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Source: *Oikos*, Vol. 69, No. 2 (Mar., 1994), pp. 318-326

Published by: Blackwell Publishing on behalf of Nordic Society Oikos

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## The shape of a *Gerbillus pyramidum* (Rodentia: Gerbillinae) isocline: an experimental field study

Z. Abramsky, O. Ovadia and M. L. Rosenzweig

Abramsky, Z., Ovadia, O. and Rosenzweig, M. L. 1994. The shape of a *Gerbillus pyramidum* (Rodentia: Gerbillinae) isocline: an experimental study. – *Oikos* 69: 318–326.

Abramsky et al. developed a new technique to measure isoclines in the field. The method is based on the single-species habitat selection theory of Fretwell. Using short term (3–4 wk) and long term (1-yr) experiments, they tested it by measuring the isocline of *Gerbillus allenbyi* competing with *G. pyramidum*. In the present study, we measured the converse isocline of *G. pyramidum* competing with *G. allenbyi*. Like the isocline of *G. allenbyi*, the isocline of *G. pyramidum* is nonlinear and agrees with the predictions of the theory of optimal density-dependent habitat selection in a two-species, shared-preference system. This is the first natural system in which both sets of isolegs and isoclines have been measured, in the field, for two competing species. A stability analysis suggested that the gerbil species can coexist under most observed density combinations.

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Isoclines have figured prominently in ecological theory for over thirty years. Competitive isoclines have been used to explain theory and to examine the general conditions that permit the coexistence of competitors (Volterra 1926, Lotka 1932, MacArthur 1972). The slope of the competitive isocline represents the competition coefficient (Vandermeer 1973). Some attempts were made to estimate species interaction coefficients in the field using data obtained from manipulation experiments. In most such studies it was assumed that the competition coefficients were constant and, consequently, that the isoclines were linear (e.g., Abramsky et al. 1979, Högstedt 1980). Attempts to measure nonlinear isoclines have been mostly limited to laboratory studies (e.g., Ayala et al. 1973, Livdahl and Willey 1991).

Abramsky et al. (1991, 1992) introduced a relatively quick method to measure linear or nonlinear competitive isoclines in the field. The method relies on the expecta-

tion that animals should adjust their spatial distribution to compensate for inequalities among habitats (Fretwell 1972). When they do, they equalize average fitness in all habitats. Suppose there are two habitats,  $i$  and  $j$ , two species (species 1 and species 2), and that their densities are  $N_1$  and  $N_2$ . In this case, the  $N_{2,i}$  individuals in habitat  $i$  will have the same average fitness as the  $N_{2,j}$  individuals in habitat  $j$ . Fretwell termed such distribution an Ideal Free Distribution (IFD). IFD is also expected in similar areas that differ only in the number of competitors (Abramsky et al. 1991). In this situation, we expect that  $N_{2,i}$  in an area with low density of a competitor will be higher than  $N_{2,j}$  in a similar area with high competitor density.

Suppose that the densities of species 1 in each of the two plots are different and fixed by experiment. For example, in Figure 1A, we excluded species 1 from plot 1 ( $N_1 = 0$ ) and put 2 individuals in plot 2 ( $N_1 = 2$ ). Individu-

Accepted 17 August 1993

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ISSN 0030-1299

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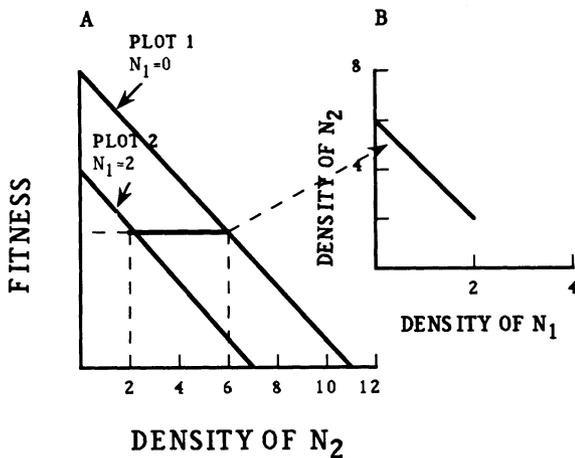


Fig. 1. A. The relationship between fitness and population density of  $N_2$  plotted as separate curves for identical areas containing different number of  $N_1$ . Note that the fitness density lines can be linear as well as nonlinear. For simplicity, we show in the figure an example with linear lines. When the ideal free distribution is attained (points at the ends of the thick lines in A), the fitness of  $N_2$  in both areas is equal. In a state space of population densities (B), the densities of the two species, in both areas, can be represented by two pairs of values that constitute a set of 2 points. The line connecting these points is a linear estimate of the isocline since all the points on this line have the same average fitness. The slope of the line is an estimate of the interaction coefficient of species 1 on species 2 ( $\alpha_{21}$ ).

als of species 2 can move freely between the two plots and attain IFD. In that case, the 2 pairs of values of  $N_1$  and  $N_2$  constitute a set of 2 points in  $(N_1, N_2)$  state space (Fig. 1B):  $(N_{1,i}, N_{2,i})$  and  $(N_{1,j}, N_{2,j})$ . Those two points lie on the same isocline of species 2. So the line connecting them is a linear estimate of the isocline in that region of the state space. Its slope is the effect of species 1 on species 2 ( $\alpha_{21}$ ).

