

Structurally complex habitat and sensory adaptations mediate the behavioural responses of a desert rodent to an indirect cue for increased predation risk

Yael Mandelik,* Menna Jones‡ and Tamar Dayan

Department of Zoology, Tel Aviv University, Tel Aviv 69978, Israel

ABSTRACT

We studied the foraging behaviour of a rocky desert rodent, the common spiny mouse (*Acomys cahirinus*), to gain insight into how structural complexity of habitat influences responses to an indirect cue for the level of predation risk. We used artificial food patches to compare the foraging response of free-ranging common spiny mice in a habitat gradient, which varied in structural complexity, between dark and moonlit nights. Close proximity to continuous overhead cover was critical to the choice of foraging microhabitat in common spiny mice, and habitat structure had a stronger effect than moon phase in the evaluation of a foraging patch, consistent with results for sandy desert rodents. The structurally complex habitat of the rocky desert environment enabled spiny mice to restrict most of their foraging to large continuous areas that offered reduced levels of predation risk. When spiny mice did forage in the open, their response can be explained by the different types of movement involved in two aspects of foraging. The number of artificial food patches visited, which reflects active and high-risk movement across open ground, was curtailed on moonlit nights. However, spiny mice reduced the food density of the most distant open food patches to similar levels, and even slightly lower ones, on moonlit compared with moonless nights. Possible explanations include the level of risk engendered by the type of movement that foraging in a tray entails combined with habitat structure (specifically camouflage afforded by shadows cast by rocks), energetic compensation for risk endured to reach the tray, and the importance of vision in anti-predator strategies in this species. This first comprehensive study of a rodent living in a rocky desert habitat demonstrates the importance of structural complexity of habitat and sensory adaptations in mediating prey behaviour under predation risk.

Keywords: *Acomys cahirinus*, foraging pattern, giving-up density, habitat structure, moonlight, predation risk, predator refuges, rocky desert, structural complexity.

INTRODUCTION

Predation has been shown to influence prey species both directly, by the removal of prey individuals, and indirectly, through behavioural responses of prey to the risk of predation

* Address correspondence either to Yael Mandelik or Tamar Dayan. e-mail: myael@post.tau.ac.il or dayant@post.tau.ac.il

‡ Current address: School of Zoology, University of Tasmania, Hobart, Tasmania 7004, Australia.

Consult the copyright statement on the inside front cover for non-commercial copying policies.

(Paine, 1966; Sih, 1987; Lima, 1998). Predation risk influences both activity pattern and habitat use (Werner *et al.*, 1983; Berger, 1991; Wooster and Sih, 1995; Abramsky *et al.*, 1996). Its effects are most commonly detected through changes in foraging behaviour (Caraco *et al.*, 1980; Lima and Valone, 1986; Werner and Anholt, 1993).

For many animals, foraging behaviour can be regarded as a reflection of the balance between two opposing demands for increasing fitness: maximizing energy intake and avoiding predation (Price, 1984; Lima *et al.*, 1985; Abrahams and Dill, 1989; Lima and Dill, 1990; Nonacs and Dill, 1990). The ratio between these two conflicting demands is used in assessing the perceived importance of different variables to the forager, including perceived risk of predation (Abramsky *et al.*, 2002).

Both predators and prey use sensory facilities (auditory, visual and chemosensory are common ones) to detect each other's presence so as to capture or evade capture. If a particular set of environmental conditions enhance the hunting ability of the predator, prey may perceive these conditions as a cue for increased risk of predation. Similarly, prey are likely to perceive varying degrees of risk depending on how their sensory adaptations match changing environmental conditions (e.g. Webster and Webster, 1971).

Well-adapted foragers change their foraging in response to predation risk, even if that risk is indirect. In particular, rodents that live in sandy deserts reduce their activity and avoid open habitats on moonlit nights when predation risk is high (Lockard and Owings, 1974; Kaufman and Kaufman, 1982; Kotler, 1984a,b; Price *et al.*, 1984; Bowers, 1988; Kotler and Brown, 1988; Daly *et al.*, 1992; Kotler *et al.*, 1993). Owls specialize on rodents and, as both visual and auditory hunters, their hunting efficacy is enhanced by increased illumination (Dice, 1945; Clarke, 1983; Kotler *et al.*, 1988; Longland and Price, 1991).

Many prey spend much of their time in or near refuges from predators (Sih, 1997). Refuge types vary from holes (e.g. crevices or burrows), which physically exclude a larger predator, to more physically complex habitats (e.g. dense vegetation or macrophytes, woody debris and screes of cobbles, or larger rocks and boulders in both terrestrial and aquatic environments), which impede the ability of the predator to detect prey, impede movement of the predator, or increase the probability that prey will elude or evade the predator (e.g. Witter and Lee, 1995; Caley and Stjohn, 1996; Pyron *et al.*, 1999; Corona *et al.*, 2000; Manatunge *et al.*, 2000). Environmental heterogeneity affects the behaviour and density of both predator and prey (Abramsky *et al.*, 1992). Relatively few studies have addressed the influence of physical habitat complexity on the anti-predator responses of the prey (e.g. mainly in fish and aquatic systems; Persson and Eklov, 1995; Caley and Stjohn, 1996; Manatunge *et al.*, 2000; Anderson, 2001).

In this paper, we study a nocturnal murid rodent, the common spiny mouse (*Acomys cahirinus*), which lives in rocky environments in Israel, including the boulder-strewn escarpments of rocky deserts (Shkolnik, 1971, 1988; Mann, 1986; Kronfeld *et al.*, 1996). There it is subject to predation by owls. In contrast to sandy deserts, in which permanent shrubs provide discrete patches of shelter in a sea of open space (Brown *et al.*, 1988), rocky deserts offer a greater total area of refuge and a gradient in refuge types. These range from large areas of jumbled boulder fields providing continuous overhead cover and absolute refuge from raptorial predators such as owls, to open space that varies both in escape distance to cover and in the range of directions in which cover is available. Rodents foraging in rocky deserts are not obligated to cross open spaces regularly.

