

# Agricultural farming alters predator–prey interactions in nearby natural habitats

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## Abstract

Agricultural farming is a major consumer of global arable lands and has a direct effect on species decline through habitat destruction. However, agricultural endeavours can also evoke indirect threats that will result in behavioural modifications of indigenous species. In a desert ecosystem, where a political border led to a farming dichotomy between intensive cultivates in Israel and intact lands in Jordan, we compared the foraging behaviours and abundances of the red fox and two species of gerbils, close to and distant from farms, and during two moon phases. We estimated fox and gerbil foraging levels by track counts, and measured gerbil time allocation, vigilance and apprehension by the giving-up density method. While foxes were significantly more abundant and active at locations close to farms, gerbils were significantly more abundant and active at locations distant from farms. Moreover, the typical reduction in food consumption during full-moon nights was exhibited only at locations close to farms. These results could suggest that indicators of predation risk, such as illumination intensity or distance to cover, are not universal, and their effectiveness may depend indirectly on anthropogenic activities, such as agricultural farming. The results could also suggest that although intensive agricultural endeavours benefit foxes, they might increase the predatory pressure on gerbils in addition to the already known effects of habitat loss. Therefore, agriculture acts as a double-edged sword by reducing natural habitats, while at the same time changing the predator–prey natural balance.

## Introduction

Human population growth has been a key factor in reshaping the natural environment (Holdren & Ehrlich, 1974; Thompson & Jones, 1999; Liu *et al.*, 2003), with agricultural sprawl playing a major role (FAO, 2004). The direct effects of agricultural expansion are the destruction of natural habitats and species extinction, resulting in local and global biodiversity crisis (Sotherton, 1998; Green *et al.*, 2005; Tscharncke *et al.*, 2005).

Several modelling methods have been developed to assess species decline in relation to agricultural intensification, incorporating mostly landscape and habitat variables as the main factors (Heikkinen *et al.*, 2004; Green *et al.*, 2005). There are, however, other repercussions to agricultural farming. One potential factor is the augmenting effect of human-dominated habitats on invasive and commensal species abundance (Yom-Tov & Mendelsohn, 1988; Tscharncke *et al.*, 2005). The consequences of these demographic changes for the survival of indigenous species are often unknown. In desert ecosystems, agriculture introduces

additional water and hence nutrition resources to a relatively oligotrophic environment (Balba, 1995), thereby opening new opportunities for invasive and generalist species at the expense of the specialist indigenous ones.

The complex dynamic of predator–prey interaction is usually maintained in a steady state under natural stable ecosystems (Begon, Harper & Townsend, 1996). This long-term equilibrium allows the development of ‘foraging games’ between predators and their prey (Brown, Laundré & Gurung, 1999; Kotler *et al.*, 2002). However, if an ecosystem undergoes significant changes during a short period of time, it can give rise to a shift in the types and abundance of predators that may affect prey species both through direct mortality and through changes in the predator–prey interactions. Consequently, prey species are likely to adopt new strategies to avoid the increased predation risk, while maintaining their energy gain demands.

The southern Arava desert ecosystem, shared by Israel and Jordan, represents a dichotomy in farming activity. On the Israeli side of the border, sandy habitats are covered with numerous patches of modern agricultural farms,

whereas the Jordanian side is sparsely inhabited by a more traditional pastoral society of nomadic herdsman and traditional farmers. The peace treaty signed by the two countries may bring an end to this developmental dichotomy, but meanwhile it has provided the opportunity for a collaborative study of the effects of habitat proximity to modern farming on native species.

The current study examines the effect farmed lands have on an invasive predator population and the secondary effect on its prey behaviour. We predicted that fox population would be higher around farmlands, resulting in altered predator–prey interactions and modified prey behaviour in nearby natural habitats.

## Materials and methods

### Studied species

Two species of gerbils live in the southern Arava Valley: the pssamophilic *Gerbillus gerbillus* and the ‘soil generalist’ *Gerbillus nanus* (Harrison & Bates, 1991; Mendelsohn & Yom-Tov, 1999). Zahavi & Wahrman (1957) have found that in the Arava *G. nanus* solely populates salt marshes, whereas *G. gerbillus* inhabits the adjacent sand dunes. This information has been confirmed by Shanas *et al.* (2006), who have also found the two species to co-occur on semi-stable sand dunes, close and far from farms. Both species are nocturnal (Harrison & Bates, 1991) and granivores (Bar, Abramsky & Gutterman, 1984; Abramsky, Brand & Rosenzweig, 1985). The specific diet of these species in the Arava Valley is unknown; however, it is possible that they have different preferences due to an inter-specific competition. According to the IUCN Red Book, *G. gerbillus* is classified as vulnerable within its natural distribution (Shalmon, 2002).

