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Foraging games between gerbils and their predators: temporal dynamics of resource depletion and apprehension in gerbils

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ABSTRACT

Predator–prey interactions constitute a foraging game when prey individuals manage risk from predators and predator individuals manage fear in their prey. As tools for managing risk, clever prey can use time allocation and apprehension (redirecting attention from foraging to predator detection). One such foraging game occurs between gerbils and their predators on the sand dunes of the Negev Desert. Here, interacting species of gerbils compete for patches of seeds that renew daily by afternoon winds. In such circumstances, gerbils are expected to deplete resource patches over the course of the night, the predators are expected to hunt when gerbil activity is highest, and gerbils are expected to be most apprehensive when predators are most active and most deadly. We tested these predictions for gerbils in two field experiments using seed trays to measure resource depletion, gerbil activity and apprehension over the course of the night, between the bush and open microhabitats and at four moon phases (new, half waxing, full and half waning). Gerbils depleted seed resources more quickly in the bush microhabitat than the open and more quickly at new moon than at other moon phases. Gerbil activity at new moon was high throughout most of the night, but decreased towards dawn. In contrast, activity at full moon was generally low, but increased towards dawn. The two gerbil species *Gerbillus andersoni allenbyi* and *G. pyramidum* partitioned the night, with *G. pyramidum* visiting resource patches earlier in the night and encountering a richer, but more risky environment, and *G. a. allenbyi* foraging later in an environment characterized by fewer seed resources, but lower risk. The same pattern extended over moon phases, with *G. pyramidum* foraging relatively more at full and waning half moon. Apprehension by gerbils was higher early in the night than later and higher at full moon than new moon. Schedules of apprehension changed according to moon phase and may have differed between the two gerbils. Finally, apprehension was higher in the open microhabitat, although the opposite was true at the beginning of the night. This foraging game affects three trophic levels, including the effect of the gerbils on the availability and

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distribution of seeds, the competitive interaction between the two gerbil species and the predator–prey interaction between gerbils and owls.

Keywords: apprehension, ecology of fear, foraging behaviour, foraging games, game theory, gerbils, giving-up density, optimal patch use, owls, predator–prey interactions, resource depletion, risk of predation, temporal partitioning, vigilance.

INTRODUCTION

The interaction between predators and their prey often constitutes a foraging game. Prey individuals must balance conflicting demands of food and safety in an effort to manage risk from their predators (e.g. Sih, 1980; McNamara and Houston, 1992; Kotler and Blaustein, 1995). Meanwhile, predators may alter their distribution and intensity of foraging effort to manage fear in their prey (Brown *et al.*, 1999). The behavioural tools available to clever prey include time allocation (where, when and for how long to forage; Bouskila, 2001) and vigilance (Kaitala *et al.*, 1989; Lima and Dill, 1990; McNamara and Houston, 1992; Lima, 1998; Brown, 1999). The predator's behavioural tools include time allocation, patch departure rules, its willingness to sustain injury and stealth (Brown *et al.*, 1999). Together, they constitute a game in which the prey's best behaviour depends on that of the predator and vice versa (e.g. Brown *et al.*, 2001).

The gerbils that inhabit the sandy habitats of the Negev Desert, Israel, and their predators (e.g. barn owls, *Tyto alba*; red fox, *Vulpes vulpes*; greater horned vipers, *Cerastes cerastes*) probably play such a game. The two most common species of gerbils on Negev Desert sand dunes are Allenby's gerbil (*Gerbillus andersoni allenbyi*, mass 24 g; we have previously referred to this animal as *Gerbillus allenbyi*) and the greater Egyptian sand gerbil (*Gerbillus pyramidum*, mass 39 g). Both species are nocturnal, burrow-dwelling granivores that compete strongly (Abramsky *et al.*, 1985, 1990, 1991; Abramsky and Pinshow, 1989; Mitchell *et al.*, 1990; Rosenzweig and Abramsky, 1997). They respond to predatory risk as a foraging cost by reallocating foraging effort to safe times and places (e.g. Kotler *et al.*, 1991; Rosenzweig and Abramsky, 1997). They co-exist on seed resource patches that are renewed daily from the redistribution of sand and seed by the wind (G. Ben-Natan, B.P. Kotler and Z. Abramsky, in prep.) and are depleted from the foraging of gerbils each night. Various trade-offs in harvest rates and foraging costs lead to temporal partitioning of activity times between the two gerbil species (Kotler *et al.*, 1993; Ziv *et al.*, 1993). The larger species, *G. pyramidum*, forages earlier in the night and experiences richer seed patches due to its ability to get to seed patches more quickly, harvest them faster and exclude *G. a. allenbyi* from rich patches. The smaller species, *G. a. allenbyi*, forages later in the night because of its ability to forage profitably at lower seed densities than its competitor (Kotler *et al.*, 1993; Ziv *et al.*, 1993; Brown *et al.*, 1994; Kotler and Brown, 1999).

As a game, the foraging decisions of individual gerbils affect the value of foraging decisions of others. Activity by gerbils will affect the value of foraging by other gerbils by affecting resource availability and by attracting predators; activity by gerbils will affect the value of foraging by predators by providing feeding opportunities. Activity by predators will affect the value of foraging by other predators by scaring gerbils and making them less active and more apprehensive (less catchable); activity by predators will affect the value of foraging by gerbils by increasing their mortality risk. The hypothesized foraging game involves both clever predators and clever prey.

Here, our experiments focus on the prey's perspective. We seek the shadow of the predators revealed by the behaviour of the prey (Rosenzweig, 2001). In a Negev Desert nature reserve, we used experimental food patches to measure each gerbil species' giving-up densities and level of apprehension. The data allowed us to test predictions regarding how giving-up densities and apprehension should vary with time during the night, with microhabitat (bush *vs* open) and moon phase.

PREDATOR–PREY FORAGING GAME ON A PULSED RESOURCE

Here we formalize two predictions central to our foraging experiments. First, over the course of a night, gerbils should become less apprehensive. Second, gerbils should be more apprehensive in the presence of more moonlight and in the open microhabitat. While seemingly intuitive, these predictions actually require and follow from the ESS conditions of a foraging game between clever prey and clever predators when the prey forage for a pulsed and depletable resource.

Consider a prey species harvesting a pulsed resource (let R_0 be the size of the initial resource pulse). Between resource pulses, foraging activity by the prey deplete resources (let $R(t)$ describe the remaining abundance of resources at time t after the pulse). While foraging, the prey are subject to predation. The prey can elect to allocate time either to foraging or to remaining safely inactive in their burrows (let $p(t)$ be the probability that a given prey individual forages at time t). While foraging, the prey harvest resources (let harvest rate, f, be an increasing function of R) and incur risk (let risk of predation, μ (units of per time), increase with the number of active predators where $q(t)$ describes the probability that a given predator is active at time t). While foraging, the prey can use apprehension, u, to regulate food intake and safety; apprehension is the amount of attention prey individuals devote to predator detection at the expense of feeding activities. Let apprehension vary from 0 to $1 : 0 \leq u \leq 1$.

