments for periods of several months to study the effects of chronic risk of predation on their activity and foraging behavior. We did so in the presence and absence of a larger competitor, *G. pyramidum*, whose population sizes we adjusted in rodent-proof enclosures.

One of our principal goals was to compare the results of these experiments with those we obtained with risk pulses that we had maintained for only 2 h at a time (Abramsky et al. 1998). During such short risk pulses, gerbils reduced their predation risk by decreasing their use of riskier habitat patches without taking interspecific competition into account.

Our results suggest that gerbil behavior is as much influenced by the chronic risk of predation as by a 2-h pulse (Fig. 2; ANCOVA, $F_{[1,152]} = 7.9$, $p = 0.005$). *Gerbillus allenbyi* reduced its activity in the presence of simulated

moonlight and did so quantitatively, i.e., the brighter the light shining on a spot, the greater the reduction until at about 55 m from the light source, the influence of the light vanished (Figs. 1 and 2). Moreover, the reduction persisted even in the presence of the further opportunity that might have been created by its competitor *G. pyramidum*. This is especially interesting and deserves more extensive comment.

Gerbillus pyramidum competes severely with *G. allenbyi* (Abramsky et al. 1990, 1991; Ziv et al. 1993). Abramsky et al. (1991) also discovered that *G. allenbyi* behaved as if *G. pyramidum* was a competitor. Their equation (Abramsky et al. 1991) for the competitive interaction coefficient of *G. pyramidum* on *G. allenbyi* was $AGA = 86.3 - 4.00AGP + 0.35AGP^2/2 - 0.008AGP^3/3$. Despite the gap of 12 years between studies, the first three terms of that equation were very close to those that we measured in enclosure 3 in the present study. The principal difference was the lack of a cubic term in enclosure 3. But in the older study, the cubic term was associated with values of AGP above 20, a set of values beyond those in enclosure 3. Therefore, our experiments reconfirmed quantitatively the strength of competition from *G. pyramidum* (Fig. 6).

Yet the 2-h pulses of extra predation risk completely overwhelmed the behavioral effects of interspecific competition. Perhaps the short temporal scale of the experiments might explain this surprising result. Indeed, the risk allocation hypothesis of Lima and Bednekoff (1999) is based on the notion that prey adaptively allocate their foraging efforts, and thus, their exposure to predation risk across high- and low-risk situations (Sih et al. 2000).

But now we discover that the imposition of chronic risk (lasting more than 6 months) yielded quite similar results. In the presence of simulated moonlight, *G. allenbyi* ceases behaving as if *G. pyramidum* competes with it. Instead, they redistribute their foraging activity to avoid much of the risk associated with the light. This shift is not categorical (i.e., some use of illuminated patches continues), illustrating that *G. allenbyi* foraging continues to be sensitive to intraspecific competition. Only the interspecific competition was ignored.

But *G. allenbyi* does not entirely ignore *G. pyramidum* (Fig. 5A). When we set up a subplot with *G. pyramidum* and then illuminated its twin, we observed a more intense avoidance of the illuminated side than when *G. pyramidum* was entirely absent. This response went beyond mere neutralization of the interspecific competition. A subplot with no light and some *G. pyramidum* was actually more attractive to *G. allenbyi* than a subplot with neither light nor *G. pyramidum* (Figs. 5A and 6). The chronic predation risk had transformed the *G. pyramidum* from a negative influence to a positive influence (i.e., a mutualist).

Two things might help to explain why predation utterly neutralizes competition between the gerbil species: (1) the threat of losing a bit of a meal to a competitor may be trivial compared with the threat of never having a chance to eat again and (2) the competitors might alter their behavior in the presence of predation risk in such a way that makes them much less effective competitors.

The first possibility is the "life-dinner" principle (Dawkins and Krebs 1979); however, continual loss of meals might also amount to a loss of life. Therefore, if the life-dinner principle was at work in the pulsed-risk experiments,

then gerbils should have behaved less tolerantly toward competition during the chronic risk experiments.

