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FORAGING GAMES BETWEEN GERBILS AND THEIR PREDATORS: SEASONAL CHANGES IN SCHEDULES OF ACTIVITY AND APPREHENSION

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ABSTRACT

The interactions between predators and prey often constitute foraging games where prey manage risk and predators manage fear. Tools available to prey to manage risk include time allocation and apprehension. Such a game exists between gerbils and their predators in sandy habitats in the Negev Desert. Pulses of seeds made available daily by wind action result in a tightly choreographed game of changing seed availability and changing gerbil and predator behavior throughout the night. This outcome depends on summer conditions, especially the mobile sandy substrate that allows for daily renewal of resources. But winter conditions are far different: colder temperatures and wet, immobile substrate that stymies seed renewal. Here, we examined nightly patterns of time allocation and apprehension in gerbils in summer and winter. Gerbils showed higher GUDs (giving-up density, a measure of time allocation) and higher selectivity for full resource patches over micropatches (a measure of apprehension) in winter than in summer. Also, gerbils showed stronger responses of GUDs to moon phase and time of night in the summer and stronger responses of selectivity to moon phase and microhabitat in the winter. In summer, gerbils use apprehension and, especially, time allocation to manage risk; in winter, gerbils rely more on apprehension. These results show how a forager's use of time allocation and apprehension depends on the nature of resource renewal and the cost of thermoregulation while foraging. Such factors can vary greatly across seasons and result in very different tactics for animals managing food and safety through foraging behavior.

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INTRODUCTION

The interactions between prey and their predators often constitute foraging games. For "clever" prey animals able to make behavioral decisions to balance conflicting demands of food and safety, the value of their decisions depends on what their predators are doing. Such behavioral decisions include time allocation of when and where to forage and how long to exploit resource patches. Also included is the vigilance or apprehension level of the forager. Prey individuals use tools such as these to manage risk. For "clever" predators able to make foraging decisions that affect prey encounter rate and catchability of prey, the value of their decisions depends on what their prey are doing. Such behavioral decisions include when and how long to hunt and how often to revisit particular patches. Also included is the boldness or willingness of the predator to incur injury while attacking prey. Predators use such tools to manage the fear and catchability of their prey. Together they provide the frequency dependence of payoffs necessary for an evolutionary game.

One such game includes the interaction of seed-eating gerbils living on sand dunes in the Negev Desert of Israel and their predators (Kotler et al., 2002). The gerbils include Allenby's gerbil, *Gerbillus andersoni allenbyi* (24 g), and the greater Egyptian sand gerbil, *G. pyramidum* (40 g). They are the focus of this paper. The predators include barn owls (*Tyto alba*), red foxes (*Vulpes vulpes*), and greater sand vipers (*Cerastes cerastes*). Because this game is played out on a mobile, sandy substrate, predictable afternoon winds redistribute sand and seed and result in daily renewal of resource patches of seed (Ben-Natan et al., 2004). The pulses of seeds and the depletion by the foraging activity of the gerbils set the stage for a highly choreographed game in which gerbils forage heavily when seeds are most abundant early in the night, predators follow suit, and gerbils respond with high levels of apprehension. Then, as gerbils deplete seeds as the night progresses, their activity falls off. Predator activity declines and gerbil apprehension declines. These schedules of gerbil activity and apprehension are modified by factors affecting the ability of predators to encounter and kill prey, namely microhabitat structure and moonlight (Kotler et al., 2002).

The nature of this game depends critically on the daily pulses of seeds and their rapid depletion. However, the gerbils live in a highly seasonal environment. Certain aspects of the environment are dependable. For example, moderately strong afternoon winds blow out of the west-northwest nearly every day of the year. But rain is limited almost exclusively to the winter months. As a result, the sand substrate can be quite wet on many or even most winter days. The sand may be dry on the surface, but completely wet just a centimeter or two below the surface. This may be enough to prevent or greatly reduce the redistribution of sand and seed by the winds and the daily renewal of seed resource patches. And even under the best of conditions, the size of the daily pulses of seed renewal in the winter must necessarily be smaller than in the summer because there are fewer seeds to be blown around after a year of depletion by the rodents. Consequently, patterns of gerbil activity and apprehension may look very different in winter months than in summer months. Also, winter months are colder and temperatures may

approach freezing in the late hours of the night. Thus, because of high thermoregulatory costs, the energetic cost of foraging can increase greatly over the course of the night.

Overall, we expect that rising metabolic costs from the energetic cost of thermoregulation over the course of a winter night should lead to rising foraging cost and less intense patch use. Furthermore, reduced daily resource renewal in the winter should make foraging more dispersed and resource depletion more gradual. This should equilibrate foraging activity over the course of the night and make time allocation a less effective tool for managing risk of predation, leaving gerbils to place more emphasis on other means.

Here, we report on an experiment with the two species of gerbils on the sand dunes of Be'er Asluj in the Negev Desert, Israel. We conducted the experiment during both summer and winter months in which we measured the link of gerbil activity and apprehension in the context of moon phase and microhabitat. The summer experiment was previously reported (Kotler et al., 2002). We report on the winter results for the first time and compare them to the summer results with its contrasting conditions.

