Research article

Giving-up densities of foraging gerbils: the effect of interspecific competition on patch use

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Abstract. We studied the effect of a dominant species, *Gerbillus pyramidum* (Egyptian sand gerbil), on the patch use of its subordinate competitor, *G. andersoni allenbyi* (Allenby's gerbil), to better understand interspecific competition between the two species. We used manipulated resource patches (seed trays) covered with cages with two adjustable species-specific gates (either opened or closed to the bigger-dominant species, but always opened to the subordinate one). We recorded species tracks around and on the seed trays and giving-up densities (GUDs) of seeds in the trays after each night of foraging. *G. a. allenbyi* depleted seed patches to a lower level whenever *G. pyramidum* was given the opportunity to forage on the seed trays (i.e., present on the grid). This result held regardless of whether *G. pyramidum* was actually present at a particular station. We suggest that competition from *G. pyramidum* occurs both directly by interference, in which *G. a. allenbyi* is forced to be active in the late part of the night, and indirectly by exploitation via resource depletion by *G. pyramidum* in the early part of the night. The results suggest that interspecific competition from *G. pyramidum* reduces seed availability and the richness of the environment for *G. a. allenbyi* enough to affect the marginal value of energy for *G. a. allenbyi* individuals and cause them to experience lower costs of predation and manifest lower GUDs.

Key words: gerbils, giving-up density, interspecific competition, Israel, optimal-patch use

Introduction

Interspecific competition is known to have a major role in desert rodent communities (e.g., Brown, 1975; Rosenzweig, 1977; Price, 1986; Kotler and Brown, 1988). Interspecific competition is often divided into exploitation and interference (Krebs, 1972; Begon *et al.*, 1986). In the first, individuals of the two species do not interact directly with each other, but have indirect effects via the utilization of a shared resource in short supply. In the second, individuals of a dominant species directly prevent individuals of a subordinate species from utilizing the shared resource by, for example, monopolizing food patches. While exploitative competition does not require a direct interaction between individuals, interference must always have an impact on the way the shared

resource is exploited (e.g., patch-use behavior). Hence, when studying interspecific competition that involves interference, one must understand how resource exploitation is affected both directly by the interference behavior and indirectly by the change in resource abundance available to the subordinate species. This is especially important when two species strongly overlap in their diet and foraging behavior, because resource exploitation and foraging ability may provide an advantage to the subordinate species that allows it to coexist with the dominant species (Vance, 1984; Kotler and Brown, 1988). The goal of the present work is to study the effect of interference competition by one gerbil species (the dominant) on the foraging and patch-use behavior of another gerbil species (the subordinate), and to understand how both interference and exploitation shape the competitive relationship between the two.

The gerbil community of the sandy habitats of the Western Negev Desert in Israel consists of five species (Zahavi and Wharman, 1957; Abramsky *et al.*, 1985). The two most common species – *Gerbillus andersoni allenbyi* (mean body mass = 26 g) and *G. pyramidum* (mean body mass = 40 g) – have been intensively studied during the last 20 years (e.g., Rosenzweig and Abramsky, 1986; Abramsky *et al.*, 1990, 1991; Mitchell *et al.*, 1990; Kotler *et al.*, 1991, 1993a, b; Brown *et al.*, 1994). These studies have shown that, due to their diet (Bar *et al.*, 1984) and habitat-use overlap (Abramsky *et al.*, 1990), the two species compete: each gerbil species reduces its foraging and non-foraging activities as a result of an increase in the activity and density of the other species (Abramsky and Pinshow, 1989; Abramsky *et al.*, 1990; Mitchell *et al.*, 1990; Ziv, 1991); each species alters its use of habitats in response to increases in the densities of the other species (Rosenzweig and Abramsky, 1986; Abramsky *et al.*, 1990); and *G. a. allenbyi* is active later in the night as a result of the activity of *G. pyramidum* early in the night (Kotler *et al.*, 1993a; Ziv *et al.*, 1993). Using field experiments, Abramsky *et al.* (1991, 1992, 1994) measured the strength of competition, the isoclines of the interaction, and the costs of interference competition leading to temporal partitioning (Abramsky *et al.*, 2000).