We used artificial food patches to compare the foraging response of free-ranging common spiny mice in a habitat gradient that varied in structural complexity, between dark and moonlit nights. We sought to address the following questions:

- What are the foraging habitat preferences of common spiny mice in rocky desert terrain?
- How does moon phase affect foraging behaviour?
- Does the moon have the same influence as in sandy deserts?
- If the effect is different, can it be explained by the differences in structural complexity of the habitat or by the particular sensory adaptations of this rodent species?

MATERIALS AND METHODS

Study system

Common spiny mice are nocturnal, omnivorous rodents that are distributed throughout the Middle East, to western India in the east, south-eastern Europe in the north, and to northern and eastern Africa in the south. During the day, *Acomys cahirinus* shelters under boulders in crevices and in burrows. Thus it is susceptible primarily to predation by nocturnal predators: foxes, snakes and owls. At our study site at Ein Gedi, near the Dead Sea in Israel, nocturnally active Blanford's foxes (*Vulpes cana*) and saw-scaled vipers (*Echis coloratus*) are potential predators. However, these species rely primarily on senses other than vision (Lloyd, 1981; Kotler *et al.*, 1992; Bouskila, 1995), so moonlight is less likely to affect their hunting success. The most common of the owl species that prey on spiny mice at Ein Gedi is Hume's tawny owl, *Strix butleri* (Paz, 1986). Its foraging habits at Ein Gedi have not been studied in detail, but pellets found in the area contained spiny mouse remains (Y. Mandelik, unpublished data). The overwhelming majority of rodents at these sites are spiny mice of two species: our study animal, the nocturnal common spiny mouse, and its congener, the golden spiny mouse (*A. russatus*), which is active during the day (Shkolnik, 1971; Kronfeld *et al.*, 1994).

Foraging measurements

We used the giving-up density technique (Brown, 1988) to estimate changes in the perceived risk of predation in different illumination conditions (new/full moon) and different micro-habitats. Aluminium trays (30 × 20 × 4 cm), each containing 2 g of crushed and sieved sunflower seeds (1–2 mm diameter pieces without husks) mixed in 2 litres of sifted substrate from Ein Gedi, were used as an enriched artificial patch for foraging. The trays were open to foraging from dusk until dawn of the following day (before first light), when each tray was checked for footprints and foraged trays were sieved to collect the remaining seeds. The seeds were then cleaned of debris and weighed. The result is the giving-up density. Giving-up densities are expected to represent the harvest rate that just balances the perceived costs of foraging. These costs include metabolic costs, perceived predation costs, missed opportunity costs (Brown, 1988) and costs of interference (Kotler and Brown, 1988).

To hold costs other than predation constant, we performed four experiments within two consecutive months, using an identical experimental setup. Changes in giving-up density

could thus be attributed to changes in predation risk. Giving-up densities should rise with increased perceived risk of predation. Hence giving-up densities should be higher in open habitats or during periods of high illumination.

To ensure that common spiny mice were responsible for the foraging data analysed, each foraged tray was inspected for *Acomys* footprints (clearly distinguishable from other small mammals by size and shape). The data were excluded in only one case (when footprints of a shrew as well as those of *Acomys* were recorded in a tray). 'Contamination' of the foraging measures by the diurnal golden spiny mouse, *A. russatus*, foraging at night is extremely unlikely (Elvert *et al.*, 1999; Kronfeld-Schor *et al.*, 2001; Shargal *et al.*, 2001). A population study (Elvert *et al.*, 1999; Kronfeld-Schor *et al.*, 2001; Shargal *et al.*, 2001), in which the mice were offered extra food in larger quantities than in this research, showed the clear diurnal activity pattern of *A. russatus*. Trays that had not been foraged were sieved at least every second night and the seed replaced.

Study sites

Experiments were carried out simultaneously at two field sites in the Ein Gedi Nature Reserve: an escarpment slope west of Kibbutz Ein Gedi and a slope near the Ein Gedi Field School. Because of their proximity to human settlements, both experimental sites were exposed to a gradient of artificial illumination. Light intensities were highest near the settlement and decreased with distance from it. As these sites are approximately 2 km apart, their spiny mouse populations were different (Shargal, 1997).

Both sites comprise an open and a boulder habitat. The open habitat is a scree of small rocks with dispersed boulders of various sizes that are not continuous with one another and do not have many interstices to offer refuge from predators for the mice. The edge of the boulder habitat has a gradient of boulder density. Near the open habitat, boulders are either discrete or are in contact with only a small number of other boulders. Boulder density rises as one moves into the boulder habitat, until, at 10 m from the edge of the open habitat, the boulder field is dense and jumbled, offering continuous overhead cover and numerous and varied hiding places. Within these two habitats we compared two microhabitats. These were defined as follows:

- *Under-boulder microhabitat* was defined as the well-protected space under some of the boulders. We chose spaces under boulders that provided overhead cover, were small enough to provide refuge from owls and foxes, and were continuous with the main boulder field so that the mice did not have to take significant predation risks to reach the tray.
- *Between-boulder microhabitat* was defined as areas within the dense boulder field that were surrounded by boulders but lacked overhead cover. Sites were approximately 2.5 m away from the adjacent under-boulder site (with slight differences in the exact distance depending on the physical structure of the area) and provided the opportunity of escape to the continuous boulder field in at least three directions.
- *Open-near microhabitat* was defined as open habitat, approximately 2.5 m away from the edge of the boulder field. Escape to the safety of the underside of boulders was possible in only one direction.
- *Open-far microhabitat* was defined as being 5 m from the edge of the boulder field and about 15 m from the under-boulder microhabitat.

This microhabitat structure enabled us to examine two factors that are expected to affect predation risk: cover and escape distances to safe habitats. The close proximity of the four trays/microhabitats to each other meant that the mice were able to run quickly between trays and hence choose directly between microhabitats and habitats. Moreover, the microhabitat structure was chosen to create a gradient in the abundance and proximity of refuges and an expected gradient in the actual and perceived risk of predation.

