

Interference competition and temporal and habitat partitioning in two gerbil species

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We have tested two hypotheses which may explain two different patterns which underlie coexistence in two species of desert gerbils (*Gerbillus allenbyi* and *G. pyramidum*). The two patterns are temporal partitioning of foraging activity and shared preference habitat selection. When sympatric, *G. pyramidum* uses the early part of the night most heavily while *G. allenbyi* is most active in the late part of the night. Although both species prefer the same habitat type (semistabilized sand dune), in the presence of *G. pyramidum*, *G. allenbyi* utilizes mainly the secondary habitat type (stabilized sand dune). The hypotheses are 1) one species is dominant (*G. pyramidum*) while the other (*G. allenbyi*) is an energetically more efficient forager, and 2) one species has the ability to quickly harvest seeds in dense resource patches and the other species can harvest seeds profitable at lower resource densities. We tested the hypotheses in an experiment conducted in four enclosed plots. Two additional unfenced plots served as controls. Two of the enclosed plots contained mixed populations of both species while the other two fenced plots contained *G. allenbyi* only. In contrast to patterns of activity of *G. allenbyi* with *G. pyramidum* present, *G. allenbyi* is also very active early in the night even on the semistabilized dunes when *G. pyramidum* is absent. The results of the experiment supported the hypothesis that interference is the key factor to understanding the coexistence of the two species. Both the temporal and spatial patterns are the result of the dominant *G. pyramidum* species excluding the energetically efficient *G. allenbyi* from the preferred time of activity and habitat type.

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Many studies on desert rodents indicate that competitive relationships are very common among coexisting species and are important for the explanation of rodent community organization (e.g., Brown 1975, Rosenzweig 1977, Abramsky et al. 1985a, Kotler and Brown 1988).

Early studies on interspecific competition provided the necessary theoretical framework to understand the importance of this process (Lotka 1925, Volterra 1926, Gause 1934). Many empirical studies were able to show that interspecific competition actually occurs (see review papers of Connell 1983 and Schoener 1983). However, the mechanisms that allowed the species to coexist were usually not explored. Recently, a new mechanistic

approach based on optimal foraging and habitat selection theories has provided several mechanisms to explain species coexistence (e.g., Rosenzweig 1981, Brown 1986, 1989a,b, Price 1986, Schoener 1986, Kotler and Brown 1988). A mechanism of coexistence is composed of two essential features (Begon et al. 1986, Kotler and Brown 1988): a) a resource axis of environmental heterogeneity and b) an evolutionary trade-off between the abilities of the coexisting species to utilize various parts of the axis. The trade-offs may rely exclusively on exploitation competition, resulting in each species utilizing partly different resources (MacArthur 1972, Tilman 1982, Vance 1984). The trade-offs

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may also be based on interference competition, resulting in dominance behavior of one species while the second species is more efficient at resource exploitation (Vance 1984).

The sandy habitats of the Western Negev Desert are inhabited by two common species of gerbils, *G. allenbyi* and *G. pyramidum* (Zahavi and Wharman 1957, Abramsky et al. 1985a). The gerbils provide a good system for studying mechanisms of coexistence. Results of earlier studies show that the two species compete (Abramsky and Pinshow 1989, Mitchell et al. 1990), and the magnitude of the competition was measured experimentally (Abramsky et al. 1991, 1992). Although both species prefer the semistabilized dune (Abramsky et al. 1990), they co-occur sympatrically in three habitat types – shifting dunes, semistabilized dunes, and stabilized sand fields (Abramsky et al. 1985b, Rosenzweig and Abramsky 1986). Where all three habitat types are found, the distribution of species densities follow the “centrifugal community organization” model (Rosenzweig and Abramsky 1986). The two species are nocturnal, inhabiting burrows during the day and consuming and collecting seeds and vegetative material while foraging during the night. Both species are mostly granivorous and have similar diets (Bar et al. 1984).

Recent field studies on these two gerbil species have revealed that they have two distinct activity patterns that may contribute to their coexistence. Abramsky et al. (1990) have studied experimentally the habitat preference of the two gerbil species in an area with two habitat types (semistabilized dune and stabilized sand). When rare, both species prefer the semistabilized dune. Habitat preference changes as a function of intraspecific and interspecific densities. In the presence of a relatively low density of *G. pyramidum*, *G. allenbyi* shifts its habitat preference to the stabilized sand. In contrast, the preference of *G. pyramidum* for the semistabilized dune increases in the presence of high density of *G. allenbyi*. This type of response follows the predictions of the shared habitat preference community organization model (Pimm et al. 1985, Abramsky et al. 1990), and is often found in interference systems.

A recent study (Kotler et al., unpubl.) has demonstrated that the two gerbil species also show temporal partitioning in their above-ground activity. *G. pyramidum* is mostly active during the first part of the night while *G. allenbyi* is mostly active during the later part of the night.

Why do the gerbils show both the spatial and the temporal segregational patterns? Could the two patterns reflect the same underlying cause?