Gerbil habitat–selection behavior (Rosenzweig and Abramsky, 1986; Abramsky *et al.*, 1990) and timing of nightly above-ground activity (Kotler *et al.*, 1993a; Ziv *et al.*, 1993; Ziv and Smallwod, 2000) are important components in interspecific competition. The dominant *G. pyramidum* monopolizes the semi-stabilized habitat type (the preferred habitat for both species) in the first hours of the night, and prevents individuals of *G. a. allenbyi* from exploiting resource patches at that time there. *G. a. allenbyi* exploits resource patches at low intensity during the first hours of the night in the stabilized sands (the less preferred habitat). However, towards midnight, immediately after *G. pyramidum* stops foraging, *G. a. allenbyi*'s activity in the semi-stabilized dunes increases dramatically. For the remainder of the night, it uses both

habitat types equally. Thus, interference competition by *G. pyramidum* has an essential role in the gerbils' habitat selection behavior and timing of activity.

Previous studies have shown that *G. a. allenbyi* can forage in poorer patches as well as in patches that were already depleted by *G. pyramidum* earlier in the night. This results from its ability to reduce seed resources to a lower density (Kotler and Brown, 1990; Kotler *et al.*, 1993a; Brown *et al.*, in press) due to its lower energetic cost of foraging (Linder, 1988). Furthermore, interference by *G. pyramidum* and the ability to reduce seed resources to a lower density allow the two species to coexist (Kotler *et al.*, 1993a; Ziv *et al.*, 1993; Brown *et al.*, 1994).

In general, the ecology of *G. a. allenbyi* and *G. pyramidum* has been studied mainly from two directions. The first direction has dealt with studies on the competitive relationship and habitat selection of the two species in enclosed grids, where population densities could be controled. The second direction has dealt with studies on the foraging behavior of the species on manipulated seed patches in different situations (e.g., different habitat types) in open grids. While the first revealed the interference competition by *G. pyramidum* (above), the second revealed the ability of *G. a. allenbyi* to forage seed levels to a lower density (above). However, it is not known in what way interference competition by *G. pyramidum* affects the patch use behavior of *G. a. allenby*, and whether any effect is contributed directly by the presence of *G. pyramidum* in resource patches, or indirectly by a change in the background environment. This information is important because in the large areas where the two species overlap, the patch use behavior of *G. a. allenbyi* and its ability to gain energy and coexist depend highly on the interspecific interaction between these two ecologically related species. This information could be obtained by using manipulated seed patches in enclosed grids, where population densities were controled, and manipulating access of *G. pyramidum* to seed trays. This is the issue that motivated the present study.

Given the interference competition by *G. pyramidum* and the importance of foraging behavior by *G. a. allenbyi*, we chose to study the effect of *G. pyramidum* on the patch use of *G. a. allenbyi* in enclosed grids. More specifically, we were interested in two questions: (1) Does *G. a. allenbyi* change its patch use when *G. pyramidum* can forage on the same seed patch? And if it does, (2) Does it happen directly via the presence of *G. pyramidum* at the seed patch's station or indirectly? To answer these questions we measured patch use by *G. a. allenbyi* in two situations: (1) Presence and absence of *G. pyramidum* at stations with artificial seed patches, and (2) Availability and unavailability of seed patches to *G. pyramidum* by covering artificial seed patches with cages perforated with adjustable species-specific gates.

We show that *G. a. allenbyi* deplete seed patches to a lower level whenever *G. pyramidum* is given the opportunity to forage on the seed patches. We also

show that this result holds both when *G. pyramidum* is actually present and when it is absent at a station area. We suggest how *G. pyramidum* can directly and indirectly affect the patch use of *G. a. allenbyi*. Finally, we incorporate interference and exploitative competition between the species to reveal the overall effect of *G. pyramidum* on *G. a. allenbyi*.

