A field test of the centrifugal community organization model using psammophilic gerbils in Israel’s southern coastal plain

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ABSTRACT

Background: An optimal habitat selection model called centrifugal community organization (CCO) predicts that species, although they have the same primary habitat, may co-exist owing to their ability to use different secondary habitats.

Goal: Test the predictions of CCO with field experiments.

Species: The Egyptian sand gerbil (40 g), Gerbillus pyramidum, and Allenby’s gerbil (25 g), G. andersoni allenbyi.

Site: Ashdod sand dunes in the southern coastal plain of Israel. Three sandy habitats are present: shifting, semi-stabilized, and stabilized sand. Gerbils occupied all three habitats.

Methods: We surveyed rodent abundance, activity levels, and foraging behaviour while experimentally removing G. pyramidum.

Results: Three predictions of the CCO model were supported. Both species did best in the semi-stabilized habitat. However, they differed in their secondary habitats. Gerbillus pyramidum preferred the shifting sand habitat, whereas G. a. allenbyi preferred the stabilized habitat. Habitat selection by both species depended on density. However, in contrast to CCO, G. pyramidum dominated the core habitat and excluded G. a. allenbyi. We term this variant of CCO, ‘asymmetric CCO’.

Conclusions: The fundamental feature of CCO appears valid: co-existence may result not because of what each competing species does best, but because of what they do as a back-up. But in contrast to the prediction of the original CCO model, all dynamic traces of interaction can vanish if the system includes interference competition.

Keywords: asymmetric centrifugal community organization, Gerbillus andersoni allenbyi, Gerbillus pyramidum, giving-up density, habitat selection, mechanism of co-existence.

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INTRODUCTION

The theory of centrifugal community organization (CCO) involves two competing species that share a preference for one of three habitats (the core), but differ in their abilities to use the other two, less suitable (marginal) habitats. Based on optimality principles, the theory predicts that, at low population densities, both species should use only the core habitat. If its density increases, each species should also use its distinct secondary habitat. Then, at very high densities of both species, both should use all three habitats (Rosenzweig and Abramsky, 1986). Competitive co-existence is achieved by virtue of the two marginal habitats because each species has the advantage in a different one of them. The unique property of CCO is that co-existence is achieved not by what the competing species do best, but by what they do as a back-up (Rosenzweig and Abramsky, 1986, Rosenzweig, 1989).

Using field survey data, Rosenzweig and Abramsky (1986) predicted that CCO ought to characterize the psammophilic gerbil community in the southern coastal plain of Israel. The sandy landscape of the southern coastal plains is characterized by transverse dunes comprising three gerbil habitats that are associated with different exposures to the strong west–southwest winter winds (Tsatz, 1990). The well-vegetated, semi-stabilized sand habitat on the dune crest and the wind-sheaned north-eastern facing slopes is preferred over sparsely vegetated, shifting-dune habitat on south-west facing windward dune slopes, and the thickly vegetated stabilized sand habitat in the sheltered groves between the sand dunes (Darin and Nukrian, 1991). Rosenzweig and Abramsky (1986) hypothesized that the two most common rodent species, the Egyptian sand gerbil (40 g), Gerbillus pyramidum, and Allenby’s gerbil (25 g), G. andersoni allenbyi, should prefer the semi-stabilized habitat because it might provide the best combination of food (seeds) and shelter (perennial bushes). They hypothesized that the secondary habitat of the larger, faster G. pyramidum should be the relatively risky, but resource-rich shifting dune habitat and that the smaller, slower G. a. allenbyi should prefer the relatively safer stabilized habitat. If the two species are density-dependent habitat selectors, then at low densities both species should use only the core semi-stabilized habitat. As densities increase, each species should start to use its own secondary habitat together with the core. At very high densities, both species should use all three habitats. The aim of this study was to test these predictions experimentally and thus provide the first field test of centrifugal community organization in animal communities.

METHODS

We established six 140 × 60 m survey grids in the Ashdod sand dunes, southern coastal plain of Israel. Each grid contained 32 stations arrayed in four lines with eight stations each (20-m spacing). We located each grid such that it contained an equal area (70 × 60 m) of two habitat types separated by a distinct border. The six grids included two replicates of each possible pair-wise combination of habitat (shifting and stabilized, shifting and semi-stabilized, stabilized and semi-stabilized). We tested the CCO theory by combining seasonal rodent sampling with experimental removal of G. pyramidum.