Study design

We investigated this gradient by placing an artificial food patch (a tray of seeds and substrate) in each of the four microhabitats. Each of the two sites had a total of 20 trays, organized in five stations (approximately 30 m apart), with four trays in each station, one in each of the four microhabitats. The distance between stations was selected on the basis of spiny mouse daily movements (Shargal, 1997) to minimize the incidence of individual mice feeding in more than one tray in each microhabitat type, thereby maximizing (within practical constraints) the independence of the data from different trays in the same microhabitats.

We carried out two new moon and two full moon experiments within a 2-month period. Comparisons of full or new moon data from consecutive months enabled us to account for any seasonal variation that might occur in the 2 weeks between the new and full moon experiments. We conducted each experiment for three nights: the night of the full/new moon and the two previous nights. We used the nights before the full moon rather than those after because the 'window of darkness', the dark period in the night between either sunset and moonrise or moonset and sunrise, occurs late in the night before a full moon. In the nights after the full moon, this window occurs at the beginning of the night, coinciding with the peak foraging period for rodents and is, therefore, more likely to influence mouse behaviour (A. Bouskila, personal communication).

Before starting the experiments, mice were familiarized with both the tray system, including the novel food type, and the specific location of trays in each site and station. Before each experiment, we did three nights of prebaiting to allow time for the mice to discover that all the trays were open.

Data analysis

Two types of data were collected: the number of trays foraged in each microhabitat, recorded as the number of trays with nocturnal spiny mouse footprints or diggings, and the giving-up density, recorded as grams of seeds remaining in each foraged tray. These data represent two aspects of foraging behaviour. The number of trays foraged is a measure of the number of trays encountered that are acceptable to the foraging mouse and reflects the extent to which the mice move around each habitat (Kotler *et al.*, 1993). Because giving-up densities and number of trays foraged measure different aspects of foraging behaviour, they can be positively, negatively or not correlated at all. We analysed only nights when no predators were seen or heard.

Since our results were found to deviate significantly from a normal distribution, and variances in different microhabitats were not equal (the use of various transformations did not change either of these results), we used the non-parametric Mann-Whitney *U* and the Kruskal-Wallis tests to determine the effects of moon phase and different microhabitats

on giving-up density. We used a contingency table approach to detect changes in the number of trays foraged. We used one-way chi-squared tests to compare differences among stations, sites, nights and experiments. We analysed the effect of moon phase and microhabitat using a three-way frequency analysis and log-linear modelling (Tabachnick and Fidell, 1989). Moon and microhabitat were the independent variables. Whether trays were foraged or not (yes/no) was the dependent variable. As there was a dependent variable, we were only interested in the two-way and higher-level interactions between variables.

RESULTS

We heard or saw predators on the study site on several nights of the experiments. We heard a Blanford's fox within the field school site during the three nights of the second new moon experiment and also saw a fox on one of those nights. We clearly heard calls of *Strix butleri* near the field school site during the last night of the second full moon experiment. The presence of these predators appeared to have a dramatic effect on foraging, which dropped so low that it may have obscured the effect of the microhabitats and moon phases. Although this decline is interesting in itself, we excluded these data points from the analysis. Therefore, the analyses include data from six nights of full moon and six nights of new moon for the kibbutz site, and five and three nights of full moon and new moon, respectively, for the field school site – that is, a total of 180 trays for the new moon phase and 220 trays for the full moon phase.

To explore the possibility that we could combine data from the two sites, the two experiments for each moon phase, nights within experiments and stations, we tested for differences in their giving-up densities and number of trays foraged. No significant differences were found between the two sites in either giving-up density or the number of trays foraged. Significant differences between the experiments were found only in the new moon phase, with an increase in the number of trays foraged in the second compared to the first month's experiment in the open-far microhabitat ($\chi^2 = 4.57$, d.f. = 1, $P = 0.033$). These results allowed us to reject the possibility of short-term effects of season (on food, temperature, humidity and more) or different populations of mice and to combine the data from the two sites and from the two experiments (within each of the moon phases). When testing for differences between nights within each of the moon phases, significant differences were found only in the full moon phase in the boulder habitat, with lower giving-up densities in the second night of the full moon phase (the night before the night of the actual full moon) ($\chi^2 = 6.72$, d.f. = 2, $P = 0.034$), compared to the other two nights.

At both field sites, we found differences between stations that we can attribute to an artificial illumination gradient. In both moon phases, giving-up densities in the boulder habitat were significantly higher in the stations closer to the settlements and gradually decreased with the distance from them ($\chi^2 = 10.46$, d.f. = 4, $P = 0.033$ for the full moon experiment; $\chi^2 = 20.4$, d.f. = 4, $P < 0.001$ for the new moon experiment). A parallel pattern was found in the number of trays foraged in the open habitat, with an increased number of trays foraged with distance away from the settlements, but only in the field school site in the full moon experiment ($\chi^2 = 18.74$, d.f. = 8, $P = 0.016$). These patterns generally follow a gradient in artificial illumination coming from external electrical lighting from the settlements below and at one end of both study sites. As such, the lighting affected the stations closest to the settlement, and the topography of the sites meant that the boulder habitat

was more affected than the open habitat. Moonlight was sufficiently strong to override the effects of the artificial lighting. As the artificial illumination was constant throughout all the experiments, we will not consider it further.