The second possibility or "competitive amelioration" is somewhat more promising. We know that *G. pyramidum* interfere with *G. allenbyi* in the absence of experimental predation risk (Ziv et al. 1993). Under risk of predation, perhaps the territorial aggressiveness of *G. pyramidum* decreased. Abramsky et al. (1998) suggested that the aggressive behavior of *G. pyramidum* might be eliminated in the presence of predation risk. Indeed, previous work showed that under risk of predation, *G. pyramidum* did decrease its activity (Abramsky et al. 1996). This would attenuate the competition. Obviously, more needs to be done to establish the significance of this possibility.

Another hypothesis of competitive amelioration does not seem to hold promise here. It is that under risk of predation, *G. pyramidum* altered its habitat selection in such a way that weakened the competition. Indeed, in the presence of predation risk, *G. pyramidum* did change its habitat use. However, it shifted its activity towards the (safer) bush microhabitat in a way similar to the shift exhibited by *G. allenbyi*. Thus, the habitat shifting should have increased the probability of encounter of the two species and increased interspecific competition.

Werner (1991) and Werner and Anholt (1996) observed quite a different outcome when they combined interspecific competition and predation in an experiment with anuran larvae. Despite the presence of a nonlethal predator, competitors significantly affected growth rates and death by starvation of both large and small larvae.

We are not sure what caused the difference between the anurans and the rodents. Perhaps it arose from the fact that we measured behavior rather than growth and survival. If so, and competition was negatively having an impact on gerbil growth and survival in the presence of the chronic predation risk, then maybe reduced growth and survival are the best that the gerbils can manage. Or perhaps, instead, reduced growth and survival would have been evidence that gerbils are not well adapted to chronic predation risks.

In fact, we must not forget the simplest overall explanation for the similarity of responses between time scales. We assume that gerbil behavior has already fully evolved and that it is capable of appropriate, selectively mature responses to predation threats at all scales of time. But these facts may not be true. Predation threats in the desert may be so episodic that potential victims have no possibility to adapt to chronic threats. The only evidence against that hypothesis is the single difference we did observe (i.e., in the presence of chronic predation risk, *G. allenbyi* did treat *G. pyramidum* as a mutualist, something that they did not do in the presence of 2-h risk pulses).

Chronic risk may not be a rare phenomena in deserts and other ecosystems. In many deserts, including the Israeli one, large shrubs that can serve as a hunting perch for avian predators are relatively rare. Such perches may be used frequently by avian predators, and thus, the area around these shrubs may suffer from chronic risk of predation. Indeed, hunting from a perch is a very common hunting method for barn owls (e.g., Bunn et al. 1992; Taylor 1994).

Several other studies on gerbils lend support to the hypothesis that predation is of much more importance to

gerbils than competition. We conducted experiments to neutralize extra predation (Abramsky et al. 2002) or extra competition (Abramsky et al. 2000) with added food. It took about twice as much extra food to neutralize the disadvantage of extra predation than it did to neutralize the disadvantage of extra competition. Studies on the energetic costs of predation risk are even more dramatic and have been studied in the field (Brown et al. 1994) and in an aviary (Kotler and Blaustein 1995) in *G. allenbyi* and *G. pyramidum*. Both studies concluded that foraging costs on gerbils are mostly from costs arising from risk of predation.

The present study concerned itself with the effects of interspecific competition and risk of predation on the behavior of *G. allenbyi*. It did not focus on the behavior of *G. pyramidum*. In fact, we have not conducted such studies and do not know how they would turn out. But the results obtained in the two unenclosed plots (4 and 5) may hint at what to expect.

In these unenclosed plots, we detected no difference in the densities of the two species between the illuminated and control subplots (Fig. 4). However, the two species did use the two subplots differently. After the moonlight treatment began, the smaller *G. allenbyi* shifted much of its activity to the control subplots (from 0.52 ± 0.07 to 0.37 ± 0.05 before and after the light treatment began, respectively). We might suspect that by doing so *G. allenbyi* opened foraging opportunities for *G. pyramidum*. However, *G. pyramidum* did not change its use of the experimental and control subplots significantly (i.e., its proportion before illumination was 0.69 ± 0.24 and afterwards was 0.61 ± 0.20). Perhaps this reflects the superior antipredator adaptations of *G. pyramidum*.