The red fox *Vulpes vulpes* has a naturally wide distribution and has also been successfully introduced to many new localities (Nowak, 1999). Within Israel, *V. vulpes*’ natural distribution extends to the southern Arava, where it was present in very low densities until recent years (Mendelsohn & Yom-Tov, 1999). However, this highly opportunistic and adaptable species is now abundant near settlements and farmed lands on the Israeli side of the Arava (B. Shalmon and R. Hefner, pers. comm.; U. Shanas, unpubl. data). It is an omnivorous predator, feeding on rodents (including gerbils), reptiles, insects as well as agricultural crops (Nowak, 1999; Lenain, Olfermann & Warrington, 2004). Therefore, *V. vulpes* can act as a model species for commensal predators that benefit from agricultural development and affect its natural surroundings at the same time.

Other potential predators of gerbils in the region are owls and snakes, both of which are present in very low densities. In recent years, golden jackals, historically not native to the region, have also invaded the southern Arava from the northern region of Israel but these are still rare. Stray dogs and cats are very scarce and usually exterminated by the local nature authorities (B. Shalmon, pers. comm.).

### Study site

The study was conducted in the southern Arava Valley desert, a region that lies within the Dead Sea rupture, at the northern end of the Great Rift Valley (avg. 50 m above sea level). The average annual rainfall is ~20 mm and average daily temperatures range from 15.5 °C in the winter to 33 °C in the summer (Dafni, 2000). The southern Arava region is politically divided by the Israeli and Jordanian border. Study sites were located between 695/710 and 295/320 UTM, close to farmed lands in Israel and distant from farmed lands in Jordan (see experiments for details). All sites, close and distant from farms, were located on semi-stable sands dominated by very low densities of *Haloxyylon persicum* shrubs.

The most common cultivars of the close agricultural farms were dates and seasonal crops, including watermelons, melons and onions. These cultivars make suitable food sources for the omnivorous *V. vulpes* (Harrison & Bates, 1991), but do not provide seeds for the granivorous gerbils (Bar *et al.*, 1984). Rodenticides are not commonly used in the agricultural farms, and the use of insecticides does not seem to have a significant effect on invertebrates of nearby sandy habitats (U. Shanas *et al.*, unpubl. data).

### Gerbil and fox foraging behaviour experiment

Gerbil and fox foraging behaviours were studied at locations close to and distant from agricultural farms, both in relation to microhabitat and during different moon phases. To examine the effect of *V. vulpes* predatory pressure on gerbil time allocation, the giving-up density (GUD) method was used. GUD refers to the density of available resources left behind by foragers in a resource patch following exploitation (Brown, 1988). GUD is a measure of foraging efficiency and provides an indication of when the cost of resource retrieval in a patch equals or outweighs its benefits. The benefit of resource consumption is simply the energy gain, whereas the costs may include the energy expenses of foraging, predation risk and missed opportunities of exploiting possibly richer patches or performing alternative valuable activities (Brown, 1988, 1999; Hughes & Ward, 1993). Hence, GUD provides a good method for studying predatory pressure in the field by revealing differences in gerbil foraging behaviour between locations close to and distant from farms.

We used plastic seed trays (45 cm in diameter and 7 cm deep, Keter Plastic Ltd., Hertzelia, Israel) containing 3 g of millet seeds mixed with 6.5 L of sand as artificial food patches for the assessment of GUD. We placed the trays randomly in 18 locations, nine of them close to farmed lands (0.05–0.2 km from the nearest farm) and nine distant from farmed lands (4–8 km from the nearest farm). Because there are practically no sand dunes distant from farms left on the Israeli side of the border, all sites distant from farms were located in Jordan while all sites close to farms were located in Israel. All sites (close and distant from farmed lands) were

located within the narrow (10 km wide) Arava Valley. All the sites had similar characteristics of substrate, vegetation and climatic conditions.

To assess distance-to-cover behaviour, we placed the seed-trays in two microhabitats. In each location, we set three trays at the margin (0–0.5 m) of a vegetation patch (bush microhabitat) and three in the open (10–12 m away from the vegetation patches, open microhabitat). Vegetation patches (*H. persicum* shrubs) were 15–30 m apart.