Habitat and microhabitat preferences

Giving-up densities were significantly higher in the open than in the boulder habitat within both moon phases ($z = -6.74$ for the new moon, $z = -5.16$ for the full moon, both $P < 0.001$) (Table 1). Moreover, the number of trays foraged was significantly lower in the open than in the boulder habitat within both moon phases ($\chi^2 = 11.76$, d.f. = 1 for the new moon, $\chi^2 = 31.36$, d.f. = 1 for the full moon, both $P < 0.001$) (Table 1). When the microhabitats within each habitat were analysed (Fig. 1), we found significant differences only between the boulder microhabitats. The giving-up densities were higher in the between-boulder microhabitat than in the under-boulder microhabitat in both moon phases ($z = -2.94$, $P = 0.003$ for the new moon phase, $z = -5.34$, $P < 0.001$ for the full moon phase) (Fig. 1a). Between the two microhabitats in the open there were no significant differences in giving-up density in either of the moon phases. In the three-way log-linear modelling of the effects of microhabitat and moon on the number of trays foraged, we found a highly significant effect of microhabitat on foraging ($\chi^2 = 153.58$, d.f. = 3, $P < 0.001$) (Table 2). Within microhabitats, there was a greater difference (in parameter estimates and in real values) between the two boulder microhabitats (under-boulder and between-boulder) and the two open microhabitats (open-near and open-far) than between microhabitats within the two main habitat types (Table 2, Fig. 1b). The effect of microhabitat ($P < 0.001$ and larger parameter estimates) was stronger than the effect of moon phase ($P < 0.01$) (Table 2).

Effect of moon phase

Moon phase was found to influence habitat (Table 1) and microhabitat use (Fig. 1). The giving-up densities did not vary significantly between full moon and new moon in the boulder habitat (Table 1) or in the under- and between-boulder microhabitats (Fig. 1a). In the open habitat, the giving-up densities were significantly higher at new moon than at full moon ($z = 2.33$, $P = 0.019$). At the microhabitat level, these differences were significant

Table 1. Mean giving-up densities and number of trays foraged in the boulder and open habitats, in the full moon and new moon experiments

Variable	Full moon	New moon
Giving-up density (g)		
Boulder habitat	1.22	1.17
Open habitat	1.52	1.61
Trays foraged (n)		
Boulder habitat	85	88
Open habitat	26	48

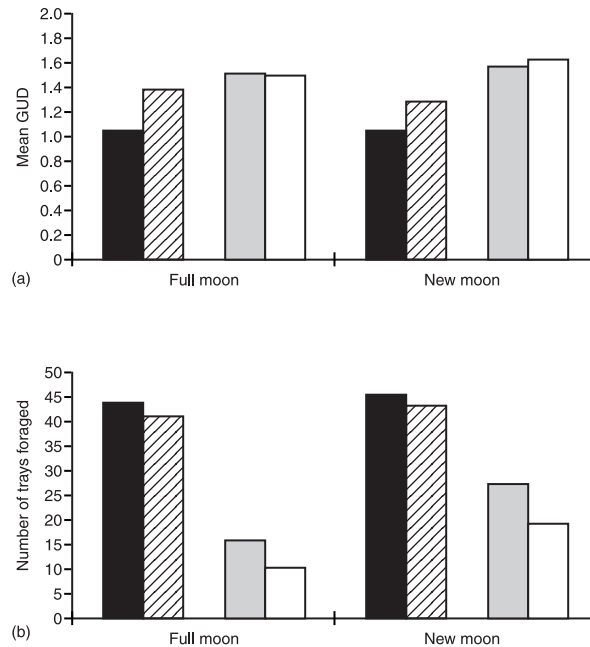


Fig 1. Microhabitat level differences in (a) giving-up densities (GUD) and (b) the number of trays foraged comparing the under-boulder (■) with the between-boulder (▨) microhabitat and the open-near (■) with the open-far microhabitat (□), in the new moon phase and full moon phase.

only in the open-far microhabitat ($z = 2.31$, $P = 0.02$; Fig. 1a). Sample sizes (i.e. number of trays foraged) in the analysis of giving-up densities in the open habitat were small (open-near: new moon, $n = 28$; full moon, $n = 16$; open-far: new moon, $n = 20$; full moon, $n = 10$; Fig. 1b). To test for any interaction between microhabitat and moon phase, we also undertook a two-way analysis of variance based on ranks of giving-up densities (Conover and Iman, 1981) (Table 3). As before, the effect of microhabitat was highly significant ($F = 30.92$, d.f. = 3, $P < 0.001$), while the effect of moon and the interaction were not significant ($F = 2.05$, d.f. = 1, $P = 0.15$ for the moon effect; $F = 1.5$, d.f. = 3, $P = 0.21$ for the interaction). We found a highly significant effect of moon phase on the number of trays foraged ($\chi^2 = 8.11$, d.f. = 1, $P = 0.004$) (Table 2). More trays were foraged in new moon than in full moon in the open habitat ($\chi^2 = 6.541$, d.f. = 1, $P = 0.011$) but not in the boulder habitat (Table 1). Within the open habitat, the strongest effect of moon phase was in the open-far microhabitat (greatest parameter estimates and values) followed by open-near microhabitat (Table 2; Fig. 1b). The lack of interaction between moon phase and microhabitat (removed from model) indicates that the effect of moon phase on the number of trays foraged was consistent across microhabitats.

We repeated these tests comparing only the two actual nights of the full moon (from both months) with all nights of the new moon experiments to exclude the possibility of the use of the window of darkness. The results for microhabitat and habitat use within each of the moon phases were very similar to those found when using all nights of the full moon experiments.

Table 2. Summary of hierarchical log-linear model of the effect of moonlight and microhabitat on the number of trays foraged

Source of variance	<i>G</i> -score (likelihood ratio χ^2)			Standardized log-linear parameter estimates ($\lambda/\text{SE}(\lambda)$) for each microhabitat				
	χ^2	d.f.	<i>P</i>					
Microhabitat $\times$ number of trays foraged	153.58	3	< 0.001		<i>UB</i>	<i>BB</i>	<i>ON</i>	<i>OF</i>
				Yes	4.831	3.338	-5.673	-8.012
				No	-4.831	-3.338	5.673	8.012
Moon phase $\times$ number of trays foraged	8.11	1	0.004		<i>New moon</i>		<i>Full moon</i>	
				Yes	2.911		-2.911	
				No	-2.911		2.911	

Note: The final model includes two of the two-way interactions (all three main effects were included by default). *N* = 360, constant = 2.52. *Abbreviations:* UB = under-boulder microhabitat, BB = between-boulder microhabitat, ON = open-near microhabitat, OF = open-far microhabitat.