We assume that a prey's harvest rate while foraging declines with apprehension according to

$$f = (1 - u)f_{\max} \tag{1}$$

and that its risk of predation declines with apprehension according to

$$\mu = m/(k + bu) \tag{2}$$

where m is a prey's encounter rate with predators (m increases with $q(t)$ and the ease with which a predator can detect its prey), k is the inverse of the predator's deadliness in the absence of prey apprehension, and b is the benefit of apprehension in reducing predator deadliness (Brown, 1999). Equations (1) and (2) deal with ecological time and functional responses of the predators and gerbils; they assume that the population densities are fixed.

At the evolutionarily stable strategy (ESS), a prey's or a predator's strategy is the best it can do given the behaviours of the other prey and predators. To develop predictions, we will draw on three necessary conditions on behaviours that must be satisfied at the ESS:

1. The prey must, throughout the period, balance their foraging costs and benefits.
2. The prey must choose their optimal level of apprehension given resource abundances and predation risk (Brown, 1999).

3. The predators must have equal foraging opportunities throughout the night (Brown *et al.*, 2001).

The prey's objective is to manage risk by selecting its optimal activity schedule, $p^*(t)$, and level of apprehension when active, $u^*(t)$. The challenge is to balance food and safety. The predator's objective is to manage fear by selecting its optimal activity schedule, $q^*(t)$, in response to the activity and apprehension of the prey. Its challenge is to be active when prey are most apt to be encountered, but not so active that prey become too difficult to capture as a consequence of induced apprehension.

1. At each point in the night, resource abundances should provide a harvest rate f that balances the metabolic (c), predation ($\mu F/(\partial F/\partial e)$) and missed opportunity costs of foraging ($-c_0$):

$$f = (c - c_0) + \mu F/(\partial F/\partial e) \tag{3}$$

where F is survivor's fitness and $\partial F/\partial e$ is the marginal fitness value of energy, and e is the prey's energy state (Brown, 1992). Because prey foraging activity can only deplete resources ($R(t)$ must decline or remain constant with time), for sustained foraging activity by the prey, $f_{\max}$ *must decline with time following the resource pulse*. And to maintain the balance of costs and benefits in equation (3), μ *must decline*. These reductions occur because predator activity declines with time ($q(t)$ declines with t), as we shall see below.

2. The optimal level of apprehension, u^*, at any point in time satisfies (Brown, 1999):

$$u^* = \sqrt{\frac{mF}{bf_{\max}(\partial F/\partial e)}} - k/b \tag{4}$$

If this expression yields values greater than 1 or less than 0, then the optimal level of apprehension is simply 1 and 0, respectively.

How does the optimal level of apprehension change with time? Equation (4) is ambiguous because both encounter rate with predators, m, and maximum foraging rate, $f_{\max}$, decline with time – each with opposite effects on u^*. To see how net apprehension changes with time, we need to make a number of substitutions. Equation (2) for μ can be substituted into equation (3). Furthermore, $f = (1 - u)f_{\max}$ can be substituted into equation (3) to form an expression for $f_{\max}$ that, in turn, can be substituted into equation (4). The resulting expression can be arranged as:

$$(u^*)^2 = \frac{(1-u)mF(k+bu)}{b(\partial F/\partial e)(c-c_0)(k+bu)+mF} - k/b \tag{5}$$

While equation (5) has not been written as an explicit function of u, it is monotonic in m for values of u on the interval [0,1] (this requires that $b > 1$, otherwise apprehension is useless). *As m and $f_{\max}$ decline with time, the apprehension level of those prey actively foraging also declines.*

The prey's encounter rate with predators, m, has three components:

- The activity level of the predators, q.
- The total number of predators in the population, P.
- The ease with which an active predator can detect a prey, a.

Combining, $m = aqP$.

How does changing the prey encounter rate with its predators influence prey apprehension? In the present experiment, this question is relevant because moonlight may make it easier for owls to detect rodents (Kotler *et al.*, 1988; Longland and Price, 1991). To evaluate this effect, we must consider how increasing a (by increasing moonlight, for instance) influences the activity of prey and predators, and the depletion of resources.

3. The predators equalize opportunity throughout the night. That is, at each point in the night, the predators have the same expected harvest rate, and this harvest rate, θ, must just balance their foraging costs (Brown *et al.*, 1999). The constant harvest rate results from the predator's adjustment of its ESS level of activity, and the concomitant effects this has on prey apprehension and activity levels. The predator's constant harvest rate is:

$$\theta = \mu pN/qP \tag{6}$$

where N is population density of prey. The right-hand side of (6) gives the expected harvest rate of an actively foraging predator individual (the numerator gives the rate at which all of the actively foraging predators kill prey, and the denominator divides this among the active predators).

We can substitute aqP for m into equation (2), and equation (2) for μ into equation (6):

$$\theta = apN/(k + bu) \tag{7}$$

As the predator's encounter rate with prey increases, the prey must either become less active ($p^*(t)$ declines) and/or the prey must become more apprehensive ($u^*(t)$ increases) to maintain the ESS condition given by equation (7). Although (7) need only be true within a single night, it will remain the same across nights so long as the population sizes and energy states of the prey and predators change very little from night to night. Either a reduction in prey activity or an increase in prey apprehension will cause a reduction in the rate at which the prey deplete resources. Hence, as a increases, $f_{\max}(t)$ increases. This ensures an increase in $u^*(t)$. *If the predator's encounter rate with their prey varies from pulse to pulse, then the prey will reduce resources more slowly and be more apprehensive during those pulses with higher predator encounter rates.*

If moonlight increases the encounter rate of predators on gerbils, then we expect gerbils to be more apprehensive on nights with full moon than on nights with no moon. Waning (moonrise during the night) and waxing (moonset during the night) moons provide opportunities for predator encounter rates to increase and decline, respectively, during the night. In the case of a waxing moon, apprehension should be high early in the night and drop precipitously as both resources and the predator's encounter rate decline. In the case of a waning moon, apprehension should remain flatter during the night, as there is an inverse relationship during the night between resource abundance and the predator's encounter rate. In a similar manner, we may expect gerbils to be more apprehensive in the open microhabitat where encounter rates are higher than in the bush microhabitat. For instance, owls appear to be more effective and deadly with moonlight and in the open microhabitat (Kotler *et al.*, 1988; Longland and Price, 1991).

Overall, at the ESS, gerbils and their predators should adjust their activity such that the risk to a foraging gerbil per gram of seed harvested remains constant during the night (Brown *et al.*, 2001). Apprehension enters into the ESS conditions through its effect on prey harvest rates and on risk of predation. As resources decline, the ESS solution is for the activity of both prey and predators to decline, apprehension on the part of the gerbils to decline and the catchability of prey to increase. The rate and extent to which prey deplete resources should decrease with predator deadliness and increase with the effectiveness of apprehension. These strongly linked patterns of resource depletion, gerbil activity and apprehension are adjusted for moon phase and bush/open microhabitats through their effects on mortality inflicted by the predators.

In the two experiments that follow, we provide tests for some of the assumptions and some of the predictions of the theory outlined above. We focus on the links between resource availability, gerbil activity and apprehension in the context of moonphase and microhabitat. We do not examine directly the issue of predator activity patterns. In the first experiment, we test the assumption of nightly depletion of seed resources by gerbils. We also examine how resource depletion is modified by moon phase and microhabitat. In the second experiment, we measure the activity and apprehension of gerbils during the night as influenced by moon phase and microhabitat. We verify that: (1) the temporal depletion of seeds is gradual during the night, but more rapid in the bush microhabitat than in the open, and more rapid during no moon than full moon; (2) gerbil apprehension declines with time during the night; (3) gerbil apprehension is higher in the open than in the bush microhabitat, with this difference declining during the night; and (4) gerbil apprehension increases with moonlight both within and among nights.