To examine the effect of moon phase on foraging behaviour, we set the trays during full-moon and moonless nights at the beginning of January 2004. We set the seed-trays at six of the 18 locations (three close to and three distant from farmed lands) simultaneously for two consecutive nights and then moved to set in new locations until all locations were sampled. We set the trays before dusk, and sifted the remaining seeds from the sand of each tray at dawn. The weight of the remaining seeds from each tray provided the measure of GUD.

We assessed gerbil and fox foraging by the number of times they crossed smoothed transects of sand, indicated by their tracks. At each location, we smoothed a single 65-m-long transect divided into ten 2 m<sup>2</sup> quadrates with 5 m intervals (measured between the ends of adjacent quadrates). The distance between a transect centre and the closest seed-tray was about 50 m (sufficient to avoid bias from gerbil foraging on the trays). Only full crossings of a gerbil or a fox were counted. Although *G. gerbillus* has hairy soles compared with *G. nanus*, it was impossible to distinguish between the tracks of the two species due to the similarity in their foot size, the nature of the soil and the wind regime in the study sites. The results for both species were therefore combined.

### Gerbil apprehension experiment

While the GUD method provides insights into the foraging behaviour of gerbil, it does not explain the behavioural motives. We therefore studied gerbil apprehension at locations close to and distant from farmed lands during full-moon and new-moon phases. Apprehension is defined as a measure of vigilance and refers to the amount of a forager's attention that is diverted away from foraging tasks to predator detection (Dall, Kotler & Bouskila, 2001; Kotler *et al.*, 2002). We expected that a forager's apprehension would rise with increasing predatory pressure (Brown, 1999; Brown *et al.*, 1999; Kotler *et al.*, 2002).

Two locations were used, one close to farmed lands (0.05 km) in Israel and one distant from farmed lands (*c.* 6 km) in Jordan, during two consecutive full-moon and moonless nights in June 2004. We laid sets of two seed-trays (see the GUD experiment) at 20 different sites (10 sets on one night and 10 others on the following night) in both locations simultaneously. Each night, we placed five sets at the margin of a vegetation patch (bush microhabitat) and five sets 10–12 m away from vegetation (open microhabitat). Each set consisted of one high-density seed-tray (HDT, 'full' tray containing 3 g of millet seeds mixed thoroughly with

6.5 L of sand) and one low-density seed-tray (LDT, 'bottom' tray containing 2 g of millet seed mixed into 3.25 L of sand and placed on the bottom of the tray, with the remaining 3.25 L of seedless sand covering on top).

Kotler *et al.* (2002) used full trays and bottom trays with the same amount of seeds. Diminishing returns from the full trays made the bottom trays relatively more attractive. Thus, differences in selectivity for full trays over bottom trays were viewed by temporal inspection during the night. Military border rules prevented us from accessing the trays during the night and quantifying temporal patterns of patch exploitation and apprehension. We therefore decreased the quality of the bottom trays by adding a lower density of seeds. Thus, differences in the GUDs between HDTs and LDTs can provide a measure of apprehension, even if trays are preyed upon all night long, as HDTs will maintain a higher quality of the patch for a longer period of time.

### Data analysis and statistics

We used locations as replicates for track counts and GUD. As the track counts were not affected by the spatial organization of the trays, each night was considered separately ( $n = 18$ ). To estimate gerbil and fox spatial distribution, we compared the number of locations that had tracks. We estimated gerbil and fox activity by averaging the number of all quadrates that had crossings to yield crossings per metre square for each location separately. Moon phase and proximity to agriculture were used as factors for yielding  $2 \times 2$  contingency tables for the fox and for the gerbil. We applied the Yates correction for continuity in order to perform  $G$ -tests, using log-linear models (Zar, 1999) for all the tables.

For GUD calculation, we considered only those locations where food consumption from the seed-trays occurred during both moon phases. In each location, we averaged the numbers of seeds left in all trays from the two consecutive nights followed by averaging all locations of the same kind. Both visited and unvisited trays within each location were included in the analysis, thus making both food consumption and activity extant the factors that were considered for GUD evaluation of foraging activity. A three-way ANOVA was performed to test for the between-subject differences in GUDs close to and distant from farms, during full-moon and moonless nights, and in bush and open microhabitats (*i.e.* the effect of distance to cover). As the effect of distance to cover was not significant, the data of the bush and open microhabitat were combined. Consequently, a two-way ANOVA was performed to test for the between-subject differences in GUDs close to and distant from farmed lands and during full-moon and moonless nights. The proportion of locations with recorded tray activity was used to estimate gerbil distribution and activity levels ( $G$ -test). This value of activity was then compared with the track counts activity estimator.