PREDATOR–PREY FORAGING GAME ON A PULSED RESOURCE

We have previously shown (Kotler et al., 2002) that in a foraging game such as the one described for gerbils, three conditions must hold at the Evolutionarily Stable Strategy (ESS):

1. The prey (i.e., the gerbils) must, throughout the night, balance their foraging costs and benefits. At each point in the night, foragers should allocate enough time to foraging such that the resource abundances available provide a harvest rate (f) that balances the metabolic (c), predation ($\mu F/(\partial F/\partial e)$), and missed opportunity costs of foraging ($-c_o$):

$$f = (c - c_o) + \mu F/(\partial F/\partial e) \quad (1)$$

   where F is survivor's fitness, $\partial F/\partial e$ is the marginal fitness value of energy, μ is the risk of predation, and e is the prey's energy state (Brown, 1992). Providing prey foraging activity depletes resources, for sustained foraging activity the harvest rate of the prey must decline with time following the resource pulse. To maintain the balance of costs and benefits of foraging, μ must decline, providing harvest rates are declining due to resource depletion in patches**.** These reductions occur because predator activity declines with time. Rapid depletion of resources will lead to marked declines in both predator and prey activity over the course of the night, while more gradual depletion will lead to more even distribution of foraging activity across the night.
2. The prey must choose their optimal level of apprehension, given resource abundances and predation risk (Brown, 1999). Apprehension is attention a prey individual directs towards predator detection (see below), and increases its safety, but reduces its harvest rates. The optimal level of apprehension, u^*, at any point in time satisfies (Brown, 1999):

$$u^* = \sqrt{mF/(bf_{max}(\partial F/\partial e))} - k/b \quad (2)$$

where m is the encounter rate of predators with their prey, k is the inverse of the predator's lethality in the absence of apprehension, and b is the effectiveness of apprehension in reducing mortality. To the extent that m and f_{max} decline with time, the apprehension level of those prey actively foraging also declines (Kotler et al., 2002).

3. The predators must have equal foraging opportunities throughout the night (Brown et al., 2001). That is, at each point in the night, the predators have the same expected harvest rate, and this harvest rate or probability of prey capture, 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.

$$\theta = apN/(k + bu) \quad (3)$$

where N is the population density of prey and p is the probability that a prey individual forages. 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 eq 3. Equation 3 need only be true within a single night, but 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. However, moonlight and microhabitat can alter values for encounter rate, predator lethality, and effectiveness of apprehension. So, we expect activity patterns and apprehension to alter with moonphase and microhabitat.

GAUGING APPREHENSION

Apprehension is one tool available to the clever forager. It is attention directed towards predator detection that may come at the expense of attention directed towards foraging tasks. Apprehension may be based on foreboding due to fear and dread based on the forager's estimation of predatory risk, and serves to increase the prey's ability at early predator detection. We are interested in apprehension insofar as it affects foraging, and so we operationally 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; Dall et al., 2001). The implication is that a more apprehensive forager is more prone to make foraging mistakes that reduce its ability to harvest resources. 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). In general, apprehension should increase in situations where predators are more lethal and where predators are more likely to be encountered (Brown, 1999; Brown et al., 1999).

We can gauge apprehension by applying our operational definition. 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). We expect more apprehensive foragers to be less able to estimate the scale of patchiness. Both over- and underestimation of patch size reduce harvest rates and patch value. Thus, a forager that is more apprehensive will perceive a patch in which it must estimate the location of patch boundaries to be less valuable than when the same forager is less apprehensive.

One can reveal changes in apprehension by offering a forager paired food patches that differ in the ease with which patch boundaries can be estimated. Here we use patch types created by mixing together measured amounts of seeds and sand in an aluminum tray. In one tray, the seeds were mixed randomly into all of the sand substrate (Full tray), and in the other, the same aliquot of seeds was mixed randomly into the sand of the bottom half of the patch only (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, it is difficult to assess the boundary line between the upper half without food and the lower half with all of the food (Schmidt and Brown, 1996; Kotler et al., 2002). Mistakes regarding the location of patch boundaries and such are easy to make. In contrast, the patch boundaries of the Full tray are always obvious to the forager, i.e., the surface of the sand and the bottom and edges of the tray. As apprehension increases, the forager should make more mistakes in the Bottom tray, but not the Full tray, and the value of the Full tray relative to the Bottom tray should increase. At the same time, factors that alter apprehension are not expected to affect the energetic cost of patch exploitation or missed opportunity costs because the same amounts of sand and seed are used in each.

METHODS

We performed the experiments at Be'er 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* (24 g) and *G. pyramidum* (39 g) are the two most common species of rodents, with *G. henleyi* (pygmy gerbil, 12 g), *Meriones sacrementi* (Buxton's jird, 120 g), and *Jaculus jaculus* (common jerboa, 55 g) also present, but rare. Barn owls (*Tyto alba*) and red foxes (*Vulpes vulpes*) are common predators in the area and often roost or den nearby.

We conducted the experiments on two 2.56 ha grids on which we have conducted studies since 1986. The grids contain a mix of stabilized and semi-stabilized sand habitats. For live-trapping, grids are arrayed 9×9 with 20 m between stations. Within the 9×9 layout, we used stations located at the intersections of even-numbered rows and columns (4×4 layout with 40 m between stations) for seed tray stations. We have quantified the habitat at each station on the grids (Brown et al., 1994).

