

## Influence of cover on the foraging behavior of Negev Desert gerbils

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### Abstract

We studied the influence of cover types on the foraging behavior of two coexisting gerbils (*Gerbillus pyramidum* and *Gerbillus andersoni allenbyi*) by experimentally manipulating cover patches in an otherwise natural setting in the sandy habitats of Negev Desert, Israel. Two types of cover manipulation were carried out, “low” (10cm high) and “high” (30cm high), and these were compared to natural, thinly vegetated cover (the control). We used artificial food patches (seed trays) to record the foraging behavior of the gerbils. The gerbils showed significantly lower GUDs (giving up density: the amount of seeds remaining in a food patch following a forager’s visit) in artificial resource patches (seed trays) located in the low cover patches as compared to high cover and control patch types. This result indicates lower cost of foraging in low cover stations due to reduced predation risk. In addition, in low cover stations, the dominant species *G. pyramidum* had significantly lower GUDs compared to *G. a. allenbyi*, indicating higher foraging efficiency. In high cover stations, the gerbils had their highest GUDs, even more than control treatment, suggesting less preference for habitats where cover merely acts as an obstruction for predator detection instead of providing safety. Cover manipulation also had a significant effect on habitat quality. The numbers of gerbil burrows were significantly greater in low cover stations than the other two types, suggesting a preference for habitats in which high quality refuges (from foxes) are abundant. In addition, the gerbils showed significant differences in GUDs across moon phases in different cover types. Fox activity was significantly higher in control as compared to high and low cover stations. This was in accordance to the gerbil’s greater apprehension there as indicated by higher selectivity for “full” resources patches when compared to more-difficult-to-exploit “bottom” patches along different periods of night.

**Keywords:** Vegetation types, giving up density, moon phases

## Zusammenfassung

Untersucht wurde der Einfluss unterschiedlicher Vegetationsbedeckungs-Typen auf das Sammelverhalten zweier co-existierender Rennmausarten (*Gerbillus pyramidum* und *G. andersoni allenbyi*) durch die experimentelle Manipulation der Vegetationsdecke in einem ansonsten natürlichen Habitat in der Negev Wüste (Israel). Es wurden zwei Arten der Manipulation der Vegetation durchgeführt: „niedrig“ (10 cm Höhe) und „hoch“ (30 cm Höhe). Diese Versuchsflächen wurden mit natürlich dichtbewachsenen Kontrollflächen verglichen. Es wurden künstliche Samenfallen verwendet, um die Sammelaktivität der Rennmäuse dokumentieren zu können. Die beiden Rennmausarten zeigten eine signifikant niedrigere GUD (giving up density: die Anzahl von in der Samenfalle verbliebenen Samen nach Aufsuchen durch die Rennmäuse) an künstlichen Sammelplätzen in der Manipulationsvariante „niedrig“ im Vergleich zur Manipulationsvariante „hoch“ und den Kontrollflächen. Dieses Ergebnis weist auf einen niedrigeren Sammelaufwand in Bereichen mit niedriger Vegetation aufgrund einer geringeren Bedrohung durch natürliche Feinde hin. Zusätzlich zeigte die dominante Art *G. pyramidum* bei niedriger Vegetationshöhe im Vergleich zu *G. a. allenbyi* eine signifikant niedrigere GUD. Dies ist als eine effektivere Sammelaktivität von *G. pyramidum* zu werten. In höherwüchsiger Vegetation wiesen beide Rennmausarten die höchste GUD auf, die sogar höher lag als im Bereich der Kontrollflächen. Dies weist auf eine geringere Bevorzugung von Habitaten, in der die Vegetation kaum als Hindernis für das Erkennen von Räubern wirkt, aber Schutzfunktion besitzt, hin. Die Manipulation der Vegetationsdecke hat einen erheblichen Einfluss auf die Habitatqualität. Die Anzahl von Bauten war signifikant höher in Bereichen mit niedriger Vegetation als in den beiden Vergleichs-Vegetationstypen. Dies legt eine Bevorzugung von Habitaten, in denen hochwertige Schutzbereiche häufig sind, nahe. Daneben zeigten die Rennmäuse signifikante Unterschiede im Hinblick auf die GUD in aufgrund der Mondphasen in den unterschiedlichen Vegetationstypen. Die Aktivität des Fuchses als einem der Hauptfeinde der Rennmäuse, war im Bereich der natürlichen Kontrollflächen signifikant höher als in niedriger bzw. höherer Vegetation. Dies ist in Übereinstimmung mit einer dort erkennbaren höheren Fluchtbereitschaft der Rennmäuse, die auch durch eine während der Nacht zu beobachtenden Bevorzugung von reichhaltigen Nahrungsplätzen erkennbar wird, zu sehen.