Two potential mechanisms have been suggested to explain coexistence in this system. An underlying assumption of the two hypotheses is that seed resources are renewed on a daily basis. In particular, Kotler and Brown (1990) and Kotler et al. (unpubl.) suggest that the available seed resources for the rodents in the area are renewed daily by the relatively strong afternoon

winds that re-distribute and expose buried seeds. These mechanisms yield predictions regarding temporal partitioning (Kotler et al., unpubl.) and shared habitat preference (Abramsky et al. 1990) and are as follows:

1) Interference (*G. pyramidum*) versus foraging efficiency (*G. allenbyi*). Interference from the bigger (mean mass 40 g) *G. pyramidum* on the smaller and energetically more efficient (Linder 1988, Kotler and Brown 1990, Ziv 1991) *G. allenbyi* (26 g) should result in temporal and habitat partitioning. In time, *G. pyramidum* will be mostly active during the first part of the night as a result of its ability to monopolize recently renewed, rich seed patches. But as seed resources are depleted from patches, resource harvest rates decline (Kotler and Brown 1990). As foraging becomes less valuable, *G. pyramidum* will become inactive and cease to interfere with *G. allenbyi*. *G. allenbyi* will be active during the later part of the night as a result of its higher foraging efficiency and the absence of foraging costs due to interference by *G. pyramidum*. During the later part of the night, *G. allenbyi*, due to its energetic efficiency, will be able to profit from resource patches already utilized, partly depleted, and abandoned by *G. pyramidum*. Regarding the habitat scale, when active, *G. pyramidum* will exclude *G. allenbyi* from the best habitat. Interference can explain both described activity patterns.

2) Foraging efficiencies at high (*G. pyramidum*) versus low (*G. allenbyi*) resource density, mediated by body size and a trade-off of foraging speed versus foraging efficiency. With regard to time scale, although both species will become active as soon as daylight diminishes, the fast *G. pyramidum* will, on the average, arrive at and utilize the rich patches first but will quit foraging early as resource patches are depleted. Since the smaller and more efficient *G. allenbyi* can benefit from a seed patch already visited and abandoned by *G. pyramidum* (Kotler and Brown 1990, Ziv 1991), it will continue to forage in patches after they are no longer profitable for *G. pyramidum*. Therefore, *G. allenbyi* will remain active longer. Similar arguments can be made with regard to the habitat used by the two species. *G. pyramidum* has an advantage in rich seed patches, especially in the loose sand of the semistabilized dune where its advantage in harvest rates may be greatest (Kotler and Brown 1990) while *G. allenbyi* is the more efficient forager in both habitats at low seed densities. Thus, it can use rich or poor seed patches in the semistabilized dune and patches in the harder-to-forage stabilized sand as well. The trade-off of foraging speed versus foraging efficiency may explain the habitat pattern (Abramsky et al. 1990). However, this trade-off cannot explain the temporal partitioning of the night since it predicts that the species will show nested temporal activity pattern (Brown 1988, Kotler et al., unpubl.), namely both species will be active during the first part of the night while only *G. allenbyi* will be active during the second part of the night.

Table 1. Numbers of gerbils in the experimental and control grids. *G. pyramidum* was artificially introduced onto the enclosures while *G. allenbyi* was able to regulate its densities via species-specific gates (see text).

| | Control grids | | Experimental grids (Enclosures) | | | |
|---------------------|---------------|---|------------------------------------|---|---|---|
| | 1 | 2 | 3 | 5 | 4 | 6 |
| <i>G. allenbyi</i> | 6 | 5 | 4 | 5 | 9 | 7 |
| <i>G. pyramidum</i> | 3 | 2 | 6 | 5 | 0 | 0 |

We now review the testable predictions of each hypothesis. Since we have previously demonstrated temporal partitioning (Kotler et al., unpubl.) and a shared preference habitat distribution (Abramsky et al. 1990), we place particular emphasis on the interference hypothesis.

The two hypotheses can be compared by removing *G. pyramidum* from some plots and comparing *G. allenbyi* activity pattern to control plots with *G. pyramidum*. According to the foraging efficiency hypothesis, removal of *G. pyramidum* from an area should have a relatively small effect on the activity pattern of *G. allenbyi*. The reason is that this hypothesis predicts a nested activity pattern in the presence of *G. pyramidum* (Kotler et al., unpubl.). In contrast, if the interference hypothesis is valid, in the absence of *G. pyramidum*, *G. allenbyi* should shift its behavior and be active mostly in the earlier part of the night. In the presence of *G. pyramidum*, *G. allenbyi* will be mostly inactive during that part of the night. Regarding habitat use, under both hypotheses, *G. allenbyi* should show different habitat preference in the presence of *G. pyramidum* than in its absence. *G. allenbyi* should show an apparent preference for the less favorable habitat when *G. pyramidum* is present and active. Without *G. pyramidum*, the preference of *G. allenbyi* may vary between preferring the best habitat to no preference, depending on its density (Abramsky et al. 1990). The same habitat shift should be seen in time concerning habitat use when both species are present.

Methods

Study site and enclosures

The study was conducted in the Holot Mashabim Nature Reserve (31°01'N, 34°45'E) situated in the Haluza region 35 km south of Beer Sheva, Israel. The area is characterized by long west-to-east ranges of dunes that provide two main habitats, semistabilized dunes and stabilized sand (Danin 1978). Average annual precipitation at the site is 108 mm. Rainfall is limited to winter, and dew forms on approximately 250 nights per year. Northwesterly winds prevail in the area and usually occur in mid- and late afternoon.

Six one-hectare (100×100 m) grids are located in the area, four of them enclosed by rodent-proof fences. Each 1-ha plot contains similar proportions of semistabilized dune and stabilized sand. Fencing, consisting of 6 mm mesh hardware cloth, is buried 40 cm below the soil surface and extends 60 cm above ground. The top 15 cm of both sides of the fence are covered with aluminum flashing to prevent individual rodents from climbing over. All fences are perforated with adjustable gates with small openings (19.7 mm in diameter) that only *G. allenbyi* can traverse. The four enclosures are arranged in 2 pairs (grids 3 and 4, and grids 5 and 6), each sharing a common 100 m fence. These enclosures have also been used for other experimental studies (e.g., Abramsky et al. 1990, 1991). The other two grids are unenclosed and served as controls.

