

## Seeds redistribution in sand dunes: a basis for coexistence of two rodent species

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Spatial and temporal heterogeneity is a major factor structuring communities and contributing to coexistence of the species they contain. In this study we examine a critical aspect of environmental heterogeneity that is assumed to promote coexistence in two gerbil species of the Western Negev Desert. Previous studies assumed that temporal partitioning, in activity time, is the result of daily redistribution of seeds that the dominant species is the first to utilize while the sub-ordinate and efficient species is being pushed to use the later and poorer part of the night. We tested the assumption that daily afternoon winds generating spatial and temporal heterogeneity in seed availability by the redistribution of sand and seeds. This was done by comparing plots experiencing normal wind condition with manipulated plots where wind action was diminished by a shade-cloth fence. Our results show that considerable amount of sand and seeds are redistributing regularly on a time scale of a single day. Our results also show that gerbil foraging behavior is strongly related to the pattern of the redistribution dynamics of the seeds. When we prevented redistribution of seeds, gerbil foraging activity was reduced considerably. However, both seed redistribution and gerbil activity did not change much on control plots. Furthermore, the two gerbil species responded differently to the reduction in seed redistribution. The larger *Gerbillus pyramidum* was shown to be more sensitive to the reduction than the smaller *G. a. allenbyi*. Daily variability in the availability of seed resources is probably the niche axis which, together with the trade-off in foraging efficiency of the species, forms the mechanism for the coexistence of the two gerbil species in the semi-stabilized sands.

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The temporal pattern and variance of resource renewal can influence foraging behaviors, population ecology, and interactions of the consumer species with other competitor species. At one extreme, resources may renew continuously as in a chemostat. As in Tilman's consumer-resource theory, species coexistence occurs when there are several resource types, and competitors vary in their foraging efficiency on each (Tilman 1980, 1982). At the other extreme, resources may renew as sharp pulses irregularly or on an annual basis (Armstrong and McGehee 1976, Brown 1989b). This creates

great temporal variability in resource availability, encouraging consumers to harvest resource when rich and to use dormancy, food caches, or high foraging efficiency to survive periods of paucity. Competitors can coexist on such pulses if there is a trade-off in foraging efficiency between garnering the resource when it is abundant versus when it is scarcer. Seed production in desert systems often conform to annual pulses and so such a mechanism may explain coexistence between some desert granivores. Intermediate between these two scales, resources may renew daily or as more frequent pulses. For

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example, nectar resources may renew during the night and reach peak abundances in the morning (Schaffer et al. 1979). At first glance such daily renewal seems less likely for seeds in deserts. However, in some desert systems, and particularly those with sand dunes, daily winds may redistribute sand and seeds, and regularly renew and create patches of seeds for desert granivores. Here, we are interested in whether such daily renewal does occur, and whether this renewal may provide the temporal variance in food availability necessary for the coexistence of two sand-dune inhabiting gerbil species.

The question of how similar species coexist on limited resources has received much attention in the last 20 years (Schoener 1986a). Coexistence can be investigated by using a mechanistic approach (Schoener 1986b, Brown 1989a). Typically, a mechanism of species coexistence requires two properties. The first is some sort of variability in the environment. This is often referred to as a niche axis or an axis of environmental heterogeneity. Examples might be food types that differ in size, microhabitats that differ in predatory risk, or even food densities that vary over time or space. The second is that individuals of different species must excel at exploiting different aspects of this environmental variance. That is to say, to coexist, species must differ in their abilities to exploit different parts of the niche axis. The trade-off may be evolutionary, but must result in each species having a part of the niche axis that it can exploit better than any of its potential competitors (reviewed by Schoener 1986b).

A mechanistic approach has been applied successfully in the study of heteromyid desert rodents (Brown 1973, 1989a, Rosenzweig 1973, Kotler 1984, Price and Waser 1985), fringillidae granivorous birds (Schluter and Grant 1984), and even herbaceous plants (Tilman 1982, 1986a,b). Desert rodents were found well suited for the study of coexistence (Kotler and Brown 1988). In Israel, extensive research has been conducted on coexisting species from the Gerbillidae family.

The two most common species of gerbils in the Negev Desert, *Gerbillus pyramidum* and *G. andersoni allenbyi*, coexist over a wide range of sandy habitats in the northwestern Negev Desert and along the Mediterranean coast (Abramsky et al. 1985). The two species are similar in their general ecology, with both consuming mostly seeds (Bar et al. 1984), living in burrows, and emerging at night to forage. They are known to compete strongly (Abramsky 1988, Abramsky and Pinshow 1989, Mitchell et al. 1990, Abramsky et al. 1991, 1994).

Kotler and co-workers (Kotler et al. 1993, Ziv et al. 1993, Brown et al. 1994) have hypothesized that the coexistence of these two species depends on temporal variability in resource abundance (Brown et al. 1994). The proposed axis of environmental heterogeneity is daily variability in the availability of seed resources. Kotler et al. (1993) have assumed that the strong daily

afternoon winds redistribute seeds and uncover concentrations of buried seeds previously deposited in wind shadows. The renewed and newly created seed patches are then depleted during the night by the foraging rodents.