GAUGING APPREHENSION

In the foraging game played out between a forager and its predator, apprehension is one tool available to the clever forager. We define apprehension as attention redirected from foraging to predator detection in a manner that lowers both predatory risk and feeding rate (Brown *et al.*, 2001). The greater an animal's apprehension, the greater its ability to detect a predator, but the poorer its ability to harvest resources (Dall *et al.*, 2001). Vigilance is a special case where apprehension is total (i.e. no foraging at all occurs when an animal is vigilant). The optimal level of apprehension balances reductions in risk with reductions in harvest rates (Brown, 1999). Thus, apprehension should increase when predators are more deadly and where predators are more likely to be encountered (Brown, 1999; Brown *et al.*, 1999).

The apprehensiveness of a forager can be difficult to measure in nature. One might simply use the giving-up density in a food patch (Brown, 1988). However, things other than risk may change over the course of a night, so it would be best to have a measure that is independent of total foraging effort. To obtain it, we can take advantage of how apprehension involves a redirection of attention from a variety of foraging tasks, including the forager's ability to detect the boundaries of resource patches or to estimate resource densities (vague boundaries; Schmidt and Brown, 1996; Fierer and Kotler, 1999). For instance, we expect apprehensive foragers to be less able to estimate the scale of patchiness. The direction of the error matters little – overestimation or underestimation of patch size – as both reduce harvest rates.

The more demanding the foraging task in terms of patch assessment, search and harvest, the more patch performance should decline with apprehension. One can reveal changes in apprehension by offering a forager paired food patches that differ in complexity and thus in how demanding they are to the forager. Here we use two patch types, one in which seeds were mixed randomly into a sand substrate ('full tray') and the other in which the same aliquot of seeds was mixed randomly into the sand of the bottom half of the patch ('bottom tray'). The latter patch is more demanding in two respects: first, it is harder to search for seeds lower in the substrate and, second, there is an advantage to assessing the boundary line between the upper half without food and the lower half with all of the food (Schmidt and Brown, 1996).

As apprehension increases, the value of the full tray should increase relative to the bottom tray. To direct its foraging to the micropatch at the bottom of such a tray, a gerbil must dig past a great deal of sand devoid of seeds. Only then can it search effectively for food. Going too far would make it more likely to miss seeds; not going far enough would cause it to begin searching at a depth devoid of seeds. Both types of mistakes lower harvest rates and patch value (Schmidt and Brown, 1996). More importantly, both types of mistakes should be more likely for an animal directing its attention to predator detection. In addition, digging through sand is likely to make it more difficult for a gerbil to detect an approaching predator, further aggravating the decline in foraging performance with apprehension. With increasing apprehension, the forager should be less able to distinguish the boundaries of micropatches, making the bottom tray less valuable and leading the gerbil to exhibit more and more selectivity for the full tray relative to the bottom tray. Hence, selectivity for the seeds of the full tray relative to the bottom tray measures apprehension in the experiments.

METHODS

We performed experiments at Bir Asluj, Holot Mashabim Nature Reserve, Negev Desert, Israel. The area contains mosaics of stabilized and semi-stabilized sand on longitudinal sand dunes. The dominant perennial plant species are *Artemesia monosperma* and *Retama raetam*. *Gerbillus andersoni allenbyi* and *G. pyramidum* are the two most common species of rodents, with *G. henleyi* (pygmy gerbil, mass 12 g), *Meriones sacramenti* (Buxton's jird, mass 120 g) and *Jaculus jaculus* (common jerboa, mass 55 g) also present, but rare. Barn owls (*Tyto alba*) and red foxes (*Vulpes vulpes*) are common predators in the area and frequently roost or den nearby.

Resource depletion experiment

The foraging game predicts a decline in gerbil activity during the night as resources wane. It further predicts that the schedule of resource depletion will change with moon phase through its effect on the risk of predation. To test these predictions, we used two 2.56 ha grids which we have studied since 1986. The grids contain a mix of stabilized and semi-stabilized sand habitats. For live-trapping, trap stations were arrayed 9×9 with 20 m between stations. Within the 9×9 layout, we set seed-tray stations at the intersections of even numbered rows and columns (4×4 layout with 40 m between stations).

We wished to determine the rates of depletion of seed resources during the course of the night as a function of hour, microhabitat and moon phase. To do this, we selected six seed-tray stations per grid (total of 12). At each station, we arranged six seed trays like spokes on a wheel (this reduces edge effects, if any). Each seed tray was provisioned with 3 g of millet seed mixed randomly into 5 litres of sifted sand. For bush and open microhabitats, we placed the trays of half of the stations in the open (open microhabitat) and the trays of the other half around a large shrub (bush microhabitat). Every 2 h during the night, we visited each station, selected one tray at random from each station, identified tracks to species on that tray, and collected the remaining seeds from the tray. These seeds were returned to the laboratory, cleaned of sand and debris, and weighed. Revisiting stations and harvesting the next tray six times during the night gave us temporal snapshots of patch depletion. We repeated this for two nights at each moon phase of full, waning half moon, new and waxing half moon. On the second night of each two-night sequence, we switched the microhabitat of the trays of a station. We ran the experiment during November and December 1998.

Apprehension experiment

The most novel predictions of the theory concern how gerbil apprehension changes with resource depletion during the night, with microhabitat and with moon phase. We measured apprehension using the selectivity of gerbils for seed trays with different micropatch structure.

Four seed trays were present at each station, a pair in each microhabitat. One tray of each pair had seeds mixed throughout the sand of the entire tray ('full tray'). The other had seeds mixed into half of the sand of the tray and then spread along the bottom of the tray, with the remaining sand (containing no seeds) spread over the top ('bottom tray').

We used selectivity for the full tray as our gauge of apprehension. An increase in apprehension should be manifested as an increase in selectivity for the full tray. In support of this metric, we note that fox squirrels (*Sciurus niger*) became more selective for a full tray compared with a micropatch tray when patches were shifted from near trees (safe) to away from trees (risky) (Schmidt and Brown, 1996).

We used Manly's index to calculate selectivity for the full tray versus that for the bottom tray (Chesson, 1983; Schmidt and Brown, 1996):

$$\frac{\{\ln \text{proportion of seeds remaining in full tray}\}}{\begin{array}{c}\{\ln(\text{proportion of seeds remaining in bottom tray}) + \\ \ln(\text{proportion of seeds remaining in full tray})\}\end{array}}$$

We expect selectivity for the full tray to be greater than 0.5, and this selectivity should increase with the forager's apprehension.

Using the two types of trays, we performed experiments in July and August 1998. We used a single grid and placed seed trays at all 16 seed-tray stations. At each station, we placed four trays: a pair (full tray and bottom tray) in the bush microhabitat and another pair in the open. We divided the 16 stations into 4 four-station sub-grids. Every $2\frac{1}{4}$ h over the course of the night, we opened the trays of one of the stations of each sub-grid (four stations at a time across the grid), allowed the gerbils to forage and then collected the remaining seeds from all four trays from each of the four stations $2\frac{1}{4}$ h later. Before collecting seeds from a tray, we identified the tracks in the tray's sand to species. We then sifted the remaining seeds from the tray and returned them to the laboratory, where seeds were cleaned and weighed.