Seasonal sampling

We conducted five sampling rounds during December 1993, and March, May, August, and October 1994. With one exception, each round consisted of five nights of live-trapping, two nights of scoring activity in giving-up densities of see conducted in October 1994.

Live-trapping

We censused gerbil population trap baited with millet seeds. Captured G. pyramidum and so that we could identify sp.

Sand-tracking

To quantify their habitat preferences, we (Kotler, 1985) as revealed by two plots of sand (sand of a perennial shrub (bush habitat). Following a night 5-point scale to score rods the plot covered with track station, we used the mean as dependent variable for inter-

Seed trays

Following Brown (1988), we relative foraging efficiency for quality and foraging efficiency foraging profit than one with foraging up density is the most resource patches that are not Brown et al., 1994a).

We measured giving-up density (aluminium trays). We filled each of sifted sand. We placed pairs of habitat, at the four central stations of these four seed tray pairs no giving-up density for each micrometer. After smoothing the surrounding of dusk and checked them at dark shape and the species-specific overnight. Then we sifted them in the laboratory, cleaned them giving-up densities.

G. pyramidum

To experimentally assess the habitat preferences, we conducted June 1995). We used eight
nights of scoring activity in sand-tracking stations (Kotler 1985), and five nights of measuring giving-up densities of seeds in experimental food trays (Brown, 1988). Trapping was not conducted in October 1994 when harsh weather would have biased our results.

Live-trapping

We censused gerbil populations using mark and recapture methods. We set a Sherman live trap baited with millet seeds at each station. Traps were set out at dusk and checked at dawn. Captured G. pyramidum and G. a. allenbyi individuals were given a species-specific toe clip so that we could identify spoor in tracking stations and seed trays.

Sand-tracking

To quantify their habitat and microhabitat use, we measured the gerbil’s ‘activity density’ (Kotler, 1985) as revealed by sand tracking (Abramsky et al., 1990; Mitchell et al., 1990). We smoothed two plots of sand (sand-tracking plots: 45 × 45 cm) at each station, one at the margin of a perennial shrub (bush microhabitat) and one 23 m from the shrub’s edge (open micro-habitat). Following a night of activity, we examined the sand-tracking plots and used a 5-point scale to score rodent activity based on track density (0 = no tracks, 4 = 100% of the plot covered with tracks). Since both microhabitats were not always available at each station, we used the mean activity density of each microhabitat across the entire plot as the dependent variable for inter-habitat comparisons.

Seed trays

Following Brown (1988), we used giving-up densities to estimate habitat preference and relative foraging efficiency for each species. Giving-up density varies inversely with habitat quality and foraging efficiency: a habitat with a low mean giving-up density yields more foraging profit than one with a high giving-up density. And a species with a lower mean giving-up density is the more efficient forager – that is, it can profitably utilize depleted resource patches that are no longer profitable to its competitor (Brown, 1988; Rosenzweig, 1991, Brown et al., 1994a).

We measured giving-up densities in artificial resource patches (45 × 60 × 2.5 cm deep aluminium trays). We filled each tray with 3 g of millet seeds mixed thoroughly into 5 litres of sifted sand. We placed pairs of seed trays, one in the bush and one in the open micro-habitat, at the four central stations of every half-grid. Since nightly giving-up densities from these four seed tray pairs may not be independent, we used the log-transformed mean giving-up density for each microhabitat from these four stations as our dependent variable. After smoothing the surrounding sand with a rubber squeegee, we filled trays with seeds at dusk and checked them at dawn. We revisited the stations in the morning and used spoor shape and the species-specific toe clips to identify which species had foraged in the tray overnight. Then we sifted the sand to remove remaining seeds, brought the seeds to the laboratory, cleaned them of debris, and weighed them (Satorius GmbH) to obtain the giving-up densities.