The proposed trade-off is foraging efficiency (defined here as the ratio of harvest rates to foraging costs) at high (*G. pyramidum* more efficient than *G. a. allenbyi*) versus low (*G. a. allenbyi* more efficient than *G. pyramidum*) resource abundance (Kotler and Brown 1990).

Evidence for the trade-off is as follows. The larger body size of *G. pyramidum* (39 g versus 25 g) allows it to reach and to aggressively monopolize concentrations of seeds, giving it an advantage at high resource densities and forcing *G. a. allenbyi* to pay an additional cost due to interference (Ovadia 1999). The smaller body size of *G. a. allenbyi*, with especially low metabolic rate (Linder 1988), and overall lower energetic foraging costs confer greater foraging efficiency that result in lower giving-up densities (i.e. the resource density at which *G. a. allenbyi* leaves a depleted resource patch (Kotler et al. 1993, Brown et al. 1994). In addition, it was shown in laboratory experiments (Kotler and Brown 1990) and also in the field (Ovadia 1999, Ovadia et al. 2001), that food handling time of *G. pyramidum* was significantly shorter than that of *G. a. allenbyi*'s. This gives *G. pyramidum* an advantage when resource density is high and harvest rates are mostly limited by handling times. The advantage disappears at low seed densities when search contributes more to harvest rate.

The expected result from the above scenario is temporal partitioning, with *G. pyramidum* foraging earlier in the night than *G. a. allenbyi* (Kotler et al. 1993, Ziv et al. 1993). Manipulation experiments of Ziv et al. (1993) showed that the earlier part of the night is indeed the preferred foraging time for both species, probably due to high resource densities that are depleted during the night (Kotler et al. 1993). Ziv et al. (1993) concluded that the primary reason for the temporal partitioning is the aggressive behavior of the larger *G. pyramidum*. This aggressive behavior results in *G. pyramidum* excluding *G. a. allenbyi* from the preferred time of the night and from the best habitat (Abramsky et al. 1990, Ziv et al. 1993).

While the trade-off is well understood, only circumstantial evidence supports the assumption of daily renewal of seed resources that is crucial for the mechanism. Here, we test the hypothesis that spatial and temporal heterogeneity in seed abundance, caused by the daily afternoon winds, provides the axis of environmental heterogeneity necessary for the coexistence between the two gerbil species. We used two techniques: a) we quantified soil and seed flow to evaluate daily wind-dependent redistribution of resources in sandy habitats, and b) we estimated and compared gerbil

foraging efforts in natural and in manipulated areas where wind action is experimentally reduced.

Following the above stated hypothesis we generated these predictions:

- 1) soil and seed accumulation will decline as a result of experimental reduction in wind velocities.
- 2) Gerbils will show less activity on wind-sheltered places than on those same places prior to wind manipulation due to reduced seed accumulation.
- 3) Gerbils will show less activity on wind-sheltered places than on places exposed to normal wind conditions.
- 4) After wind manipulation is removed, the gerbil activity and soil accumulation will return to pre-manipulated levels.
- 5) There should be a positive correlation between soil accumulation, seed density, and gerbil level of activity.
- 6) *G. pyramidum* presence in the wind-sheltered places should be lower than that of the more efficient *G. a. allenbyi* because of the presumed lower resource density resulting from low rate of seed renewal.
- 7) Soil and seeds will accumulate in seed traps as a result of wind action.

## Methods

### Research area

The study was carried out in a semi-stabilized sandy habitat at Holot Mashabim Nature Reserve (31°01' N, 34°45' E) situated in the Halutza region, 35 km south of Beer-Sheva, Israel. The elevation at the site is 360 m, with average annual precipitation of 108 mm and dew forming on about 250 nights a year. Vegetation in this area is characterized by the community of *Retama retam* and *Artemisia monosperma* (Zohary 1982). Dunes in this stage of stabilization also show dead remnants of *Stipagrostis scoparia* (Danin 1978). The prevailing wind is mainly Northwesterly and blows in the mid and late afternoon (Fig. 2.14 in Pye and Tsoar 1990).

### Data collection

We conducted experiments in the spring (May), and summer (September) of 1998, in which we manipulated wind velocities and quantified the consequences on gerbil foraging activity and the movement of soil and seeds. We manipulated wind velocities by constructing wind barriers made of shade-cloth. During each experiment, we placed 12 stations in the semi-stabilized sand dunes. Experimental stations consisted of four 80 × 80

cm sub-plots aligned according to the main wind direction (Fig. 1). The sub-plots were marked by a small stone at each corner, and were otherwise undistinguished from their surroundings. In each sub-plot we placed a soil trap, buried with its top flush with ground level. These soil traps were constructed of two plastic containers: a smaller 500 ml cup (opening area of about 70 cm<sup>2</sup>) tightly fitted within a larger container and covered by a hardware mesh (1 cm pore size). In this way, traps could be extracted and repositioned without disturbing the soil surface, and rodents could not access the accumulated sample within.