Species densities and experimental design

To detect the activity pattern of *G. allenbyi* in the presence and absence of *G. pyramidum*, we introduced individuals of *G. pyramidum* onto the four enclosed grids in two different densities (Table 1). Five and six individuals of *G. pyramidum* were introduced to grids 5 and 3, respectively, while 0 individuals of *G. pyramidum* were present on grids 4 and 6. In addition, 3 and 2 individuals of *G. pyramidum*, respectively, inhabited naturally control grids 1 and 2. As noted, *G. allenbyi* freely entered and exit fenced plots through species-specific gates, and adjusted its density in response to that of its competitor (*G. pyramidum*) and itself (Table 1). Previous experiments (Abramsky et al. 1991, 1992) showed that without *G. pyramidum*, *G. allenbyi* equally used the two adjacent enclosures, suggesting an "Ideal Free Distribution" (Fretwell and Lucas 1970, Fretwell 1972).

We marked animals with species-specific toe-clips to help in identifying tracks: the outside left hind toe for *G. pyramidum* and the outside right hind toe for *G. allenbyi*. Forty "sand-tracking" stations (0.4 by 0.4 m) were set in each of the six grids (Kotler 1985, Mitchell et al. 1990). In the four enclosed plots, 20 stations were placed in the semistabilized dune and 20 in the stabilized sand of each grid. We smoothed the sand in tracking-stations (using household squeegees) before sunset and again after each time we read plots. We scored plots for rodent activity by estimating % coverage by tracks on a scale of 0 to 4. Zero indicated no footprints at all and 4 indicated 100% coverage. Scores could be assigned to species on the basis of species-specific toe clips, which were easily discerned in the smooth sand. This method has been used in recent studies (e.g., Kotler 1985, Abramsky and Pinshow 1989, Abramsky et al. 1990, 1991, Mitchell et al. 1990) and was found to be an accurate indicator of activity level. As we censused activity levels several times during the night, scores for any plot were rarely above 3 (< 1.8% for *G. allenbyi*

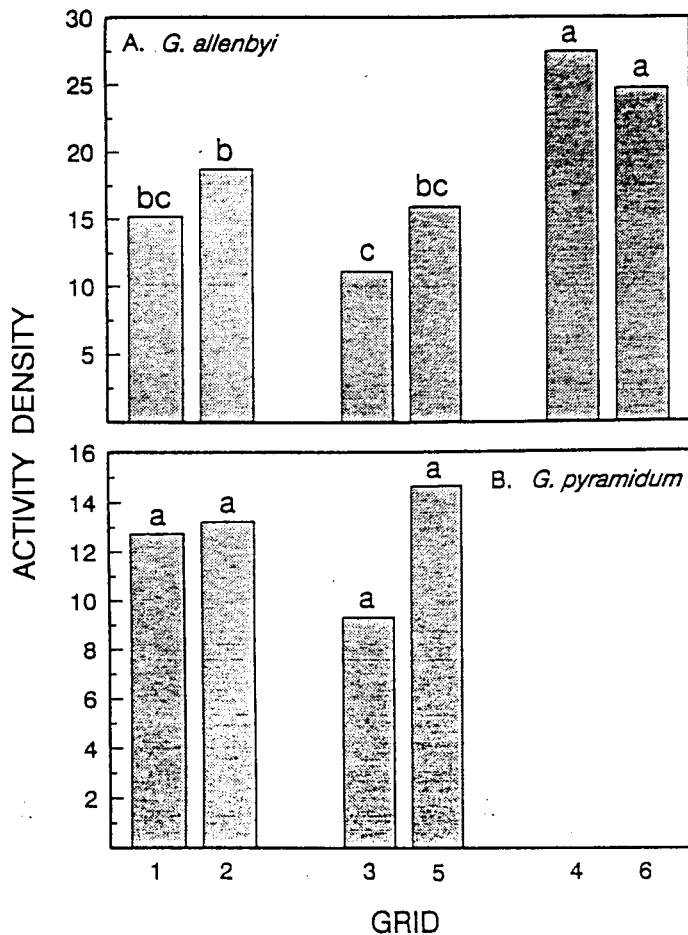


Fig. 1. Activity density values of *G. allenbyi* (A) and *G. pyramidum* (B) in the different grids. Bars which share the same letter are not significantly different ($p > 0.05$, ANOVA, multiple range test).

and 0.8% for *G. pyramidum*). Thus, the activity of one individual could not "cover up" tracks made earlier. We termed the sum of scores of a species for all plots in a grid as "activity density", which served as the dependent variable for the analysis. A high and significant correlation exists between the species' activity and population densities (Abramsky and Pinshow 1989, Mitchell et al. 1990), with sand tracking yielding more sensitive data for measuring habitat use and species interactions (Abramsky et al. 1990, 1991). For the habitat use analysis, sand-tracking scores were summed separately for each habitat in each plot.

We took measurements of footprint coverage on each grid five times every night (20.00, 22.00, 24.00, 02.00, 04.00). It took 10–15 min to read the forty stations in each grid. Last light during the experiment was at 18.10, while first light in the morning was at 04.55. The experiment continued for four consecutive nights.