**Schlüsselbegriffe:** Vegetationstypen, giving up density, Mondphasen

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## Introduction

Cover is an essential part of all habitats, and lack of this feature can limit an animal's space use and its movement across

the landscape. The availability of cover helps moderate predation risk by providing individuals with refuges and safe opportunities for foraging. For example, many

small mammals prefer foraging close to vegetation (Brown et al. 1988, Kotler et al. 1988, Kotler et al. 1991, Abramsky et al. 1996). Animals change their allocation of time and their levels of vigilance behavior under varying amounts of cover. Small mammals and birds may spend considerable amount of their time being vigilant when foraging in open and away from shrub or tree cover (Barnard 1980, Leger et al. 1983, Cassini 1991, Otter 1994, Tchabovsky et al. 2001). Rodents make decisions about where to forage based on the quality and quantity of vegetative cover and moonlight conditions (Kotler et al. 1991). However, cover can affect prey animal in two opposing ways. It can provide safety from physical forces (wind, rain etc.) and biotic agents (predator attacks); on the other hand, it can also affect their predator-detection ability by obstructing sight lines and vision (Lazarus & Symonds 1992). Cover offers different kinds of foraging opportunities to different species, changing the cost-benefit decision of when to flee (Fernández-Juricic et al. 2002).

The desert ecosystem, because of sparse plant cover (4-10%) generates many open areas. These open areas pose high predation risk for smaller mammals and reptiles from their avian, reptilian, and mammalian predators. This predation risk has been known strongly to influence animal activity (e.g., Brown 1988, Hughes & Ward 1993, Vásquez 1994) and foraging behavior (Kotler 1984, Brown 1988). The availability of cover (e.g. shrubs) in the desert

landscape plays a vital role in providing some degree of safety to the prey species, as well as influencing the availability of food (seed trapping due to wind shadow) (Parmenter & MacMahon 1983, Hughes & Ward 1993, Brown et al. 1994).

The importance of cover on the foraging behavior of desert gerbils was studied in the sandy habitats of the Negev desert in southern Israel. The study animal consisted of two granivorous rodent species, *Gerbillus andersoni allenbyi* (Allenby's gerbil), and *G. pyramidum*, (greater Egyptian sand gerbil) which coexist in the semi-stabilized sand dunes (Abramsky et al. 1985, Kotler et al. 1993). The two species are very similar except in their body size (Zahavi & Wharman 1957, Abramsky et al. 1985). *G. pyramidum*, is the bigger and dominant species. It forages early at night, exploits richer patches, and excludes the *G. a. allenbyi* by interference competition, forcing the latter to forage late at night at poor resource patches (Kotler et al. 1993). The smaller *G. a. allenbyi* on the other hand is more efficient forager, and thereby benefits from patches already abandoned by *G. pyramidum* (Kotler & Brown 1990, Ziv et al. 1993). These gerbils alter their foraging behavior in response to increased predatory risk from owls, and snakes (Kotler et al. 1991, Brown et al. 1994). Predation risks from owls forces both the species to forage less and avoid the open microhabitat (Abramsky et al. 1996, Kotler et al. 1991, 1992), while in the presence of snakes they shift their activity to the open microhabitat (Kotler et al. 1992, 1993).

However, in presence of foxes, the two-gerbil species reduce their foraging activity, but there is no difference in foraging under bush and open microhabitats (Ovadia 1999). Compared to open habitats, both the gerbil species prefer the bush microhabitat habitat where they are the most efficient foragers.

In this sandy habitat of the Negev desert, two types of shrub structures are common. The ground hugging shrubs with dense and thick thorns that possibly influences (reducing) prey capture by hindering predators, by increasing their risk of injury (see Brown & Kotler 2004), and thus reducing risk of predation. The second types of shrubs are of thinly vegetated type, providing only shade and concealment to rodents, but do not deter predators. Thus, there possibly is a differential risk of predation with relation to shrub cover type in this habitat. Few studies have addressed the influence of such cover types on foraging behavior of small mammals in desert environment. Therefore, here we investigated the influence of two cover types which differ in their properties of providing safety and concealment, on foraging behavior of two coexisting rodents in the Negev desert. We experimentally manipulated the availability of cover types in the sandy habitats, thus manipulating the predator lethality towards the rodents. In addition, through artificial food patches, we used foraging behavior to interpret their risk of predation.