Table 3. The effect of moon phase and microhabitat on giving-up densities as determined by a two-way analysis of variance based on ranks of giving-up density

Variable	d.f.	MS	<i>F</i>
Microhabitat	3	75415.06	30.92*
Moon phase	1	3294.2	2.05
Microhabitat $\times$ moon	3	5879.34	1.5

* $P < 0.001$.

DISCUSSION

Common spiny mice prefer to forage where there is continuous overhead cover. Mice foraged more patches to a lower giving-up density in the boulder habitat than in the open. Within the boulder habitat, mice showed a strong preference for the under-boulder microhabitat. They show these preferences in the summer when snakes are present in the boulder field and in the winter when they are not (Jones *et al.*, 2001). These results conform in general to studies on quadrupedal sandy desert rodents, which show a preference for foraging in the safer environment of the cover provided under bushes (e.g. Kotler, 1984a; Kotler *et al.*, 1991, 1993, 1994) where the capture success of owls is lower (Kotler *et al.*, 1988; Longland and Price, 1991). In the more dangerous open habitat, our microhabitat designations influenced the number of trays foraged but not the giving-up density. These results suggest that the 2.5 m difference in escape distance to cover between the two open microhabitats represented a sufficiently greater risk of predation so that the mice found fewer of the open-far microhabitat trays. Once they had found a tray, however, the lack of strong differences in giving-up density between the two open microhabitats indicates that the chance of evading predation by running back to cover is uniformly high between 2.5 and 5 m from shelter. This difference between finding trays and foraging in them may reflect differential sensitivity to risk during the two components of foraging behaviour (discussed later).

Moon phase may create temporal heterogeneity in both the true and the perceived risk of predation (e.g. Clarke, 1983; Kotler *et al.*, 1994; but see Longland and Price, 1991). In this rocky desert environment, moon phase affected the foraging behaviour of common spiny mice only in the open habitat. The lack of a moonlight effect in the boulder habitat can be explained by the structure of the respective microhabitats. The under-boulder microhabitat provides complete shade from moonlight and refuge from hunting owls. The between-boulder microhabitat is a complex system of small open areas nestled in hollows between jumbles of different-sized boulders. This structure provides extensive shading for large parts of the night, creating a safe 'window of opportunity' that mice can use to forage in these areas. Even when the moon is overhead, there is a complex of shaded patches that provides substantial camouflage for foraging mice (see later discussion on shade patterns). As a consequence of their strong preference for foraging in the boulder field, the mice are exposed to changes of moon phase during a relatively small proportion of their foraging time. This represents a major difference in how moonlight affects foraging of rodents in sandy deserts and relates to the structural complexity of the habitat. We propose that the extensive boulder fields in this type of rocky desert may enable common spiny mice to largely confine their foraging to a habitat that provides continuous good protection from owls, and thus they mostly evade the enhanced risk of foraging in moonlight. With the continuous nature of the overhead shelter in the boulder field, excursions into open habitat are likely to be deliberate and discrete foraging trips. In contrast, in sandy deserts, open habitat crossings between bushes may be a regular and obligatory aspect of foraging.

The effect of habitat on foraging behaviour in common spiny mice was stronger than the effect of moon phase. These results agree with findings from a study of actual predation risk (Longland and Price, 1991), which showed much stronger effects of habitat type than moonlight on capture rates by owls. The variation in protection afforded by open and sheltered habitats appears to be greater than the differences in level of risk between moonless and moonlit nights.

When common spiny mice did forage in the open, moon phase strongly affected both the number of trays that they visited and the extent of their foraging in those trays. They visited fewer trays on moonlit compared with moonless nights, the number visited decreasing with increasing distance from overhead shelter in both moon phases. This result agrees with expectation. Studies on sandy desert rodents have shown that foraging activity increases the exposure of prey species to predators (Clarke, 1983; Longland and Jenkins, 1987; Daly *et al.*, 1990) and, specifically, that owls usually attack only moving prey (Metzgar, 1967; Kaufman, 1974). The number of trays visited reflects the extent of active movement across open habitat to reach the trays, so the fewer trays an individual visits, the less exposure it will have to predators. Owls are visual predators, so this risk is likely to be enhanced with higher illumination regimes. The trade-off between resource gain and predation risk is likely to be less profitable for the mice during nights of the full moon.

The effect of moonlight on foraging intensity in the two open microhabitats did not conform to the expectation that enhanced risk should result in reduced foraging (higher giving-up densities). Indeed, the giving-up densities were lower at full moon than at new moon and this happened in the more dangerous open-far microhabitat, at a greater distance from shelter, rather than in the open-near microhabitat. These results need to be interpreted cautiously, however, because the sample sizes for giving-up densities in the open

microhabitats were small (relatively few trays were foraged there). Moreover, while statistically significant, the differences are so minute that their biological significance must not be overstated.

Most studies of the effect of moon phase on rodent foraging activity in sandy deserts have reported reduced foraging in the open habitat (e.g. Kaufman and Kaufman, 1982; Price *et al.*, 1984; Kotler and Brown, 1988; Longland and Price, 1991; Abramsky *et al.*, 1996), or in both bush and open habitats (Brown *et al.*, 1988; Kotler *et al.*, 1991), on nights of increased predation risk (presence of owls or added illumination), whereas others have not reported any response (Bouskila, 1995). A lack of response to moonlight has been explained as reflecting predator facilitation (Bouskila, 1995), as a result of seasonal changes (Lockard and Owings, 1974; Alkon and Saltz, 1988), or as being dependent on the extent to which rodents and their predators rely on vision and hearing (Longland and Price, 1991). Predator facilitation, between snakes in the boulder field and owls in the open (Jones *et al.*, 2001), is unlikely to have influenced our results, however, as we worked in late winter before snakes became active. In the narrow time frame of this study, it is also unlikely that seasonal changes could have been a factor.