Methods

Measuring optimal patch use with giving-up density

To measure the patch use of *G. a. allenbyi*, we applied Brown's optimal patch use theory (Brown, 1988). We preferred this theory over the marginal value theorem (Charnov, 1976) for two reasons. First, the marginal value theorem assumes that the overall resources in the environment are not depleted by the animals during foraging, while Brown's theory allows for resource depletion in the environment. In the gerbil system, resource (i.e., seeds) depletion may be very important: resource depletion and daily renewal of seed resources is thought to be the environmental axis promoting coexistence between these species (Kotler *et al.*, 1993a; Ziv *et al.*, 1993; Brown *et al.*, 1994). Second, while the marginal value theorem does not consider the costs of foraging in a patch other than the cost of not foraging in another higher-density patch, Brown's theory considers three foraging costs – metabolic, predation and missed opportunity (see below). All three costs were found to be important for gerbils and to differ significantly between the two species (Linder, 1988; Kotler *et al.*, 1991, 1993b; Kotler 1992). Furthermore, Brown (1992) showed that four different models of patch use resulted in the same optimal patch use rule as in Brown (1988).

Brown (1988) showed that an optimal forager should leave a patch when its harvest rate (H) is less than or equal to the sum of its metabolic (C), predation (P), and missed opportunity (MOC) costs of foraging : $H \leq C + P + MOC$ (or, $H/(C + P + MOC) \leq 1$). This ratio determines the density to which a forager can profitably depress the resources of a patch (Brown, 1988). Hence, the resource density left in a patch reflects the value at which a forager can no longer forage profitably. This is called the giving-up density (GUD). Because foragers of a given species share similar characteristics, the average resource density left in patches indicates their species-specific foraging ability (Tilman, 1982; Vance, 1985; Brown, 1988). Brown's theory allows us to study the effect of different factors (both abiotic and biotic) on foraging behavior by comparing differences in patch use values of individuals when everything but the studied factor is similar for all individuals (Kotler *et al.*, 1991; Kotler, 1992;

Brown *et al.*, 1994). For example, we can study the effect of one species' abundance on the patch use of its competitor.

Patch use can be measured with artificial resource patches. For example, aluminum trays filled with millet seeds mixed thoroughly into sifted substrate may serve as resource patches for granivorous rodents (e.g., Brown 1986; Kotler *et al.*, 1991; Bowers *et al.*, 1993). The amount of seeds remaining in a tray after a night of foraging is the GUD (Brown, 1986, 1988; Kotler and Brown, 1988). Differences in GUDs imply a difference in the net gain because foragers reduce resource density in patches only when their benefits exceed their costs.

Study site

We conducted our study in the Holot Mashabim Nature Reserve (31°01′ N, 34°45′ E) situated in the Haluza region, 35 km south of Beer-Sheva, Israel. The area is characterized by long west-to-east ranges of sand dunes that provide two main habitats – semi-stabilized dunes and stabilized sands (Danin, 1978). Average annual precipitation at the site is 108 mm. Rainfall is limited to winter, and dew forms on approximately 250 nights per year. Northwesterly winds prevail in the area and usually occur in mid- and late afternoon.

Species densities, tracks and identification

We studied gerbils in enclosed grids (see below). We left the enclosed grids open to rodent movement for 6 months prior to the experiment to allow rodents to freely colonize the grids and achieve natural densities. This also allowed rodents to equalize food resources inside and outside of grids. So, background food resources should have been equal on both grids. We then closed the grids, captured all resident rodents using Sherman live traps, and marked individuals of *G. a. allenbyi* with a species-specific toe clip – outer toe of the right hind foot. We had 28 and 32 individuals of *G. a. allenbyi* in grids 1 and 2, respectively. Individuals of *G. a. allenbyi* on the different grids did not differ in body mass ($F = 0.130$, $p = 0.720$ and $F = 3.723$, $p = 0.067$ for males and females, respectively). All captured individuals of *G. pyramidum* were removed from the grids and brought to the lab. (Evidently, we failed to capture two small individuals of *G. pyramidum* which we recorded later on during the experiment by using the sand tracking technique.) In the lab, we selected those individuals of *G. pyramidum* that were larger than 50 g for introduction in the second part of the experiment (see below). We marked the selected individuals of *G. pyramidum* with a species-specific toe clip – outer toe of the left hind foot.

The species-specific marking helped to identify rodent tracks to species, both in the station area and in seed trays. We could therefore identify both the

species that were present in the station area determine the species that last foraged in each tray. This method has been used in recent studies and was found to be accurate (e.g., Kotler, 1985; Abramsky and Pinshow, 1989; Abramsky *et al.*, 1990, 1991; Mitchell, 1990).