However, *G. pyramidum* did respond to illumination. In the illuminated subplot, it shifted its activity to the safer microhabitat under bushes (0.50 ± 0.04) relative to the control subplot (0.35 ± 0.05) (Student's *t* test, $t_{19} = 2.60$, $p < 0.03$). *Gerbillus pyramidum* also responded to illumination by being less active the closer it was to the centre of a subplot where the light pole was placed (i.e., $y = -0.15 + 0.012x$ where x was the distance from the centre and y was the AGP; $r = 0.26$, $p \ll 0.001$). These results seemed to suggest that *G. pyramidum* responded to illumination similar to *G. allenbyi*.

Yet, *G. pyramidum* did not seem to be able to take advantage of the new foraging opportunities created by the shift in AGA, and did not increase its use of the illuminated subplot. Possibly the reduction of competition from *G. allenbyi* was matched almost exactly by the increase in risk, thus requiring no change in *G. pyramidum*. However, this seems unlikely given that risk is so much more costly than competition for gerbils (Brown et al. 1994; Kotler and Blaustein 1995; Abramsky et al. 2002). Therefore, the results again suggest that under risk of predation interspecific competition between the two gerbil species is negligible. Nevertheless, since the densities of *G. pyramidum* during this study were usually low (Fig. 4), one must be very cautious about these conclusions.