G. pyramidum removal experiment

To experimentally assess the predictions of CCO and facilitate study of G. a. allenbyi’s habitat preferences, we conducted a removal of G. pyramidum lasting 13 nights (25 May to 6 June 1995). We used eight grids in total, four of which contained the semi-stabilized/
stabilized habitat combination and four that contained the stabilized/shifting habitat combination. Each grid was composed of four lines 25 m apart. Each line had 10 pairs of spoor-tracking stations (15-m intervals). We trapped experimental and control grids simultaneously and removed all *G. pyramidum* individuals trapped for seven consecutive nights from two of the four combined replicates. The other two were used as controls. We discouraged re-colonization by neighbours *G. pyramidum* by also placing traps at 25-m intervals around the periphery of the experimental grids. Immediately after these seven nights of trapping, we conducted two nights of sand tracking followed by two additional nights of removal trapping, and then again two nights of sand tracking.

**Data analysis**

We used a four-way analysis of variance (ANOVA) to determine the effect of protocol, period, habitat, microhabitat, and species on per-tracking-plot activity density. We used a two-way ANOVA to determine the effect of habitat and species on giving-up density. We analysed the effect of removal of *G. pyramidum* on *G. a. allenbyi* habitat use with analysis of covariance (ANCOVA) [dependent variable = the proportion (arcsine transformed) of activity density per tracking plot in the ‘preferred habitat’ relative to the total activity density in the two habitats combined (‘relative preference’ (Abramsky et al., 1990))].

We used isodar analysis (Morris, 1987) to determine whether *G. pyramidum* or *G. a. allenbyi* are density-dependent habitat selectors. A habitat isodar is a line of equal fitness drawn in a state space of the population densities of a species in two habitats. A significant, positively sloped isodar indicates that a species selects habitat in a manner consistent with ideal habitat selection (Fretwell and Lucas, 1970; Fretwell, 1972). In our study, due to the low abundances of *G. pyramidum* and *G. a. allenbyi* in the stabilized and shifting habitat respectively (see Results), only two analyses were feasible: the activity density of *G. pyramidum* in the semi-stabilized/shifting habitat combination and that of *G. a. allenbyi* in the semi-stabilized/stabilized habitat combination. We included the activity density of the competing species in our isodar regressions to search for interspecific competition (Morris, 1989).

**RESULTS**

**The relationship between density and activity level**

The activity densities of *G. a. allenbyi* (AGa) and *G. pyramidum* (AGp) were each significantly correlated with their own respective species densities (DGa for *G. a. allenbyi* and DGP for *G. pyramidum*). For *G. a. allenbyi*, the relationship was linear (AGa = 0.119 × DGa + 0.072; $r^2 = 0.756$, $P < 0.0001$), whereas for *G. pyramidum* the relationship approached an asymptote (AGp = 0.194 × DGP − 0.012 × DGP$^2$ + 0.006; $r^2 = 0.736$, $P < 0.0001$).

**Activity pattern**

Overall activity was highest in the semi-stabilized (SM) habitat, followed by the stabilized (ST) and shifting (SH) habitats (Table 1). The species differed in their habitat use. *Gerbillus pyramidum* biased its activity towards the semi-stabilized habitat, followed by the shifting and then the stabilized habitats. *Gerbillus a. allenbyi* biased its activity towards the stabilized

<table>
<thead>
<tr>
<th>Table 1. Results of four-way ANOVA, by type, and species on the giving-up density in three sand habitats.</th>
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</thead>
<tbody>
<tr>
<td>Source</td>
</tr>
<tr>
<td>Period (P)</td>
</tr>
<tr>
<td>Habitat (H)</td>
</tr>
<tr>
<td>Microhabitat (M)</td>
</tr>
<tr>
<td>Species (S)</td>
</tr>
<tr>
<td>S × H</td>
</tr>
<tr>
<td>S × M</td>
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<tr>
<td>S × P</td>
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<tr>
<td>S × H × P</td>
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<tr>
<td>S × M × P</td>
</tr>
<tr>
<td>S × M × H</td>
</tr>
<tr>
<td>Residual</td>
</tr>
</tbody>
</table>

habitats, followed by the semi-stabilized, and was significantly more active in semi-stabilized habitats, whereas *G. a. allenbyi* was highest, both species used the stabilized the most. Gerbil activity also differed between species, with *G. a. allenbyi* being more active in the semi-stabilized (0.238 ± 0.029 respectively) and *G. a. allenbyi* (0.145 ± 0.026). Each species was a density-independent isodar (AGpSM = 0.60, CI(P = 0.05) = 0.10, 0.10) and density-dependent isodar (AGpSM = 1.25, CI(P = 0.05) = 0.25, 0.25) for *G. pyramidum* and *G. a. allenbyi* respectively. Mean giving-up density was the highest in the stabilized habitats (0.786 ± 0.035) and the lowest in the semi-stabilized habitats (0.586 ± 0.029).
Field test of the CCO model

