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

Gideon Wasserberg,^{1*} Burt P. Kotler,² Douglas W. Morris³
and Zvika Abramsky⁴

¹USGS Wisconsin Cooperative Wildlife Research Unit, Department of Wildlife Ecology, University of Wisconsin, Madison, WI, USA, ²Mitrani Department of Desert Ecology, Jacob Blaustein Institute for Desert Research, Ben-Gurion University of the Negev, Midreshet Ben-Gurion, Israel, ³Department of Biology, Lakehead University, Thunder Bay, Ontario, Canada and ⁴Department of Life Sciences, Ben-Gurion University of the Negev, Beer-Sheva, Israel

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.

* Address all correspondence to G. Wasserberg, Department of Wildlife Ecology, University of Wisconsin, 207 Russell Laboratory, 1630 Linden Drive, Madison, WI 53706, USA. e-mail: wasserberg@wisc.edu
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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 (Tsoar, 1990). The well-vegetated, semi-stabilized sand habitat on the dune crest and the wind-sheltered 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 troughs between the sand dunes (Danin 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 seeds 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 use (Kotler, 1985) as revealed by sand two plots of sand (sand-tracks of a perennial shrub (bush) habitat). Following a night on a 5-point scale to score rodent tracks the plot covered with tracks at station, we used the mean activity as a dependent variable for inter-

Seed trays

Following Brown (1988), we measured relative foraging efficiency for quality and foraging efficiency of foraging profit than one with giving-up density is the most resource patches that are not

Brown *et al.*, 1994a).

We measured giving-up density (aluminium trays). We filled each tray with sifted sand. We placed pairs of trays in each habitat, at the four central stations. These four seed tray pairs measured giving-up density for each microhabitat. After smoothing the surrounding sand at dusk and checked them at dawn for shape and the species-specific tracks overnight. Then we sifted the trays in the laboratory, cleaned them and measured giving-up densities.

To experimentally assess the habitat preferences, we conducted live-trapping on 6 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 gerbils' '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 microhabitat). 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 microhabitat, 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 neighbouring *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 ($AGa = 0.119 \times DGa + 0.072$; $r^2 = 0.756$, $P < 0.0001$), whereas for *G. pyramidum* the relationship approached an asymptote ($AGp = 0.194 \times DGp - 0.012 \times DGp^2 + 0.006$; $r^2 = 0.736$, $P < 0.0001$).

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 1. Results of four-way ANOVA for type and species on the

Source
Period (P)
Habitat (H)
Microhabitat (M)
Species (S)
S × H
S × M
S × P
S × H × P
S × M × P
S × M × H
Residual

habitat, followed by the shifting habitat, which was significantly more active in the shifting habitats, whereas *G. a. allenbyi* almost completely avoided the shifting habitat. In the highest, both species used the shifting habitat. Gerbil activity also differed between the three sand habitats. *G. a. allenbyi* were more active in the semi-stabilized (0.238 ± 0.029 respectively) and stabilized (*G. a. allenbyi*). Microhabitat use differed between the three sand habitats.

Each species was a density-dependent habitat selector. Its isodar ($AGpSM = 0.6 \times DGpSM + 0.072$) was significantly better than the shifting habitat ($AGaST = 1.258 \times AGaST + 0.072$) than 0 [CI($P = 0.05$) = 0.238 ± 0.029 respectively] (*G. a. allenbyi*). Microhabitat use differed between the three sand habitats.