We created seed resource patches for the gerbils using $60 \times 45 \times 3$ cm aluminum trays. Each seed tray was provisioned with 3 g of millet seed mixed into 5 l of sifted

sand. Following foraging in the seed trays, we took seed remains back to the laboratory for cleaning of sand and debris and for weighing to determine the amount of seeds remaining in the resource patch, i.e., the giving-up density, GUD. We used GUDs to quantify activity time.

We measured how apprehension changed as a function of hour, microhabitat, and moon phase as follows. Four seed trays were present at each station, two in each microhabitat, bush and open. Each of the two trays in a microhabitat at a station contained one of two different patch types, Full or Bottom. Gerbils have greater selectivity for the Full tray over the Bottom tray, with the selectivity for the Bottom tray decreasing yet further with greater levels of apprehension. Thus, we gauged apprehension by selectivity for the Full tray compared to the Bottom tray.

We performed the following experiment in July and August, 1998 and again in the winter of 1999–2000. We used a single grid and placed seed trays at all 16 seed-tray stations. At each station, we placed 4 trays, a Full tray and a Bottom tray in the bush microhabitat and a Full and a Bottom tray in the open. We divided the 16 stations into 4 four-station sub-grids. Then, every two and a quarter hours (summer) or three and a quarter hours (winter) over the course of the night, we opened the trays of one of the stations of each sub-grid (four stations at a time), allowed the gerbils to forage, and then collected the remaining seeds from all 4 trays from each of the four stations two and a quarter (three and a quarter) hours later. The different length time intervals used in summer and winter allowed for the same number of intervals to be used, but should have had little effect on GUDs as GUDs are determined by foraging costs and food availability at large in each time interval. We identified the tracks in the tray's sand to species, and assigned trays accordingly (*G. a. allenbyi* only, *G. pyramidum* only, or both). We then closed the trays and the following morning sifted the remaining seeds from the trays to obtain the GUDs. After closing one set of trays at one station, we opened another set at the next station for the next two and a quarter hour (three and a quarter hour) time period. We ran 4 temporal replicates total over the course of each night. We rotated stations in each sub-grid according to a Latin square during the night. Also, we rotated the first station in a sub-grid to be used each night over a 4-night sequence according to a Latin square. In each time period, we ran a total of 16 trays arrayed at four stations; on each night we ran a total of 64 trays. We repeated each 4-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. Altogether, we ran the experiment for 32 nights in each season, for a total of 64 nights.

We analyzed data using partially hierarchical analysis of variance for amount of seeds remaining in foraging trays (log-transformed for normality; a measure of foraging activity) or on the selectivity for the full tray (a measure of apprehension). We used Manly's index for depletable resources to calculate selectivity (Chesson, 1983; Schmidt and Brown, 1996; Kotler et al., 2002):

$$\frac{\{Ln(\textit{proportion of seeds remaining in Full tray})\}}{\{Ln(\textit{proportion of seeds remaining in Bottom tray}) + Ln(\textit{proportion of seeds remaining in Full tray})\}}$$

RESULTS

AMOUNT OF SEEDS LEFT IN TRAYS

We start by presenting the results from the amount of seeds left in seed trays at the end of each time period, i.e., giving-up densities (GUDs; Brown, 1988). Here we are using the GUDs primarily as an indicator of foraging activity in that time period, although they also reflect the foraging efficiencies and foraging costs of the gerbils. With regard to foraging activity, lower GUDs indicate more seeds removed from trays and therefore greater activity.

We consider how GUDs vary according to the main effects of season, moon phase, microhabitat, time of night, and species of gerbil. Giving-up densities differed between seasons, with GUDs in winter being higher than GUDs in the warmer summer (M.S. = 254.629, $F_{1, 4027} = 254.629$, $p << 0.001$; Fig. 1). Higher winter GUDs may be the result of the higher energetic cost of foraging due to the cost of thermoregulation on cold winter nights, and reflect lower winter activity.

Moon phase also affected GUDs, with lower GUDs on nights with a new moon and a waxing half moon (moonlight early in the night) and higher GUDs at full moon and at the waning half moon (moonlight later in the night) (M.S. = 9.289, $F_{3, 4027} = 41.453$, $p << 0.001$; Fig. 1). The higher GUDs on moonlit nights likely reflect the higher risks of predation on those nights.

Gerbil GUDs differed over the course of the night (M.S. = 1.779, $F_{3, 4027} = 7.939$, $p < 0.001$; Fig. 2). Since new sets of seed trays were opened for each time period, this reflects changing foraging costs and activity over the course of the night. In particular, GUDs dropped from the first time period to the second, and then increased from the third to the fourth. The generally increasing costs towards the end of the night may reflect resource depletion and increasing energetic costs of foraging due to the cost of thermoregulation as the night gets progressively colder, especially in the winter.

GUDs differed between the bush and open microhabitat, with gerbils foraging bush trays to lower seed densities (M.S. = 0.658, $F_{1, 4027} = 2.937$, $p = 0.0433$, one-tailed test; bush = 1.287 (.017 SE), open = 1.35 (.019 SE)). This may reflect the greater safety offered by the bush microhabitat from predators such as owls and foxes.

The gerbil species differed in their GUDs (M.S. = 2.214, $F_{2, 4027} = 9.878$, $p < 0.001$; Figs. 1 and 3). Overall, we found the lowest GUDs in trays foraged by both species, followed by trays foraged by *G. a. allenbyi*, followed by trays foraged by *G. pyramidum*. This contrasts somewhat from previous results in which *G. a. allenbyi* had lower GUDs (Brown et al., 1994).