In each time period of the night, we ran a total of 16 trays arrayed at four stations; each night, we collected data from four time periods for a nightly total of 64 trays. Over the course of four nights, we rotated the time period of each station of a sub-grid according to a Latin square. We repeated each four-night Latin square at the new moon, waxing half moon, full moon and waning half moon. We then repeated data collection at each moon phase twice. Altogether, this yielded 32 nights of data.

We analysed the data using log-linear models of multi-way contingency tables for number of trays foraged (indicated as G statistics), and partially hierarchical analysis of variance (indicated as F statistics) for amounts of seeds remaining in trays (log-transformed for normality).

RESULTS

The two experiments provide information on the effects of time of night, microhabitat, moon phase and gerbil species on patch depletion (resource depletion experiment) and apprehension (apprehension experiment).

Resource depletion experiment

To analyse the amount of seeds remaining, we used moon phase, day, microhabitat and time period within the night as independent variables in a partially hierarchical analysis of variance (ANOVA) where day is nested within moon phase and all other variables are fully crossed. To analyse the data on the number of trays visited, we used a log-linear analysis on a multi-way contingency table formed by all combinations of time period within the night, moon phase, species, microhabitat and the number of trays foraged. The amount of seeds found in trays at each time period declined gradually during the night (MS = 3.403, $F_{1,340} = 10.38$, $P < 0.001$; Fig. 1). More seeds were harvested in the bush than the open microhabitat (MS = 3.129, $F_{1,340} = 9.543$, $P = 0.002$; Table 1). Also, more seeds were harvested during new moon than during the other moon phases (MS = 7.176, $F_{3,4} = 9.43$, $P < 0.01$; Table 1). Finally, resource depletion was more rapid and more complete during new moon than during the other moon phases (time × moon phase interaction: MS = 0.66, $F_{15,340} = 2.011$, $P = 0.014$; Fig. 1). These values indicate how resource availability changes during the night.

The two gerbil species differed in their foraging patterns during the night (based on frequencies of trays foraged) and in their rates of resource depletion at the stations that each frequented (based on seeds remaining in the tray). To allow meaningful comparisons between the species (i.e. to avoid excessive numbers of empty cells), we based our analysis of seeds remaining in trays on mean values for each moon phase according to time period, species and microhabitat. We recognized three categories for species: stations at which the tracks of *G. a. allenbyi* only were visible in the sand of the tray, stations at which the tracks of *G. pyramidum* only were visible, and stations at which the tracks of both were visible.

The observed pattern of resource depletion and activity of the gerbil species mostly conformed to previous observations (e.g. Brown *et al.*, 1994). For moon phase, gerbils visited more trays during the full moon and waning half moon (moon rise around midnight) and less during waxing half moon (moon set around midnight) and new moon (number of trays foraged × moon phase: $G = 21.78$, d.f. = 3, $P < 0.001$; Table 2). Although this last result

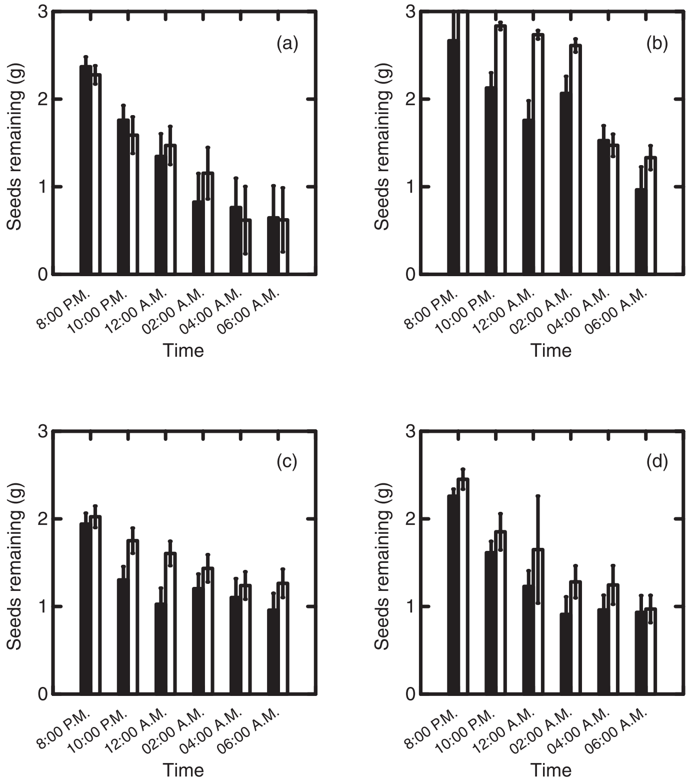

Fig. 1. Amount of seeds remaining (g) in the resource depletion experiment (means are back-transformed; standard error bars reflect the natural log-transformed data) as a function of time of night and according to microhabitat (bush or open) for (a) new moon, (b) waxing half moon, (c) full moon and (d) waning half moon phases. ■, bush; □, open microhabitat.

is surprising, the gerbils nonetheless exploited seed trays more thoroughly during the new moon and waning half moon than the waxing half moon and full moon (amount of seeds left in trays: $F_{3,44} = 9.743$, $P = 0.001$). For time of the night, the number of seed trays visited increased over the course of the night (number of trays foraged × time period: $G = 24.55$, d.f. = 5, $P < 0.001$; Table 2) and the amount of seeds remaining in trays generally declined ($F_{5,44} = 8.88$, $P < 0.001$; Fig. 1). These results reflect resource depletion in the trays and in the environment during the course of the night.

In terms of species, *G. a. allenbyi* visited more trays than *G. pyramidum* ($G = 354.62$, d.f. = 2, $P < 0.001$) by virtue of being far more common. More importantly, *G. pyramidum* visited trays earlier in the night than *G. a. allenbyi* (number of trays foraged × species × time: $G = 21.70$, d.f. = 10, $P < 0.025$; Table 2) and thereby encountered a richer environment (trays visited only by *G. pyramidum* in a given time period tended to be richer than those visited by *G. a. allenbyi* or by both species; MS = 0.317, $F_{2,44} = 2.402$, $P = 0.05$, one-tailed test; Fig. 2). These results are in keeping with *G. pyramidum* arriving at resource patches earlier and operating in an effectively richer environment than *G. a. allenbyi*, as reported previously (e.g. Kotler *et al.*, 1993; Ziv *et al.*, 1993). Finally, *G. pyramidum* visited more seed trays

Table 1. Mean (back-transformed) amount of seeds remaining in a tray in the patch depletion experiment according to moon phase and microhabitat

	Microhabitat			
	Bush		Open	
Moon phase	Mean	Standard error	Mean	Standard error
New	0.585	0.124	0.666	0.124
Half-wax	0.965	0.087	1.439	0.053
Full	1.091	0.074	1.302	0.061
Half-wane	1.079	0.079	1.164	0.075

Note: The standard errors are for the log-transformed data.