Sand tracking allowed us to detect the activity pattern of *G. allenbyi* in the absence or presence of *G. pyramidum* in enclosed and control plots. We calculated habitat selectivity as the ratio between the sum of track scores on plots in the semistabilized dune and the sum of track scores on both the semistabilized dune and the

stabilized sand plots of each grid. A value of 0.5 indicates equal habitat use by a species, while higher or lower values indicate preference for the semistabilized dune or the stabilized sand, respectively.

We found no significant differences in the activity density of either species on the 4 different days ($F=0.06$, $P=0.98$ for *G. pyramidum*; $F=1.42$, $P=0.24$ for *G. allenbyi*). Also, no significant difference (2-way ANOVA) existed between replicate grids (Fig. 1). Therefore, we lumped together the data from all days and grids that belonged to the same treatment.

We used repeated measures ANOVA to compare between the behavior of the rodents during the night in different treatments and different times. We used Scheffé multiple range test to test between the behavior of the rodents in similar hours.

Results

The temporal scale

Activity of the species – temporal partitioning

Because different grids included different densities of

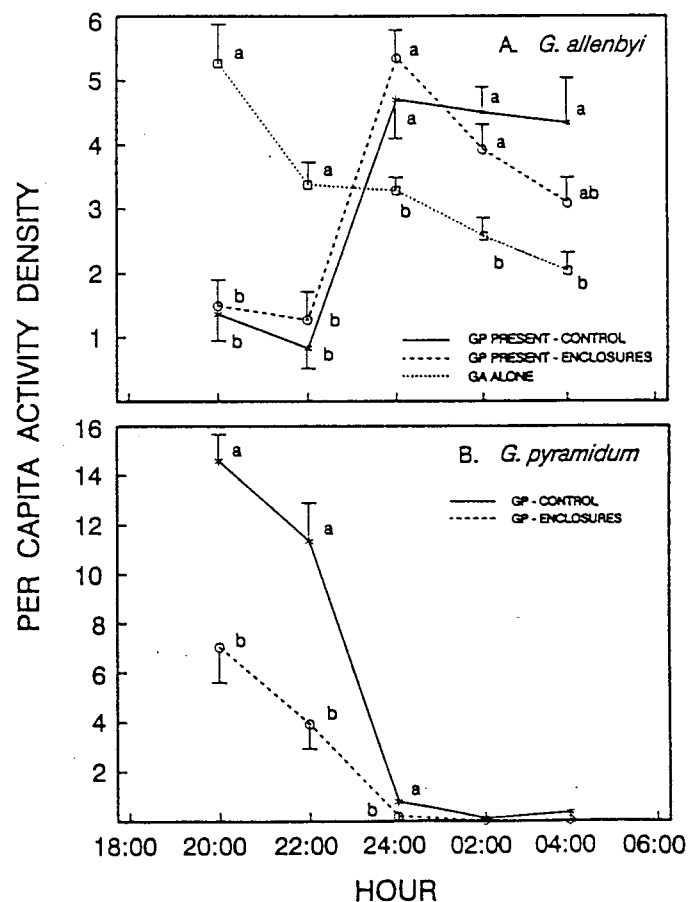


Fig. 2. Per capita activity density values (\pm SE) of *G. allenbyi* (A) and *G. pyramidum* (B) during different hours in the control and enclosed grids. Points of the same hour which share the same letter are not significantly different ($p > 0.05$, Scheffé multiple range test).

Table 2. Repeated measures ANOVA testing the effect of hour and treatment on the species' per capita activity density.

| <i>G. allenbyi</i> | | | | | | |
|---------------------------|--------|----|-------|------|--------|--|
| Source | SS | DF | MS | F | P | |
| <i>Between subjects</i> | | | | | | |
| Day | 15.3 | 3 | 5.1 | 2.4 | 0.1 | |
| Treatment | 1.6 | 2 | 0.8 | 0.4 | 0.7 | |
| Subjects w. groups | 38.2 | 18 | 2.1 | | | |
| <i>Within subjects</i> | | | | | | |
| Hour | 93.6 | 4 | 23.4 | 22.4 | <0.001 | |
| Day × Hour | 28.9 | 12 | 2.4 | 2.3 | 0.025 | |
| Treat × Hour | 161.6 | 8 | 20.2 | 19.4 | <0.001 | |
| Hour × Subjects w. groups | 75.1 | 72 | 1.0 | | | |
| <i>G. pyramidium</i> | | | | | | |
| Source | SS | DF | MS | F | P | |
| <i>Between subjects</i> | | | | | | |
| Day | 7.1 | 3 | 2.4 | 0.3 | 0.8 | |
| Treatment | 205.4 | 1 | 205.4 | 26.7 | <0.001 | |
| Subjects w. groups | 84.6 | 11 | 7.7 | | | |
| <i>Within subjects</i> | | | | | | |
| Hour | 1623.6 | 4 | 405.9 | 68.3 | <0.001 | |
| Day × Hour | 63.9 | 12 | 5.3 | 0.9 | 0.6 | |
| Treat × Hour | 244.1 | 4 | 61.0 | 10.3 | <0.001 | |
| Hour × Subjects w. groups | 261.6 | 44 | 5.9 | | | |

the species, we calculated the per capita activity for each species by dividing the activity density in each grid by the density of individuals there. *G. allenbyi* and *G. pyramidium* showed temporal partitioning in time of activity on both the control and the enclosed grids where *G. pyramidium* was present (Fig. 2A and 2B). *G. pyramidium* was active from dusk, with the highest per capita activity density occurring at 20.00 (per capita activity density = 14.6 in the control and 7.03 in the enclosures). *G. pyramidium* per capita activity density declined sharply during the following hours, reaching very low values by 24.00 (per capita activity density = 0.80, 0.14, 0.37 in the control and 0.19, 0.04, 0.02 in the enclosures at 24.00, 02.00, 04.00, respectively). Per capita activity densities of *G. pyramidium* in both control and enclosures were significantly higher before midnight than after midnight ($P < 0.05$, Scheffé multiple range test; Fig. 2B).