There were several significant interactions between the main effects. One is the interaction between time and moon phase (M.S. = 3.782, $F_{9, 4027} = 16.875$, $p << 0.001$; Fig. 2). Here, the overall pattern of decreasing GUDs early in the night and increasing GUDs later on is seen at all moon phases save for the waning half moon. In these cases, moonlight appears to be related to risk of predation, and foraging patterns change accordingly with moon phase as the moonlit hours of the night change.

The other significant interactions include differences across seasons or between

species and are of greater interest here. With regard to species, the gerbils differed in their pattern of GUDs over the course of the night (M.S. = 0.926, $F_{6, 4027} = 4.293$, $p < 0.001$; Fig. 3). For trays foraged by *G. a. allenbyi*, GUDs dropped from the first time period to the second, and remained more or less constant for the remainder of the night. For trays foraged by *G. pyramidum* only, GUDs remained low through the first three time periods before increasing at the end. This may reflect the interference between the two gerbils and the temporal partitioning that results from it (Kotler et al., 1993; Ziv et al., 1993).

Interactions involving season allow us to compare gerbil foraging in summer versus winter. Significant interactions occurred between season and moon phase (M.S. = 2.694, $F_{3, 4027} = 12.020$, $p << 0.001$; Fig. 1), season and time of night (M.S. = 1.032, $F_{3, 4027} = 4.608$, $p = 0.003$; Fig. 3), and season and species (M.S. = 1.120, $F_{2, 4027} = 4.999$, $p = 0.007$; Fig. 3). With regard to moon phase, summer GUDs are highest at the brightest moon phases (full and waning half moon), while winter GUDs differ little among moon phases—with the exception of higher GUDs at the waning half moon. With regard to time of night, summer GUDs dropped over the course of the night until rising at the last time period. Winter GUDs differed little over the course of the night, with the lowest GUD occurring at the second time period. Interestingly, the number of trays visited by gerbils increased during the night for the summer data (from 613 to 682 per time period), but decreased sharply during the winter (from 488 to 266). Both of these results are consistent with the prediction of less variation in resource depletion and foraging activity during the winter, but may also have resulted from higher summer densities. Also, the two gerbil species showed similar GUDs in the winter time (with trays foraged by both species being lower than trays foraged by either species by itself), although in the summer *G. a. allenbyi* had the lowest GUDs.

Finally, there were two significant three-way interactions, both of which involved species and season. One involved species, season, and moon phase (M.S. = 1.790,

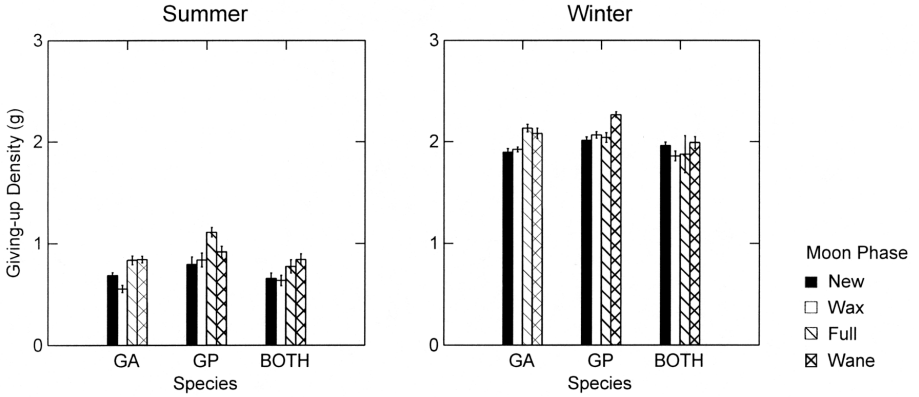


Fig. 1. Mean giving-up densities (GUDs; back-transformed from the log-transformed data) for trays foraged by *Gerbillus andersoni allenbyi*, *G. pyramidum*, or both according to season and moon phase. Error bars give standard errors for the log-transformed data.

$F_{6, 4027} = 7.987$, $p << 0.001$; Fig. 1) and the other involved species, season, and time of night (M.S. = 0.644, $F_{6, 4027} = 2.873$, $p = 0.009$; Fig. 3). The species × season × moon phase interaction comes about because in the summer both species have high GUDs at the full and the waning half moon and low GUDs at the new and the waxing half moon, while in the winter, *G. a. allenbyi* shows little response to moon phase whereas *G. pyramidum* shows the highest GUDs at the waning half moon. The species × season × time interaction comes about because both species show similar summer patterns

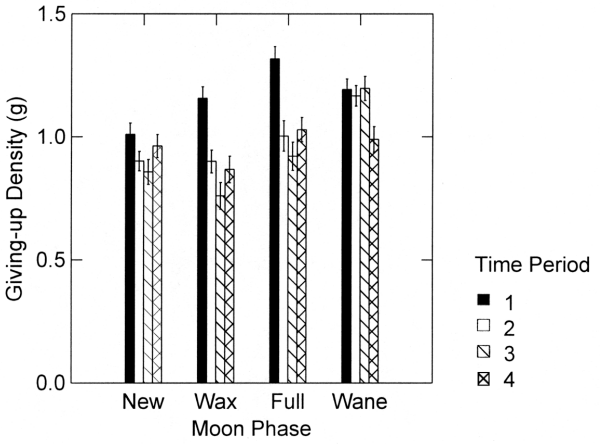


Fig. 2. Mean giving-up densities (GUDs; back-transformed from the log-transformed data) according to moon phase and time of night. Error bars give standard errors for the log-transformed data.