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References

- Abrams, P.A. 1977. Density-independent mortality and interspecific competition: a test of Pianka's niche overlap hypothesis. *Am. Nat.* **111**: 539–552.
- Abramsky Z., Rosenzweig, M.L., Pinshow, B., Brown, J.S., Kotler, B.P., and Mitchell, W.A. 1990. Habitat selection: an experimental field test with two gerbil species. *Ecology*, **71**: 2358–2369.
- Abramsky, Z., Rosenzweig, M.L., and Pinshow, B. 1991. The shape of a gerbil isocline. *Ecology*, **72**: 329–340.
- Abramsky, Z., Ovadia, O., and Rosenzweig, M.L. 1994. The shape of a *Gerbillus pyramidum* (Rodentia: Gerbillinae) isocline: an experimental field study. *Oikos*, **69**: 318–326.
- Abramsky, Z., Strauss, E., Subach, A., Kotler, B.P., and Riechman, A. 1996. The effect of Barn Owls (*Tyto alba*) on the activity and microhabitat selection of *Gerbillus allenbyi* and *G. pyramidum*. *Oecologia* (Berl.), **105**: 313–319.
- Abramsky, Z., Rosenzweig, M.L., and Subach, A. 1997. Gerbils under threat of owl predation: isoclines and isodars. *Oikos*, **78**: 81–90.
- Abramsky, Z., Rosenzweig, M.L., and Subach, A. 1998. Do gerbils care more about competition or predators? *Oikos*, **83**: 75–84.
- Abramsky, Z., Rosenzweig, M.L., and Subach, A.A. 2000. The energetic cost of competition: gerbils as moneychangers. *Evol. Ecol. Res.* **2**: 279–292.
- Abramsky, Z., Rosenzweig, M.L., and Subach, A. 2002. The cost of apprehensive foraging. *Ecology*, **83**: 1330–1340.
- Bar, Y., Abramsky, Z., and Gutterman, Y. 1984. Diet of gerbilline rodents in the Israeli desert. *J. Arid Environ.* **7**: 371–376.
- Begon, M., Harper, J.L., and Townsend, C.R. 1996. *Ecology: individuals, populations, and communities*. Blackwell Scientific Publications, Oxford.
- Brown, J.S., Kotler, B.P., and Valone, T. 1994. Foraging under risk of predation: a comparison of energetic and predation costs in a Negev and Sonoran Desert rodent community. *Aust. J. Zool.* **42**: 449–466.
- Bunn, D.S., Warburton, A.B., and Wilson, R.D.S. 1992. *The barn owl*. T&AD Poyser, London.
- Clarke, J.A. 1983. Moonlight's influence on predator/prey interactions between short-eared owls (*Asio flammeus*) and deer mice (*Peromyscus maniculatus*). *Behav. Ecol. Sociobiol.* **13**: 205–209.
- Daly, M.R., Wilson, B.P., and Jacobs, L.F. 1992. Behavioral modulation of predation risk: moonlight avoidance and crepuscular compensation in nocturnal desert rodent, *Dipodomys merriami*. *Anim. Behav.* **44**: 1–9.
- Dawkins, R., and Krebs, J.R. 1979. Arms races between and within species. *Proc. R. Soc. Lond. B Biol. Sci.* **205**: 489–511.
- Dayton, P.K. 1973. Two cases of resource partitioning in an intertidal community: making the right prediction for the wrong reason. *Am. Nat.* **107**: 662–670.
- Fretwell, S.D. 1972. *Population in a seasonal environment*. Princeton University Press, Princeton, N.J.
- Fretwell, S.D., and Lucas, H.L., Jr. 1970. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta Biotheor.* **19**: 16–36.
- Gause, G.P. 1934. *The struggle for existence*. Hafner, New York.
- Gilpin, M.E. 1972. Enriched predator-prey systems. *Theoretical stability*. *Science* (Wash., D.C.), **177**: 902–904.
- Holland, J.N., DeAngelis, D.L., and Bronstein, J.L. 2002. Population dynamics and mutualism: functional responses of benefits and costs. *Am. Nat.* **159**: 231–244.
- Holt, R.D. 1984. Spatial heterogeneity, indirect interactions, and the coexistence of prey species. *Am. Nat.* **124**: 377–406.
- Hurlbert, S.H. 1984. Pseudoreplication and the design of ecological field experiment. *Ecol. Monogr.* **54**: 187–211.
- Janzen, D.H. 1976. The depression of reptile biomass by large herbivores. *Am. Nat.* **110**: 371–400.
- Kaufman, D.W., and Kaufman, G.A. 1982. Effect of moonlight on activity and microhabitat use by Ord's kangaroo rat (*Dipodomys ordii*). *J. Mammal.* **63**: 309–312.
- Kotler, B.P. 1984. Effects of illumination on rate of resource harvesting in a community of desert rodents. *Am. Midl. Nat.* **111**: 383–389.
- Kotler, B.P., and Blaustein, L. 1995. Titrating food and safety in a heterogeneous environment: when the risky and safe patches of equal value. *Oikos*, **74**: 251–258.
- Kotler, B.P., and Holt, R.D. 1989. Predation and competition: the interaction of two types of species interactions. *Oikos*, **54**: 256–260.
- Kotler, B.P., Brown, J.S., and Subach, A. 1993. Mechanisms of species coexistence of optimal foragers: temporal partitioning by two species of sand dune gerbils. *Oikos*, **67**: 548–556.
- Krebs, C.J., Keller, B.L., and Tamarin, R.H. 1969. *Microtus* population biology: demographic changes in fluctuating populations of *M. ochrogaster* and *M. pennsylvanicus* in Southern Indiana. *Ecology*, **50**: 587–607.
- Lima, S.L. 1987. Distance to cover, visual obstructions, and vigilance in house sparrows. *Behaviour*, **102**: 231–238.
- Lima, S.L., and Bednekoff, P.A. 1999. Temporal variation in danger drives anti-predator behavior: the predation risk allocation hypothesis. *Am. Nat.* **153**: 649–659.
- Lockard, R.B., and Owings, D.H. 1974. Moon-related surface activity of bannertail (*Dipodomys spectabilis*) and Fresno (*D. nitratoides*) kangaroo rats. *Anim. Behav.* **22**: 262–273.
- Longland, W.S., and Price, M.V. 1991. Direct observation of owls and heteromyid rodents: can predation risk explain microhabitat use? *Ecology*, **72**: 2261–2273.
- Lotka, A.J. 1932. The growth of mixed populations: two species competing for a common food supply. *J. Wash. Acad. Sci.* **22**: 461–469.
- MacArthur, R.H. 1972. *Geographical ecology*. Harper & Row, New York.
- May, R. 1981. Models for two interacting populations. *In* *Theoretical ecology, principles and applications*. Edited by R.M. May. Saunders, Philadelphia. pp. 78–104.
- Mitchell, W.A., Abramsky, Z., Kotler, B.P., Pinshow, B., and Brown, J.S. 1990. The effect of competition on foraging activity in desert rodents: theory and experiments. *Ecology*, **71**: 844–854.
- Paine, R.T. 1974. Intertidal community structure. Experimental studies on the relationship between a dominant competitor and its principle predator. *Oecologia* (Berl.), **15**: 93–120.
- Paine, R.T., and Vadas, R.L. 1969. The effects of grazing by sea urchins on benthic algae populations. *Limnol. Oceanogr.* **14**: 710–719.
- Price, M.V., Waser, N.M., and Bass, T.A. 1984. Effects of moonlight on microhabitat use by desert rodents. *J. Mammal.* **65**: 353–356.
- Rosenzweig, M.L. 1981. A theory of habitat selection. *Ecology*, **62**: 327–335.
- Rosenzweig, M.L., and Abramsky, Z. 1997. Two gerbils of the Negev: a long-term investigation of optimal habitat selection and its consequences. *Evol. Ecol.* **11**: 733–756.