In practice, to measure the slope of the isocline of species 2 in different regions of the state space, you have to: 1) show that the two experimental plots are so similar that in the absence of species 1, species 2 uses them equally; 2) fix the density of the first species so the two plots have different  $N_1$  values; 3) allow free movement of individuals of  $N_2$  between plots; and 4) repeat the experiment using different density combinations of  $N_1$  and  $N_2$  so as to sample different regions of the state space.

Using short-term (3–4 wk, Abramsky et al. 1991) and long-term experiments (1 yr, Abramsky et al. 1992), we tested the new method and measured the isocline of *Gerbillus allenbyi* ( $N_1$ ) in the presence of *G. pyramidum* ( $N_2$ ). Both gerbil species are common in the Negev desert, Israel. We predicted the shape of the isocline from a combination of theory and our previous studies of habitat selection (Rosenzweig and Abramsky 1986, Abramsky et al. 1990). The estimated nonlinear isoclines of *G. allenbyi* agreed with those predictions (Abramsky et al. 1991, 1992).

The present study uses the same method and the same gerbil species to measure the isocline of *G. pyramidum*. We show that the shape of *G. pyramidum* isocline also agrees with the predictions of our previous studies (Abramsky et al. 1990). This increases confidence in the new method and allows us to assess the stability of the two species system. This is the first natural system in which both sets of isoclines were measured, in the field, for two competing species.

## Methods

### Study species

*G. allenbyi* (26 g) and *G. pyramidum* (40 g) are sympatric in a wide range of sandy habitats in the Western Negev Desert (Abramsky et al. 1985). We built six 1-ha enclosures to study their interaction at Holot Mashabim Nature Reserve (31°01'N, 34°45'E). We set up the enclosures in three pairs (1a and 1b; 2a and 2b; 3a and 3b), so that each shared one of its fences with its paired enclosure. Each pair was at least 70 m from its nearest neighbor. We also established two 1-ha unfenced plots as controls. All 1-ha plots contained similar proportions of two habitat types – semistabilized dune and stabilized sand. (More detailed information about the species and the plots are in Abramsky et al. 1990, 1991.)

We installed 6 weight-specific gates, at 15 m intervals, in the fences shared by each pair of enclosures. The heavier *G. pyramidum* easily passes through these gates, but the lighter *G. allenbyi* cannot use them at all. We tested the gates in the laboratory and the field data supported our assumption that only adult *G. pyramidum* could use the gates. Only mature individuals of both species were used in the experiment.

Mammal populations enclosed for long periods often show artifacts (fence effects, Krebs et al. 1969). To avoid such problems, we conducted each experimental test during a relatively short time. Between experimental sets (2–3 wk), and during the rest of the year (7 months), gates in the fences were opened to the outside so that animals and resources would attain similar levels inside and outside the plots. This tactic appeared to succeed (Abramsky et al. 1991). Hence, we benefited from controlling population densities without paying the costs associated with fence effects in the target species (the one whose isocline we want to measure).

### Experimental setup

We varied the densities of both species according to a protocol described below. We introduced different numbers of *G. allenbyi* to each side of an enclosure pair and measured the response of *G. pyramidum* which was also introduced into the enclosures but was free to move between the two adjacent enclosures.

Table 1. Initial densities of *Gerbillus allenbyi* (GA) that were introduced to the six enclosures during the 7 experimental tests. The experimental tests were divided to three sets that were conducted in different months. Since individuals of *G. pyramidum* (GP) could move freely between two pair of enclosure plots we show the total numbers introduced to each pair, but actually introduced equal numbers (as equal as possible) to each plot of a pair. Enclosures were arranged in three pairs, each connected by a common fence perforated by 6 species specific gates (1a and 1b; 2a and 2b; 3a and 3b).

EXP. SET	I				II				III					
	1		2		3		4		5		6		7	
Exp. test	GA	GP	GA	GP	GA	GP	GA	GP	GA	GP	GA	GP	GA	GP
1a	1	7	0	4	25	13	25	9	25	6	22	4	22	2
1b	28		18		15		11		9		36		36	
2a	2	14	0	14	19	12	16	9	16	3	23	13	23	5
2b	31		22		5		4		3		36		36	
3a	28	14	23	14	15	12	14	9	14	3	28	10	28	5
3b	11		8		30		29		29		12		12	

## Experimental protocol

In the three pairs of enclosed plots we conducted 7 experimental tests in which each plot (*G. allenbyi*) and each pair of plots (*G. pyramidum*) received a unique experimental treatment (Table 1). We varied the densities so that the set of density combinations occupied as much of the state space as possible and as uniformly as possible. In the first two experimental tests, we sampled much of the state space to search for large differences in slopes (Fig. 2A). This gave us a general idea about the shape of the isocline. If the isocline is nonlinear – as we indeed suspected and confirmed – reducing the distance between each pair of experimental points in the state space improves the accuracy of the isocline estimate. During the last 5 experimental tests, we reduced those distances (Fig. 2B and 2C).