Table 2. Number of trays foraged according to moon phase, microhabitat, species and time period for the resource depletion experiment

		Species					
		G. a. allenbyi		*G. pyramidum*		Both	
Moon phase	Time	Bush	Open	Bush	Open	Bush	Open
New	1	3	2	1	0	1	2
	2	2	4	1	1	2	1
	3	6	6	0	0	1	1
	4	8	5	0	0	0	1
	5	7	8	1	0	0	1
	6	9	8	0	1	0	0
Half-wax	1	2	1	0	0	0	1
	2	4	1	0	0	0	0
	3	5	0	0	1	0	1
	4	3	3	0	0	0	0
	5	9	10	0	0	0	0
	6	8	8	1	1	0	1
Full	1	4	4	1	0	3	3
	2	9	4	2	0	1	2
	3	10	7	0	1	0	2
	4	8	7	2	1	0	2
	5	10	9	0	1	1	1
	6	10	9	1	2	0	0
Half-wane	1	6	3	1	0	0	0
	2	7	5	3	0	1	1
	3	7	8	3	1	0	0
	4	8	7	2	2	1	0
	5	9	8	2	1	0	0
	6	9	9	1	3	1	0

Note: Time represents sequential 2 h time periods after sunset. See Fig. 1.

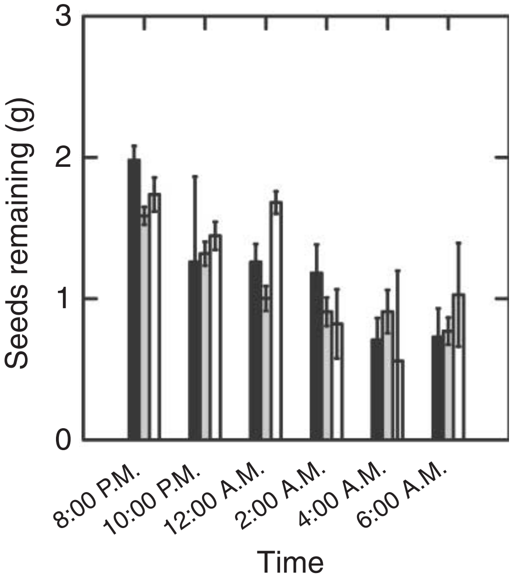

Fig. 2. Amount of seeds remaining (g) in the resource depletion experiment (means are back-transformed; standard error bars reflect the natural log-transformed data) as a function of time of night and species. □, *Gerbillus pyramidum*; ▨, *G. a. allenbyi*; ■, both species.

during the riskier conditions of full and waning half moon than during the new and waxing half moon, especially compared with *G. a. allenbyi* ($G = 16.22$, d.f. = 6, $P < 0.025$; Table 2).

Apprehension experiment: activity levels and seeds harvested

To examine foraging in the apprehension experiment, we start with the intensity of foraging activity as revealed by the numbers of trays foraged and the amounts of seeds left in resource trays. We used similar ANOVA and log-linear models as in the previous experiment to analyse seeds remaining in patches and frequency of patch visits, respectively. Because of the nature of the apprehension experiment (fresh trays presented in every time period), these data better reflect the potential intensity of activity in each time period.

As in the previous experiment, gerbil foraging was affected by moon phase and time of night. Fewer feeding trays were foraged during full moon and waning half moon than during the waxing half moon or new moon (number of trays foraged × moon phase: $G = 30.95$, d.f. = 3, $P < 0.001$; Table 3). The number of trays foraged and the intensity of patch use declined with time of night (number of trays foraged × time period: $G = 23.98$, d.f. = 3, $P < 0.001$; number of trays foraged × time period × microhabitat: $G = 15.34$, d.f. = 3, $P < 0.001$, Table 3; amount of seeds remaining in trays: MS = 1.838, $F_{3,2489} = 8.686$, $P < 0.001$, Fig. 3).

The high abundance of *G. a. allenbyi* relative to *G. pyramidum* meant that *G. a. allenbyi* visited more trays in total ($G = 1034.80$, d.f. = 2, $P < 0.001$; Table 3). More interestingly, we observed a time × moon phase interaction in both number of trays foraged ($G = 54.77$, d.f. = 9, $P < 0.001$; Table 3) and intensity of seed tray use (amount of seeds remaining: MS = 2.58, $F_{9,2489} = 12.192$, $P < 0.001$, Fig. 3). At full moon, the number of trays visited was

Table 3. Number of trays foraged according to moon phase, microhabitat, species and time period for the temporal changes in the apprehension experiment

		Species					
		G. a. allenbyi		*G. pyramidum*		Both	
Moon phase	Time	Bush	Open	Bush	Open	Bush	Open
New	22:15	42	41	30	25	18	26
	24:30	63	64	22	24	7	5
	02:45	80	82	11	6	5	6
	05:00	87	79	4	8	0	3
Half-wax	22:15	27	21	29	23	15	27
	24:30	55	55	26	26	15	14
	02:45	79	82	16	10	0	4
	05:00	84	86	9	6	1	1
Full	22:15	21	19	16	8	20	25
	24:30	28	18	10	12	22	15
	02:45	50	42	14	24	21	17
	05:00	66	68	10	6	7	12
Half-wane	22:15	35	32	26	29	30	28
	24:30	54	48	22	20	14	21
	02:45	39	46	22	18	9	11
	05:00	50	48	15	11	8	13

low, but tended to increase throughout the night. Also, foraging intensity within patches tended to increase in those patches that were visited. At new moon, activity was uniformly high, with perhaps a slight decline towards dawn. Similarly, the intensity of patch use decreased at the end of the night. For half moon, the number of seed trays visited and intensity of patch use declined during the waning moon (moon present in the second half of the night) and vice versa for the waxing moon. In general, tray use intensified with increased darkness regardless of time of night.

The number of seed trays visited also showed temporal partitioning. As the night progressed, the number of trays foraged by *G. a. allenbyi* compared to those foraged by *G. pyramidum* increased ($G = 326.30$, d.f. = 6, $P < 0.001$; Table 3). In addition, the number of trays visited showed that the species respond differently to changes in moon phase ($G = 120.02$, d.f. = 6, $P < 0.001$; Table 3); *G. a. allenbyi* was more sensitive to moon phase than *G. pyramidum*. Finally, the number of trays visited was affected by the interaction of time, moon phase and species ($G = 80.01$, d.f. = 18, $P < 0.001$; Table 3). For *G. a. allenbyi*, the number of trays visited increased during the night at both full and waxing half moon. The number of trays visited changed little during the night for the waning half moon. Activity was high at new moon.