G. allenbyi showed very low per capita activity during the first two time periods (20.00, 22.00) both in the control and in enclosures where *G. pyramidium* was present (Fig. 2A). Its per capita activity density strongly and significantly increased towards 24.00 and then declined moderately until the end of the night. The per capita activity density of *G. allenbyi* in the control grids increased, between 22.00 to 24.00, approximately 5.7 times (from 0.83 at 22.00 to 4.70 at 24.00), and approximately 4.2 times in the enclosed grids where *G. pyramidium* was present (from 1.27 at 22.00 to 5.35 at 24.00). Per capita activity densities of *G. allenbyi*, in both control and enclosures when *G. pyramidium* was present,

were significantly different before 22.00 and after 22.00 ($P < 0.05$; Fig. 2A).

We tested the similarity of the per capita activity density patterns in the control and the enclosed grids where *G. pyramidium* was present using 2-way ANOVA (grids and hours as factors). No significant difference was found between these ($F = 2.14$, $p = 0.085$). These results are encouraging since they suggest no effect of the fences on the activity of the gerbils.

The results strongly suggest that the two species are active at different parts of the night. *G. pyramidium* is active mostly until 22.00 while *G. allenbyi* is active mostly after 22.00. The per capita activity density of *G. allenbyi* before 24.00 is very low. Thus, as previously demonstrated (Kotler et al., unpubl.), temporal partitioning was present. We can now examine its underlying causes.

When G. pyramidium is absent, G. allenbyi shifts its activity to the earlier part of the night

On grids without *G. pyramidium* (enclosures 4 and 6), the pattern of per capita activity for *G. allenbyi* differed from that described above. Without *G. pyramidium*, *G. allenbyi* was most active immediately after twilight (Fig. 2A, dotted line). Thereafter, *G. allenbyi* per capita activity declined moderately until the end of the night. Per capita activity of *G. allenbyi* in the different treatments changed significantly between hours (Table 2, repeated measures ANOVA). The per capita activity of *G. allenbyi* was significantly higher during the earlier part of the night (in the enclosed grids where *G. pyra-*

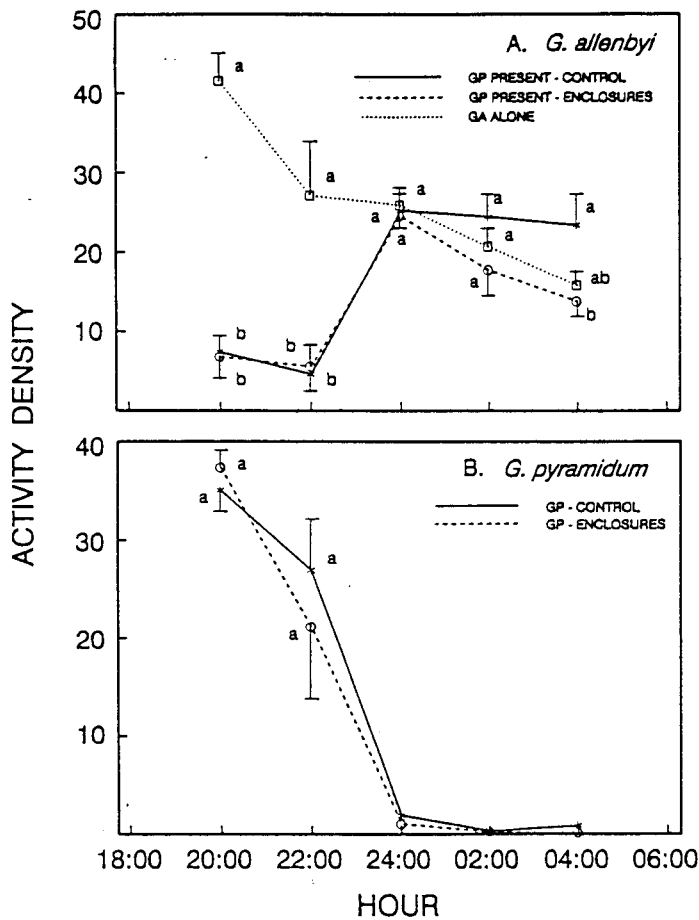


Fig. 3. Activity density values (\pm SE) of *G. allenbyi* (A) and *G. pyramidum* (B) during different hours in the control and enclosed grids. Points of the same hour which share the same letter are not significantly different ($p > 0.05$, Scheffé multiple range test).