The experimental tests were divided into three sets: two experimental tests in July, three in August, and two in September. Before each set we trapped and removed all animals from the six fenced plots, marked them individually by ear and by front limb toe clipping, and marked them as to species by amputating an outside left (*G. pyramidum*) or right (*G. allenbyi*) hind toe. Individuals were kept in the laboratory for a maximum of six days to minimize chances of behavioral alternation. We simultaneously introduced the appropriate initial densities of *G. allenbyi* and *G. pyramidum* to each plot during the first two experimental tests (first set). Since *G. pyramidum* was free to move between a pair of enclosures, we introduced equal numbers (as equal as possible) of the initial densities of *G. pyramidum* to each plot of a pair. In the last five experimental tests, we tested for an equal distribution (at 2, 4, 6, 10, 12, and 14 animals per pair of enclosures) of *G. pyramidum* in the absence of *G. allenbyi* by sampling the number of tracks left in the sand (see later). Once this was accomplished, appropriate numbers

of *G. allenbyi* were also introduced into the enclosures (Table 1). Care was taken not to return an animal to the pair of plots on which it was initially caught.

After each density alteration (experimental test) animals were allowed to habituate to their new surroundings during two nights. On the following 2–3 nights, we measured rodent activity in each plot by identifying and counting footprints on 40 smoothed sites ( $0.4 \times 0.4$  m). Twenty such smoothed sites were located in the stabilized sand habitat of each 1-ha enclosure and 20 in the semistabilized dune. The sites were smoothed late in the afternoon and were read the following morning. The score given to a site depended on the footprint coverage, and ranged from 0 (no tracks) through 1 (1/4 track coverage), 2 (1/2 track coverage), 3 (3/4 track coverage), to a score of 4 (full track coverage). This scoring technique has been used successfully by several scientists in the last several years (Abramsky et al. 1990, 1991, 1992, Mitchell et al. 1990, Kotler et al. 1993, Ziv et al. 1993). Scores could be assigned to species on the basis of the species-specific toe clips. These were easy to discern in the smooth sand. (For more details about the experimental protocol see Abramsky et al. 1991, 1992).

## The relationship between activity density and population density

Sampling the number of tracks in the sand does not interfere with the rodents' natural behavior throughout the night. Abramsky and Pinshow (1989), Abramsky et al. (1990, 1991, 1992), Ziv et al. (1993), and Mitchell et al. (1990) showed that activity data can better assess interactions between these two gerbil species than can data obtained from trapping. Nevertheless, activity of the rodents should be, and is, significantly correlated with

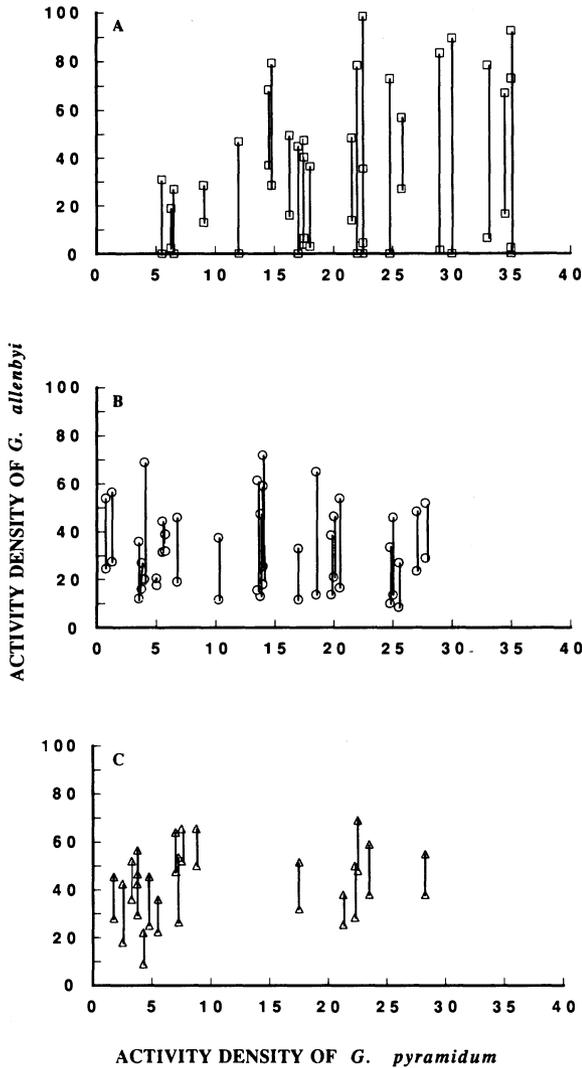


Fig. 2. The experimental design and the deterministic null hypothesis. Each pair of points represents one sampling period. The AGA values (Y-axis) show the actual values of AGA in the two adjacent enclosures. The AGP values are the mean total AGP values in two adjacent enclosures. Equal subdivision is the null hypothesis because it assumes *G. pyramidum* distribution is uninfluenced by AGA and that it equally utilizes the two adjacent enclosures. Activity density in each plot was estimated as the sum of species-specific footprint scores in 40 sites  $\text{ha}^{-1}$ . A – First set (experimental tests 1–2); B – Second set (experimental tests 3–5); C – Third set (experimental tests 6–7).

density (Mitchell et al. 1990, Abramsky and Pinshow 1989, Abramsky et al. 1990).