Table 1. Results of four-way ANOVA of the effect of sampling period, habitat type, microhabitat type, and species on their activity density

<table>
<thead>
<tr>
<th>Source</th>
<th>d.f.</th>
<th>SS</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Period (P)</td>
<td>4</td>
<td>14.498</td>
<td>3.624</td>
<td>81.014</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Habitat (H)</td>
<td>2</td>
<td>4.959</td>
<td>2.48</td>
<td>55.424</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Microhabitat (M)</td>
<td>1</td>
<td>0.903</td>
<td>0.903</td>
<td>20.183</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Species (S)</td>
<td>1</td>
<td>0.587</td>
<td>0.587</td>
<td>13.124</td>
<td>0.0003</td>
</tr>
<tr>
<td>S × H</td>
<td>2</td>
<td>23.885</td>
<td>11.942</td>
<td>266.934</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>S × M</td>
<td>1</td>
<td>0.016</td>
<td>0.016</td>
<td>0.356</td>
<td>0.5513</td>
</tr>
<tr>
<td>S × P</td>
<td>4</td>
<td>0.242</td>
<td>0.060</td>
<td>1.35</td>
<td>0.2506</td>
</tr>
<tr>
<td>S × H × P</td>
<td>16</td>
<td>8.111</td>
<td>0.507</td>
<td>11.331</td>
<td>0.0001</td>
</tr>
<tr>
<td>S × M × P</td>
<td>8</td>
<td>0.191</td>
<td>0.024</td>
<td>0.534</td>
<td>0.8320</td>
</tr>
<tr>
<td>S × M × H</td>
<td>4</td>
<td>0.430</td>
<td>0.108</td>
<td>2.404</td>
<td>0.0491</td>
</tr>
<tr>
<td>Residual</td>
<td>435</td>
<td>19.506</td>
<td>0.045</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

habitats, followed by the semi-stabilized and then the shifting habitats. Gerbillus pyramidum was significantly more abundant than G. a. allenbyi in the shifting and semi-stabilized habitats, whereas G. a. allenbyi was significantly more abundant in the stabilized habitat (Fig. 1A). This habitat ranking remained consistent throughout most of the study, with G. a. allenbyi almost completely avoiding the shifting habitat and G. pyramidum almost completely avoiding the stabilized habitat. However, in August 1994 when densities were highest, both species used all three habitats (Fig. 1B,C).

Gerbil activity also differed significantly between microhabitats (Table 1). Both species were more active in the bush than in the open (mean ± standard error: 0.313 ± 0.034 and 0.238 ± 0.029 respectively for G. pyramidum; 0.395 ± 0.042 and 0.296 ± 0.036 respectively for G. a. allenbyi). Microhabitat preference for the bush microhabitat was consistent across all three sand habitats.

Isodar analysis

Each species was a density-dependent habitat selector. For G. pyramidum, the intercept of its isodar (AGpSM = 0.6 × AGpSH + 0.212; \( r^2 = 0.806, P < 0.0001 \)) was significantly greater than 0 [CI(\( P = 0.05 \)) = 0.06], indicating that the semi-stabilized habitat was quantitatively better than the shifting habitat. For G. a. allenbyi, the intercept of its isodar (AGaST = 1.258 × AGaSM + 0.237; \( r^2 = 0.377, P = 0.001 \)) was also significantly greater than 0 [CI(\( P = 0.05 \)) = 0.23], indicating that, in the presence of G. pyramidum, G. a. allenbyi perceives the stabilized habitat to be quantitatively better than the semi-stabilized habitat.