Mean giving-up density was highest in the semi-stabilized (mean ± standard error: 0.786 ± 0.029) and stabilized habitats (0.786 ± 0.029) and was lowest in the semi-stabilized habitat. Mean giving-up density in the semi-stabilized habitats did not

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

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

habitat, 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 \pm 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 ($AGpSM = 0.6 \times AGpSH + 0.212$; $r^2 = 0.806$, $P < 0.0001$) 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 ($AGaST = 1.258 \times AGaSM + 0.237$; $r^2 = 0.377$, $P = 0.001$) 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 \pm 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

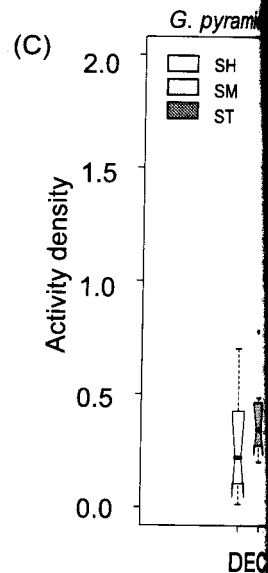
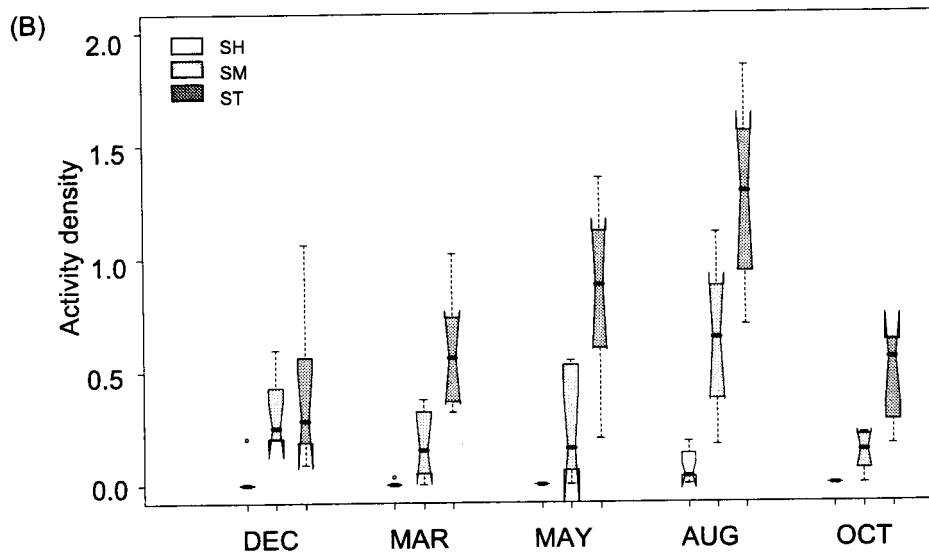
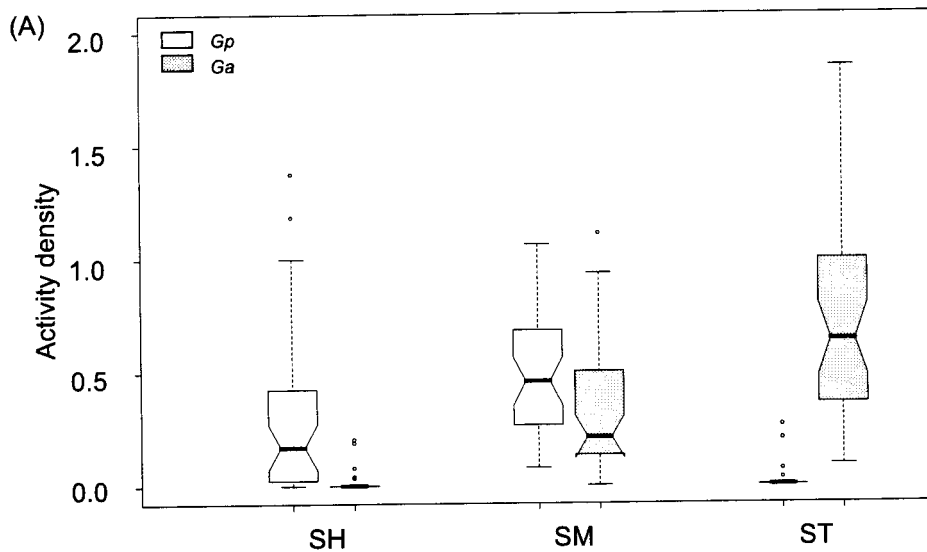


Fig. 1. Box-and-whiskers plots of activity between the three habitats. Each box has lines at the lower quartile and upper quartile, and whiskers extending from each end of the box to show the range of the data. Whiskers are outliers. Boxes which differ at the 5% significance level are indicated by different patterns.