In Fig. 2 we show the experimental coverage in a state space of activity densities of the two rodent species. To generate this figure we used the actual activity densities of *G. allenbyi* (AGA) in each of the adjacent enclosures. For *G. pyramidum* (AGP), which had access to both plots of each pair, we graphed its average activity densities in the two adjacent plots.

## Previous results

Using the same enclosures, Abramsky et al. (1990) showed that the habitat distribution of *G. allenbyi* and *G. pyramidum* follow the predictions of shared preference community organization (Pimm et al. 1985, Rosenzweig 1991). The biological basis of shared preference exists in the interaction of those two gerbils, as follows. When rare, both species prefer to utilize the same habitat, the semistabilized dune. As their populations increase, both begin to forage in a secondary habitat, the stabilized sand. When *G. allenbyi* is common, and there are even a few individuals of *G. pyramidum*, then *G. allenbyi* reverses its preference from the semistabilized dune to the stabilized sand. The reverse interspecific effect is not as strong, and *G. pyramidum* never prefers the stabilized sand even in the presence of high densities of both species (Abramsky et al. 1990).

Isolegs are lines in the state space of population densities that divide the space into different behavioral zones. Shared preference systems yield characteristic isoleg patterns corresponding to what we have previously found for *G. allenbyi* and *G. pyramidum*. *G. allenbyi* has two isolegs with negative slopes and *G. pyramidum* has one

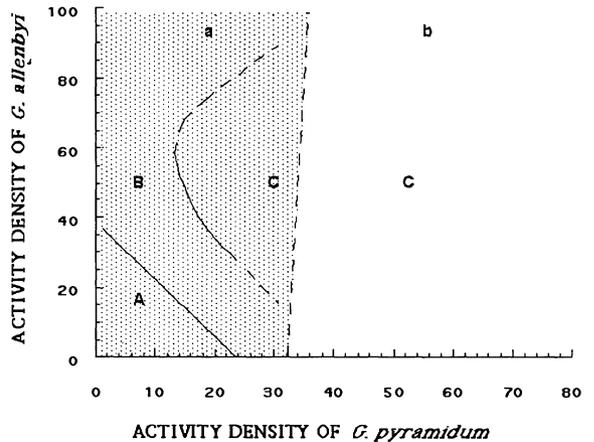


Fig. 3. The shape and location of the three isolegs of *G. allenbyi* and *G. pyramidum* (adopted from, and explained in detail in Abramsky et al. 1990). *G. allenbyi* has two isolegs (the two lines on the left) while *G. pyramidum* has one positively sloped isoleg (the broken line on the right). The second isoleg of *G. allenbyi* is partly represented by a continuous line, where many data points support the negative slope, and partly by a broken line where too few data exist. Upper case letters represent the three different behavioral zones of *G. allenbyi* and lower case letters represent the two different behavioral zones of *G. pyramidum*. The shaded area represent the first (a) behavioral zone of *G. pyramidum*. In zone Aa, both species prefer the same habitat, the semistabilized dune. In zone Ba, *G. pyramidum* prefers the semistabilized dune and *G. allenbyi* exhibits random utilization of both habitats. In zone Ca, *G. allenbyi* exhibits apparent preference for the stabilized sand and *G. pyramidum* exhibits preference for the semistabilized dune. In zone Cb, *G. allenbyi* exhibits apparent preference for the stabilized sand and *G. pyramidum* selects the semistabilized dune but also uses the stabilized sand.

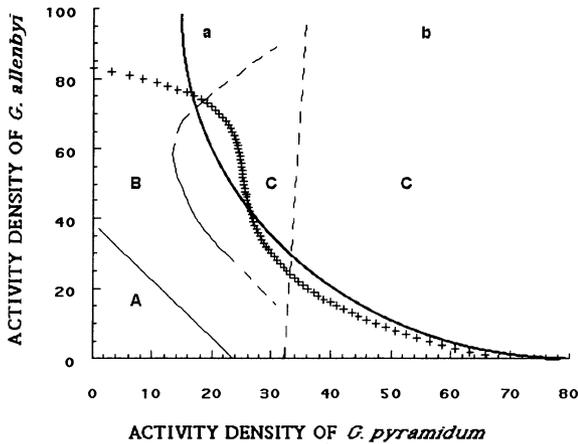


Fig. 4. The two expected *G. pyramidum* isoclines that can be predicted from the isocline graph, depending on the shape of the second *G. allenbyi* isocline. If the second *G. allenbyi* isocline in zone (a) does not have a positive slope, the *G. pyramidum* isocline should be almost vertical in this region because habitat overlap is minimal in zone Ca. However, if the positive slope of the isocline is real then the *G. pyramidum* isocline should become less steep on the left as it goes into a zone of higher habitat overlap (zone Ba).

isocline with a positive slope (details of the explicit shapes and number of isoclines are presented in Abramsky et al. 1990). The two *G. allenbyi* isoclines divide the state space of activity density into three zones: A – it predominantly uses the semistabilized dune; B – it uses both habitats about equally; and C – it shows an apparent preference for the stabilized sand (Fig. 3). However, our confidence in the second *G. allenbyi* isocline varies depending on whether we drew it as a solid line or not (Abramsky et al. 1990). In the region of  $30 < AGA < 60$ , we have many data points to support its negative slope. Thus, the isocline was drawn as a continuous line. Above and below this region we have too few data (three and one data points, respectively) to decide the exact shape or slope of the isocline. We show our lack of confidence in the shape and location of the second isocline at  $AGA < 30$  and  $AGA > 60$  by drawing it with broken lines. The *G. pyramidum* isocline divides the state space into two zones: a – it predominantly uses the semistabilized dune; b – it often accepts the stabilized sand (although its average use of the semistabilized habitat never falls as low as 50%). These zones overlap to create four different regions in the state space (see Fig. 3): Aa, Ba, Ca, and Cb.