We evaluated differences in apprehension levels by log transforming (the log transformation is applied to represent

**Table 1** Effect of resource availability on animal selectivity

Comparison resources C versus B	% Available	% Used	Manly–Chesson selectivity index <sup>a</sup>	Manly–Chesson standardized index <sup>b</sup>
C	80	40	0.5	0.14
B	20	60	3	0.86

Notes: In this example (after Garshelis, 2000), the selectivity is higher for B, despite C being a richer resource. In the actual calculations, standardized values (<sup>c</sup>) were log transformed.

<sup>a</sup>Selectivity indices (example for C): % used in C/% available in C.

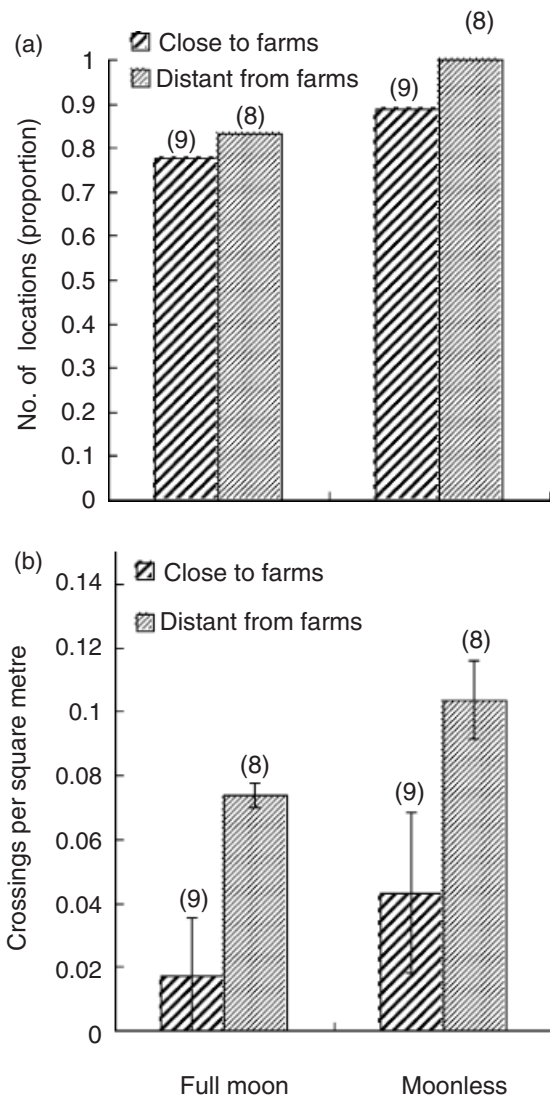
<sup>b</sup>Selectivity indices standardized so that they total 1. The equation for the Manly–Chesson standardized index is (example for C) C selectivity/(B selectivity+C selectivity).

the depletion of the food patch during the night; Kotler *et al.*, 2002) the Manly–Chesson standardized selectivity index (Garshelis, 2000) for the HDT and LDT paired GUD values ( $n = 10$ , Table 1). A selectivity index value higher than 0.5 indicates that the animals prefer the predicted patch, HDT (Garshelis, 2000; Kotler *et al.*, 2002). Therefore, high selectivity values (above 0.5) indicate high apprehension as the animals prefer the better, more secure food source over the poorer, less secure food source (Kotler *et al.*, 2002). A three-way ANOVA test of between-subject effects on the standardized selectivity indices revealed no significant effect of microhabitat. Therefore, a two-way ANOVA test of between-subject effects for only moon phase and proximity to farms was performed on the combined bush and open microhabitat data.