## Material and Methods

We performed the experiment at Beer Asluj in the Holot Mashabim Nature Reserve (31°01'N, 34°45'E), northwestern Negev Desert, Israel, during the summer of 2004 (July through September). The site is composed of stabilized sand dunes, semi-stabilized sand dunes, rocky slopes, and loess plains. This area receives an average of approximately 110mm rainfall per year, mainly restricted to winter months (December–March). The dominant perennial plant species are *Artemisia monosperma* and *Retama raetam* (Abramsky et al. 1985). Rodent species in the sandy habitat include *G. a. allenbyi* (Allenby's gerbil, 25g), *G. pyramidum* (greater Egyptian sand gerbil, 40g), *Meriones sacramenti* (Buxton's jird, 120g; rare), and *Jaculus jaculus* (common jerboa, 50–70g). All of these species are nocturnal, burrow dwelling, and mostly granivorous (Bar et al. 1984). The predatory species include red foxes (*Vulpes vulpes*), barn owls (*Tyto alba*) and desert diadema snakes (*Spalerosophis diadema*). The experiment was carried out on two 2.56 ha grids. Each grid contained 81 stations arranged in 9 x 9 arrays with 20 meters between stations. Both grids covered a mosaic of sandy habitats. In these two grids, the rodents were censused for three nights at the beginning and at the end of experiment by setting Sherman live traps baited with millet seeds at each station of the grids. Captured individuals of *G. a. allenbyi* and *G. pyramidum* were toe clipped (species-specific marks) for identification in the sand tracking strips.

The 9 x 9-grid layout was further divided into two sub-grids (4 x 4 layouts) and on each sub-grid; we had four seed tray stations, each separated by an alternate row and column (40m between stations). We manipulated cover to gerbils by adding artificial coverings made up of black polygal plastic sheets, approximately 1m x 1m dimension. These artificial covers were held horizontally above the ground by steel reinforcing bar (rebar) stakes at selected stations on the sub-grids. We used two levels of cover for the experiment i.e. “low” and “high”. The control stations had no artificial covers and consisted of thinly vegetated shrubs. For the high cover, polygal sheets were suspended above the ground at heights of 30cm. This allowed both foxes and gerbils to move under them. This cover type provided concealment for the gerbils (by the shadows that they cast), but not shelter. For the low cover, the polygal sheets were suspended 10cm above the ground, thereby allowing only gerbils to move underneath. This type of cover provided both concealment and refuge for the gerbils. At each cover type station, 40 polygal sheets were added to the natural habitat (i.e. 160 in each grid). We distributed the covers at each station within a 5 meters radius ( $\sim 78\text{m}^2$  area) of a centrally located natural bush. We also counted the number of burrows (identified by presence of gerbil tracks) before and at the end of the experiment in each circular plot to quantify any changes in habitat use following added cover. The black polygal sheets were perforated with numerous

holes to reduce any unnatural build up of temperature or humidity that may affect the behavior of gerbils or reptilian predators. In total, we established four patches of each cover type in the two grids. We used plastic seed trays (38cm x 28cm x 10cm) as artificial resource patches. Each contained 3g of millet seed mixed into 3 L of sieved sand taken from the vicinity of the stations. We used these trays to assess giving up densities (GUDs; Brown 1988) for rodents. These trays are representative of the natural foraging conditions that are experienced by gerbils, and provide for diminishing returns, i.e., declining harvest rates with time spent in the tray (Kotler & Brown 1990); they do not provide “free lunches” (Brown 1988). In addition, gerbils employ a quitting harvest rate rule when exploiting these resource patches (Garb et al. 1999). Pairs of seed trays were placed in each microhabitat at each station, one pair in the open and one pair in the bush. Of each pair, one was a “full” tray and other a “bottom” tray. In the full tray, the millet seed was mixed evenly with 3 L of sand and spread throughout the tray; in the bottom tray, the millet was mixed with half the quantity of sand (1.5 L), spread along the bottom of the tray, and then covered with the remaining sand on top. Selectivity by gerbils for the full trays provides us with the measurement of level of apprehension faced by the gerbils (Kotler et al. 2002) in different cover levels. We used Manly’s index for selectivity on depletable resources to calculate selectivity for the full tray (Chesson 1983, Schmidt &

$$\{Ln (\text{proportion of seeds remaining in Full tray})\}$$

$$\{Ln (\text{proportion of seeds remaining in bottom tray}) + Ln (\text{proportion of seeds remaining in Full tray})\}$$

Brown 1996, Kotler et al. 2002): This provided a measure of apprehension, an indicator of the amount of attention a forager redirects from foraging tasks to predator detection, with higher selectivity reflecting higher apprehension (Kotler et al. 2002). GUD data were log – transformed for normality for the analysis, but presented in original values in the figures for better clarity.