As the habitat overlap varies, so should the strength of the competition between the species. It should be intense in Aa, and strong in Ba, and Cb. But it should be very weak in Ca where species overlap very little in habitat use. Our previous study examined the regions except for Aa and confirmed the above.

## Predictions of the current experiment

The first prediction tests whether we have succeeded in matching the pairs of plots. If they are well-matched, then in the absence of *G. allenbyi*, *G. pyramidum* will find the two adjacent plots equally suitable. We should find equal activity densities of *G. pyramidum* between adjacent plots.

The second prediction tests whether *G. pyramidum* treats *G. allenbyi* as a competitor. If it does, then *G. pyramidum* will exhibit higher activity densities in plots with lower density of *G. allenbyi*.

The third prediction deals with the isocline shape. It stems from the isoclines of the shared habitat preference model as summarized above (Fig. 3). This prediction says: competition is relatively high at both low and high densities of *G. pyramidum*, when habitat overlap is high, and low at intermediate densities of *G. pyramidum*, when habitat overlap is relatively low. In Fig. 4 we draw two expected isoclines that can be predicted from the isocline graph, depending on the shape of the second *G. allenbyi* isocline. If the isocline in zone (a) does not have positive slope, the *G. pyramidum* isocline should be almost vertical in this region because habitat overlap is minimal in zone Ca. However, if the positive slope of the isocline is real then the *G. pyramidum* isocline should become less steep on the left as it goes into a zone of higher habitat overlap (zone Ba).

## Data reduction

We summed the activity density score of each species over all 40 sand tracking sites. The sum is the total activity density for the species in the plot during one night. A species could have no more than 320 total activity density units in a pair of plots (80 stations multiplied by a maximum score of 4). However, activity density rarely exceeded 100 for *G. allenbyi* (AGA) and never exceeded 70 for *G. pyramidum* (AGP). Scores of 3 or higher occurred

Table 2. Analysis of covariance conducted to examine the effect of day, experimental test, and experimental set on the estimated isocline's slopes of *G. pyramidum*.  $N = 64$ ;  $R^2 = 0.80$ .

Variable	SS	DF	MS	F	P
AGA	0.20	1	0.20	7.89	0.008
AGP	0.20	1	0.20	8.07	0.007
Day	0.18	4	0.04	1.78	0.150
Exper. test	0.09	1	0.09	3.51	0.068
Exper. set	0.21	2	0.10	4.14	0.023
AGA*Day	0.20	4	0.05	2.03	0.109
AGA*Exper. test	0.08	1	0.08	3.27	0.078
AGA*Exper. set	0.21	2	0.11	4.28	0.021
AGP*Day	0.12	4	0.03	1.22	0.317
AGP*Exper. test	0.01	1	0.01	0.30	0.585
AGP*Exper. set	0.28	2	0.14	5.68	0.007
Error	0.99	40	0.03		

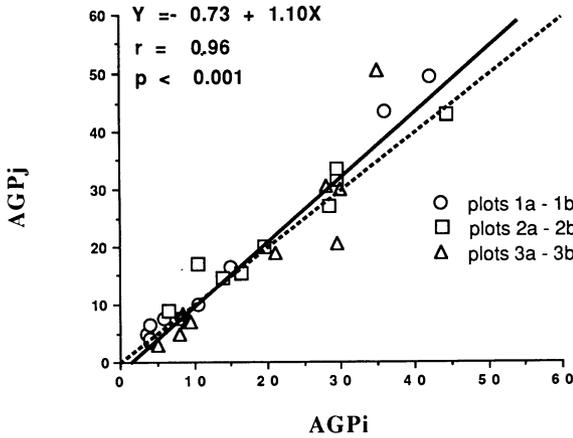


Fig. 5. The activity density of *G. pyramidum* is similar in connected adjacent enclosures without *G. allenbyi*. *i* and *j* correspond to numbers of adjacent plots in each pair of enclosures (plots 1a and 1b (squares), 2a and 2b (O), and 3a and 3b ( $\Delta$ )). The dotted line shows exactly equal usage between enclosures of a pair (slope = 1.0). The fitted thick line is Bartlett's best fit regression. Its slope and intercept are not significantly different from 1 and 0, respectively.

only in 9% of the cases during the entire study and empty sites occurred 40% of the time. Because gerbil activity density did not saturate our tracking sites, the upper bound of 320 did not obscure differences between moderate and relatively high activity densities.