## Results

### Gerbil and fox activity

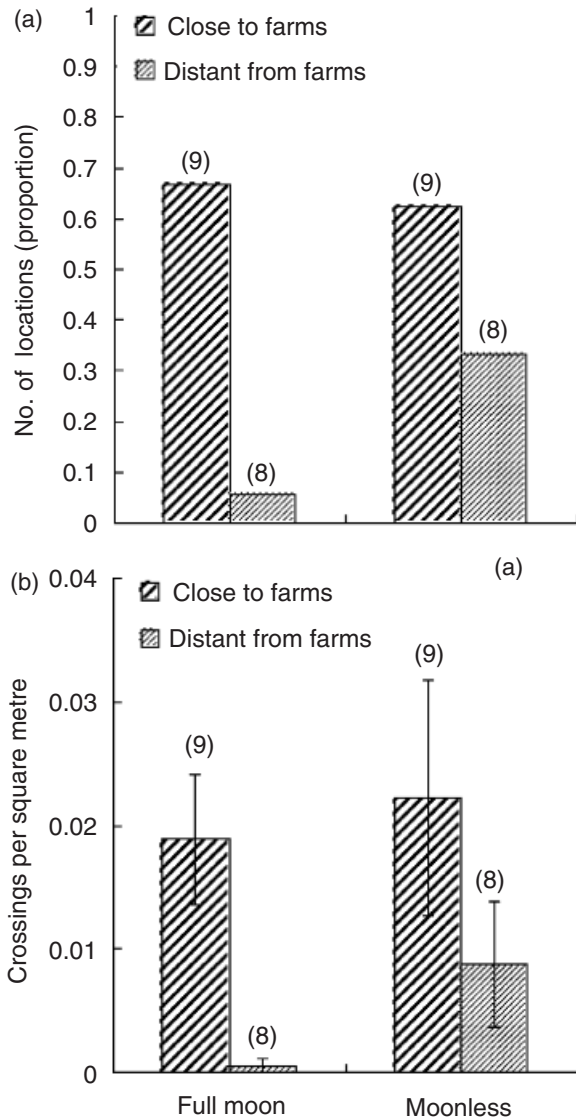
Gerbil activity extant, indicated by the number of locations that showed gerbil tracks and by the number of locations that showed gerbil food consumption activity, was not affected ( $G = 0.04$ , d.f. = 1, NS; and  $G = 0.365$ , d.f. = 1, NS, respectively) by either moon phase or proximity to farms (Fig. 1a). However, gerbil activity intensity, measured by the numbers of gerbil crossings in a plot, was significantly higher ( $G = 33.457$ , d.f. = 1,  $P < 0.001$ ) at locations distant from farmed lands compared with locations close to farmed lands, and on moonless nights for both (Fig. 1b). In contrast, fox activity extant, indicated by the number of locations that showed fox tracks, and activity intensity, measured by the number of fox crossings in a plot, were both significantly higher close to farmed lands ( $G = 215.94$ , d.f. = 1,  $P < 0.001$ ; and  $G = 60.483$ , d.f. = 1,  $P < 0.001$ , respectively) (Fig. 2a and b). Fox activity dropped during full-moon nights only at locations distant from farmed lands (Fig. 2a and b). No other predators' tracks or other rodent species' tracks were found in the sites during the experimental nights.



**Figure 1** Gerbil activity levels ( $n$  values in parentheses): (a) activity extant measured as the proportion of locations with recorded tracks ( $G$ -test, NS) and (b) activity intensity measured by track counts as mean ( $\pm$  SE) crossings per square metre ( $G$ -test,  $P < 0.001$ ) ( $n = 18$  for all full-moon nights;  $n = 9$  for moonless nights in locations close to farmed lands; and  $n = 8$  for moonless nights in locations distant from farmed lands).

### Gerbil GUD

Distance to cover had no effect on gerbil GUDs (three-way ANOVA,  $F_{3,1} = 0.792$ , NS). When data of distance to cover were combined, proximity to farmed lands did not significantly affect GUD values (two-way ANOVA,  $F_{1,2,1} = 3.62$ , NS). However, GUDs were significantly higher on full-moon nights than on moonless nights (two-way ANOVA,  $F_{1,2,1} = 9.177$ ,  $P < 0.01$ ). The interactions between proximity to farmed lands and moon phase also had a significant effect on GUD values (two-way ANOVA,