- Rosenzweig, M.L., and MacArthur, R.H. 1963. Graphical analysis and stability conditions of predator-prey interactions. *Am. Nat.* **97**: 209–233.
- Sih, A. 1982. Foraging strategies and the avoidance of predation by an aquatic insect, *Notonecta hoffmanni*. *Ecology*, **63**: 786–796.
- Sih, A., Ziemba, R., and Harding, K.C. 2000. New insights on how temporal variation in predation risk shapes prey behavior. *Trends Evol. Ecol.* **15**: 3–4.
- Taylor, I. 1994. *Barn owls*. Cambridge University Press, London.
- Thorson, J.M., Morgan, R.A., Brown, J.S., and Norman, J.E. 1998. Direct and indirect cues of predatory risk and patch use by fox squirrels and thirteen-lined ground squirrels. *Behav. Ecol.* **9**: 151–157.
- Vance, R.R. 1978. Predation and resource partitioning in one predator–two prey model communities. *Am. Nat.* **112**: 797–813.
- Volterra, V. 1926. Variations and fluctuations of the numbers of individuals in animal species living together. *In* *Animal ecology*. Edited by R.N. Chapman. McGraw-Hill Companies, New York.
- Werner, E.E. 1991. Nonlethal effects of a predator on competitive interactions between two anuran larvae. *Ecology*, **72**: 1709–1720.
- Werner, E.E., and Anholt, B.R. 1996. Predator-induced behavioral indirect effects: consequences to competitive interactions in anuran larvae. *Ecology*, **77**: 157–169.
- Ziv, Y., Abramsky, Z., Kotler, B.P., and Subach, A. 1993. Interference competition and temporal and habitat partitioning in two gerbil species. *Oikos*, **55**: 237–246.