In the manipulation stage of the experiment, 4 m long plastic nets (shade cloth of 40% porosity) were placed in a semi-circular configuration between the second and third sub-plots (as shown in Fig. 1). The nets, reaching from ground level to the height of 1 m, provided a barrier that reduced wind velocities and impact, while minimizing local turbulence which could complicate sand and seed dynamics. The nets have the additional advantages in being inexpensive, easy to handle, and having limited effect both in time and in space (below).

We estimated gerbil foraging efforts and soil accumulation for a period of 15 days: five days prior to manipulation (installing fences), five days during manipulation, and an additional five days after the removal of the wind brake. At dawn each day, we scored the density of tracks that each gerbil species left during that night by distinguishing newly laid tracks from those of previous nights. At the same time, we weighed and removed the content of the soil traps. Density of tracks was scored as an index ranging from 0 (no tracks) to 4 (100% coverage of the census sub-plots), as has been done in other studies with these gerbils (Abramsky et al. 1990, Kotler et al. 1993, Ziv et al. 1993, Brown et al. 1994). At the end of each experiment, soil traps were left in the field to accumulate sand and seeds for an additional 48 hours without shade cloth fences.

The samples taken at the end of the experiments (accumulation over 48 hours), were placed in paper bags and taken to the laboratory for germinating in the greenhouse. The germination process took place in flower pots with water added ad lib. Each sample was placed in as many pots as it took to make sure the layer originating from the field did not exceed 2 cm in depth. In each pot, seedlings were counted and identified. This procedure allowed us to assign minimum quantities and relative qualities to wind-dependent redistribution of soil and seed in time and space.

### Data reduction

Repeated measured ANOVAs were used for the analysis of both soil accumulations and gerbil activity using the SuperANOVA statistical package (Abacus Concepts Inc.

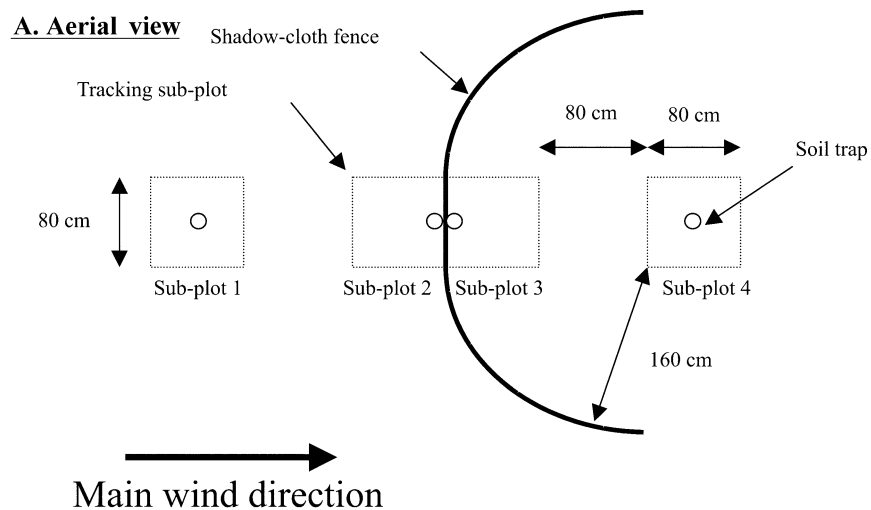
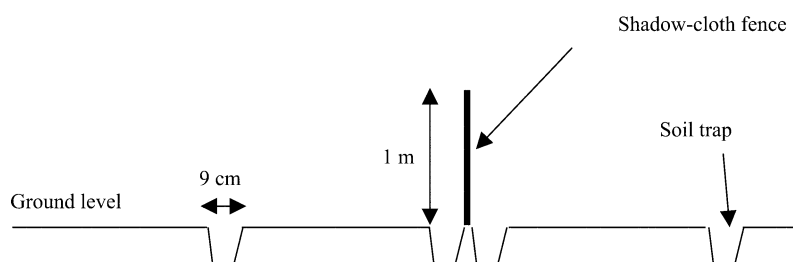


Fig. 1. Experimental set-up; four sub-plots aligned according to the main wind direction (generally from the north-west). In each sub-plot, a soil trap is placed with its tip flush with ground level. The station is divided into two by a porous fence configured in a semicircle. (A) aerial view, (B). cross-section view.

**B. Cross-section view**



1989). Three within-subject effects were considered: sub-plot (relative position within the station;  $df = 3$ ), day (in the period of treatment;  $df = 4$ ) and treatment (pre-fence, fence, and post-fence;  $df = 2$ ), with stations being the replicates. Planned comparisons were generated according to prediction specified, namely comparison among sub-plots in the same treatment and comparison among treatments within each sub-plot. In all of our analyses, we have considered the possibility of inflated F-statistic values, and in our report we refer to the probabilities of the adjusted F-statistic according to Huynh and Feldt (Abacus Concepts Inc. 1989, von Ende 2001). The main factor responses (and their interactions) are presented in ANOVA tables while the specific planned comparisons appear in appendix tables A, B and C. All planned comparisons have  $df = 1$ , and full descriptions of the results are detailed in the text.

Since the activity of gerbils can vary greatly across days, we standardized the results to allow comparisons. Thus, we analyzed the proportion of nightly activity on each sub-plot out of the sum of activity in the whole station (the set of four sub-plots in that location). Data shown are after arcsin transformation.