Experimental designs

We used two one-hectare (100 × 100 m) grids enclosed by rodent-proof fences to experimentally set population densities (see Abramsky and Pinshow (1989), Abramsky *et al.* (1990) for the original use of the enclosures). Fencing, consisting of 6 mm mesh hardware cloth, was buried 40 cm below the soil surface and extended 60 cm above ground. The top 15 cm of both sides of the fence were covered with aluminum flashing to prevent rodents from climbing over.

We established 10 stations in the semi-stabilized dune habitat of each grid. A station was an area of approximately 1 m^2 in which gerbil tracks could be easily seen. We distributed the stations in two lines, five stations per line. The distance between neighboring stations in a line was 10 m, while the distance between lines was 25 m. We noted gerbil tracks in the sand nightly at each station.

We used aluminum trays (45 × 60 × 2.5 cm deep; hereafter, seed trays) as artificial resource patches to measure the patch use of *G. a. allenbyi*. We placed one seed tray at each station. We filled each tray with 3 g of millet seeds mixed thoroughly into 5 l of sifted sand. Each evening we placed the seeds in all the trays, and we sifted the sand from each tray to recover its remaining seeds the next morning. We cleaned the non-harvested seeds, and weighed the remainder to obtain the GUD.

We covered each seed tray with a mesh hardware cloth cage (66.5 × 46 × 40 cm tall) perforated with a gate with two adjustable opening positions – full opening, allowing individuals of both species to visit the seed tray (hereafter, fully open), and small opening (19.7 mm in diameter), allowing only individuals of *G. a. allenbyi* to visit the seed tray (hereafter, partially open). This adjustable-gate method has been successfully used in other experimental studies to limit access to just *G. a. allenbyi* (e.g., Abramsky *et al.*, 1990, 1991; Ziv *et al.*, 1993).

We used natural densities of *G. a. allenbyi* in both grids during the entire experiment. In the first part of the experiment, grids contained only individuals of *G. a. allenbyi*. We designed this part of the experiment to test whether the artificial gate and its positions bias foraging behavior of *G. a. allenbyi*. We introduced seed trays for the first 2 days without measuring GUDs to familiarize the rodents with the availability of artificial resource patches. Thereafter, we partially closed the gates of the seed tray cages on one of the grids. We left the second grid's seed tray cages open (fully open). We collected GUDs in both

grids for 4 days and then changed the positions of the gates. We then collected GUDs for an additional 4 days.

After the first 8 days, we introduced five individuals of *G. pyramidum* to each grid (i.e., second part of the experiment). We introduced only individuals of *G. pyramidum* that were larger than 50 g to guarantee that only individuals of *G. a. allenbyi* could pass through the species-specific gates and gain access to seed trays. We allowed individuals to become familiar with seed trays for 2 days, after which we repeated the experimental protocol of the first part of the experiment.

Results

Temporal and spatial variability

We tested the effect of days and grids on GUDs of *G. a. allenbyi* to look for differences due to temporal and spatial variability. A two-way ANOVA revealed a significant difference among days ($F_{14,206} = 6.107$, $p < 0.001$), but not among grids ($F_{1,206} = 0.872$, $p = 0.352$). In the first part of the experiment, *G. a. allenbyi*'s GUDs were significantly correlated with the day on which data were collected ($r = -0.78$, $p < 0.001$). However, we did not find a significant correlation between days and GUDs in the second part of the experiment ($r = 0.22$, $p = 0.957$). We do not have any particular explanation for these differences. We considered whether or not moonlight affects the foraging decision of gerbils in the two parts of the experiment differently (Kotler *et al.*, 1991, 1993). In fact, GUDs are correlated to moonlight in a way very similar to days ($r = -0.78$, $p < 0.001$ and $r = 0.32$, $p = 0.255$ for the first and the second part of the experiment, respectively). Therefore, to avoid ambiguities, we do not compare *G. allenbyi*'s GUDs of the first with the second part of the experiment.