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

Source	d.f.
Habitat (H)	2
Species (S)	1
H × S	2
Residual	540

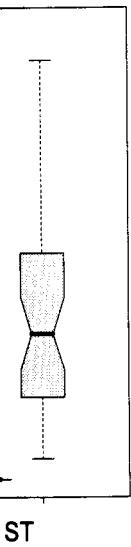
were used much less frequently than in the stabilized habitat (14 and 159 times respectively). Within the semi-stabilized habitat, *G. a. allenbyi* had a significantly lower giving-up density than *G. pyramidum* (Fig. 2).

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

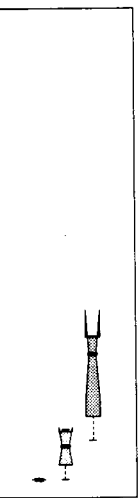
(0.76 g) was significantly higher than in the semi-stabilized and shifting habitats. *G. pyramidum*'s least preferred

The effect of *G. pyramidum*

In the semi-stabilized/stabilized habitats, the use of *G. pyramidum* to about one-third of the experimental grids of the shifting habitat was reduced to zero by *G. pyramidum* completely. The relative use of both the semi-stabilized and stabilized habitats



ST



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times respectively).
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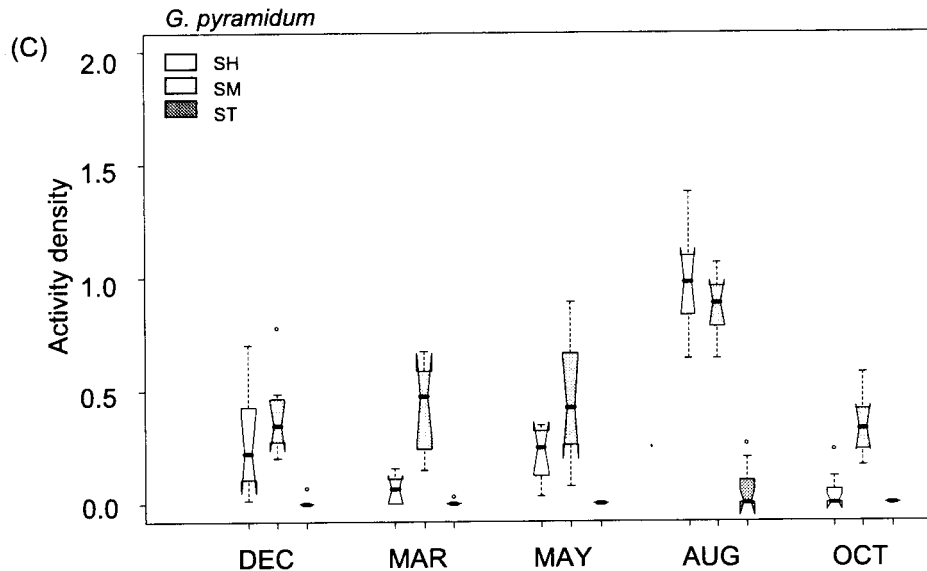


Fig. 1. Box-and-whiskers plots of the distribution of *G. a. allenbyi* (Ga) and *G. pyramidum* (Gp) activity between the three habitats (A), and for each species between the sampling periods (B, C). The box has lines at the lower quartile, median, and upper quartile values. The whiskers are lines extending 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 2. Results of two-way ANOVA of the effect of habitat type and species on log(giving-up density)

Source	d.f.	SS	MS	F	P
Habitat (H)	2	1.662	0.831	6.226	0.0021
Species (S)	1	0.268	0.268	2.009	0.1569
H × S	2	0.516	0.258	1.934	0.1455
Residual	540	72.069	0.133		

(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. pyramidum*'s least preferred habitat.