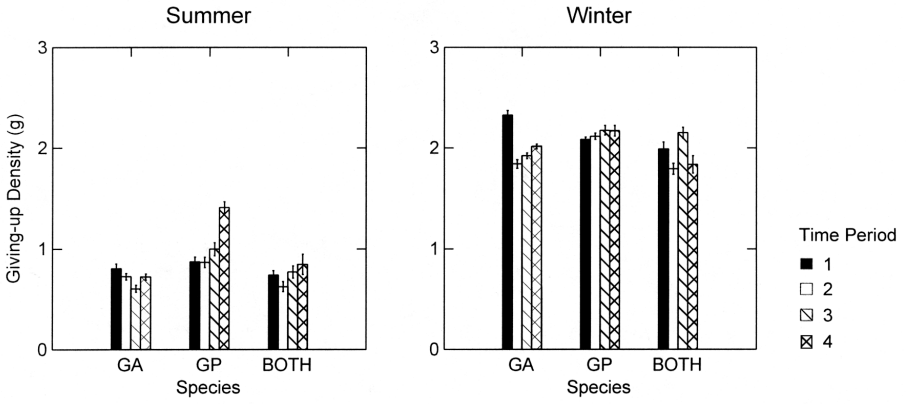


Fig. 3. Mean giving-up densities (GUDs; back-transformed from the log-transformed data) for trays foraged by *Gerbillus andersoni allenbyi*, *G. pyramidum*, or both according to time of night. Error bars give standard errors for the log-transformed data.

(falling activity throughout the night, with an increase in the last time period), but in the winter, *G. a. allenbyi* shows falling activity from the first time period to the second and slight increases thereafter whereas *G. pyramidum* shows nearly constant activity throughout.

The above analysis did not include the three-way interaction moon phase × time of night × season due to an empty cell (the last time period of the night, in the winter, during the waning moon). To estimate the strength of this interaction, we re-analyzed the data using only the first three time periods of the night. This yielded a significant three-way interaction (M.S. = 1.227, $F_{6, 3084} = 5.786$, $p << 0.001$), although its meaning is difficult to interpret.

SELECTIVITY FOR THE FULL TRAY

Selectivity for the full tray provides our measure of apprehension, with higher values of selectivity corresponding to higher levels of apprehension. The main effects of season (M.S. = 0.574, $F_{1, 2505} = 24.331$, $p < 0.001$; Fig. 4), microhabitat (M.S. = 0.094, $F_{1, 2505} = 4.001$, $p = 0.046$; Fig. 5), and moon phase (M.S. = 0.276, $F_{3, 2505} = 11.693$, $p < 0.001$; Fig. 6) all significantly affected selectivity. Selectivity was higher in the winter than the summer, higher in the open than the bush microhabitat, and higher during the full and waning half moon than during the new and waxing half moon phases. Overall, higher levels of selectivity and apprehension prevailed where and when GUDs were also higher.

Significant interactions of the main effects included time of night and moon phase (M.S. = 0.053, $F_{9, 2505} = 2.237$, $p = 0.017$; Fig. 4), time of night and microhabitat (M.S. = 0.077, $F_{3, 2505} = 3.269$, $p = 0.017$; Fig. 5), and a marginally significant interaction of microhabitat and moon phase (M.S. = 0.052, $F_{3, 2505} = 2.195$, $p = 0.087$). The time by moon phase interaction reflects increasing selectivity with time of night at the waning

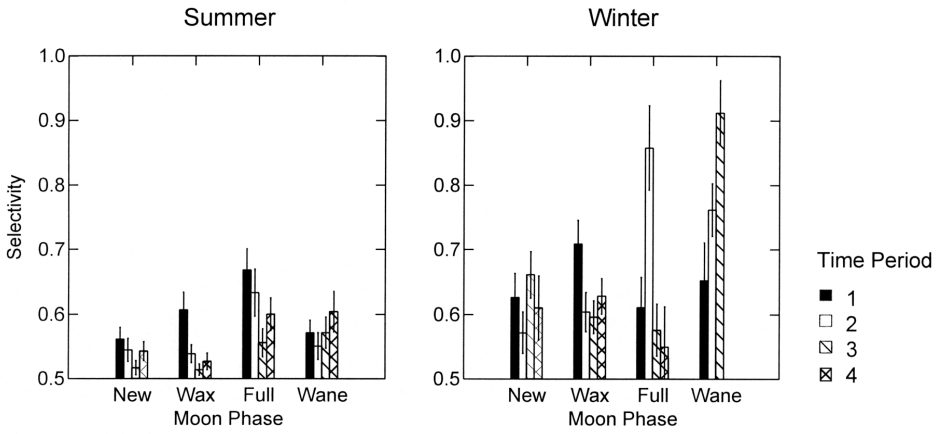


Fig. 4. Mean selectivity for the full tray (a measure of apprehension) according to season, moon phase, and time of night. Error bars give standard errors.

half moon contrasting with declining selectivity with time of night at the waxing half moon (both corresponding with greater selectivity/apprehension during the moonlit hours of the night when predators are more lethal and encounter rates higher) and other moon phases. The time × microhabitat interaction reflects an inconsistent effect of the microhabitat over the hours of the night.