We used nonlinear regression to analyze the data. We treated the estimated isocline slopes obtained from experimental tests of each set as independent of all other observations. Abramsky et al. (1991) showed that experimental tests in different sets had no significant effect on the magnitude of competition of *G. pyramidum* on *G. allenbyi* in the same set of enclosures. We tested the effect of experimental tests, and days within each experimental test by analysis of covariance (Table 2) and found that both contributed an insignificant amount of the variance of rodent activity. However, since we intentionally sampled different regions of the state space in each of the 3 experimental sets, we expected, and obtained (Table 2), a significant difference between slopes obtained from the 3 sets. The hypothesized nonlinear shape of the isocline accounts for differences between slopes of different experimental sets (Fig. 4). Isocline slopes estimated from the region  $AGP > 30$  are expected to be relatively high, slopes estimated from the region  $10 < AGP < 30$  are expected to be low or even zero, while those from the region  $AGP < 10$  are expected to be very low or very high depending on the specifics of the hypothesis. Earlier studies (Abramsky et al. 1991, 1992), in which densities of the rodents were replicated between experimental sets, have shown that the temporal element in this system is not important. For these reasons, we used all the results in the nonlinear regression to estimate the isocline of *G. pyramidum*.

## Results

### 1) In the absence of *G. allenbyi*, *G. pyramidum* equally utilizes the two plots of each enclosure pair

Prior to experimental test 3–7, *G. pyramidum* was alone in the two adjacent plots. We used these data to test whether *G. pyramidum* equally used the two adjacent plots of each pair of enclosures. The data appear in Fig. 5.

If the data fit the hypothesis, they should fall along a

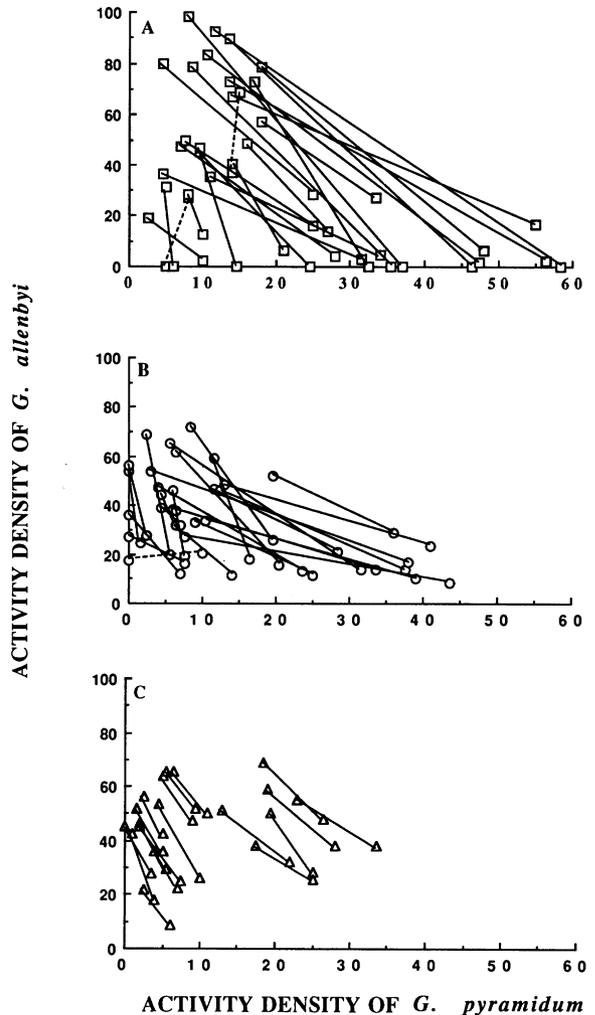


Fig. 6. *G. allenbyi* competes with *G. pyramidum*. The results of the competition experiments are plotted in a state space defined by the activity densities of both species. The activity densities of both species from each pair of adjacent plots sampled simultaneously define two points. The line that connects these points is the linear estimate of the isocline and the inverse of its slope estimates the competition coefficient ( $\alpha_{p,a}$ ) in that region of the space. The vast majority of the slopes are negative suggesting that the isocline is also negative throughout the state space of competitor densities. A – First set (experimental tests 1–2); B – Second set (experimental tests 3–5); C – Third set (experimental tests 6–7).

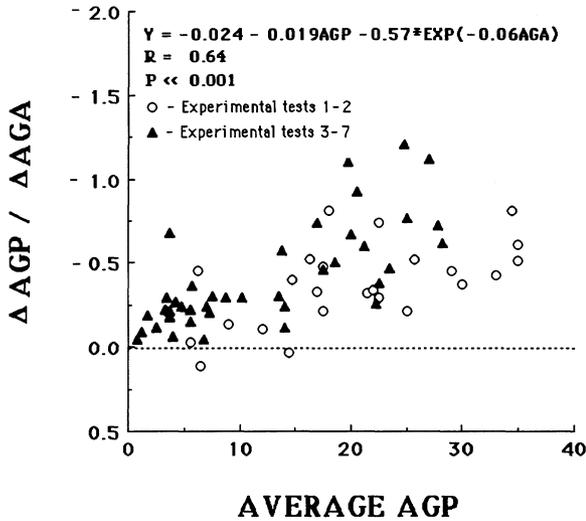


Fig. 7. The relationship between the magnitude of competition ( $\Delta AGP/\Delta AGA$ ) and the average activity density of *G. pyramidum* (AGP). Competition also depends upon AGA, as noted by the complete regression equation. The broken line separates the zone of negative competition coefficients from that of positive ones.

straight line with slope 1 and intercept 0. Bartlett's best fit regression of AGP in one plot (i) against AGP in the adjacent plot (j) yielded a line with a slope not significantly different from unity and an intercept not significantly different from zero ( $p < 0.01$ ). Similar results were obtained when data from the 3 pair of enclosures were analyzed separately.