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

In the semi-stabilized/stabilized habitat combination, we reduced the activity of *G. pyramidum* 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. pyramidum* completely. The reduction of *G. pyramidum* density increased *G. a. allenbyi*'s relative use of both the semi-stabilized and shifting habitats (Table 3, Fig. 3), demonstrating

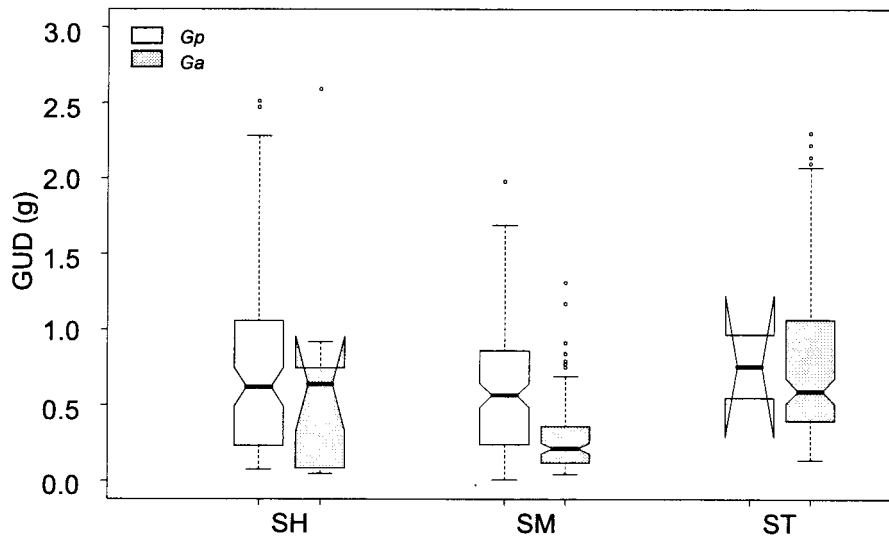


Fig. 2. Box-and-whiskers plots of the giving-up-density (GUD) distribution of *G. pyramidum* (Gp) and *G. a. allenbyi* (Ga) between the three habitats. The box has lines at the lower quartile, median, and upper quartile values. The whiskers are lines extending from each end of the box to show the extent 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.

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

Table 3. Results of ANOVA for *G. a. allenbyi* (AGa), and control plots (AGc) use of the semi-stabilized

Source	df	MS	F	P
Habitat (H)	2	0.11	0.16	0.85
AGp	1	0.11	0.16	0.85
AGa	1	0.14	0.20	0.63
AGp × H	2	0.12	0.17	0.83
Error	24	0.10		
$R^2 = 0.782$				

PREF(SM)

0.14

0.10

0.08

0.06

0.04

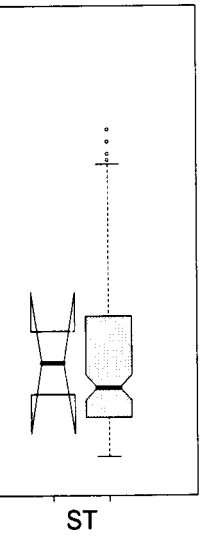
0.02

0

PREF(SH)

Fig. 3. The effect of removal of *G. pyramidum* on the relative preference of *G. a. allenbyi* for the shifting [PREF(SH)] and semi-stabilized [PREF(SM)] habitats. ■, experimental.

was significantly greater than in the control plots. In the removal plots, the part of *G. a. allenbyi*



ation of *G. pyramidum* (Gp) lower quartile, median, and the box to show the extent of boxes whose notches do not significance level. Habitats:

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3A) was much lower than combination, we conducted s, the activity density of nce of *G. a. allenbyi* for ent to two *G. pyramidum* e from a slight preference r the stabilized habitat. *G. pyramidum* activity had ivity levels, the preference s than 0.5 (mean relative

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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*