The species differed in their response to moon phase (M.S. = 0.074, $F_{6, 2505} = 3.130$, $p = 0.005$; Fig. 6) and to microhabitat (M.S. = 0.082, $F_{2, 2505} = 3.475$, $p = 0.031$; Fig. 7). Both interactions reflect mostly differences in selectivity for trays foraged by one species versus those foraged by two.

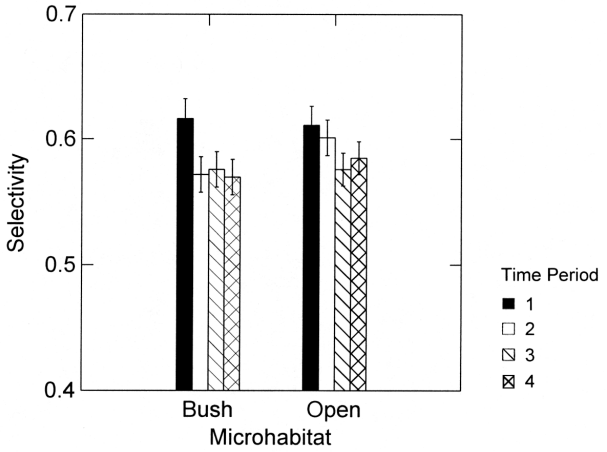


Fig. 5. Mean selectivity for the full tray (a measure of apprehension) according to microhabitat and time of night. Error bars give standard errors.

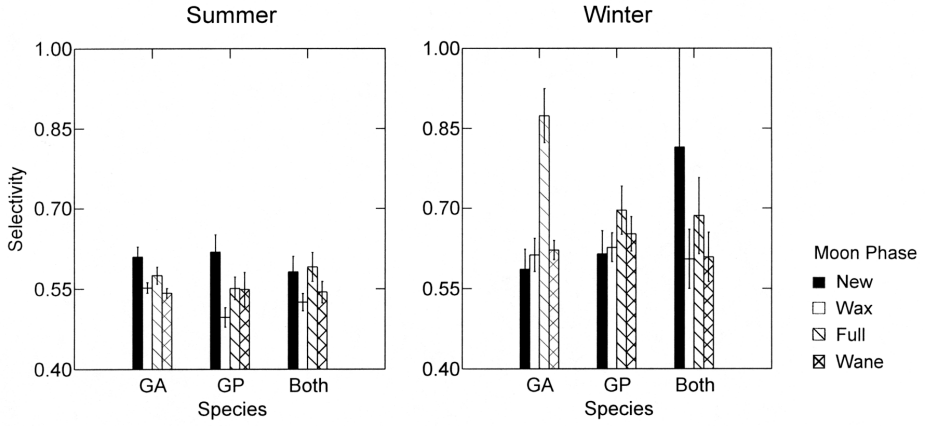


Fig. 6. Mean selectivity for the full tray (a measure of apprehension) according to season, species, and moon phase. Error bars give standard errors.

More of interest to us are the significant interactions involving season. The reaction of rodents to moon phase (M.S. = 0.067, $F_{3, 2505} = 2.852$, $p = 0.036$; Fig. 4), time of night (M.S. = 0.157, $F_{3, 2505} = 6.656$, $p << 0.001$; Fig. 4), and microhabitat (M.S. = 0.124, $F_{1, 2505} = 5.243$, $p = 0.022$; Fig. 7) all differed between season. The species also differed in how season affected their response to moon phase (M.S. = 0.114, $F_{6, 2505} = 4.836$, $p < 0.001$; Fig. 6). Interestingly, effects of both moon phase and microhabitat on selectivity were more pronounced in the winter than in the summer. This suggests that in situations where predator lethality varies, apprehension is a more important tool for managing safety in winter while time allocation is more important in summer. Contrast this to the effect of time of night, which should mostly affect encounter rates with predators (as gerbil activity and therefore predator activity decline with the depletion of resources). Selectivity in the summer dropped during the course of the night before increasing again at dawn. In contrast, winter selectivities began the night high and dropped for the second time period before increasing for the third and decreasing again for the fourth. In both seasons, patterns of selectivity over time of night are similar to patterns of time allocation, implying the use of both time allocation and apprehension. With regard to seasonal differences between the species in their response to moon phase, the two gerbil species showed similar patterns in winter, but contrasting patterns in the summer when *G. a. allenbyi* showed less response to moon phase.

As with the GUD analysis above, our analysis of the selectivity data did not include the interaction of moon phase × time of night × season due to an empty cell. We thus re-analyzed the data including this interaction, but for the first three time periods of the night only. The interaction was significant (M.S. = 0.092, $F_{6, 1882} = 3.771$, $p = 0.001$; Fig. 4). While in the summer, selectivity mostly dropped over the first three time periods at all moon phases, in the winter selectivity dropped during the new and waxing half moon, but increased over time during the full moon and the waning half moon.