For *G. pyramidum*, the number of trays visited at full moon was low and varied little during the night. A waxing half moon yielded a high number of seed trays visited early in

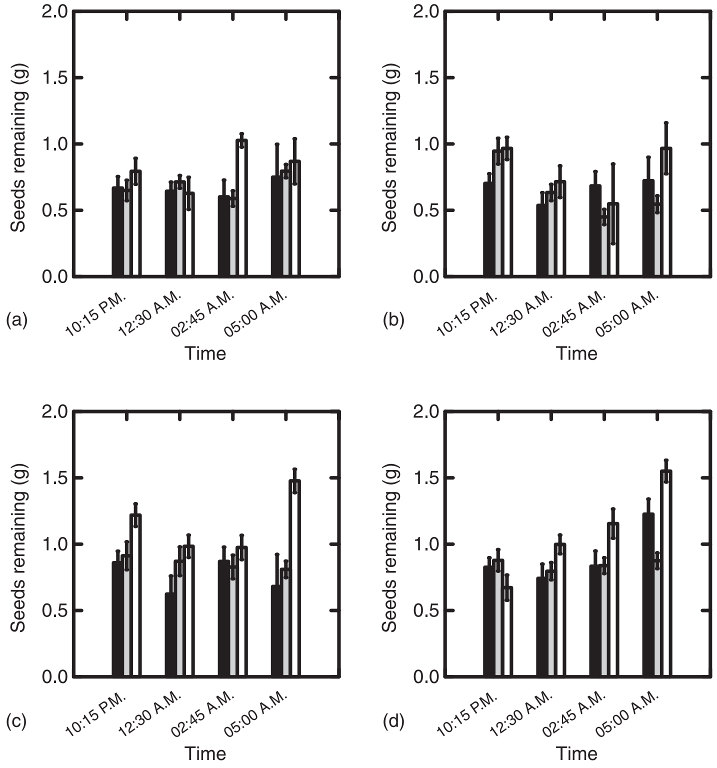

Fig. 3. Amount of seeds remaining (g) in the apprehension experiment (means are back-transformed; standard error bars reflect the natural log-transformed data) as a function of time of night and species for (a) new moon, (b) waxing half moon, (c) full moon and (d) waning half moon phases. □, *Gerbillus pyramidum*; ▨, *G. a. allenbyi*; ■, both species.

the night, while both new moon and the waning half moon yielded declining activity during the night. Overall, temporal partitioning was most extreme during the new moon and the waxing half moon. The end of nights with new moon or waxing half moon were dominated by *G. a. allenbyi* when risk and resource availability were lowest. Temporal partitioning was less extreme during full moon and the waning half moon, when moonlight imposed greater risk later in the night.

The interaction of microhabitat and moon phase (MS = 0.569, $F_{3,2489} = 2.69$, $P = 0.045$; Fig. 4) reflects avoidance of the open microhabitat at full moon and the lack of microhabitat effects at other moon phases.

Apprehension experiment: selectivity for different tray types

We now examine changes in apprehension using the selectivity metric. As predicted by the theory of the foraging game, the selectivity of the gerbils for the ‘full tray’ decreased throughout the night until the last time period near dawn when it unexpectedly rose (Tables 4 and 5). Moon phase had a similar effect on selectivity (apprehension), with gerbils

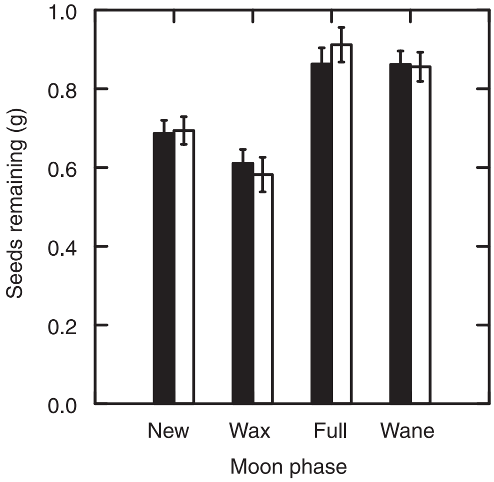

Fig. 4. Amount of seeds remaining (g) in the apprehension experiment (means are back-transformed; standard error bars reflect the natural log-transformed data) as a function of microhabitat and moon phase. ■, bush; □, open microhabitat.

showing greatest selectivity (most apprehension) at full moon and lowest selectivity (least apprehension) at new moon (Tables 4 and 5).

There was a small, but significant effect of microhabitat on selectivity. Although the unadjusted means are nearly identical for the bush and open microhabitats (0.565 ± 0.008 and 0.562 ± 0.007 respectively; mean ± standard error), the adjusted least square means show that gerbils are more selective (more apprehensive) in the open (0.591 ± 0.010) than in the bush (0.559 ± 0.011) microhabitat.

We observed two significant interactions and one non-significant trend. The first significant interaction included time of night and microhabitat (Tables 4 and 5). Early in the night, gerbils showed more selectivity (greater apprehension) in the bush than in the open microhabitat. Thereafter, they showed more selectivity (greater apprehension) in the open. The second significant interaction was between time of night and moon phase (Table 4, Fig. 5). Schedules of selectivity (apprehension) over the course of the night changed according to moon phase. During the new moon, selectivity was low (apprehension was low) and changed little during the night; during the waxing half moon when the early hours of the night were moonlit, gerbils were more selective (more apprehensive) early in the night, but less selective (less apprehensive) after the moon had set. During the full moon, gerbils showed a particularly high selectivity (especially apprehensive) early in the night. During the waning half moon when the early hours of the night were dark, selectivity was low (apprehension was low) early and later increased.

A trend involved a three-way interaction of time of night, moon phase and gerbil species (Table 4, Fig. 6). Part of this result comes from trays that both species exploited. To the extent that the trend is real, *G. a. allenbyi* tended to manifest more selectivity (more apprehension) than *G. pyramidum* early in the night and *G. pyramidum* more than *G. a. allenbyi* later on.

Table 4. ANOVA table for the temporal changes in the apprehension experiment, with selectivity for the micropatch (either 'full' or 'bottom') tray as the dependent variable

Source	d.f.	MS	*F*	*P*
Moon phase	3	0.129	3.794	0.028
Date {moon phase}	28	0.034	1.897	0.004
Grid	3	0.385	1.921	< 0.40
Station {grid}	12	0.271	15.251	< 0.001
Time	3	0.087	4.878	0.002
Microhabitat	1	0.082	4.596	0.032
Species	2	0.002	0.097	0.908
Moon phase × microhabitat	3	0.017	0.942	0.420
Moon phase × time	9	0.034	1.904	0.048
Moon phase × species	6	0.029	1.623	0.138
Time × microhabitat	3	0.060	3.348	0.019
Time × species	6	0.013	0.755	0.605
Microhabitat × species	2	0.023	1.314	0.269
Moon phase × microhabitat × species	6	0.011	0.616	0.718
Moon phase × microhabitat × time	9	0.020	1.142	0.330
Moon phase × time × species	18	0.028	1.588	0.057
Time × microhabitat × species	6	0.027	1.535	0.164
Error	780	0.018		

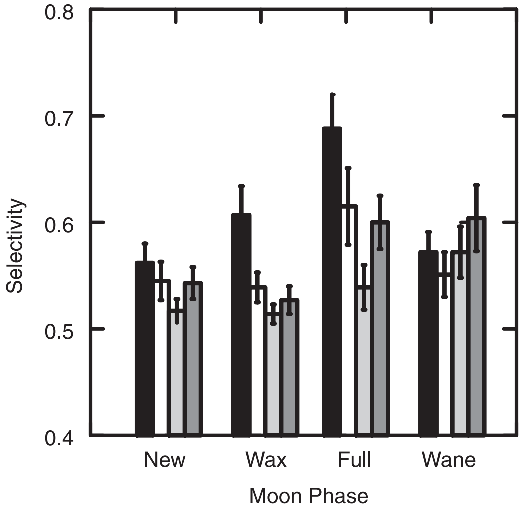

Fig. 5. Selectivity in the apprehension experiment according to moon phase and time of night. ■, 22:15 h; □, 24:30 h; ▒, 02:45 h; ▓, 05:00 h.