Source	d.f.	SS	MS	F	P
Habitat (H)	1	0.208	0.208	26.235	<0.0001
AGp	1	0.063	0.063	7.933	0.009
AGa	1	0.041	0.041	5.192	0.031
AGp × H	1	0.000	0.000	0.041	0.842
Error	27	0.215	0.008		

$R^2 = 0.782$

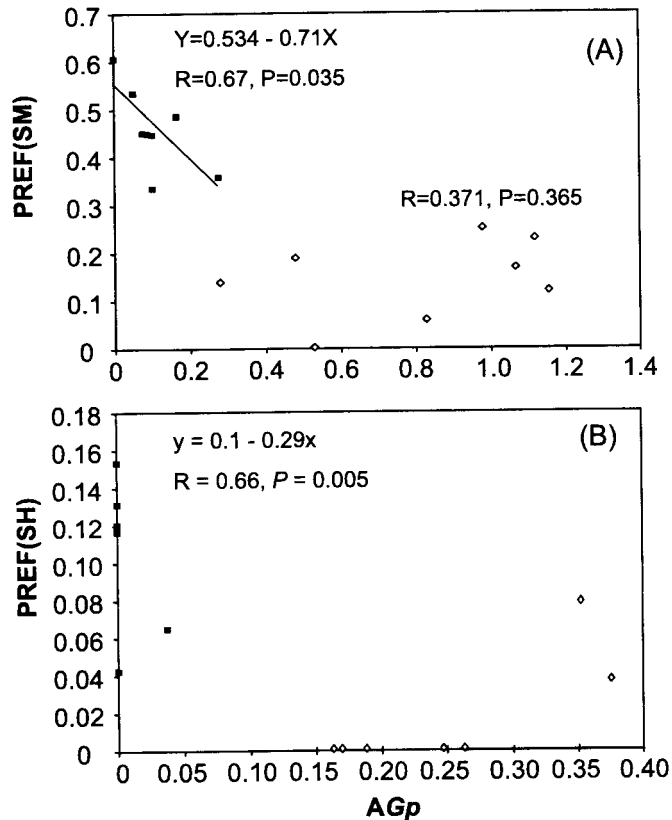


Fig. 3. The effect of removal of *G. pyramidum* on the relative preference of *G. a. allenbyi* for the semi-stabilized [PREF(SM)] habitat in the semi-stabilized/stabilized (ST) habitat combination (A), and for the shifting [PREF(SH)] habitat in the shifting/stabilized habitat combination (B). \diamond , control; \blacksquare , 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 preferred habitat. Abramsky *et al.*

The

G. a. allenbyi

Activity data (Fig. 1) show that *G. a. allenbyi* uses the semi-stabilized habitat combination (I) and the shifting habitat. After the shifting habitat from 0 to 100% of the habitat. The reason it uses the shifting habitat is its predation risk characteristics adapted (Kotler *et al.*, 1991):

G. pyramidum

The second and third habitats are the semi-stabilized habitat respectively. Preference for the semi-stabilized habitat is supported by its activity data. *G. pyramidum* almost completely avoids the semi-stabilized habitat present there only at very high densities. *G. pyramidum* uses the stabilized habitat (II) and the shifting habitat (I) more than in the other two habitats. This is consistent with its relative fitness being less disadvantageous in the semi-stabilized habitat.

Both

The CCO model predicts that both species will extend their activities in the semi-stabilized habitat. This analysis (see text) reveals that both species are indeed densitophobous in their third-choice habitats. *G. a. allenbyi* uses other habitat combinations mainly in periods when *G. pyramidum* is not present. This occurred in this case, too.

The two

One of the predictions of the CCO model is that competing species use the core habitat. This is the implicit assumption of the CCO model. If competition is not considered, the core habitat is important. Faced with density-dependent competition, two individuals per hectare are not enough. On the other hand, the density-dependent

hypothesis that the primary habitat preference of *G. pyramidum* is the semi-stabilized habitat. Abramsky *et al.* (1990) and Brown *et al.* (1994a) 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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