In addition, at the stations with added cover i.e. high and low cover stations; we placed two additional “assay” trays each containing approximately 3gm of seed mixed evenly with 3 litres of sand. We placed one directly under a polygal cover (“under tray”) and the other in open besides it. We then measured the giving up densities (GUDs) for these trays. This allowed us to assess the efficacy of the polygal sheets as covers.

We used sand tracking to aid in measuring the activities of foxes, snakes, and gerbils in the experimental plots in two different ways. First, for each seed tray, we smoothed an area of approximately 30cm in width surrounding the tray using a household squeegee. This allowed us to identify the gerbil species that visited or foraged in the tray. Second, two sand tracking transects of 180 meter length and 45cm width were laid between the rows of seed tray stations (along the three cover types) on each full grid to quantify the activities of gerbils, foxes, and snakes on

the grids. These transects included both open and bush microhabitats. Along each transect, we permanently marked a short 2m segment in the open microhabitat and another along the margin of a nearby shrub every 20m. We recorded fox and snake activities along the entire length of each transect, and gerbil activity in each of the short tracking segments. We also set out a third transect on the last row of each grid, used exclusively to record fox tracks. We checked transects for tracks three times per night (23.30 hrs, 02.30 hrs and 05.30 hrs). The activity of foxes and snakes were quantified based on the number of spoor crossings from one side of the plot to the other. The experiment was carried out in different moon phases (new, waxing, full and waning) as light intensity plays an important role in influencing the activity patterns of gerbils with relation to predators and also in the ability of predators to detect and capture the prey (Kotler et al. 1991).

## Results

### *Effect of polygal sheet as covers: giving up densities in “Assay” seed trays*

We start by presenting the results from amount of seeds left in “assay” seed trays, which allowed us to assess the efficacy of polygal sheet (cover) in the added cover areas. Gerbil GUDs indicate different amounts of foraging activity in the different cover types. It also reflects their for-

aging efficiencies and costs, i.e. lower GUDs indicate lower costs and higher activity.

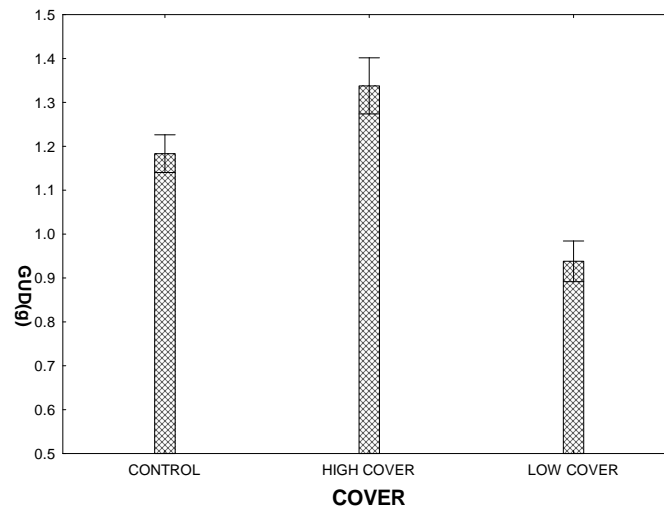
GUDs were significantly lower in assay trays in low cover than in the high cover stations (ANOVA,  $F_{1, 372} = 193.86$ ,  $p < 0.001$ , Means; Low cover = 1.25g (0.043 SE), High cover = 2.1g (0.039 SE)). Comparing GUDs from trays kept directly under the polygal covers with those from nearby trays in the open helped to determine the perceived risk of predation in the area directly under and between the artificial cover types. In low cover stations, GUDs differed significantly between the “under” and open trays, with gerbils reducing the “under” trays to lower seed densities (ANOVA,  $F_{1, 201} = 6.8698$ ,  $p = 0.009$ , Means; under trays = 1.15g (0.057 SE), open trays = 1.35g (0.048 SE)). This reflects the greater level of safety in the areas directly under cover. Interestingly, however, in high cover stations, the GUDs did not differ significantly between under and open assay trays (ANOVA,  $F_{1, 204} = 2.6113$ ,  $p = 0.107$ , Means; under = 2.15 g (0.059 SE), open = 2.01g (0.055 SE)). In fact, the GUDs for assay trays kept directly under cover were nominally higher than in open. Results stated above clearly reflect that artificial polygal sheets had indeed acted as covers for the gerbil species in the sandy habitat, as desired in our experimental set up.