Foraging patterns

Mean giving-up density was lowest in the presumptive core semi-stabilized habitat (mean ± standard error: 0.474 ± 0.023 g) than in the shifting (0.723 ± 0.056 g) and the stabilized habitats (0.786 ± 0.040 g) (see Table 2). Mean giving-up density of G. a. allenbyi was lowest in the semi-stabilized habitat. Mean giving-up densities in the shifting and stabilized habitats did not differ significantly (Fig. 2). However, trays in the shifting habitat
were used much less frequently than in the stabilized habitat (14 and 159 times respectively). Within the semi-stabilized habitat, G. a. allenbyi had a significantly lower giving-up density than G. pyramidum (Fig. 2).

For G. pyramidum, there was no significant difference in giving-up density between habitats, although there was a trend towards a lower density in the semi-stabilized habitat (Fig. 2). However, sample size in the stabilized habitat was very small (n = 2; stabilized habitat used only in August when gerbil densities were at their highest). Nevertheless, in August, despite the small sample, G. pyramidum’s giving-up density in the stabilized habitat

**Table 2. Results of two-way ANOVA (density)**

<table>
<thead>
<tr>
<th>Source</th>
<th>d.f.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Habitat (H)</td>
<td>2</td>
</tr>
<tr>
<td>Species (S)</td>
<td>1</td>
</tr>
<tr>
<td>H × S</td>
<td>2</td>
</tr>
<tr>
<td>Residual</td>
<td>540</td>
</tr>
</tbody>
</table>

(0.76 g) was significantly high in both semi-stabilized and shifting habitat. G. pyramidum’s least preferred habitat was G. pyramidum.

**The effect of G. pyramidum**

In the semi-stabilized/stabilized habitat, G. pyramidum to about one-segmental grids of the shifting habitat. G. pyramidum completely. The relative use of both the semi-st...
Field test of the CCO model

![Graph showing activity density for G. pyramidalum across different months]

**Fig. 1.** Box-and-whiskers plots of the distribution of *G. a. allenbyi* (Ga) and *G. pyramidalum* (Gp) activity between the three habitats (A), and for each species between the sampling periods (B, C). The box has lines at the lower quartile, median, and upper quartile values. The whiskers are lines extending from each end of the box to show the extent of the rest of the data. Dots beyond the ends of the whiskers are outliers. Boxes whose notches do not overlap indicate that the medians of the two groups differ at the 5% significance level. Habitats: SH = shifting, SM = semi-stabilized, ST = stabilized.

<table>
<thead>
<tr>
<th>Source</th>
<th>d.f.</th>
<th>SS</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Habitat (H)</td>
<td>2</td>
<td>1.662</td>
<td>0.831</td>
<td>6.226</td>
<td>0.0021</td>
</tr>
<tr>
<td>Species (S)</td>
<td>1</td>
<td>0.268</td>
<td>0.268</td>
<td>2.009</td>
<td>0.1569</td>
</tr>
<tr>
<td>H x S</td>
<td>2</td>
<td>0.516</td>
<td>0.258</td>
<td>1.934</td>
<td>0.1455</td>
</tr>
<tr>
<td>Residual</td>
<td>540</td>
<td>72.069</td>
<td>0.133</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

(0.76 g) was significantly higher than in the other two habitats (0.249 and 0.174 g for the semi-stabilized and shifting habitat respectively), suggesting that the stabilized habitat is *G. pyramidalum*’s least preferred habitat.

**The effect of *G. pyramidalum* removal on the habitat use of *G. a. allenbyi***

In the semi-stabilized/stabilized habitat combination, we reduced the activity of *G. pyramidalum* to about one-sixth of that in the controls (53.25 vs. 9.082). In the experimental grids of the shifting/stabilized habitat combination, we managed to eliminate *G. pyramidalum* completely. The reduction of *G. pyramidalum* density increased *G. a. allenbyi*’s relative use of both the semi-stabilized and shifting habitats (Table 3, Fig. 3), demonstrating...
a competitive effect of *G. pyramidum* on *G. a. allenbyi*. As measured by the increase of *G. a. allenbyi* activity after *G. pyramidum* reduction, the effect did not differ between the two habitat combinations (Table 3).