Table 5. Values for selectivity (used to gauge the level of apprehension) according to time of night, moon phase and the interaction of moon phase and microhabitat (mean ± standard error)

	Time (h)			
	22:15	24:30	02:45	05:00
Selectivity	0.609 ± 0.013	0.557 ± 0.012	0.537 ± 0.010	0.571 ± 0.012

	Moon phase			
	New	Half-wax	Full	Half-wane
Selectivity	0.546 ± 0.009	0.554 ± 0.010	0.612 ± 0.015	0.572 ± 0.013

	Moon phase							
	New		Half-wax		Full		Half-wane	
Microhabitat	Bush	Open	Bush	Open	Bush	Open	Bush	Open
Selectivity	0.544 ± 0.015	0.549 (0.013)	0.560 (0.015)	0.547 (0.013)	0.614 (0.022)	0.609 (0.019)	0.573 (0.018)	0.571 (0.019)

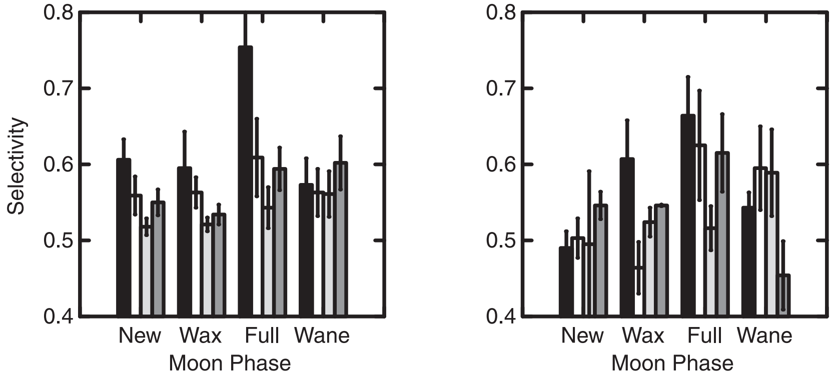

Fig. 6. Selectivity in the apprehension experiment according to moon phase, time of night and species: (a) *G. a. allenbyi*, (b) *G. pyramidum*. ■, 22:15 h; □, 24:30 h; ▒, 02:45 h; ▓, 05:00 h.

DISCUSSION

The foraging game between gerbils and their predators begins with a daily pulse of seeds created by wind-blown sand and the subsequent depletion of this seed pulse by gerbils. Seeds are produced only once a year on the sand dunes of Bir Asluj in response to winter rains. This annual crop ripens through the spring, rarely lasting into the early summer. It rapidly disappears from plants and from the surface of the ground due to primary dispersal of seeds by water and wind and exploitation and secondary dispersal by migratory birds and resident birds, ants and mammals. The dispersed seeds enter the seed bank. Thereafter, seeds are made available by winds that blow nearly every afternoon (G. Ben-Natan, B.P. Kotler and Z. Abramsky, in prep.). Wind creates new seed patches by uncovering, redistributing and depositing seeds in wind shadows and depressions. This sets the stage for the nightly depletion of seeds and the foraging game between gerbils and their predators.

When modelling such a system in which resources are produced in temporal pulses, several predictions emerge. They include a tight linkage between depletion of resources by the gerbils, declining gerbil activity, declining predator activity and declining apprehension by gerbils. They also include shifts of schedules of gerbil activity and apprehension according to changes in environmental conditions that alter predator deadliness or the effectiveness of apprehension in reducing predator deadliness.

$f_{\max}$ must decline with time following the resource pulse. This prediction requires that the activity of the prey and that of the predators decline as resources are depleted. Results from the first experiment show that resources are depleted by the gerbils over the course of the night. The patterns of resource depletion from the first experiment closely matched patterns of gerbil activity from the second experiment. Gerbil activity at new moon was high throughout most of the night, but decreased towards dawn.

As m and $f_{\max}$ decline with time, the apprehension level of those prey actively foraging also declines. Apprehension is one of two tools available to foragers for managing risk (Brown, 1999; Brown *et al.*, 2001). Heightened apprehension improves the prey's detection of predators. However, it diminishes harvest rates and the forager's ability to accurately assess patch value. In the case of *G. a. allenbyi*, increased apprehension leads to more random search paths in the foraging patch with greater re-sampling of areas previously foraged (Dall *et al.*, 2001). This should lead to a lower harvest rate of resources. Because of the benefits of apprehension in increased predator detection and the cost of lower harvest rates, there should be an optimal level of apprehension (Brown *et al.*, 2001).

To reveal evidence for the gerbils' use of apprehension, we used the ability of gerbils to respond to micropatch structure as evidenced by seeds removed from full trays relative to bottom trays. Schmidt and Brown (1996) found that the ability of squirrels to take advantage of micropatches declined as food patches were moved from a safe to a risky microhabitat. We have preformed experiments in a large aviary in which we experimentally manipulated the risk of predation and observed changes in the selectivities of gerbils that are consistent with our suggestion that they reflect apprehension (J.S. Brown and B.P. Kotler, in prep.). And, as we note in the next paragraph, changes in selectivities in the gerbils for full patches relative to bottom patches quantified the gerbils' response to micropatch structure and followed closely the predictions of the foraging game, strongly suggesting that changes in such selectivities reflect changes in apprehension.

Apprehension for both species of gerbils increased in circumstances when encounter rates with predators should be high. Apprehension was highest early in the night when seed resources, gerbil activity and, presumably, predator activity were highest. The high availability of resources early in the night causes high gerbil activity, which, in turn, attracts predators. To this, the gerbils respond with heightened apprehension.

The prey will reduce resources more slowly and be more apprehensive during resource pulses offering predators higher encounter rates on their prey. The gerbils deplete seeds more quickly under safe than risky circumstances. Gerbils depleted seed resources more quickly in the bush than the open microhabitat, where the gerbils are more exposed to predators, and more quickly at new moon than at other moon phases, when moonlight renders predators more deadly (Kotler *et al.*, 1988, 1991). In contrast, activity at full moon (slow depletion) was generally low, but increased towards dawn. Gerbil activity according to time of night, moon phase and microhabitat tended to reflect patterns of apprehension. Apprehension was higher at full moon than new moon, and our work and that of others has demonstrated that predators such as the barn owls present at the field site are more deadly in moonlight (e.g. Kotler *et al.*, 1988, 1991; Longland and Price, 1991). Apprehension was higher in the exposed open microhabitat, where owls are also more deadly and encounter prey more readily (Kotler *et al.*, 1988; Longland and Price, 1991). Encounter rates with predators should be high in both these contexts.

Interestingly, while apprehension was generally higher in the open microhabitat, it was higher in the bush microhabitat at the beginning of the night. Why this is so remains unclear, but possible explanations include predators directing their attacks towards the bush microhabitat early in the night when gerbil activity there was highest and the shifting activities of owls and snakes during the night (Bouskila, 2001; E. Shani, unpublished data). Also, contrary to predictions, gerbils showed heightened apprehension and low activity just before dawn. Low activity is easy to explain, since it is seen after a night of foraging and resource depletion. But we can only speculate as to the causes for heightened apprehension. Perhaps it is a response to increased predator deadliness as the sky gradually lightens and prey become easier to spot. Or perhaps it is due to greater predator activity as foxes and owls run up against the time horizon and take one last pass. Or perhaps it is a response to vipers as they set their last ambushes for the night. The behaviour of the gerbils provides fertile ground for new testable hypotheses.