In contrast, the comparison between the individual species was made by considering the actual specific

nightly activity. In comparing the activity of the two species, the comparison is between species activity at the same places, the same time, and under the exact same conditions. For species comparisons, within species standardization is not justified.

The soil accumulation comparisons were also made without standardization, considering the actual accumulation of soil mass (sand and organic matter) in the traps. Factors determining the accumulation were both at scales large enough to allow comparison between experiments, and at a scale small enough to generate meaningful variations within experiments and within stations (see Discussion).

**Results**

**The effect of the wind on short-term redistribution of soil and seeds**

We found a positive significant relationship between wind velocity and sand accumulation during the two studied seasons (Fig. 2,  $df = 25$ ,  $P < 0.001$ ,  $r^2 = 0.5$ ). For both periods, we found similar significant regressions. Figure 2 shows two things: first, there is a threshold wind speed under which no soil accumulates in the traps (the

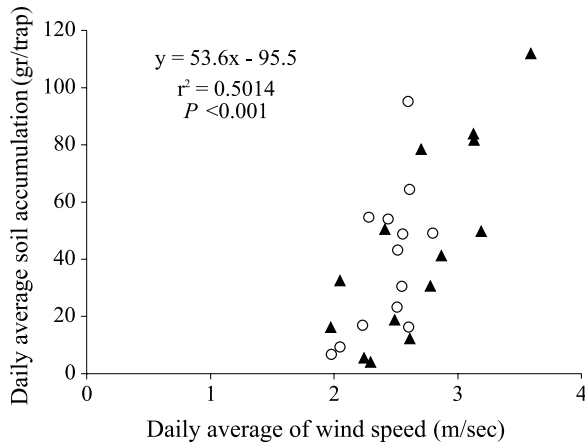


Fig. 2. Mean soil accumulation in the traps, as a function of mean daily wind velocities pooled over the two months (May black triangles, and September open circles). The positive relationship that has been found between the wind velocities and soil accumulation mass was the same for both months. The importance of these findings is in the quantification of heterogeneity in semi-stabilized sandy habitats.

zero value of accumulation in the regression is at wind velocity higher than zero); second, there is daily variation in soil redistribution. Nevertheless, on average, considerable amount of soil is redistributed on a daily basis.

In the germination experiment a positive relationship was found between the amount of soil accumulating in the soil traps and the amount of seeds germinating from that sample (seedlings =  $2 + 0.01 \times \text{soil mass}$ ;  $df = 58$ ,  $P < 0.001$   $r^2 = 0.25$ ).

### Accumulation in soil traps

Soil accumulation was used as an estimator for particle movements within the experimental unit (station) at the time of the experiment. Pooling all the experimental stations (replications) together, there are two types of comparisons to discuss: a) comparison among the four different sub-plot positions during the same treatment (i.e. variation in space), and b) comparison among the effects of different treatments on the same sub-plot

position (i.e. variation in time due to treatments effects). The statistical analysis show that soil accumulation on different sub-plots varied among treatments (significant treatment  $\times$  plots interaction). This is true for both May and September (Table 1) experiments. Here we shall discuss results of each month separately, beginning with the spatial comparison and following with the temporal comparison. Within each comparison we shall refer to variation among the appropriate sub-plots (among the same positions in the different treatments, or among different positions in the same treatments), actual significance of comparisons can be found in the appendix.

In the May experiment (Fig. 3a; Appendix Table A), no differences were found among any of the sub-plots in the pre-fence treatment (circles), with the exception of sub-plot 1. The same is true for both the fence (squares) and the post-fence (triangles) treatments. The accumulation during the pre-fence treatment was higher in all sub-plots than the other two treatments, but it shares the same pattern of sub-plot hierarchy (the ranking of the sub-plots according to their levels of soil accumulation, resulting from the micro environmental conditions), with the post-fence treatment, while both differ from the fence treatment in this respect.

The accumulation in sub-plots 1 + 3 in the presence of the fence (fence treatment) did not change after the removal of the fence (post-fence treatment). Sub-plots 2 and 4 however, show a marked decrease in accumulations during the fence treatment.

In the September experiment (Fig. 3b; Appendix Table A), no difference was found between any of the sub-plots of the pre-fence treatment. The same holds true for the post-fence treatment as well, with the exception of sub-plot 1. Also the accumulation in the sub-plots did not differ between those two treatments, (note that those are the treatments before the fences were introduced and after they were removed). In contrast, we see that in the presence of the fences (fence treatment), the hierarchy of the sub-plots changed. Only sub-plot 4 was different from sub-plot 1. The accumulation in sub-plot 1 in the presence of the fence does not differ from accumulation achieved after the fence was removed, though higher levels were recorded before the fence was installed. The

Table 1. Results of repeated-measures ANOVA of soil accumulation in May and September. P-values shown are after Huynh and Feldt correction for inflation of F-statistic values.