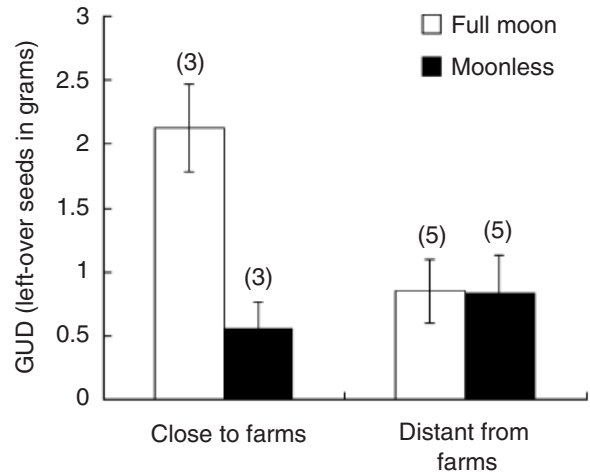


**Figure 2** Fox activity levels (*n* values in parentheses): (a) activity extant measured as the proportion of locations with recorded tracks (*G*-test,  $P < 0.001$ ) and (b) activity intensity measured by track counts as mean ( $\pm$  SE) crossings per square metre (*G*-test,  $P < 0.001$ ) ( $n = 18$  for all full-moon nights;  $n = 9$  for moonless nights in locations close to farmed lands; and  $n = 8$  for moonless nights in locations distant from farmed lands).

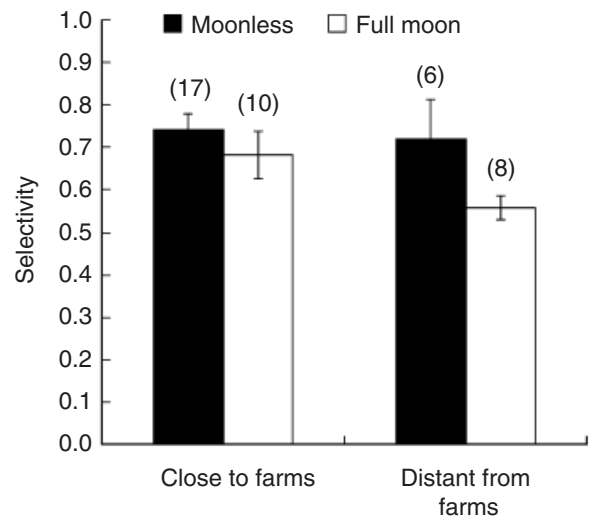
$F_{12,1} = 8.766$ ,  $P < 0.05$ ), indicating that the effect of illumination is related to the proximity to farmed lands (Fig. 3).

**Gerbil apprehension**

Distance to cover had no effect on gerbil selectivity (three-way ANOVA,  $F_{33,1} = 1.281$ , NS). When data of distance to cover was combined (Fig. 4), proximity to farms had no significant effect on gerbil selectivity (two-way ANOVA,  $F_{37,1} = 2.862$ , NS). However, moon phase had a significant



**Figure 3** Mean ( $\pm$  SE) gerbil giving-up density (GUD) values close to and distant from farmed lands during full-moon and moonless nights (*n* values in parentheses). Changes in illumination affecting GUD values are apparent only at locations close to farmed lands (two-way ANOVA, corrected model,  $P = 0.01$ ; proximity to farms, NS; moon phase,  $P = 0.01$ ; proximity to farms, \*moon phase,  $P = 0.012$ ).



**Figure 4** Mean ( $\pm$  SE) selectivity between high-density tray and low-density tray pairs close to and distant from farmed lands during moonless and full-moon nights. Only the moon phase had a significant effect on gerbil selectivity, notably in tray pairs distant from farmed lands (two-way ANOVA, corrected model,  $P = 0.05$ ; proximity to farms, NS; moon phase,  $P = 0.037$ ; proximity to farms, \*moon phase,  $P = NS$ ).

effect on gerbil selectivity (two-way ANOVA,  $F_{37,1} = 4.696$ ,  $P < 0.05$ ), which was lower during full-moon nights and especially evident in trays distant from farmed lands. The interactions between proximity to farmed lands and moon phase did not have a significant effect on gerbil selectivity (two-way ANOVA,  $F_{37,1} = 0.848$ , NS).

## Discussion

The population of predators in the southern Arava Valley has undergone remarkable changes as a result of increased development on the Israeli side of the border. Some psammophilic desert-adapted species, such as the sand fox *Vulpes rueppellii* (Schinz, 1825) and the sand cat *Felis margarita* (Loche, 1858), have been extirpated on the Israeli side (Jordanian status: unknown) (Shalmon, 2002), while generalist ones, such as the red fox, increased in number (B. Shalmon, pers. comm.). Our results confirmed these observations. Foxes were spatially more abundant throughout sites (Fig. 2a) and more active within sites (Fig. 2b) close to rather than distant from farmed lands.