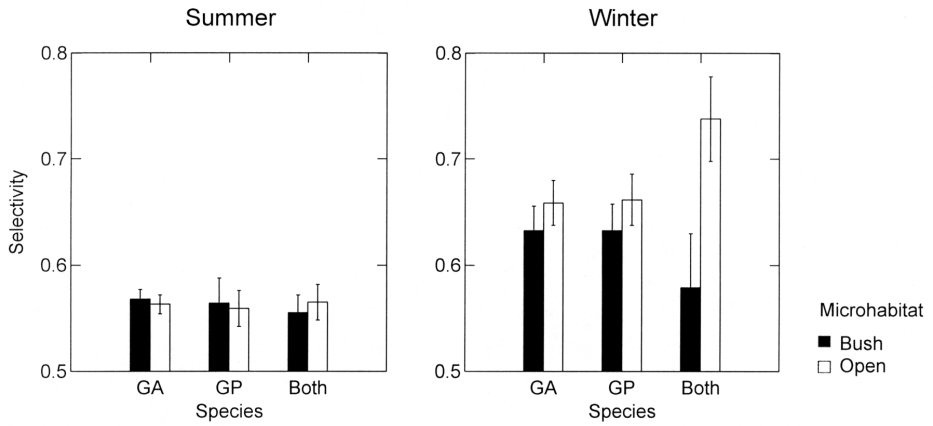


Fig. 7. Mean selectivity for the full tray (a measure of apprehension) according to season, species, and microhabitat. Error bars give standard errors

DISCUSSION

We have previously reported on and discussed the summer results (Kotler et al., 2002), so here we limit the discussion to seasonal comparisons. Such comparisons are of interest since the environment differs in many key features between summer and winter, and this has consequences for many aspects of the foraging game in the two seasons. Among these environmental features are temperature, food availability, precipitation, and the mobility of the substrate. Overall, giving-up densities are higher (indicating lower activity) in winter than in summer, in moonlit hours of the night (especially in the summer), in the open microhabitat, and early in the night and again at the very end. Also, species are similar in their timing of activity in the summer whereas in winter activity is evenly spread through the night, and *G. a. allenbyi* shows higher levels of activity than does *G. pyramidum* (Table 1). Time allocation is used by gerbils in response to factors affecting both predator lethality (moon phase, microhabitat) and encounter rates with predators (time of night). With regard to apprehension, gerbils are more apprehensive when GUDs are higher: in winter, in the open microhabitat, during moonlit hours of the night. Patterns of apprehension change seasonally and are much more pronounced in the winter (Table 2). Apprehension is used by gerbils in response to factors affecting predator lethality (moon phase, microhabitat).

In winter, overnight temperatures can approach and occationally even reach below freezing, in contrast to summer temperatures that may be 20 degrees warmer. The colder temperatures mean higher thermoregulatory costs and subsequently higher energetic costs of foraging, c. The energetic cost of foraging should also increase much more

Table 1
Summary of significant effects on giving-up densities (GUD)

Factor	Effect
Season	Winter GUDs higher than summer GUDs
Moon phase	GUDs for full moon and waning half moon greater than for new moon and waxing half moon
Time of night	GUDs highest at beginning and end of night
Microhabitat	GUDs higher in open than in bush
Species	GUDs for *G. pyramidum* higher than for *G. a. allenbyi*
Time × moon phase	Moonlight early in the night leads to higher GUDs early on and lower GUDs later
Time × species	Temporal partitioning between the species
Season × moon phase	Little change in GUDs across moon phases in winter
Season × time	Little change in GUDs during the night in winter
Season × species	Species similar in GUDs in winter
Season × moon × species	*G. a. allenbyi* changes little in its GUDs across moon phases in the winter
Season × time × species	*G. pyramidum* changes little during the night in its GUDs
Season × time × moon	No obvious patterns

Table 2
Summary of significant effects on selectivities (apprehension)

Factor	Effect
Season	Apprehension higher in winter than in summer
Moon phase	Apprehension higher at bright moon phases (full, waning half moon)
Microhabitat	Apprehension higher in the open microhabitat
Time × moon phase	Apprehension highest when moon is shining (earlier hours during the waxing moon and late hours during the waning moon)
Time × microhabitat	No obvious patterns
Species × moon phase	Similar patterns for each species
Species × microhabitat	Similar patterns for each species
Season × moon phase	Patterns more pronounced in the winter
Season × microhabitat	Patterns more pronounced in the winter
Season × time	Patterns more pronounced in the summer
Season × species × microhabitat	Patterns most pronounced in the winter, especially for trays foraged by both species
Season × species × moon phase	Both species respond to moon phase similarly in the winter; *G. a. allenbyi* less responsive in the summer
Season × time × moon	Changes in apprehension during the night much greater in winter

dramatically over a winter's night than over a summer's night. The result is that winter foraging is more biased towards the early hours of the night. Otherwise, winter conditions dictate that foraging opportunities outside of trays are fairly constant during the night and harvest rates change little. Higher winter energetic costs of foraging coupled with fewer seed resources (see below) and lower harvest rates means that there should be less foraging activity in winter, especially towards dawn.

Food availability in winter contrasts with summer in at least two ways. Regarding seeds, fewer are available in winter due to months of depletion by granivores. Also, seed germination occurs with the winter rains, and as the winter progresses into spring, greater and greater biomass of herbacious annuals become available. The rodents of our study, though mostly granivorous, can supplement their diets with green vegetations during these times up to 25% (Bar et al., 1984). The desert annual plants provide a resource that does not appear to be depleted quickly, if at all.