Source	df	May		September	
		F-value	P-value	F-value	P-value
Treatment	2	13.358	0.001	23.913	0.001
Days	4	4.572	0.025	29.650	0.001
Sub-plots	3	1.112	0.355	0.378	0.694
Treatment $\times$ days	8	2.382	0.077	23.423	0.001
Treatment $\times$ sub-plots	6	3.504	0.041	2.948	0.035
Days $\times$ sub-plots	12	1.093	0.368	0.895	0.440
Treatment $\times$ days $\times$ sub-plots	24	1.214	0.313	1.285	0.295

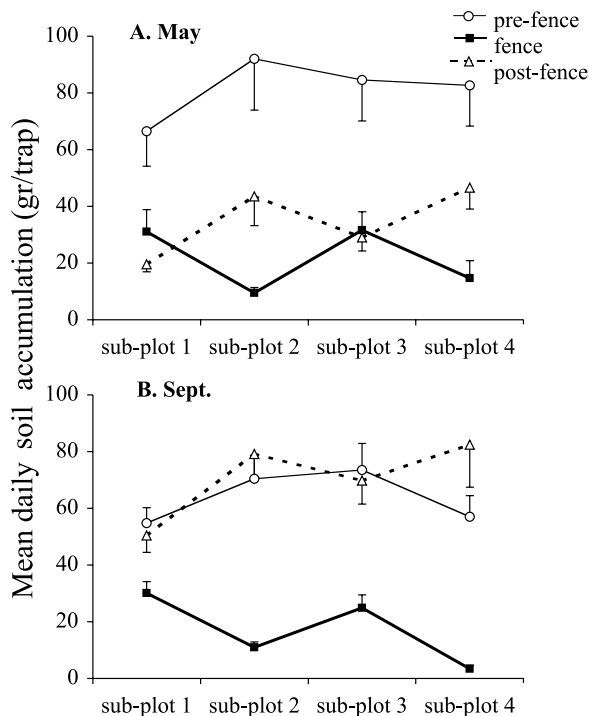


Fig. 3. Soil accumulation in soil traps (with standart error bars) during the three different treatments (pre-fence, fence and post-fence) in May (A) and September (B) in the four subplots (1–4). The general pattern from both months is that accumulation after the fence was removed, was similar to accumulation before its placement, while both patterns differ from the pattern of accumulation in its presence. Also, the effect of the fence on subplot 1 is small and it could be viewed as a control, and that subplot 4, that exhibits the highest effect of the fence, decline significantly in the fence presence. Thus, the effect of the shadow cloth disappears immediately after its removal and when present influences mainly subplot 4. Significance levels of comparisons among and across treatments appear in Appendix Table A.

sub-plot adjacent to the fence on the windward side (sub-plot 2) shows a dramatic decrease in accumulation levels from the other treatments, and to a lesser extent so does the adjacent sub-plot on the leeward side (sub-plot 3). The most significant observation is that the distant sheltered sub-plot (sub-plot 4) has the lowest levels of accumulation among treatments (indeed in the whole experiment).

Table 2. Results of repeated-measures ANOVA of gerbil activity in May and September. P-values shown are after Huynh and Feldt correction for inflation of F-statistic values.

Source	df	May		September	
		F-value	P-value	F-value	P-value
Treatment	2	3.260	0.062	0.130	0.084
Days	4	1.490	0.235	0.200	0.938
Sub-plots	3	1.710	0.185	1.780	0.186
Treatment × days	8	2.690	0.036	0.570	0.800
Treatment × sub-plots	6	3.560	0.004	8.370	0.001
Days × sub-plots	12	1.670	0.094	1.580	0.159
Treatment × days × sub-plots	24	0.770	0.722	1.140	0.341

In summary we emphasize two points: a) treatments with the fences absent (pre-fence and post-fence) show similarity, but differ from the fence treatment. b) The distant sub-plot on the windward side (sub-plot 1) showed the least changes in accumulation due to manipulation, while the distant sub-plot on the leeward (sub-plot 4) showed the greatest changes.

### Gerbil response to the fencing

The statistical analysis shows that gerbil activity on the different sub-plots changed among treatments (significance of the treatment × plots interaction). This is true for both the May (Table 2) and September experiments. In the pre-fence treatment, gerbil activity was similar on all four sub-plots during both seasons (Fig. 4a, b; Appendix Table B). Similar results were obtained for the post-fence treatment in May (Fig. 4a; Appendix Table B), but not in September (Fig. 4b; Appendix Table B). During the fence treatment, in both periods, the activity of the gerbils on the sheltered sub-plots was significantly lower than on the non-sheltered sub-plots. Also, in both periods, the highest activity of the gerbils during the fence treatment was on sub-plot 2 adjacent to the fence on the windward side (Fig. 4a, b; Appendix Table B). The difference between that sub-plot and all other sub-plots is significant.

As in the case of the soil accumulation, gerbil preferences reverted to their original (prior to manipulation) hierarchy after the removal of the fences. This is obvious in the case of the spring experiment, but less so in the case of the summer experiment. In the September experiment, the post-fence treatment, although being different from the fence treatment, does not resemble the pre-fence treatment.