Because *G. pyramidum* activity in both experimental plots (Fig. 3A) was much lower than in the control plots in the semi-stabilized/stabilized habitat combination, we conducted separate linear regressions for each. In the experimental plots, the activity density of *G. pyramidum* (AGp) reduced considerably the relative preference of *G. a. allenbyi* for the semi-stabilized habitat (Fig. 3A). An activity level equivalent to two *G. pyramidum* individuals was enough to shift *G. a. allenbyi*’s habitat preference from a slight preference for the semi-stabilized habitat to an apparent preference for the stabilized habitat. Meanwhile, in the control plots, where AGp was always high, *G. pyramidum* activity had no effect on *G. a. allenbyi*’s preference. At these *G. pyramidum* activity levels, the preference of *G. a. allenbyi* for the semi-stabilized habitat was always less than 0.5 (mean relative preference: 0.14).

We conducted a separate isodar analysis for *G. a. allenbyi* in the removal experiment where we had a wider range of *G. pyramidum* densities. We compared the activity density of *G. a. allenbyi* (AGa) in the semi-stabilized habitat with that in the stabilized habitat, and with AGp in both habitats. The isodar revealed inter-specific competition for habitat (AGaSM = 1.2990.612 × AGpST; $r^2 = 0.497$, $P = 0.0115$) as well as a preference for the semi-stabilized habitat (significant intercept: $P = 0.031$).

For the stabilized/shifting habitat combination, we also found a significant effect of *G. pyramidum* removal on *G. a. allenbyi*’s relative preference for the shifting habitat (Fig. 3B). In removal plots, *G. a. allenbyi*’s proportional use of the shifting habitat was significantly greater for the shifting [PREF(SH)] than for the stabilized [PREF(SM)] habitat, which was expected (Table 3).

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**Table 3.** Results of ANOVA of the activity of *G. a. allenbyi* (AGa), and comparison of the activity of the semi-stabilized and shifted habitat.

<table>
<thead>
<tr>
<th>Source</th>
<th>$F$</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Habitat (H)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>AGp</td>
<td></td>
<td></td>
</tr>
<tr>
<td>AGa</td>
<td></td>
<td></td>
</tr>
<tr>
<td>AGp × H</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Error</td>
<td>2</td>
<td></td>
</tr>
</tbody>
</table>

$R^2 = 0.782$

---

**Fig. 3.** The effect of removing *G. pyramidum* on the preference of *G. a. allenbyi* for the shifting [PREF(SH)] and stabilized [PREF(SM)] habitats. The shifting habitat was significantly greater for the shifting [PREF(SH)] than for the stabilized [PREF(SM)] habitat, which was expected (Table 3).
Field test of the CCO model

Table 3. Results of ANCOVA of the effect of the activity density of *G. pyramidum* (AGp), *G. a. allenbyi* (AGa), and combination of habitat types (Habitat) on the habitat preference (proportional use of the semi-stabilized and shifting sand habitats, arcsine transformed) of *G. a. allenbyi*

<table>
<thead>
<tr>
<th>Source</th>
<th>d.f.</th>
<th>SS</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Habitat (H)</td>
<td>1</td>
<td>0.208</td>
<td>0.208</td>
<td>26.235</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>AGp</td>
<td>1</td>
<td>0.063</td>
<td>0.063</td>
<td>7.933</td>
<td>0.009</td>
</tr>
<tr>
<td>AGa</td>
<td>1</td>
<td>0.041</td>
<td>0.041</td>
<td>5.192</td>
<td>0.031</td>
</tr>
<tr>
<td>AGp × H</td>
<td>1</td>
<td>0.000</td>
<td>0.000</td>
<td>0.041</td>
<td>0.842</td>
</tr>
<tr>
<td>Error</td>
<td>27</td>
<td>0.215</td>
<td>0.008</td>
<td></td>
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</tr>
<tr>
<td>$R^2$</td>
<td></td>
<td>0.782</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

![Diagram A](image)

$Y=0.534 - 0.71X$

$R=0.67, P=0.035$

![Diagram B](image)

$y = 0.1 - 0.29x$

$R=0.66, P=0.005$

**Fig. 3.** The effect of removal of *G. pyramidum* on the relative preference of *G. a. allenbyi* for the semi-stabilized [PREF(SM)] habitat in the semi-stabilized/stabilized (ST) habitat combination (A), and for the shifting [PREF(SH)] habitat in the shifting/stabilized habitat combination (B). ○, control; ■, experimental.

was significantly greater than that in the control plots (0.1 vs. 0.002). However, in both plot types, shifting habitat use was always less than 0.5, indicating a clear preference on the part of *G. a. allenbyi* for the stabilized compared with the shifting habitat. The
effect of *G. a. allenbyi*'s own density on this preference was not significant (*t* = 0.173, *P* = 0.865).