Precipitation in the Negev Desert occurs nearly exclusively in winter months, beginning as early as November and lasting into April, with most rain falling from January through March. While lower winter temperatures and more rainfall may make it easier for rodents to maintain water balance and to encounter buried seeds, the key effect of precipitation so far as the gerbils are concerned may be in what it does to the mobility of the sandy substrate. Due to winter rains, the soil below the surface is apt to be wet. This

is in contrast to the summer when the strong afternoon northwesterly wind redistributes sand and seeds nearly every day and thus creates and renews patches of seeds (Ben-Natan et al., 2004). There are pulses of seeds made available daily in the summer, and these seeds are depleted daily as well by the foraging of ants, larks, and, most of all, gerbils. In contrast, seed resource patches are less commonly renewed in winter because the wet sand is less mobile. At the very least, resource patches are renewed less frequently. And because there are fewer seeds in the soil in winter, whatever pulses may be generated by wind action must necessarily be smaller. As a result, foraging by the gerbils in winter can be expected to rapidly eliminate richer than average opportunities early in the season and set the stage for more gradual depletion across the entire environment thereafter. Consequently, in winter, seed depletion may be a more gradual process involving much less spatial variance.

Compare these differences in the summer versus winter environment to seasonal differences in GUDs and apprehension. Overall, GUDs in winter are higher than GUDs in summer, reflecting higher energetic costs of thermoregulation while foraging. But GUDs in winter show less variation compared to the summer in response to factors such as moon phase, time of night, or species identity. Instead, while gerbils use both time allocation and apprehension in the summer, they appear to rely more heavily on apprehension to manage risk in the winter. Why should this be so?

Two features of the winter environment appear to play especially important roles. One is the reduced likelihood of the creation of daily pulses of renewal of seed availability from wind action. Because resource depletion appears to be more even and gradual in winter, i.e., less directed towards recently created rich patches, harvest rates change little during the night, and there is little premium for being the first forager, nor can changes in time allocation alter harvest rates much within a given night. Also, the decision to leave a foraging patch should be less driven by changes in harvest rates than changes in foraging costs. Foraging costs in turn are less sensitive to changes in the marginal value of energy, which in any case is high in winter.

The second factor is air temperature and its effect on the energetic cost of foraging. Nighttime temperatures in winter are cold and grow even colder as the night progresses. This increases the cost of thermoregulation and the energetic cost of being out of the burrow to forage. Winter foraging should be characterized by more constant harvest rates over the night for reasons previously discussed. If so, then foraging decisions are driven more by changing foraging costs rather than by changing harvest rates. A consequence is that gerbil activity should be more constant on a winter night up until the time when costs of foraging have risen so high as to exceed harvest rates. Higher energetic cost of foraging later in the night can reduce the number of patches that offer a profitable rate of return and so can act to limit foraging. In fact, gerbils sharply curtail the number of patches they visit later in the night. Thus, gerbils in winter appear to have less of an opportunity to manage risk using time allocation.

That leaves apprehension as a tool to manage risk. The data suggest that apprehension is an important tool in managing the tradeoff of food and safety in both summer and winter, especially regarding factors affecting predator lethality. Summer foraging then is

characterized by seed harvest rates that start out high and decline during the night in a finely choreographed game involving resource renewal, gerbil foraging activity, predator foraging activity, and gerbil apprehension (Kotler et al., 2002). The foraging game ensures that, as harvest rates decline with seed depletion, gerbil activity declines, and as gerbil activity declines, so too does predator activity. Gerbils counter high predator activity at the beginning of the night with high levels of apprehension and gradually reduce apprehension as predators become less active. Schedules of apprehension are tailored to changes in predator lethality according to moonlight and microhabitat.

In winter, apprehension may be the primary tool used, especially in response to factors affecting predator lethality, namely moon phase and microhabitat. The reason that apprehension may be relatively more important is that it continues to be effective whereas time allocation loses at least some of its value.

Interestingly, the changing relative importance of time allocation versus apprehension in managing risk in summer versus winter may have little or no impact on the interaction between the gerbils. The mechanism of coexistence of these two species of gerbils depends on daily variability of seed density (Kotler et al., 1993; Ziv et al., 1993; Brown et al., 1994), i.e., pulses of seeds made available each day by wind action (Ben-Natan et al., 2004). Tradeoffs in foraging efficiency at high and low resource densities based on body size, energetic costs of foraging (Linder, 1988), and the ability to interfere (Ziv et al., 1993) result in strong temporal patterns of activity in summertime and temporal partitioning between the species (Kotler et al., 1993, 2002; Ziv et al., 1993). But such pulses are infrequent in the winter, and time allocation plays a more minor role. In winter months when conditions for coexistence do not hold, both gerbil populations decline and reach their lowest annual densities.

We have compared the foraging behavior of two species of gerbils in two different seasons. We focused on time allocation and apprehension, tools used to mitigate interactions with predators. The changing seasonal environment, especially with regard to overnight temperature and resource patch renewal by wind action, dictate seasonal changes in gerbil behavior. In particular, gerbils rely more on apprehension and less on time allocation in winter. This has obvious ramifications regarding their interactions with predators. But it also affects the interaction between the gerbil species in that the mechanism of species coexistence becomes inoperative in winter. Despite the challenge of overwinter survivorship and the importance of winter seed germination and winter/spring breeding for gerbil population densities, much of what is important regarding species interactions occurs during the summer.

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