### *Effect of cover on rodent burrow site selection*

A comparison of censuses of burrows prior to and at the end of the experiment suggested an effect of cover on rodent patch selection. The numbers of gerbil burrows were significantly greater (ANOVA,  $F_{2,9} = 85.333$ ,  $p = 0.001$ , Means: high = 0.8, low = 3.8, control = 0.7) at low cover stations than at the other station types, suggesting a preference for patches in which high quality refuges from foxes are abundant. This preference for high quality refuge by the rodents is further corroborated by the fact that most of the gerbils captured in census trapping following the experiment (13, or 68%) were trapped in low cover stations (or very nearby).

### *The effect of different cover types on giving up densities: seed trays in station*

We come now to our main experimental results, for seed trays not placed under the covers. We found that giving up densities of seed trays at the stations differed significantly among cover types (ANOVA,  $F_{2, 810} = 56.26$ ,  $p < 0.001$ , Fig. 1), with GUDs being lowest in low cover compared to control and high cover stations. Thus, low cover provided low cost of foraging in terms of reduced predation risks. The gerbils show highest GUDs in high cover stations, even higher than the control stations, suggesting high foraging costs (planned comparison of LS means,  $F_{1, 810} = 18.01$ ,  $p < 0.001$ ) These differences in foraging activity in high cover stations suggest that the obstructive cost of cover outweighs the protective component here.



**Fig. 1:** Mean giving up densities (GUDs, for untransformed data) for trays foraged by gerbils in three cover types. Vertical bars denote 0.95 CI.

### *Effect of Moonlight*

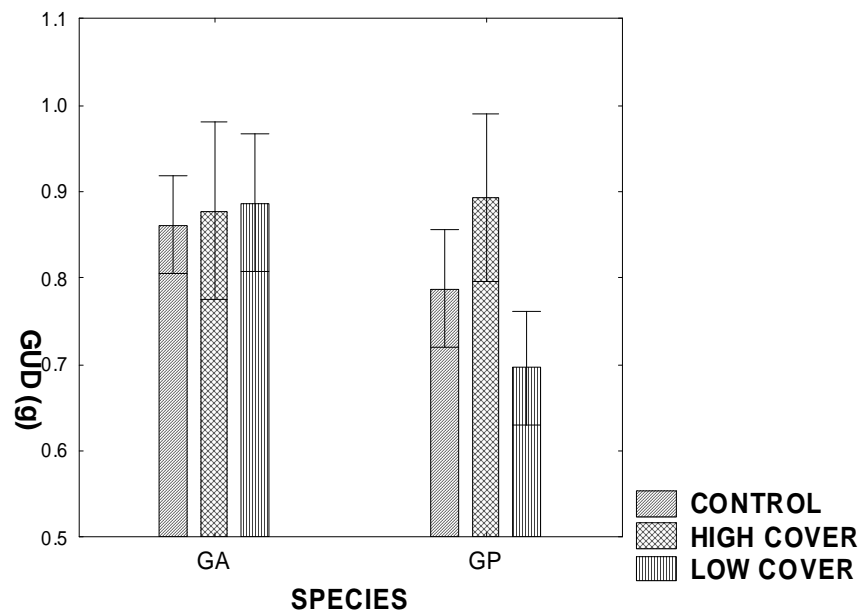
Moon phase affected GUDs in stations with different cover types, with lower GUDs on nights with waxing moon and new moon and higher GUDs at full moon and waning moon (ANOVA,  $F_{3, 810} = 28.683$ ,  $p < 0.001$ ). There were also significant interactions of moon phase and cover type on GUDs (ANOVA,  $F_{6, 810} = 3.197$ ,  $p = 0.004$ ). The GUDs in low cover stations were the lowest in all the moon phases, reflecting the lower risk of predation for gerbils in the area. High cover stations always showed higher GUDs in all the moon phases.

### *Species differences in giving up densities*

The gerbil species differed in their GUDs in different cover types (ANOVA,  $F_{2, 810} = 3.125$ ,  $p = 0.045$ , Fig. 2). Also, there was significant interaction effect between cover type and species (ANOVA,  $F_{2, 810} = 3.195$ ,  $p = 0.041$ ). The bigger, *G. pyramidum* seemed to be more responsive to cover types than the *G. a. allenbyi* (see Fig. 2).