**DISCUSSION**

In this study, we conducted the first experimental field test of the validity of centrifugal community organization in an animal community. We tested four CCO predictions (Rosenzweig and Abramsky, 1986):

1. Species do best in the same habitat (the core habitat).
2. Each species does next best in different habitats (the two secondary habitats).
3. Both species use the core habitat regardless of their population densities.
4. As gerbil densities increase, species first extend their activity to their secondary habitat and then to their tertiary habitat.

Both species do best in the semi-stabilized habitat

*G. a. allenbyi*

*Gerbillus a. allenbyi*'s preference for the semi-stabilized habitat is hidden because in the presence of *G. pyramidum*, *G. a. allenbyi* is active mostly in the stabilized habitat. *Gerbillus a. allenbyi*'s true preference for the semi-stabilized habitat emerged only when we removed *G. pyramidum*. In these experimental plots, *G. a. allenbyi* increased its activity substantially in the semi-stabilized habitat when we reduced *G. pyramidum*'s activity (regression intercept = 0.534, suggesting a preference for the semi-stabilized habitat) (Fig. 3A). Actually, in the single case when *G. a. allenbyi* was completely alone, its preference for the semi-stabilized habitat was 0.61. The significant isodar intercept in the semi-stabilized habitat in the removal experiment further substantiates *G. a. allenbyi*'s hidden preference for that habitat.

*Gerbillus a. allenbyi* had a significantly lower giving-up density in the semi-stabilized habitat even in the presence of *G. pyramidum*, indicating again that this is its preferred habitat (Rosenzweig, 1991). But how can *G. a. allenbyi* gain access to seed patches in this habitat when the dominant *G. pyramidum* is present? The answer is that its greater foraging efficiency (lower giving-up density) allows it to use poor or depleted seed patches perceived as unprofitable and little used by the more wasteful but behaviourally dominant *G. pyramidum*. Indeed, Ziv et al. (1993) and Wasserberg et al. (2006) showed that this ‘dominance versus higher foraging efficiency’ trade-off underlies temporal partitioning of the daily activity times of these species. *Gerbillus pyramidum* is active during the early part of the night, gradually depleting the new and rich food patches recently replenished by the afternoon winds (Ben-Natan et al. 2004). Once patches become unprofitable, *G. pyramidum* abandons them, allowing *G. a. allenbyi* access (Kotler et al., 1993).

*G. pyramidum*

Throughout most of the study period, *G. pyramidum* was most abundant and most active (Fig. 1) in the semi-stabilized habitat, followed by the shifting and stabilized habitats. Also, despite some seasonal variations, on average its giving-up density is lowest in the semi-stabilized habitat (Fig. 2). These results, together with the isodar analysis, support our hypothesis that the presence of the core habitat. Abramsky et al. 1986).

The first prediction

*G. a. allenbyi*

Activity data (Fig. 1) reveal results in the shifting and the secondary shifting habitat from 0.560 to 0.400 in the core habitat. The reason it was not adapted (Kotler et al., 1991). The second and third predictions refer to the second and third habitat respectively. Prediction 2 is supported by its activity data. As seen in Fig. 1, *G. pyramidum* almost completely disappeared from the semi-stabilized habitat when at very high densities, while *G. a. allenbyi* was the dominant species in the stabilized habitat (Fig. 2). The interpretation of this result is consistent with its relative abundance, which makes this type of habitat disadvantageous in the removal experiment (Fig. 2).

Both species are efficient foragers

The CCO model predicts that species that extend their activities in the shifting and stabilized habitat (see text) reveal a hidden preference. Here, the two species are indeed density-dependent, and they select their third-choice habitat in competition with the core habitat. The third habitat was more efficient and selected mainly in periods when the other two habitats were in decline. These results are consistent with the interpretation of the isodar analysis, too.