As discussed earlier, moving across open habitat to visit our artificial food patches involves active movement, increasing the risk of detection and attack by an owl. While foraging within a patch, however, mice are relatively motionless. In a rocky desert, such as at Ein Gedi, the open habitat is studded with rocks of all sizes. Although these are in full contact with the ground and do not offer any overhead protection from owls, on moonlit nights they cast sharp shadows. The patchwork of rock sizes creates a mosaic of different sizes and shapes of shadows. While foraging in a tray, a mouse may be able to use this pattern as camouflage, the shadows blending cryptically within the landscape. Cover-seeking behaviour in highly illuminated environments has been found in spiny mice (Mandelik, 1999), deermice (Clarke, 1983) and other prey species (Fenton *et al.*, 1977). Thus, the mice may perceive foraging in the open habitat on nights of the full moon to be less risky, or at least not present a greater risk, than open foraging on dark nights when there are no shadows.

It is also possible that common spiny mice compensate for the increased risk involved in travelling to the open habitat trays, especially the open-far microhabitat, by foraging longer once they reach them. Because these food patches are less likely to be visited by spiny mice, there could be a profitable trade-off between increased risk in reaching the tray and less depleted food reserves once the tray is reached.

Common spiny mice probably use vision more than hearing to detect predators. They have less developed middle-ear cavities than many sandy desert rodents (Longland and Price, 1991), better visual information-processing capabilities and they use visual information more than, for example, mongolian gerbils (*Meriones unguiculatus*) (Greenberg, 1986). Perhaps moonlight actually increases the ability of spiny mice to detect predators. In this case, the foraging response of spiny mice in open habitat may be a complex interplay between the elevated risk of detection by owls, reflected in fewer patches foraged on moonlit nights, and a greater chance of detecting their predators, which is indicated by the absence of the expected reduced foraging response in the open and, in particular, the open-far microhabitat. Other experimental and observational studies of desert rodents, geckos and even primates support this hypothesis (Webster and Webster, 1971; Erkert, 1974, 1976; Longland and Price, 1991; Reichmann, 1998; Zollner and Lima, 1999).

CONCLUSIONS

A growing body of research has indicated a broad range of non-lethal effects of predation risk, mediated by adaptive flexibility in prey behaviour (Lima, 1998). Selection pressure operates on prey to adapt their foraging behaviour in a very subtle manner. Foraging behaviour corresponds to continuous spatial and temporal changes in environmental conditions, including changes in competitor, food or predator densities (Abramsky *et al.*, 1997, 1998). Foragers adapt to these changes by altering their foraging pattern as a whole, or by independently altering its components according to the risk they endure. In this study of a desert rodent in a structurally complex habitat, we have shown that the response to moonlight as an indirect cue for elevated predation risk is mediated both by structural complexity of the habitat and by the sensory adaptations of the prey; the same cue for increased risk of predation was perceived differently in different habitats. Furthermore, our results suggest that the mice distinguish varying predation risk at different stages of the foraging process, and that this differential perception underlies the foraging pattern observed.

ACKNOWLEDGEMENTS

We sincerely thank Arie Landsman for his tireless and cheerful assistance in the field, the Ein Gedi Field School of the Society for the Protection of Nature in Israel for their hospitality and warmth, and the Nature Reserves Authority for their help. The manuscript benefited greatly from the comments of Burt Kotler, Mary Price and Dan Simberloff. David Wool and Leon Barmuta provided statistical advice. This research was supported by a National Geographic Society grant (6293-98) to T. Dayan and by a George S. Wise Postdoctoral Fellowship in Life Sciences to M. Jones.

REFERENCES

- Abrahams, M.V. and Dill, L.M. 1989. A determination of the energetic equivalence of the risk of predation. *Ecology*, **70**: 999–1007.
- Abramsky, Z., Shachak, M., Subach, A., Brand, S. and Alfia, H. 1992. Predator–prey relationships: rodent–snail interactions in the central-Negev desert of Israel. *Oikos*, **65**: 128–133.
- Abramsky, Z., Strauss, E., Subach, A., Kotler, B.P. and Riechman, A. 1996. The effects of barn owls (*Tyto alba*) on the activity and microhabitat selection of *Gerbillus allenbyi* and *G. pyramidum*. *Oecologia*, **105**: 313–319.
- Abramsky, Z., Rosenzweig, M.L. and Subach, A. 1997. Gerbils under threat of owl predation: isoclines and isodars. *Oikos*, **78**: 81–90.
- Abramsky, Z., Rosenzweig, M.L. and Subach, A. 1998. Do gerbils care more about competition or predation? *Oikos*, **83**: 75–84.
- Abramsky, Z., Rosenzweig, M.L. and Subach, A. 2002. The costs of apprehensive foraging. *Ecology*, **83**: 1330–1340.
- Alkon, P. and Saltz, D. 1988. Influence of season and moonlight on temporal activity patterns of Indian crested porcupines (*Hystrix indica*). *J. Mammal.*, **69**: 71–80.
- Anderson, T.W. 2001. Predator responses, prey refuges, and density-dependent mortality of a marine fish. *Ecology*, **82**: 245–257.
- Berger, J. 1991. Pregnancy incentives, predation constraints and habitat shifts: experimental and field evidence for wild bighorn sheep. *Anim. Behav.*, **41**: 61–77.
- Bouskila, A. 1995. Interactions between predation risk and competition: a field study of kangaroo rats and snakes. *Ecology*, **76**: 165–178.