### Species responses to the manipulation

Forging activity of both species was similar in all sub-plot except sub-plot 4 which is the sheltered sub-plot farthest from the fence (Fig. 5; Appendix Table C). On this sub-plot, the activity of *G. pyramidum* was lower than that of *G. a. allenbyi* (one-way planned comparison

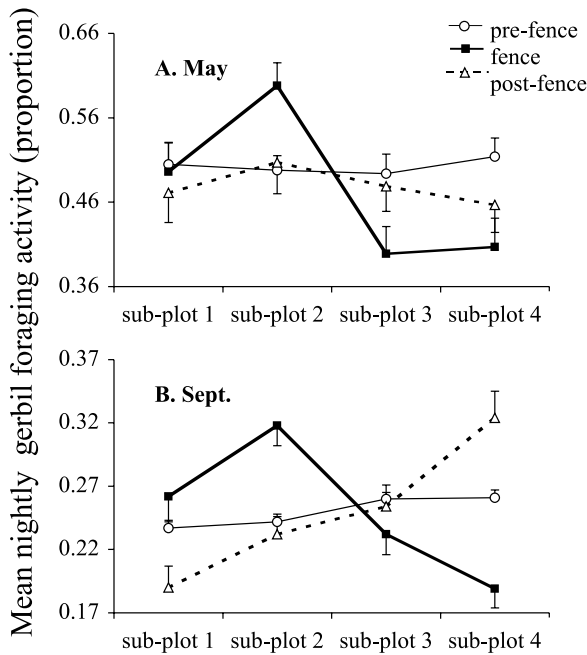


Fig. 4. Proportions (arcsin transformed) of gerbil foraging activity (with standard error bars) during the three different treatments (pre-fence, fence and post-fence) in May (A) and September (B) in the four sub-plots (1-4). In general it can be said that gerbils had increased their activity in the windward side of the fence, while reducing activity on the leeward side. Furthermore, gerbil activity showed no preference of any certain sub-plot before the manipulation, and reverting to this condition after the manipulation stopped (in the case of the May experiment). Also, that sub-plot 1 could be viewed as a control, since its values do not change as a function of the three treatments. Sub-plot 4 declines significantly in the presence of the fence. Significance levels of comparisons among and across treatments appear in Appendix Table B.

of repeated measure ANOVA:  $df = 1$ ,  $F = 2.97$ ,  $P < 0.05$ ). For both species, the highest activity was recorded in sub-plot 2 (the closest sub-plot to the fence on the windward side), and the lowest in the sheltered sub-plots.

## Discussion

Our results show that there is a significant redistribution of the habitat substrate on a very short time scale, a time scale of a single day (Fig. 2). More importantly, we have evidence linking seed resource redistribution to substrate movement (the germination experiment). From this, we can state that redistribution of seed resources in the sandy habitat of the northwestern Negev occurs on a short-time scale.

Further support for this contention comes from the reaction of the system to the manipulation in the time frame of five days (Fig. 3a, b). It is vitally important to note that the system resumes its original configuration after the fence removal. This strongly suggests that the

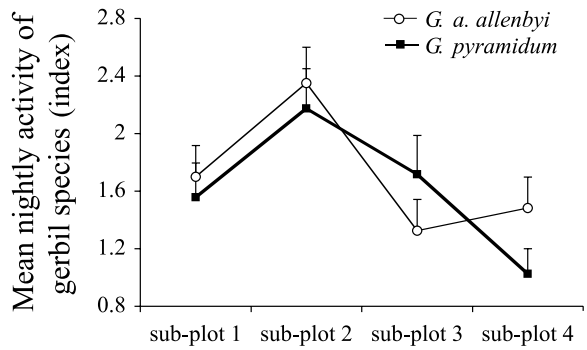


Fig. 5. Mean gerbil nightly activity (with standard error bars) for the two species, *G. pyramidum* and *G. a. allenbyi*, during the manipulation period in the May experiment. The results show that the activity of *G. pyramidum* was significantly lower only in the leeward side of the fence than that of *G. a. allenbyi* (one-way planned comparison of repeated measure ANOVA:  $df = 1$ ,  $F = 2.97$ ,  $P = 0.05$ ). Significance levels of comparisons among and across treatments appear in Appendix Table C.

changes we observe in soil accumulation following fence installation was not by chance (changing back when the fence was removed). This also shows that the changes caused by the fence treatment was local both in time and in space, showing no lasting effects.

The general effect of a fence on redistribution of sand is well known: wind breakers of this sort stabilize and trap fields of sand when positioned correctly (Kerr and Nigra 1952). The wind velocities in the vicinity of such fences are reduced, and some of the air is pushed back, resulting in wind flow circumventing the fence rather than breaking before it. This reduces considerably the formation of turbulent areas in the vicinity of the wind breaker. The fence effect on wind velocities is known also at a small spatial scale down to centimeters adjacent to the fence (Seginer 1975).

In this study we wanted to reduce wind velocities with minimum disturbance to the area under investigation. Therefore we chose to use shade cloth. Indeed, sub-plot 1 is a reasonable control in being relatively unaffected by manipulation. However, the effect of the fence on redistribution of substrate and resources in sub-plot 4 was significant, resulting in reduced sand movement (Fig. 3a, b). The intriguing pattern of accumulation in sub-plots 2 and 3 is the result of sand grains meeting the fence with some force and falling just after it (sub-plot 3). Indeed we have observed in the field the building of miniature sand dunes leeward of our fences with crests (the location of the particle deposition) immediately (less than a cm) after the fence.