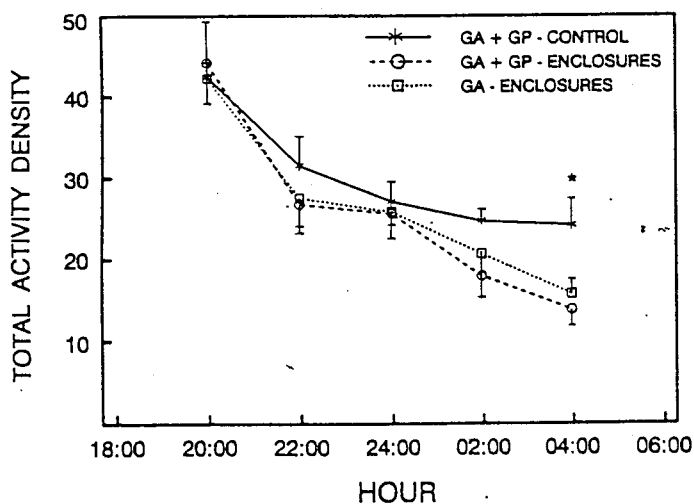


Fig. 4. Total activity density (\pm SE) of both species in the different treatments. A * represents a significant ($P < 0.05$) difference between that point and the other two in the same time interval.

midum was absent) than on either the control grids ($F=42.3$, $p < 0.001$) or the enclosures where both species were present (approximately four times higher in the absence than in the presence of *G. pyramidum*; $F=39.52$, $p < 0.001$).

These results suggest that *G. allenbyi* prefers to forage in the first part of the night, but is usually excluded from that period by *G. pyramidum*.

Density dependent effects on activity of *G. allenbyi*

Analysis of activity density (sum of a species' activity scores in one grid) of each species revealed temporal partitioning (Fig. 3). Also, the results show that activity density of *G. allenbyi* is similar on all treatments after 22.00 regardless of treatment (Fig. 3A). In addition, the summation of total activity density of both gerbil species on a grid within any given time periods are similar (not significantly different) (Fig. 4 and Table 3). This is true for all treatments and time periods except for the last census (04.00) where the total activity density on the control grids was significantly higher than on the enclosed grids (Fig. 4).

Given the result that total activity in each plot is similar for a given period of the night, the activity of each individual must be influenced by the activity of con- and hetero-specific individuals.

We tested the effect of intraspecific density and interspecific activity density on per capita activity of a species by using step-wise multiple linear regression. The per capita activity of each species correlated negatively and significantly with its own population density and the other species' activity density. This suggests that both inter- and intraspecific relationships are important in determining the per capita activity density of the gerbils (Table 4).

Interestingly, relative effects of interspecific competition reflect differences in body mass and metabolic rate. The ratio between the reduction of the per capita activity by con- and hetero-species on *G. allenbyi* (Table 4) is $(0.07/0.21 =) 0.33$, in comparison to $(0.36/1.67 =) 0.22$ for *G. pyramidum*. Thus, the reduction in per capita activity of *G. allenbyi* by *G. pyramidum* is $0.33/0.22 = 1.5$ times larger than the reduction of *G. pyramidum* per capita activity by *G. allenbyi*. This ratio is similar to the ratio of their metabolic rates $(40^{0.75}/26^{0.75} = 1.5)$.

We detected no significant correlation between the per capita activity density of either species and the population density of its competitor. Therefore, activity density in this two-species-system is more sensitive than density for detecting inter-specific relationships, as has been noted before (Abramsky and Pinshow 1989, Abramsky et al. 1990, 1991, 1992).

Table 3. Repeated Measures ANOVA testing the effect of hour and treatment on total activity density.

| Source | SS | DF | MS | F | P |
|---------------------------|--------|----|--------|------|--------|
| <i>Between subjects</i> | | | | | |
| Day | 903.9 | 3 | 301.3 | 2.5 | 0.09 |
| Treatment | 430.6 | 2 | 215.3 | 1.8 | 0.19 |
| Subjects w. groups | 2161.8 | 18 | 120.1 | | |
| <i>Within subjects</i> | | | | | |
| Hour | 8958.1 | 4 | 2239.5 | 34.6 | <0.001 |
| Day × Hour | 1546.2 | 12 | 128.9 | 1.9 | 0.038 |
| Treat × Hour | 373.5 | 8 | 46.7 | 0.7 | 0.67 |
| Hour × Subjects w. groups | 4665.8 | 72 | 64.8 | | |

The habitat scale

Habitat selection by G. allenbyi changes in the presence of G. pyramidum

Do the results of the study also support the predictions of the shared habitat preference model for the two gerbil species (Abramsky et al. 1990)? Habitat selection by *G. allenbyi* can be studied in the first part of the night, when *G. pyramidum* is active, by comparing enclosure grids with and without *G. pyramidum*. We have not included data from the control grids in the analysis of habitat preference since a priori classification of the tracking stations by habitat were available for only the enclosures.

The prediction of the shared preference habitat selection model is that in the presence of many individuals of *G. pyramidum* (>3), *G. allenbyi* should select the stabilized sand; in the absence of *G. pyramidum*, *G. allenbyi* should show selectivity for the semistabilized dune or opportunism, depending on intraspecific density (Abramsky et al. 1990: Fig. 1b). This behavior in combination with temporal partitioning should result in changing patterns of habitat use during the night.

Repeated measures ANOVA (treatment × hour) showed that significantly different preferences were obtained for *G. allenbyi* in the presence and absence of *G.*

pyramidum both in time and space (Table 5). In plots where *G. pyramidum* was present and active, *G. allenbyi* exhibited a significant preference for the stabilized sand habitat during the first two time periods (0.12 at 20.00 and 0.25 at 22.00; Fig. 5). During later hours, when *G. pyramidum* activity ceased, the selectivity for the stabilized sand on these grids disappeared (Fig. 5). In the absence of *G. pyramidum* from the experimental grids, *G. allenbyi* exhibited opportunism throughout the night. This result is expected for the known density of *G. allenbyi* since intraspecific density affects the selectivity of *G. allenbyi* (Abramsky et al. 1990: Fig. 1b). The selectivity of *G. allenbyi* in the first two census periods, in the presence or absence of *G. pyramidum*, is significantly different (Fig. 5). These results agree with the predictions of the shared preference model of habitat selection.