The two other species

One of the predictions of niche theory is that competing species use the core habitat. However, the implicit assumption that the core habitat is the most efficient is not consistent with the observed results. As noted before, the core habitat is not the most efficient, and it is not the most important. Faced with dense populations, all the species reduced their densities. On the other hand, the density of the core habitat was not affected by the presence of the other species.
hypothesis that the primary habitat preference of *G. pyramidum* is the semi-stabilized habitat. Abramsky et al. (1990) and Brown et al. (1994b) reported similar findings.

The two species prefer different secondary habitats

*G. a. allenbyi*

Activity data (Fig. 1) and results from the removal experiment in the shifting/stabilized habitat combination (Fig. 3B) demonstrate that *G. a. allenbyi* prefers the stabilized to the shifting habitat. After *G. pyramidum* was removed, *G. a. allenbyi* increased its activity in the shifting habitat from 0 to at most 9%, showing that it spent 91% of its time in the stabilized habitat. The reason it preferred the stabilized habitat is most likely the relatively high predation risk characteristic of the shifting habitat, a risk to which *G. a. allenbyi* is poorly adapted (Kotler et al., 1991; Brown et al., 1994b).

*G. pyramidum*

The second and third habitat preferences of *G. pyramidum* are the shifting and stabilized habitat respectively. Preference for the shifting over the stabilized habitat by *G. pyramidum* is supported by its activity and partially by its giving-up density data. Throughout the study, *G. pyramidum* almost completely avoided the stabilized habitat even when *G. a. allenbyi* was present there only at relatively low densities. Also, *G. pyramidum* only used the stabilized habitat when at very high densities. Finally, when *G. pyramidum* did forage in trays in the stabilized habitat (August 1994), its giving-up density there was significantly higher than in the other two habitats. *Gerbillus pyramidum*’s aversion to the stabilized habitat is consistent with its relatively large body size and rapid movement mode, which could be disadvantageous in the more densely vegetated stabilized habitat.

Both species are density-dependent habitat selectors

The CCO model predicts that as the density of either species increases, both species should extend their activities into their second- and then their third-choice habitats. The isodar analysis (see text) reveals that with respect to their two most preferred habitat types, both species are indeed density-dependent habitat selectors (Morris, 1987). Scarcity of both species in their third-choice habitat precluded us from conducting a similar analysis for any of the other habitat combinations. Yet, the observation that the third-choice habitat was used mainly in periods when densities peaked suggests that density-dependent habitat selection occurred in this case, too.

The two species do not always both use the core habitat

One of the predictions of the CCO model is that at all density combinations, both competing species use the core habitat (Rosenzweig and Abramsky, 1986). This prediction is based on the implicit assumption of relatively symmetric exploitative competition. Interference competition is not considered. However, in our study system, interference competition is important. Faced with densities of the dominant species (*G. pyramidum*) of as low as one or two individuals per hectare, *G. a. allenbyi* shifts to using mostly its second-choice habitat. On the other hand, the dominant *G. pyramidum* always prefers the semi-stabilized habitat.
Thus the intense interference competition creates partial habitat segregation, with the dominant *G. pyramidum* excluding the subordinate *G. a. allenbyi* from the best time (the early night) (Wasserberg et al., 2006) and place (the semi-stabilized habitat). This was noted before both by Abramsky et al. (1990) and Ziv et al. (1993), although at a site with only two of the three habitats (semi-stabilized and stabilized) where the gerbils have a shared-preference community organization (Abramsky et al., 1990).

In summary, our results support three of the four predictions of centrifugal community organization: both species prefer the semi-stabilized habitat; both have a distinct second habitat preference; and both spill over into their less preferred habitats as densities increase. The discrepancy between one prediction of CCO and our results stems from the strong interference competition of *G. pyramidum*, which is able to exclude most *G. a. allenbyi* individuals from the semi-stabilized core habitat.

If, at all density combinations, both competing species use the core habitat, complete habitat separation is impossible and so, by definition, is the ‘ghost of competition past’. Thus, interference competition rescues the possibility of the ghost, in contrast to Rosenzweig and Abramsky’s (1986) prediction. It may well exist in the gerbil community of the Ashdod sand dunes. In recognition of this important difference, we suggest a new term, ‘asymmetric centrifugal community organization’, for this version of CCO. But even in asymmetric CCO, the unusual property of CCO remains intact: co-existence results not because of what the competing species do best, but because of what they do as a backup.

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Field test of the CCO model