The next step in our research was studying the response of the gerbil species to this short time-scale variation in resources. We show that gerbil foraging efforts reflect the pattern of resource variation. In sub-plots where fence effect was minimal (sub-plot 1), gerbil foraging effort was similar with and without the fences (Fig. 4a, b). At the same time, in sub-plots where the

fence effect was greatest (sub-plot 4), gerbil foraging efforts changed the most.

The dramatic increase of gerbil activity near the fence on the windward side (sub-plot 2) serve as further evidence for gerbil awareness to the resource variation. We suggest that our porous fences act the same as a fisherman's net, snaring seeds from the air flux, depositing them at the base of the fence. This strip of high level of seed availability serves as an attractant for the gerbils (Fig. 4a, b).

Again we would like to emphasize the response of the gerbils, one way to the fence installation and the opposite way to their removal, all in the time frame of just five days. In particular, the gerbils reduced their activity in the time and place where wind action was lowered, and increased their activity to known normal levels when wind action reverted to normal conditions. This means that gerbils assess and respond to the environmental variability caused by the fences in a small scale both in time (between treatments) and space (within treatments), with little evidence for any time lags.

Finally, the differential response of the gerbils to our experimental manipulation of wind support our suggested mechanism for coexistence of the two gerbil species. *G. a. allenbyi*, is the more efficient of the two gerbil species (Kotler et al. 1993, Ovadia 1999, Ovadia et al. 2001), and it was this species that showed a higher level of activity in the sheltered sub-plots (sub-plot 4, Fig. 5) than did *G. pyramidum*. This is consistent with *G. a. allenbyi* being a more efficient forager and being able to forage profitably in time and places where resources are too low for its competitor (Kotler et al. 1993, Ziv et al. 1993).

An optimal forager should keep on sampling the environment each night repeatedly (Abrahams 1986). This may explain why the two gerbil species continued visiting the wind reduced areas during the experiment. This activity level of the gerbils (both species) could be considered as the minimal investment an animal has to pay for the possibility of encountering renewed seed resources in a changing environment.

The redistribution of sand on a time scale of a single day as an outcome of afternoon winds is apparent (Fig. 2). Reduced soil movement (as in behind a wind-breaker) result in lower seed replenishment and subsequently lower gerbil activity. This result suggests that redistribution of seeds resources in the sandy habitat of the northwestern Negev occurs on a short-time scale, with the gerbils responding to the redistribution. This supports the hypothesis of daily seed renewal in the sandy habitats of the Negev Desert. Furthermore, the two gerbil species respond differently to the observed reduction in seed renewal. Taken as a whole, daily variability in the availability of seed resources (variable niche axis), together with the known aggressive behavior of *G. pyramidum* (Ovadia 1999) and greater *G. a. allenbyi*

foraging efficiency at low resource densities (Kotler and Brown 1990, Ovadia 1999) results in temporal partitioning of gerbil foraging efforts (trade-off in foraging abilities, Ziv et al. 1993), and forms the mechanism for the coexistence of the two gerbil species in the semi-stabilized sands.

The literature on coexistence mechanisms is abundant in examples of species coexisting along spatial and temporal environmental heterogeneity (Armstrong and McGehee 1976, Brown et al. 1979, Chesson and Warner 1981, Chesson 1985, Kotler and Brown 1988, Brown 1989a, Mares 1993, Vincent et al. 1996). Daily variance in resources is very common in natural ecosystems, and at least theoretically should be a suitable axis of environmental heterogeneity along which species can coexist. Yet there are few examples in the literature of very short term temporal mechanisms. The exception to this is the day/night cycle. This daily variance is well known as part of coexistence mechanisms. An example is provided by *Acomys cahirinus* and *A. russatus* in the Judaeen Desert of Israel (Jones et al. 2001). Our work shows that daily wind is another factor that generates the heterogeneity necessary to allow species coexistence. The daily wind action is a common feature of many ecosystems such as deserts and sea coasts. Consequently, many more examples of daily coexistence mechanism likely await discovery. In light of our own experience, we predict that rodent communities found on sand substrate in places like the Namib, Great Basin, and Sonoran Deserts will show similar patterns of species response to environmental heterogeneity caused by daily wind. Furthermore, we believe that intertidal ecosystems with daily wave action and variance caused by the tide should yield several examples of species coexistence on this spatio-temporal scale. Indeed we feel that the common features of a flowing substrate and a daily resource redistribution make these two ecosystems, which at first glance appear as dissimilar as can be, to represent parallel cases for some of their community structure mechanisms.

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**Appendix Table A**

Significance levels of planned comparisons of the repeated-measures ANOVA (presented in Table 1) of the sand accumulation during the two seasons: May (A) and September (B). Comparisons were made among treatments (pre-fence, fence, post-fence) and among sub-plots (1–4).