## 2) The *G. pyramidum* isocline has a negative slope. In the presence of different densities of *G. allenbyi*, *G. pyramidum* biased its activity toward the plot with the lower densities of *G. allenbyi*

In the vast majority of cases (61 of 64, Fig. 6), AGP was higher in the plot with the lower *G. allenbyi* activity density. This trend is highly significant (paired t test,  $p < 0.001$ ). That result by itself establishes that *G. pyramidum* perceives *G. allenbyi* as a competitor and that the isocline of *G. pyramidum* tends to have a negative slope.

## 3) The *G. pyramidum* isocline is nonlinear

In Fig. 6, the results from each pair of adjacent enclosures in each sampling period appear as two points. The slope of the straight line connecting each pair of points is the linear estimate of the slope of the isocline between the two points. Thus, it is also an estimate of  $\alpha_{p,a}$  the competition coefficient of *G. allenbyi* on *G. pyramidum* in the region of the state space covered by that pair of points.

We performed several nonlinear regressions using different mathematical relations to find out whether the isocline slopes vary systematically in Fig. 6. Since all resulted isoclines had the same general shape we show here only the result that gave the highest R value. The prediction (Fig. 4) is that slopes will be shallower on the right sides (zone Ca), and steeper in the middle (zone Ca). On the left, slopes might be either steeper (vertical) or shallower, depending on the shape of the second *G. allenbyi* isocline (see predictions).

Our dependent variable was the estimate of the slope. The independent variables were average AGA and average AGP. Because the two points of each experiment actually have two AGP and two AGA values (Fig. 6), we averaged them to characterize the position of the experiment in AGA, AGP space.

Fig. 7 shows the estimated slopes plotted against average AGP and the significant nonlinear regression coefficients:

$$\alpha_{p,a} = -0.24 - 0.019AGP - 0.573*EXP(-0.064AGA) \quad (1)$$

(R = 0.64;  $p < 0.001$ )

The fit is even better, though similar overall and identical in zone Ca and part of Cb, when only the data obtained in the last two experimental sets (experimental tests 3-7) were used. In these sets, the range of AGA over which competition was measured was narrower (Figs 2 and 6)

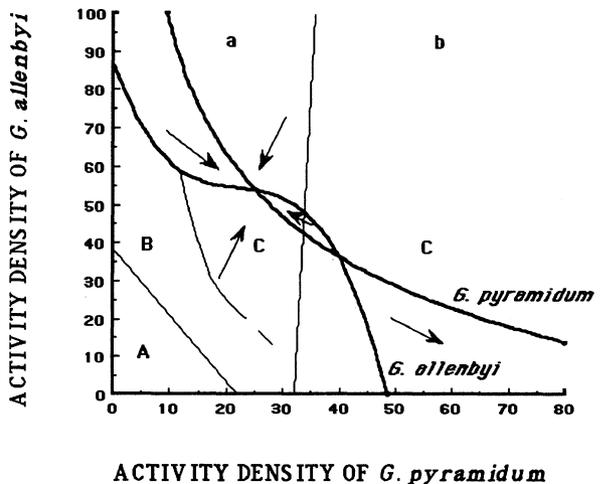


Fig. 8. The isocline of *G. pyramidum*, the isocline of *G. allenbyi* (the inverse sigmoid curve), and the isoclines of both species drawn in a state space of activity densities. *G. allenbyi* has two negatively sloped isoclines and *G. pyramidum* has one positively sloped isocline. The shape, number, and location of the isoclines were adopted from, and explained in detail in Abramsky et al. 1990. Arrows represent the trends of the population dynamics. The isoclines of *G. pyramidum* and *G. allenbyi* intersect in two locations. On the left, the equilibrium is stable since both species are mostly using different habitats (*G. pyramidum* in the semistabilized dune and *G. allenbyi* in the stabilized sand). On the right, the equilibrium is unstable since the overlap in habitat utilization has increased (*G. pyramidum* uses both habitats).

and thus the linear estimate of the slope should have been better (see experimental protocol above).

$$\alpha_{pa} = -0.26 - 0.024AGP - 0.786*EXP(-0.06AGA) \quad (2)$$

(R = 0.83; p << 0.001)

Equations (1) and (2), and the data (Fig. 7) reveal that at low AGP (<15) competition from *G. allenbyi* is weak. It increases at AGP > 15.

The variable AGA is also significant (P < 0.001). This means that the isoclines are not a family of parallel curves. But the curves become more concave upward from right to left in Fig. 8.

Solving Eq. 2 for any given values of AGA and AGP will yield the equation of the isocline. The general solution for a differential equation of the form  $dx/dy = -a - bx - d*EXP(cy)$  is  $x = [(-ab)+ac-bd*EXP(cy)]/(b^2-bc)+K*EXP(by)$ , where x is AGP, y is AGA, K is the integration constant, and a, b, c, and d are the nonlinear regression coefficients. To allow a relatively simple comparison with the isocline of *G. allenbyi* we solved Eq. 2 using the average values obtained in the earlier study (Abramsky et al. 1991: AGA = 54; AGP = 25). The resulting isocline is plotted in Fig. 8.