- Bowers, M.A. 1988. Seed removal experiments on desert rodents: the microhabitat by moonlight effect. *J. Mammal.*, **69**: 201–204.
- Brown, J.S. 1988. Patch use as an indicator of habitat preference, predation risk, and competition. *Behav. Ecol. Sociobiol.*, **22**: 37–47.
- Brown, J.S., Kotler, B.P., Smith, R.J. and Wirtz II, W.O. 1988. The effects of owl predation on the foraging behavior of heteromyid rodents. *Oecologia*, **76**: 408–415.
- Caley, M.J. and Stjohn, J. 1996. Refuge availability structures assemblages of tropical reef fishes. *J. Anim. Ecol.*, **65**: 414–428.
- Caraco, T., Martindale, S. and Pulliam, H.R. 1980. Avian flocking in the presence of a predator. *Nature*, **285**: 400–401.
- Clarke, J.A. 1983. Moonlight's influence on predator/prey interactions between Shorteared Owls (*Asio flammeus*) and deermice (*Peromyscus maniculatus*). *Behav. Ecol. Sociobiol.*, **13**: 205–209.
- Conover, W.J. and Iman, R.L. 1981. Rank transformation as a bridge between parametric and nonparametric statistics. *Am. Stat.*, **35**: 124–129.
- Corona, A., Soto, L.A. and Sanchez, A.J. 2000. Epibenthic amphipod abundance and predation efficiency of the pink shrimp *Farfantepenaeus duorarum* (Burkenroad, 1939) in habitats with different physical complexity in a tropical estuarine system. *J. Exp. Mar. Biol. Ecol.*, **253**: 33–48.
- Daly, M., Wilson, M., Behrends, P.R. and Jacobs, L.F. 1990. Characteristics of kangaroo rats, *Dipodomys merriami*, associated with differential predation risk. *Anim. Behav.*, **40**: 380–389.
- Daly, M., Behrends, P.R., Wilson, M.I. and Jacobs, L.F. 1992. Behavioural modulation of predation risk: moonlight avoidance and crepuscular compensation in a nocturnal desert rodent, *Dipodomys merriami*. *Anim. Behav.*, **44**: 1–9.
- Dice, L.R. 1945. Minimum intensities of illumination under which owls can find dead prey by sight. *Am. Nat.*, **79**: 385–416.
- Elvert, R., Kronfeld, N., Dayan, T., Haim, A., Zisapel, N. and Heldmaier, G. 1999. Telemetric field studies of body temperature and activity rhythms of *Acomys russatus* and *Acomys cahirinus* in the Judean Desert of Israel. *Oecologia (Berlin)*, **119**: 484–492.
- Erkert, H.G. 1974. The effect of moonlight on the activity of nocturnal mammals (in German, English summary). *Oecologia (Berlin)*, **14**: 269–287.
- Erkert, H.G. 1976. Light-induced activity optimum in night monkeys (*Aotus trivirgatus*) (in German, English summary). *Folia Primatol.*, **25**: 186–192.
- Fenton, M.B., Boyle, N.G.H., Harrison, T.M. and Oxley, D.J. 1977. Activity patterns, habitat use, and prey selection by some African insectivorous bats. *Biotropica*, **9**: 73–85.
- Greenberg, G. 1986. Depth perception in Mongolian gerbils (*Meriones unguiculatus*) and Spiny mice (*Acomys russatus* and *A. cahirinus*). *J. Comp. Psychol.*, **100**: 81–84.
- Jones, M.E., Mandelik, Y. and Dayan, T. 2001. Coexistence of temporally partitioned spiny mice: roles of habitat structure and foraging behaviour. *Ecology*, **82**: 2164–2176.
- Kaufman, D.W. 1974. Differential predation on active and inactive prey by owls. *Auk*, **91**: 172–173.
- Kaufman, D.W. and Kaufman, G.A. 1982. Effect of moonlight on activity and microhabitat use by Ord's Kangaroo rat (*Dipodomys Ordii*). *J. Mammal.*, **63**: 309–312.
- Kotler, B.P. 1984a. Risk of predation and the structure of desert rodent communities. *Ecology*, **65**: 689–701.
- Kotler, B.P. 1984b. Effects of illumination on the rate of resource harvesting in a community of desert rodents. *Am. Midl. Nat.*, **111**: 383–389.
- Kotler, B.P. and Brown, J.S. 1988. Environmental heterogeneity and the coexistence of desert rodents. *Annu. Rev. Ecol. Syst.*, **19**: 281–307.
- Kotler, B.P., Brown, J.S., Smith, R.J. and Wirtz II, W.O. 1988. The effects of morphology and body size on rates of owl predation on desert rodents. *Oikos*, **53**: 145–152.
- Kotler, B.P., Brown, J.S. and Hasson, O. 1991. Factors affecting gerbil foraging behavior and rates of owl predation. *Ecology*, **72**: 2249–2260.