Gerbils were also more apprehensive in the open microhabitat and at full moon. Heightened apprehension at full moon, even though gerbil activity was low, suggests that gerbils were responding to greater predator deadliness, just as theory suggests they should. In contrast, the high gerbil activity and the rapid resource depletion seen at new moon should have attracted more predators compared with full moon, yet gerbils were more apprehensive under full moon. Although gerbils were often most apprehensive when they were most active, the pattern is heavily modified by predator deadliness, and indicates complex foraging strategies.

Two interacting prey species and the foraging game. The experimental system provided us with the opportunity to examine empirically the foraging game with two prey species, *G. a. allenbyi* and *G. pyramidum*. These species are involved in a competitive game with each other, as well as in their game with the predator. Although the theory so far provides for a single predator species and a single prey, we already have expectations regarding timing of activity and apprehension for each species. The two species co-exist through the partitioning of temporal variability in the shared habitat (Kotler *et al.*, 1993; Ziv *et al.*, 1993). The theory underlying this mechanism predicts that the species will show nested periods of activity for pure exploitation competition, and temporal partitioning when interference (interference becomes an additional cost of foraging for the subordinate species) is involved. In temporal partitioning, each species directs its activity to times and resource availabilities at which it is superior to its competitor (Brown, 1989). Individuals forage when their harvest rates are higher than their energetic, predation and interference costs, with all of these costs being affected by the activity of other foragers. This is one of the conditions that must be satisfied at the ESS and helps to tie the competitive foraging game to the predator–prey game. Here, we might expect foragers to direct their attention away from foraging and towards apprehension when apprehension is more valuable or foraging is less valuable and vice versa.

Time allocation led *G. pyramidum* and *G. a. allenbyi* to partition nights, moon phase and microhabitats in a manner consistent with the former gerbil being better at interference competition, better at evading predators and less good at foraging profitably on low resource abundances than the latter gerbil (Abramsky *et al.*, 2001). *Gerbillus pyramidum* visited resource patches earlier in the night and encountered a richer, but more risky environment; *G. a. allenbyi* foraged later in an environment with fewer seed resources, but lower risk. The same pattern extended over moon phases. *Gerbillus pyramidum* foraged relatively more at full and waning half moon. This resulted in the most extreme temporal partitioning occurring at new and waxing half moon.

The timing of activity differed between the two gerbil species, as may have the timing of apprehension. As we have previously demonstrated, the two gerbils partition the night, with *G. pyramidum* being relatively more active early in the night and *G. a. allenbyi* being more active later on. Temporal partitioning was most extreme during new moon and waxing moon. At the same time, patterns of apprehension also tended to change with moon phase. Moonlight early in the night meant that apprehension was higher then, too; moonlight later in the night meant that apprehension was higher later on.

The trend from the interaction of species, moon phase and time observed in the second experiment suggests that schedules of apprehension differed between the two gerbil species.

Although patterns of apprehension of both species changed with moon phase, *G. a. allenbyi* tended to show more apprehension in the early hours of the night than its competitor and vice versa. That is, the times at which one species was relatively more active than its competitor coincide with the times at which it was relatively less apprehensive. This pattern may reflect the superior ability of *G. pyramidum* to detect the presence of predators or to escape their attacks (e.g. Kotler *et al.*, 1991). In addition, *G. a. allenbyi* has more than just predators to be apprehensive about. Because this species is subject to interference from its larger competitor, at least some of its attention may be directed to avoiding *G. pyramidum*. Thus, apprehension may be a tool used in the competitive foraging game, as well as in the foraging game between predators and prey.

In terms of competition, *G. pyramidum* pushes *G. a. allenbyi* into resource-poor, but safer times of the night. Overall, *G. pyramidum* forages in a richer, more risky environment. To this end, *G. pyramidum* has a suite of characters tailored to such an environment: high harvest rates (Kotler and Brown, 1990), an ability to interfere (Kotler *et al.*, 1993; Ziv *et al.*, 1993; Abramsky *et al.*, 2001) and an ability to avoid predators (Kotler *et al.*, 1991). The first two characteristics are important in the foraging game with *G. a. allenbyi*; the last characteristic is important in the foraging game with the predators. In contrast, *G. a. allenbyi* forages in a relatively safe, but resource-poor environment and possesses an especially low metabolic rate and energetic cost of foraging to allow for profitable foraging in a depleted world (Linder, 1988). Overall, our results support a choreographed game involving two co-adapted gerbil species competing for seed resources that are renewed daily, tightly linked to and followed closely by resource depletion by gerbils, the response of the predators to gerbil activity and the response by the gerbils to their predators manifested by changes in activity and apprehension.

Other foraging games. There are other examples of foraging games. Consider intraspecific games. The most familiar is Fretwell's ideal free distribution model for habitat selection (Fretwell, 1972). In this model, foragers are predicted to distribute themselves across habitats to equalize fitness in each (for reviews, see Brown, 1998; Tregenza, 1995; see Sih, 1998, for the ideal free distribution in predator–prey games).

Intraspecific foraging games have also been used to model diet selection on depletable resources in a patchy environment (Mitchell, 1990). Consider foragers that have two prey types from which to choose. In sufficiently rich environments, foragers should always feed selectively on the preferred prey type. But in poorer environments, selectivity depends on the competitive environment. With no competitors, a single forager should always feed opportunistically. But the more competitors that share the patch, the more a forager should behave like an expanding specialist (Holt and Kotler, 1997; Mitchell, 1990), feeding selectively at first, but gradually becoming more opportunistic as the resource patch depletes.

Bednekoff (1997, 2001) considered a foraging game for animals living in groups in which foragers could also act as sentinels. Sentinel behaviour can evolve when it is part of a trade-off of foraging and predatory risk providing non-vigilant animals that are in places typically occupied by sentinels are most at risk.

Foraging behaviour in social groups is typically modelled as a producer–scrounger game (e.g. Vickery *et al.*, 1991; Ranta *et al.*, 1993; Giraldeau and Livoreil, 1998). Typically, the producer strategy is favoured in larger groups, when the finder's share increases and when energy shortfalls are more likely (Caraco and Giraldeau, 1991).

In this article, we have examined patch depletion and apprehension in gerbils in the field under threat of predation. We have seen that apprehension is related not only to the foragers' activity, but also to conditions that affect predator deadliness and, apparently, encounter rates with predators. The environmental conditions, resource availability and depletion, the decisions of the gerbils regarding level of activity, location of activity and level of apprehension, and the decisions of the predators regarding level and timing of activity are all conjoined in the foraging game. This game affects three trophic levels, including the effect of the gerbils on the availability and distribution of seeds, the competitive interaction between the two gerbil species and the predator–prey interaction between gerbils and their predators. It is in the context of game theory that these interactions are best understood (Bouskila *et al.*, 1998). But the foraging game perspective provides even more insight. For example, when we model the system as a game, we obtain predator and prey zero-growth isoclines that are especially stabilizing (Brown *et al.*, 2001). Furthermore, the gradually changing levels of activity and apprehension by gerbils over the course of the night only emerge from foraging game models. Thus, a thorough understanding of this system requires a game theoretical approach.

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