At both low cover and control stations, trays foraged by *G. pyramidum* had significantly lower GUDs than those foraged by *G. a. allenbyi* (ANOVA, planned comparison of LS means, for low cover;  $F_{1, 810} = 12.741$ ,  $p < 0.001$ ; for control,  $F_{1, 810} = 4.138$ ,  $p = 0.042$ ). No significant differences in GUDs of *G. pyramidum* and *G. a. allenbyi* were observed in high cover stations ( $p = 0.740$ ). The total number of seed trays foraged by gerbils differed in different cover types (Chi square = 37.47,  $df = 2$ ,  $p < 0.001$ ) although this difference is clearly brought by the visitation number in low cover types (*G. pyramidum*, 213 trays vs. *G. a. allenbyi*, 119 trays). In control and high cover station, visits by *G. a. allenbyi* versus *G. pyramidum* slightly differed but otherwise were not statistically significant.





**Fig 2:** Mean giving up densities (for untransformed data) of trays foraged by *Gerbillus andersoni allenbyi* (GA) and *G. pyramidum* (GP) in three cover types. Vertical bars denote 0.95 CI.

#### *Selectivity for the full tray: gauging apprehension of gerbils*

There were significant effects of moon phase (ANOVA,  $F_{3, 696} = 6.443$ ,  $p < 0.001$ ) and cover type ( $F_{2, 696} = 51.827$ ,  $p < 0.001$ ) on selectivity. There was also a significant interaction of cover type and moon phase ( $F_{6, 696} = 2.127$ ,  $p = 0.048$ , fig. 3). Gerbils selectivity at control and high cover stations show significant effect of moon phase (ANOVA, for control:  $F_{3, 358} = 2.9956$ ,  $p = 0.030$ ; for high cover:  $F_{3, 171} = 5.410$ ,  $p < 0.001$ ). These changes in selectivity reflect the changes in the gerbils' apprehension level in unsafe patches, due to cover and varying light conditions. However, the selectivity in low cover stations reveals no significant effect of moon phases ( $p = 0.109$ ). There were no significant interactions between time of night and moon phases on selectivity of rodents, although control station show a

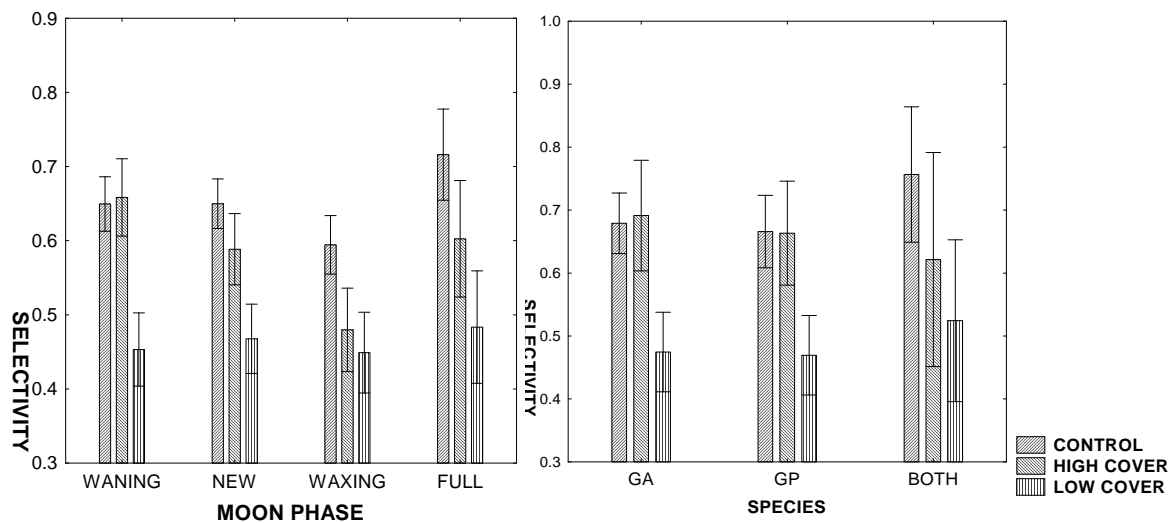
significant differences in selectivity with relation to time of the night (ANOVA, planned comparisons of LS means:  $F_{1, 696} = 3.939$ ,  $p = 0.004$ ). In control stations, selectivity is low in first part of night (19.30 to 22.30 hrs), grows to its maximum level in second part of night (23.00 to 2.00 hrs), and then again declines at the end (2.30 to 5.30 hrs). This may reflect changes in predator lethality due to changes in encounter rates with predators in different periods of night (see predator activity results below). The non-significant differences in selectivity over time of night in low cover patches suggests that gerbils perceived risk of predation is uniform throughout the night in these patches. The species-specific comparison of selectivity for full trays showed no significant difference among different cover stations. However for *G. a. allenbyi* and *G. pyramidum* together, there was

significant difference in selectivity in control and high cover station versus the low cover station (ANOVA, planned comparisons of LS means,  $F_{1, 187} = 31.932$ ,  $p < 0.001$ ).