## Discussion

Since we were not sure about the exact shape of the second *G. allenbyi* isoleg (Abramsky et al. 1990), we suggested two alternative theoretical isoclines for *G. pyramidum*. If the positively sloped part of the isoleg (represented by a broken line in Fig. 4) is real it should bend the *G. pyramidum* isocline to the left (the isocline becomes shallower) since competition from *G. allenbyi* increases as habitat overlap in zone Ba increases. If it is not, the slope of the isocline should stay close to vertical (low competition) since in this zone (Ca) habitat overlap is low.

The result of the present study supports the second alternative. The *G. pyramidum* isocline has a negative slope in zone Cb where habitat overlap is high (Fig. 8). The slope approaches a vertical slope in zone Ca where habitat overlap is low. We found no evidence of a shallower slope in zone Ba, although we had enough data in this region to search for it (Fig. 6). This result supports our earlier suspicion that the second *G. allenbyi* isoleg has a negative slope over its entire range.

The pattern of nonlinearity in the isocline (Figs 7, 8), fits the predictions of the shared preference model as represented by the particular set of isolegs measured for the two gerbil system (Abramsky et al. 1990).

The *G. pyramidum* and *G. allenbyi* isoclines cross at two points creating two equilibria (Fig. 8). The first point is in zone Ca and the second in zone Cb.

Graphical stability analysis shows that the equilibrium point in zone Ca is stable while that at zone Cb is

unstable. The "unstable equilibrium" predicts that in years with very unusual population densities, namely many *G. pyramidum* (>12 ha<sup>-1</sup>) and only a few *G. allenbyi* (<13 ha<sup>-1</sup>), the latter species may go extinct. This could not have happened in the last 12 yr because *G. allenbyi* outnumbered *G. pyramidum*, during this period, by a factor of 4–6, and *G. pyramidum* densities never exceeded 6.5 ind ha<sup>-1</sup>. However, a census from the early 1950s (Zahavi and Wharman 1956) in the Holot Halutza area (see Abramsky et al. 1985), failed to register even one *G. allenbyi* in areas where they are presently very common. Perhaps they owed their absence to the unstable equilibrium of Fig. 8.

Stability analysis is traditionally conducted on the zero isoclines. We measured the observed population growth rate of *G. pyramidum* and *G. allenbyi* using data collected in the control plots. It was -2.5 for *G. pyramidum* and -2.5 for *G. allenbyi* (Abramsky et al. 1992). Since the value of the isoclines we analyzed is slightly negative, the zero isoclines are probably located somewhat lower (toward the southwest corner of the graph). But the equilibrium points are most likely located in the same behavioral zones defined by the isolegs (zone Ca), and thus their stability analysis will yield similar results.

We have shown earlier (Rosenzweig and Abramsky 1986) that on a regional scale of several hundreds km<sup>2</sup>, the distribution of the two gerbil species follows the prediction of centrifugal community organization. Centrifugal organization requires three habitats types for coexistence (sand dunes, semistabilized sand dunes, and stabilized sand). When relatively scarce, both species prefer the same habitat type, the semistabilized dune. As densities of both species increase, *G. allenbyi* extends its habitat use to include the stabilized sand. *G. pyramidum* also shifts its habitat use to include its secondary habitat, but it chooses the open, shifting sand dunes. When densities increase further and become very high, both species may use all three habitat types. When one of the secondary habitats is missing, as is the case in the experimental enclosures, the centrifugal system should collapse, as we suggested and showed earlier (Abramsky et al. 1990), to shared-preference model. Indeed, the present study also suggests that the distribution of the gerbils follows the predictions of shared preference community structure and coexistence seems to be possible, on a local scale, in areas consisting of two habitat types (semistabilized dunes and stabilized sand).

How do the two gerbil species coexist? Earlier studies revealed that the smaller *G. allenbyi* is energetically more efficient than *G. pyramidum* (Linder 1988, Kotler and Brown 1990). In addition, field manipulation experiments, conducted in the same enclosures, supported the hypotheses that both gerbil species prefer to conduct their foraging activity in the semistabilized dune (Abramsky et al. 1990, Ziv et al. 1993) and the earlier, and preferred, part of the night (Ziv et al. 1993, Kotler et al. 1993). But, the dominant *G. pyramidum* excludes the energetically efficient *G. allenbyi* from the preferred time of activity

and habitat type (Ziv et al. 1993). Nevertheless, the efficient *G. allenbyi* can still benefit from patches of seeds already visited by *G. pyramidum* as well as use poorer patches which are unacceptable to *G. pyramidum* (Ziv et al. 1993).

The three studies in which isoclines were measured produced results that are internally consistent and repeatable. They also agree with the unusual isocline predictions made by optimal foraging theory. Thus, the combined results of all three studies in which isoclines were measured using the new method, encourage us to believe that the method of estimating them can be used reliably to measure competitive interactions in the field for species obeying an IFD.

*Acknowledgements* – This study was supported by United States-Israel Binational Science Foundation grant No. 840065 and NSF grant BSR – 8905728. The two reviewers, S. Pimm and D. Morris, have made many useful comments that helped to improve the clarity of the paper. This is publication number 170 of the Mitrani Center for Desert Ecology.

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