G. pyramidum always selects the semistabilized dune *G. pyramidum*, when active during the first two time periods, appears always to prefer the semistabilized dune (preference value of 0.64 and 0.61, respectively). This preference is only marginally significantly different from a value of 0.5 (i.e., no preference; $0.05 < P < 0.06$), possibly as a result of the relatively small sample size ($n=4$).

Table 4. The effect of intra- and interspecific activity and activity density on the per capita activity densities of *G. allenbyi* and *G. pyramidum*. DGA = Density of *G. allenbyi*, DGP = Density of *G. pyramidum*, AGA = Activity density of *G. allenbyi*, AGP = Activity of *G. pyramidum*.

| <i>G. allenbyi's</i> per capita activity density as dependent variable | | | | | |
|-------------------------------------------------------------------------|-------------|-------|---------|--------|------|
| Independent variables | Coefficient | SE | t-value | P | R |
| Constant | 5.07 | 0.596 | 8.50 | <0.001 | |
| DGA | -0.21 | 0.091 | -2.32 | <0.021 | |
| AGP | -0.07 | 0.010 | -7.49 | <0.001 | 0.57 |
| <i>G. pyramidum's</i> per capita activity density as dependent variable | | | | | |
| Independent variables | Coefficient | SE | t-value | P | R |
| Constant | 16.21 | 1.49 | 10.83 | <0.001 | |
| DGP | -1.67 | 0.28 | -5.94 | <0.001 | |
| AGA | -0.36 | 0.04 | -8.43 | <0.001 | 0.73 |

Table 5. Repeated measures ANOVA testing the effect of hour and treatment on the habitat preference of *G. allenbyi*.

| Source | SS | DF | MS | F | P |
|---------------------------|-------|----|-------|--------|------|
| <i>Between subjects</i> | | | | | |
| Day | 0.09 | 3 | 0.03 | 0.537 | 0.67 |
| Treatment | 0.05 | 1 | 0.051 | 0.841 | 0.38 |
| Subjects w. groups | 0.545 | 9 | 0.061 | | |
| <i>Within subjects</i> | | | | | |
| Hour | 0.376 | 4 | 0.094 | 1.958 | 0.12 |
| Day × Hour | 0.707 | 12 | 0.059 | 1.216 | 0.31 |
| Treat × Hour | 0.489 | 4 | 0.122 | 2.5211 | 0.05 |
| Hour × Subjects w. groups | 1.744 | 36 | 0.048 | | |

Discussion

We found that total activity density of both or one species in each of the six grids decreased during the night, but was similar across most treatments within any time period (Fig. 4). This result suggests that a certain level of total gerbil activity, perhaps related to resource levels, might exist. Results supporting this idea were reported by Mitchell et al. (1990) and Abramsky and Pinshow (1989) for gerbils foraging over the entire night.

Species coexistence is composed of two essential conditions: an axis of environmental heterogeneity and a trade-off between the coexisting species such that individuals of one species better exploit one part of the axis while individuals of the other species better exploit another (Kotler and Brown 1988, Brown 1989a, b).

Kotler et al. (1991) suggested that daily renewal of resource patches of seeds is probably the environmental axis promoting coexistence between these species. Although this suggestion is not directly supported by data,

it does agree with our understanding of the area. Seed resources at the site are renewed as a large pulse of productivity in late spring and summer following winter rains. Shortly thereafter, the seeds disperse and get buried in the sand and are later redistributed by wind, rain, changes in temperature and humidity, animal activity, and weathering. Strong daily afternoon winds also redistribute the seeds. Because seed patches are depleted by rodents during the night, a gradient of resource densities ranging from high resource densities at the beginning of the night to low resource densities at the end of the night is created by foraging activity. Earlier experiments (Abramsky et al. 1990) showed that the semistabilized dune is the preferred habitat. So there are two essential environmental axes – one in time and one in space – needed for the coexistence (Kotler and Brown, unpubl.).

Our results to date suggest that coexistence between *G. allenbyi* and *G. pyramidum* is due to a trade-off between the foraging efficiency of *G. allenbyi* and the dominance of *G. pyramidum*.

It has previously been shown for sympatric rodents with dissimilar body sizes that the smaller species are energetically more efficient foragers (Rosenzweig and Sterner 1970, Kotler and Brown 1988). Our previous work shows that *G. allenbyi* (the smaller species) is more efficient in harvesting seeds than *G. pyramidum* (Kotler and Brown 1990, Ziv 1991). The high foraging efficiency of *G. allenbyi* may be explained by inherent physiological advantages. On average it has 30%-40% lower energetic requirements than the other species resulting from lower basal metabolic rate and thermo-regulatory costs (Linder 1988).