In trays where both species had foraged, selectivity differed only between control and low cover stations (planned comparisons of LS means,  $F_{1, 187} = 7.466$ ,  $p =$

#### *Predator activity in different cover types*

Overall there was significant difference in fox activity among different cover types (ANOVA,  $F_{2, 75} = 3.779$ ,  $p = 0.027$ , Fig. 5), with maximum activity taking place in control station and the least in low cover stations. Fox visits were significantly different between low and control cover stations (planned comparison,  $F_{1, 75} =$

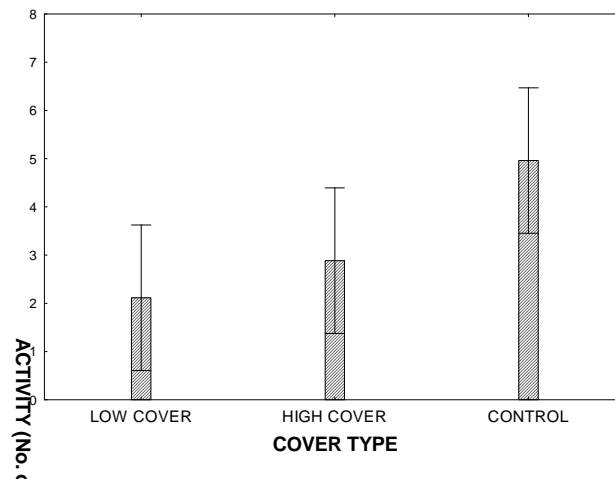


**Fig 3** (left): Mean selectivity for the full tray (a measure of apprehension) for the gerbils according to moon phases and cover type. Vertical bars denote 0.95 CI.

**Fig 4** (right): Mean selectivity for the full tray (a measure of apprehension) for *Gerbillus andersoni allenbyi* (GA) and *G. pyramidum* (GP) and both combined according to cover type. Vertical bars denote 0.95 CI.

0.006, Fig. 4), but did not differ for high cover versus control or low cover stations. The selectivity for the full tray was always high in control and high cover and the lowest in low cover stations for *G. a. allenbyi* only, *G. pyramidum* only, and both. This likely reflects that both species vary their levels of apprehension similarly across the different cover types.

7.062,  $p = 0.009$ ). Comparisons of control versus high cover station reveal a marginally significant difference in fox activity (planned comparison,  $F_{1, 75} = 3.760$ ,  $p = 0.056$ ). There was no significant difference in fox visits to low versus high cover patches ( $F_{1, 75} = 0.51$ ,  $p = 0.47$ ).



**Fig 5.** Mean fox activity (no of crossings) per night for different cover types. Vertical bars denote 0.95 CI.

The fox activity in different times of night differed significantly across the in three cover types (ANOVA,  $F_{2,152} = 3.195$ ,  $p = 0.044$ ). As previously noted, this result is in accordance with the selectivity results for both control and cover stations where the gerbil's selectivity for full tray goes up (apprehension increases) with relation to increase in fox activity. In control patches, fox activity is low (i.e. selectivity is low for gerbils) during the early part of the night, then increases in the second part (highest selectivity), before again decreasing in late night (low selectivity). The low cover station does not show any significant difference in activity across different times of night. The relationship between predator activity and selectivity in high cover stations is not clear. Unexpectedly, snake activity in different cover stations did not differ significantly ( $p = 0.078$ ).

## Discussion

The significant differences in GUDs between various cover types reveal the level of anti-predator responses by gerbils in

their foraging activity in different cover types. Giving up densities and selectivity results suggests that the low cover (10cm) is the safest habitat for the gerbils. Lower GUDs (compared to control) in low cover patches reveal that gerbils are less apprehensive in safe microhabitats, and hence devote more time there in harvesting seeds. In low cover, the presence of significantly larger numbers of burrows lends further support to this notion. The burrows in the low cover microhabitat allow easy transport of harvested seeds, and a suitable environment for consumption and storage. Low cover patches may also be sites for strong interference competition for both the gerbil species. *G. pyramidum* was a more efficient forager there, having lower GUDs, and greater numbers of visits (twice), compared to *G. a. allenbyi*. This is in contrast to previous results in natural unmanipulated conditions, where *G. a. allenbyi* was usually a better exploiter of the resources within all sandy habitats and microhabitats (Rosenzweig 1987) and thus allowing their coexistence (Brown et al.