Treatment	sub-plot	Pre-fence				Fence				Post-fence			
		1	2	3	4	1	2	3	4	1	2	3	4
A. Prefence	1	–	–	–	–	–	–	–	–	–	–	–	–
	2	*	–	–	–	–	–	–	–	–	–	–	–
	3	ns	ns	–	–	–	–	–	–	–	–	–	–
	4	ns	ns	ns	–	–	–	–	–	–	–	–	–
A. Fence	1	**	–	–	–	–	–	–	–	–	–	–	–
	2	–	***	–	–	ns	–	–	–	–	–	–	–
	3	–	–	***	–	ns	ns	–	–	–	–	–	–
	4	–	–	–	***	*	ns	ns	–	–	–	–	–
A. Postfence	1	***	–	–	–	ns	–	–	–	–	–	–	–
	2	–	***	–	–	–	**	–	–	*	–	–	–
	3	–	–	***	–	–	–	ns	–	ns	ns	–	–
	4	–	–	–	**	–	–	–	**	*	ns	ns	–
B. Prefence	1	–	–	–	–	–	–	–	–	–	–	–	–
	2	ns	–	–	–	–	–	–	–	–	–	–	–
	3	ns	ns	–	–	–	–	–	–	–	–	–	–
	4	ns	ns	ns	–	–	–	–	–	–	–	–	–
B. Fence	1	ns	–	–	–	–	–	–	–	–	–	–	–
	2	–	***	–	–	ns	–	–	–	–	–	–	–
	3	–	–	***	–	ns	ns	–	–	–	–	–	–
	4	–	–	–	***	*	ns	ns	–	–	–	–	–
B. Postfence	1	ns	–	–	–	ns	–	–	–	–	–	–	–
	2	–	ns	–	–	–	***	–	–	*	–	–	–
	3	–	–	ns	–	–	–	**	–	ns	ns	–	–
	4	–	–	–	ns	–	–	–	***	*	ns	ns	–

**Appendix Table B**

Significance levels of planned comparisons of the repeated-measures ANOVA (presented in Table 2) of the gerbil activity during the two seasons: May (A) and September (B). Comparisons were made among treatments (pre-fence, fence, post-fence) and among sub-plots (1–4).

Treatment	sub-plot	Pre-fence				Fence				Post-fence			
		1	2	3	4	1	2	3	4	1	2	3	4
A. Prefence	1	–	–	–	–	–	–	–	–	–	–	–	–
	2	ns	–	–	–	–	–	–	–	–	–	–	–
	3	ns	ns	–	–	–	–	–	–	–	–	–	–
	4	ns	ns	ns	–	–	–	–	–	–	–	–	–
A. Fence	1	ns	–	–	–	–	–	–	–	–	–	–	–
	2	–	*	–	–	**	–	–	–	–	–	–	–
	3	–	–	*	–	**	***	–	–	–	–	–	–
	4	–	–	–	***	**	***	ns	–	–	–	–	–

Appendix (Continued)

Treatment	sub-plot	Pre-fence				Fence				Post-fence			
		1	2	3	4	1	2	3	4	1	2	3	4
A. Postfence	1	ns	-	-	-	ns	-	-	-	-	-	-	-
	2	-	ns	-	-	-	*	-	-	ns	-	-	-
	3	-	-	ns	-	-	-	*	-	ns	ns	-	-
	4	-	-	-	ns	-	-	-	ns	ns	ns	ns	-
B. Prefence	1	-	-	-	-	-	-	-	-	-	-	-	-
	2	ns	-	-	-	-	-	-	-	-	-	-	-
	3	ns	ns	-	-	-	-	-	-	-	-	-	-
	4	ns	ns	ns	-	-	-	-	-	-	-	-	-
B. Fence	1	ns	-	-	-	-	-	-	-	-	-	-	-
	2	-	**	-	-	*	-	-	-	-	-	-	-
	3	-	-	ns	-	ns	***	-	-	-	-	-	-
	4	-	-	-	*	***	***	ns	-	-	-	-	-
B. Postfence	1	Ns	-	-	-	*	-	-	-	-	-	-	-
	2	-	ns	-	-	-	***	-	-	ns	-	-	-
	3	-	-	ns	-	-	-	ns	-	*	ns	-	-
	4	-	-	-	*	-	-	-	***	***	***	*	-

Appendix Table C

Significance levels of planned comparisons of the repeated-measures ANOVA of the nightly activity of the two species, *G. pyramidum* and *G. a. allenbyi*, during the manipulation period in the May experiment. Comparisons were made among sub-plots (1–4).

Treatment	sub-plot	<i>G. a. allenbyi</i>				<i>G. pyramidum</i>			
		1	2	3	4	1	2	3	4
<i>G. a. allenbyi</i>	1	-	-	-	-	-	-	-	-
	2	*	-	-	-	-	-	-	-
	3	ns	***	-	-	-	-	-	-
	4	ns	***	ns	-	-	-	-	-
<i>G. pyramidum</i>	1	ns	-	-	-	-	-	-	-
	2	-	ns	-	-	*	-	-	-
	3	-	-	ns	-	ns	ns	-	-
	4	-	-	-	*	*	***	**	-