The results of the experiment reported here provide strong support for the existence of strong asymmetrical interference competition by *G. pyramidum* on *G. allenbyi*. We showed that in the absence of *G. pyramidum*, *G. allenbyi* prefers to be active in the early hours of the night. But in the presence of *G. pyramidum*, *G. allenbyi* shifts its apparent preference to the second half of the night (Figs 2 and 3). We obtained similar effects in our analyses of habitat preference. Thus, *G. pyramidum* displaces *G. allenbyi* in both time and space. This conclusion is further supported by the estimates of intra-

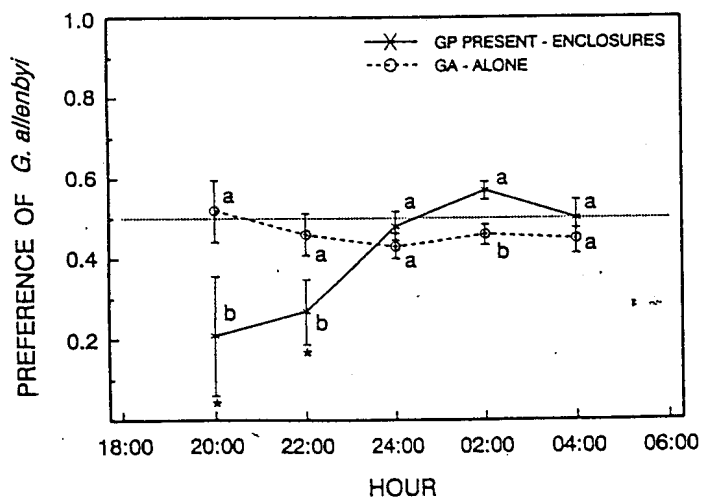


Fig. 5. The preference (\pm SE) of *G. allenbyi* for the semistabilized dune in the enclosed plots in the absence and presence of *G. pyramidum*. Points of the same hour which share the same letter are not significantly different ($p > 0.05$, Scheffe multiple range test). A * indicates that the point is significantly different than the preference value of 0.5. The data were arcsine transformed for the analysis.

and inter-specific density dependent effects on per capita activity (Table 4). Moreover, aggressive interference between gerbils, while foraging in the field, has been directly observed (Abramsky, Brown, and Kotler, pers. obs.). Finally, habitat selection isopleths measured for this system are suggestive of interspecific interference (Abramsky et al. 1990).

The combination of high energetic efficiency for *G. allenbyi* and interference activity by *G. pyramidum* results in *G. allenbyi* being more efficient in low density seed patches and *G. pyramidum* being more efficient in high density patches (Brown 1989b, Kotler et al., unpubl.). This provides the basis for species coexistence (Brown et al., unpubl., Kotler et al., unpubl.).

The results of the experiment support the prediction that one factor, interference, is probably the cause for the two observed patterns of habitat and temporal partitioning. *G. pyramidum* excludes *G. allenbyi* from the preferred earlier part of the night and from the preferred semistabilized dune habitat. When both species are present, *G. pyramidum* emerges first from its burrows and dominates the area. Most of its activity is in the preferred semistabilized dune. In the earlier part of the night *G. allenbyi* is active at a relatively low level and mostly in the stabilized sand away from *G. pyramidum*. After 22.00 *G. pyramidum* ceases most of its activity; interference costs for *G. allenbyi* drop. As a result, *G. allenbyi* becomes very active in both habitats. Since *G. allenbyi* is energetically more efficient than *G. pyramidum* in the absence of interference (Kotler and Brown 1990, Ziv 1991), it can still benefit from patches of seeds already visited by *G. pyramidum* as well as use poorer patches which are unacceptable to *G. pyramidum*. Interference can be regarded as a transient foraging cost (Kotler and Brown 1988). When *G. pyramidum* is present, *G. allenbyi* may utilize only rich patches in the semistabilized dune, but show greater use of habitats used only lightly by *G. pyramidum* (stabilized sand). Without *G. pyramidum*, more patches become profitable for *G. allenbyi*.

All the results reported earlier support the hypothesis that the spatial and temporal patterns exhibited by the two gerbil species are caused by a single mechanism, namely, interference by the bigger species on the energetically more efficient, smaller species. Is it possible that exploitation competition is also important? We think that it had only a minor role in determining the observed patterns. Assume that exploitation competition is solely responsible for the observed patterns of temporal partitioning and habitat selection. This would mean that *G. pyramidum* has an actual advantage (for whatever reason) in patch exploitation in the early parts of the night, which translates to lower quitting harvest rates and giving-up resource densities in patches (Brown 1988). This advantage lets *G. pyramidum* eliminate most foraging opportunities in the early part of the night for *G. allenbyi*. If so, then when *G. allenbyi* forages by itself in the early part of the night, it will not

exploit patches as thoroughly or harvest as much resources as would *G. pyramidum*, had it been present instead. So, when foraging costs for *G. allenbyi* drop late in the night, there will be more resources to exploit than when *G. pyramidum* is present. The result is that *G. allenbyi* activity in the later part of the night, when *G. pyramidum* is not present on the grid, should be higher than when it is present. In fact, we observed just the opposite (Figs 2 and 3). *G. allenbyi*, when alone, decreased its activity during the later parts of the night in a way similar to when *G. pyramidum* was present. As we have noted, these results are consistent with interference competition. Thus, the patterns of habitat selection in time and space resulting from the mechanism of coexistence in this system are governed by interference competition.

Understanding this gerbil community has in past research been approached in two complementary ways. One concentrates on understanding species interactions by investigating habitat selection behavior and estimating habitat selection isopleths and isoclines of species interactions (Rosenzweig and Abramsky 1986, Abramsky and Pinshow 1989, Abramsky et al. 1990, 1991, 1992). The other examines individual behavior and assesses the likelihood of different mechanisms for species coexistence (Kotler and Brown 1990, Brown et al., unpubl., Kotler et al., unpubl.). Both approaches assume optimal behavior on the part of the gerbils. The approaches have neatly converged in this paper to yield a better overall understanding of the community.

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