The GUD experiments suggest that predatory pressure is higher in locations close to farms, as food consumption activity decreased during full-moon nights only at these locations (Fig. 3). Despite no differences in the spatial distribution of gerbils close to and distant from farmed lands as indicated by track counts, higher temporal activity during both moon phases at locations distant from farmed lands suggests higher population densities or lower vigilance of gerbils living in these locations. A study by Shanas *et al.* (2006) suggested, based on trapping data, that the gerbils of the Arava Valley have higher population densities at locations distant from farms. However, the current apprehension study (Fig. 4) demonstrates that gerbils may show relatively low vigilance (lower selectivity for HDT) at locations distant from farmed lands. Therefore, lower vigilance could provide an additional explanation for higher trapping rates at locations distant from farmed lands. Not surprisingly, this lower vigilance spatially and temporally coincides with minimal fox presence (Fig. 2b).

A further support for the importance of vigilance in explaining foraging patterns is found in the gerbils' activity during different moon phases. Our study supports previous observations showing that the activity of nocturnal rodents can be higher on moonless nights (Kotler, 1984; Hughes & Ward, 1993). Therefore, if differences in GUDs were only due to differences in gerbil population densities, then we would have expected a similar increase in food consumption during moonless nights at both locations and not only at the close to farmed land locations.

We therefore suggest that the higher abundance of fox living close to farmed lands, as indicated by the track counts (Fig. 2a and b), could impose a higher predatory pressure. This pressure apparently forces the gerbils living close to farmed lands to adjust their foraging behaviour in accordance with the lunar cycle by being more active on moonless nights. Gerbils living at a distance from farmed lands, however, are probably not subjected to high predatory pressure and therefore do not need to substantially alter their activity in response to changing phases of the moon. Nevertheless, the track counts were low for these gerbils on full moon nights, suggesting compensation for the lower activity by increasing food consumption during the times at night when the moon is

low. Species richness in the highly xeric Arava Valley is relatively low (Shanas *et al.*, 2006). Consequently, other predators that can potentially elicit anti-predator behaviour, such as snakes (Bouskila, 1995) or owls (Longland & Price, 1991), are rare at the region (B. Shalmon, pers. commun.).

Although it has been shown that distance to cover can affect rodents foraging (Hughes & Ward, 1993; Kotler *et al.*, 2002), in this study we found that it had no such effect. Thus we suggest that a distance to cover of 10–12 m is not a strong cue of predation risk at locations either close to or distant from farmed lands in this region. It is possible that our study sites differ from those previously reported by having a very low density seed bank or a very rapid renewal of the seed bank due to the wind reign, a phenomenon which might drive gerbils to highly opportunistic foraging (i.e. force them to forage for their food equally in bush and open microhabitats). Alternatively, it is also possible that the *H. persicum*, shrubs which have relatively low foliage, do not provide sufficient cover against predators and hence do not make the bush microhabitat a preferable foraging ground.

In harsh desert environments, water is usually the most important limiting factor for mammals (Degen, 1997). However, in the case of the Arava Valley, which is an oligotrophic desert, intensive farming has increased the water and food resources. This change is to the benefit of the red fox and to the detriment of native prey species, such as the gerbils, which have been forced out to the remaining shrinking habitats surrounding the farms. Thus, gerbils living close to farmed lands are experiencing a decrease in abundance due to habitat loss and are also under higher predatory pressure as compared with gerbils living distant from farms. Considering that the region's farming activity has increased sand exploitation, the higher predation pressure has the potential to further threaten the already vulnerable psammophilic *G. gerbillus* (Shalmon, 2002).

As agricultural expansion continues to pose a threat to all habitat forms, it might be a greater threat to arid environment, where the transformation of the land is usually extreme. In addition to the direct effect on the landscape, the secondary and tertiary effects, such as those described here, should also be considered in the management planning of agro-environmental ecosystems. We show that farming can act as a double-edged sword by reducing native species' natural habitats, while at the same time adding competition and predation risks from other exotic and commensal organisms. In the case of the southern Arava, the agricultural development on the Israeli side is expanding in recent years to the Jordanian side, with the aid of Israeli agricultural knowledge and experts. In addition, sand mining activities are taking place on both sides of the border. Immediate action for the preservation of sandy habitat should include the declaration of new reserves on all remaining sand-dominated areas on the Israeli side, alongside a sustainable development of the Jordanian side.

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