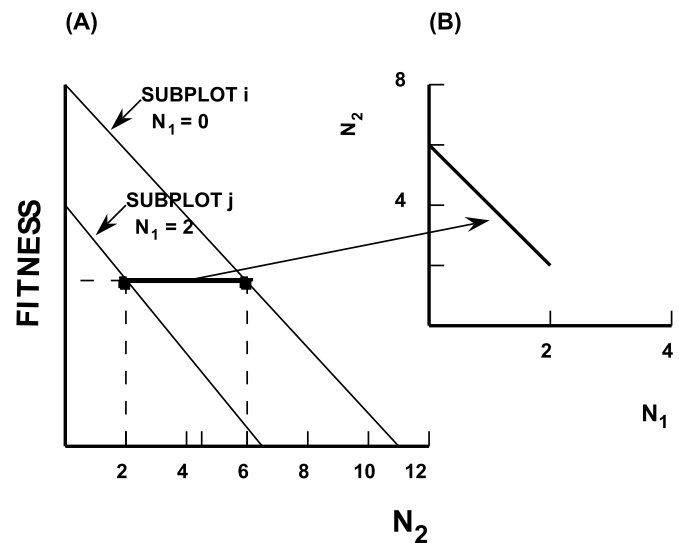
Appendix A

Estimating interaction coefficients and isoclines

Isoclines were extensively used in developing the theory that led to the understanding of the interactions between species, such as competition (e.g., Volterra 1926; Lotka 1932; Gause 1934; MacArthur 1972), predation (e.g., Volterra 1926; Lotka 1932; Rosenzweig and MacArthur 1963), and mutualism (e.g., May 1981). An isocline is a line in a state space on which every point of the state variable in question (or a fixed transformation of it such as its logarithm) has a fixed value of its time derivative. The state space has one axis for the population of each species. An example of an isocline would be the set of points at which the population of species 1 does not change. In fact, that isocline is called species 1 zero isocline. Zero isoclines play a large role in predicting what will happen to a set of interacting species (e.g., Begon et al. 1996).

Suppose there are two habitats (i and j) and two species (1 and 2) with total densities N_1 and N_2 . Let $N_{1,i}$, $N_{1,j}$, $N_{2,i}$, and $N_{2,j}$ be the habitat specific densities. If the $N_{2,i}$ individuals in habitat i have the same average fitness as the $N_{2,j}$ individuals in habitat j, then N_2 is said to be at the ideal free distribution (IFD; Fretwell and Lucas 1970). Barring complications, IFD is the ESS, which optimal individuals will try to attain. Foragers should also approach IFD when they are using habitat patches that differ only in the density of a competitor (Abramsky et al. 1991). In this situation, competitors depress the value of a patch and foragers should respond by distributing their foraging between patches inversely to the competitor's density.

Fig. A1. (A) The relationship between the fitness of species 2 and its population density (N_2) plotted as separate lines for matched patches with different population density values of species 1 (N_1). For simplicity, the figure shows an example with straight lines, although curved ones would do as well. Points at the ends of the thick horizontal line constitute an ideal free distribution of N_2 ; its individuals have the same fitness in both patches. (B) The densities of the two species at the ideal free distribution (IFD) of species 2 are transferred to a state space of population densities (N_1, N_2). The line connecting these two points is a linear estimate of the isocline of species 2 because its individuals have the same average fitness at both points of the IFD. The slope of the line estimates $\alpha_{2,1}$, which is the interaction coefficient of species 1 on species 2.



Given a forager seeking an IFD and an experimental pair of matched patches, one can estimate competitive coefficients and isoclines as follows. First, introduce some individuals of species 2, allowing them to move freely between patches i and j. Now show that species 2 moves freely between the two experimental patches and views them as equivalent. Do this by removing species 1 entirely and determine that $N_{2,i} = N_{2,j}$ at various values of N_2 . Next, reintroduce the competitor and fix its densities at $N_{1,i}$ and $N_{1,j}$. For example, set $N_{1,i} = 0$ and $N_{1,j} = 2$ as in Fig. A1A. Measure the distribution attained by species 2. The free densities they reach and the fixed densities of their competitors constitute a set of two points in (N_1, N_2) state space (Fig. A1B): $(N_{1,i}, N_{2,i})$ and $(N_{1,j}, N_{2,j})$. Because the average fitness of species 2 should be equal in the two subplots (i.e., $d(\ln N_{2,i})/dt = d(\ln N_{2,j})/dt$), the two points should lie on one isocline of species 2. So the line connecting them is a linear estimate of the N_2 isocline in the neighborhood of the two points. Its slope is negative $\alpha_{2,1}$ where $\alpha_{2,1}$ is the effect of an individual of species 1 on an individual of species 2.

Repeat the last few steps of this procedure many times with various values of N_1 and N_2 . The result will be estimates of $\alpha_{2,1}$ and isocline slopes throughout the state space. Thus, even if $\alpha_{2,1}$ depends on population densities and the isocline is curvilinear, the method will succeed.