- Kotler, B.P., Blaustein, L. and Brown, J.S. 1992. Predator facilitation: the combined effect of snakes and owls on the foraging behavior of gerbils. *Ann. Zool. Fenn.*, **29**: 199–206.
- Kotler, B.P., Brown, J.S. and Mitchell, W.A. 1993. Environmental factors affecting patch use in two species of gerbilline rodents. *J. Mammal.*, **74**: 614–620.
- Kotler, B.P., Ayal, Y. and Subach, A. 1994. Effects of predatory risk and resource renewal on the timing of foraging activity in a gerbil community. *Oecologia*, **100**: 391–396.
- Kronfeld, N., Dayan, T., Zisapel, N. and Haim, A. 1994. Coexisting populations of *Acomys cahirinus* and *A. russatus*: a preliminary report. *Isr. J. Zool.*, **40**: 177–183.
- Kronfeld, N., Shargal, E. and Dayan, T. 1996. Population biology of coexisting *Acomys* species. In *Preservation of Our World in the Wake of Change* (Y. Steinberger, ed.), pp. 478–480. Jerusalem: ISEEQS.
- Kronfeld-Schor, N., Dayan, T., Elvert, R., Haim, A., Zisapel, N. and Heldmaier, G. 2001. On the use of the time axis for ecological separation: diel rhythms as an evolutionary constraint. *Am. Nat.*, **158**: 451–457.
- Lima, S.L. 1998. Nonlethal effects in the ecology of predator–prey interaction. *BioScience*, **48**: 25–34.
- Lima, S.L. and Dill, L.M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.*, **68**: 619–640.
- Lima, S.L. and Valone, T.J. 1986. Influence of predation risk on diet selection: a simple example in the grey squirrel. *Anim. Behav.*, **34**: 536–544.
- Lima, S.L., Valone, T.J. and Caraco, T. 1985. Forging-efficiency–predation-risk trade-off in the grey squirrel. *Anim. Behav.*, **33**: 155–165.
- Lloyd, H.G. 1981. *The Red Fox*. London: Batsford.
- Lockard, R.B. and Owings, D.H. 1974. Seasonal variation in moonlight avoidance by bannertail kangaroo rats. *J. Mammal.*, **55**: 189–193.
- Longland, W.S. and Jenkins, S.H. 1987. Sex and age affect vulnerability of desert rodents to owl predation. *J. Mammal.*, **68**: 746–754.
- Longland, W.S. and Price, M.V. 1991. Direct observations of owls and heteromyid rodents: can predation risk explain microhabitat use? *Ecology*, **72**: 2261–2273.
- Manatunge, J., Asaeda, T. and Priyadarshana, T. 2000. The influence of structural complexity on fish–zooplankton interactions: a study using artificial submerged macrophytes. *Environ. Biol. Fish.*, **58**: 425–438.
- Mandelik, Y. 1999. Foraging microhabitat use and foraging efficiencies of the common spiny mouse, *Acomys cahirinus* (in Hebrew, English summary). Master's dissertation, Tel Aviv University, Tel Aviv.
- Mann, S. 1986. Rodent distribution and notes on the comparative biology of the genus *Acomys* at Ein Gedi (in Hebrew, English summary). Master's dissertation, The Hebrew University, Jerusalem.
- Metzgar, L.H. 1967. An experimental comparison of screech owl predation on resident and transient white-footed mice (*Peromyscus leucopus*). *J. Mammal.*, **48**: 387–391.
- Nonacs, P. and Dill, L.M. 1990. Mortality risk vs food quality in a common currency: ant patch preferences. *Ecology*, **71**: 1886–1892.
- Paine, R.T. 1966. Food web complexity and species diversity. *Am. Nat.*, **100**: 65–75.
- Paz, U. 1986. *Plants and Animals of the Land of Israel*. Israel: Ministry of Defence/The Publishing House, SPNI.
- Persson, L. and Eklov, P. 1995. Prey refuges affecting interactions between piscivorous perch and juvenile perch and roach. *Ecology*, **76**: 70–81.
- Price, M.V. 1984. Microhabitat use in rodent communities: predator avoidance or foraging economics? *Neth. J. Zool.*, **34**: 63–80.
- Price, M.V., Waser, N.M. and Bass, T.A. 1984. Effects of moonlight on microhabitat use by desert rodents. *J. Mammal.*, **65**: 353–356.

- Pyron, M., Covich, A.P. and Black, R.W. 1999. On the relative importance of pool morphology and woody debris to distributions of shrimp in a Puerto Rican headwater stream. *Hydrobiologia*, **402**: 207–215.
- Reichmann, A. 1998. Effects of moonlight and predation on the behavior of *Stenodactylus doriae* (abstract). *Isr. J. Zool.*, **44**: 85–86.
- Shargal, E. 1997. Population biology and ecophysiology of coexisting *Acomys cahirinus* and *Acomys russatus* (in Hebrew, English summary). Master's dissertation, Tel Aviv University, Tel Aviv.
- Shargal, E., Kronfeld-Schor, N. and Dayan, T. 2001. Population biology and spatial relationships of coexisting spiny mice of the genus *Acomys*. *J. Mammal.*, **81**: 1046–1052.
- Shkolnik, A. 1971. Diurnal activity in a small desert rodent. *Int. J. Biometeor.*, **15**: 115–120.
- Shkolnik, A. 1988. Physiological adaptation to the environment: the Israeli experience. In *The Zoogeography of Israel* (Y. Yom-Tov and E. Tchernov, eds), pp. 487–496. Dordrecht: W. Junk.
- Sih, A. 1987. Predators and prey lifestyle: an evolutionary and ecological overview. In *Predation: Direct and Indirect Impacts on Aquatic Communities* (W.C. Kerfoot and A. Sih, eds), pp. 203–224. Hanover, NH: University Press of New England.
- Sih, A. 1997. To hide or not to hide? Refuge use in a fluctuating environment. *Trends Ecol. Evol.*, **12**: 375–376.
- Tabachnick, B.G. and Fidell, L.S. 1989. *Using Multivariate Statistics*, 2nd edn. New York: Harper & Row.
- Webster, D.B. and Webster, M. 1971. Adaptive value of hearing and vision in kangaroo rat predator avoidance. *Brain Behav. Evol.*, **4**: 310–322.
- Werner, E.E. and Anholt, B.R. 1993. Ecological consequences of the tradeoff between growth and mortality rates mediated by foraging activity. *Am. Nat.*, **142**: 242–272.
- Werner, E.E., Gilliam, J.F., Hall, D.J. and Mittelbach, G.G. 1983. An experimental test of the effects of predation risk on habitat use in fish. *Ecology*, **64**: 1540–1548.
- Witter, M.S. and Lee, S.J. 1995. Habitat structure, stress and plumage development. *Proc. R. Soc. Lond. Biol. Sci. Ser. B*, **261**: 303–308.
- Wooster, D. and Sih, A. 1995. A review of the drift and activity responses of stream prey to predator presence. *Oikos*, **73**: 3–8.
- Zollner, P.A. and Lima, S.L. 1999. Illumination and the perception of remote habitat patches by white-footed mice. *Anim. Behav.*, **58**: 489–500.