1994). The strong tendency of *G. pyramidum* to forage under low cover could force *G. a. allenbyi* to feed more in the open, and thus face higher predation risk. This may cause changes in energetic state and affect the population dynamics of *G. a. allenbyi* in the habitat. Previous study by Abramsky & Pinshow (1989) reveal that the effect of *G. pyramidum* on the per capita activity of *G. a. allenbyi* is much stronger than vice versa. Therefore, it can be concluded that in low cover stations higher activity of *G. pyramidum* (i.e. number of visits) could result in more pronounced effect on *G. a. allenbyi*, and may lead to their expulsion from these patches. The lesser activity of foxes in low cover stations in comparison to control stations can also substantially increase intra-specific competition in these patches.

Organisms perceive cover differently depending on their escape strategy (Lima & Valone 1986). While some perceive it as safe, others see it as a risky habitat. Higher GUDs in the high cover stations (provides only concealment) suggests a strongly obstructive role of this cover type. High cover may have offered concealment for gerbils, but it also reduced the ability of the gerbils to detect (or see) predators. Consequently, gerbils showed lower foraging efficiency and higher level of apprehension in these habitats. In high covers patches, the gerbils apparently compensated for reduced visibility due to obstruction (therefore higher risk of mortality) by being more apprehensive (higher selectivity), devoting less time to those areas, and

quitting resource patches there at higher GUDs and higher quitting harvest rates. This signifies a threat from overhead avian predators such as Barn owls (*Tyto alba*), apart from foxes. Another possible explanation of difference in foraging behavior of gerbils in high and low cover may be attributed to the cover quality (see Bartholomew 2002) i.e. width of cover versus width of gerbils. In our experiment, the cover quality may have declined as we increase the height because it allows more lateral visibility for both avian and terrestrial predators.

Predators should choose to allocate time to microhabitats where their energetic return is greatest. For foxes hunting gerbils, this will involve the ability of the fox to encounter prey that occur in a patch, the number of gerbils found in each patch, the amount of time each prey individual devotes to that patch, their levels of apprehension, and the ability of a gerbil to escape an attack. The greater the rate of returns of resources in a patch within a cover type, the more time a predator will spend foraging in that cover type. This translates to having greater movements of a predator in such patches (Phillips et al. 2004). In our field experiment, higher activity of foxes in the control (128 crossings in tracking strips) as compared to high (67 crossings) and low cover stations (54 crossings) supports this theory. However, we also observe that the predator activity does not significantly vary between high and low stations. The lower activity of foxes in low cover stations may reflect the

poorer opportunity for foxes to detect and pursue gerbils due to safety and concealment properties of cover there, which in turn may have lead to shifts in its activity to more accessible control areas. The problem may be different in high cover stations, where the low activity of foxes may be a result of the lower activity of gerbils there (as inferred by higher GUDs). A study by Orrock et al. (2004) revealed that rodent foraging is affected by indirect cues of predation risk like microhabitat, rather than direct cues (urine scent). This is because indirect cues like microhabitat structure are much more effective in providing consistent information about risk from multiple predators (Blumstein et al. 2000). In our experiment, the significant difference in GUDs in high and low cover station may suggest the above effect.

In summary, this experiment indicated that foraging behavior of two species of gerbils is affected by the cover types differing in their concealment and safety properties. Gerbils preferred the low covers for foraging due to less risk from predators (better concealment and safety), although the dominant *G. pyramidum* showed stronger response to cover manipulations and proved to be efficient forager than the smaller *G. a. allenbyi*. This will have obvious ramifications on mechanism of species

co-existence between these gerbils in relation to availability of cover. Also, this experiment further strengthens the fact the some cover types can represent as visual obstruction, rather than safety or concealment to foraging animals thus causing increase in their vigilance behavior and affecting their actual foraging effort. The cover type also dictated changes in gerbil interactions with their predators. There was alteration in behavioral response of predator (red fox) to different cover types, which was associated with cost and benefits (accessibility and catchability of prey) of its activity across differing cover types.

To conclude, this study apart from being of ecological interest can also be of conservation value. It provides information about the changes in interactions among the gerbil species in the Negev Desert with relation to changes in landscape cover, thus providing knowledge about the mechanism of species coexistence and community organization with relation to habitat structure. This study can also be important for understanding the need for conservation of sandy habitats in desert ecosystem. The changes in vegetation cover due to browsing (and grazing) and other anthropogenic pressure may also influence the cover availability for small mammals.

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