Gate positions do not affect G. a. allenbyi's GUDs

Testing for the effect of gate position (fully open vs. partially open) on GUDs of *G. a. allenbyi* in the first part of the experiment using ANOVA showed no significant difference between GUDs in the two positions ($F_{1,116} = 3.65$, $p > 0.05$). Because GUDs of *G. a. allenbyi* in the absence of *G. pyramidum* were negatively correlated to the day on which data were collected, we also compared separately the effect of gate position in each of the 4 day periods (i.e., days 1–4 and 5–8). We found no significant difference in *G. a. allenbyi*'s GUDs in either of these time periods ($F_{1,58} = 2.84$, $p = 0.097$, and $F_{1,57} = 0.815$, $p = 0.371$ for days 1–4 and 5–8, respectively). Hence, the

different gate positions did not influence the GUD values of *G. a. allenbyi*. Thus, any differences in GUDs due to gate positions in the second half of the experiment can be attributed to the effect of access to the seed tray by *G. pyramidum*.

In the presence of G. pyramidum, G. a. allenbyi has lower GUDs when gate is fully open

We next tested for the effect of gate position on *G. a. allenbyi*'s GUDs in the presence of *G. pyramidum*. Because an earlier test showed that the different gate positions do not bias *G. a. allenbyi*'s GUDs, differences in GUDs of *G. a. allenbyi* in the presence of *G. pyramidum* should indicate an effect of *G. pyramidum* on *G. a. allenbyi*.

Two-way ANOVA showed that GUDs of *G. a. allenbyi* in the presence of *G. pyramidum* were significantly lower when gate was fully open than when it was partially open ($F_{1,89} = 5.71$, $p = 0.019$; Fig. 1A). Therefore, when *G. pyramidum* was allowed the opportunity to enter the covered seed tray, *G. a. allenbyi* depleted those seed trays to lower seed densities than when *G. pyramidum* was not allowed to do so.

We had 28 cases in which both species were present in the station area, the gate was fully open (i.e., both were allowed to forage on a seed tray), and we could unambiguously determine the last species to forage in the seed tray. In 21 cases (75%) individuals of *G. a. allenbyi* foraged last on seed trays and were responsible for the GUDs. Only in seven cases (25%) were individuals of *G. pyramidum* responsible for the GUDs. We did not distinguish between small (not captured) and large (introduced) individuals of *G. pyramidum*. Because small individuals of *G. pyramidum* show similar behavior to individuals of *G. a. allenbyi* (A. Subach, unpublished data), it is likely that the introduced individuals of *G. pyramidum* were responsible for GUDs in even less than 25% of the seed trays. Thus, in most cases *G. a. allenbyi* was the last forager on a seed tray.

G. a. allenbyi has similar GUDs in the presence and absence of G. pyramidum at a station

In the second part of the experiment, we recorded the species' tracks at the station in order to look for an effect of *G. pyramidum* on *G. a. allenbyi*'s GUDs on a finer spatial scale (station). In some cases, only *G. a. allenbyi* was present at the station, while in others both species were present. Although we cannot know whether individuals of both species were present simultaneously, a difference in GUDs when *G. pyramidum* was absent vs. when it was present at the
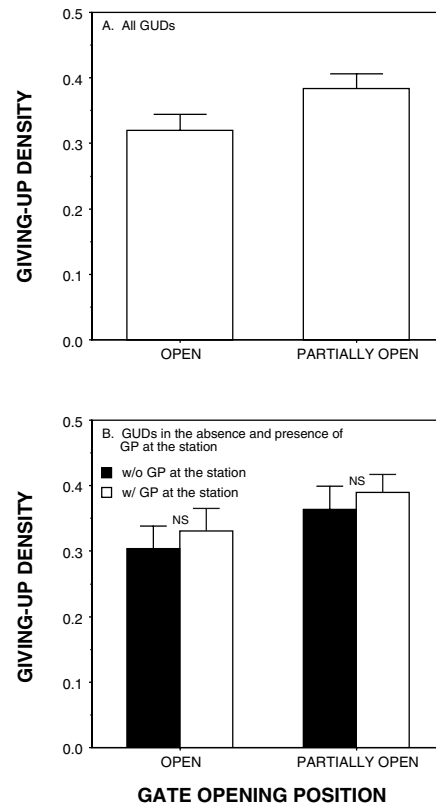
Figure 1. GUDs of *G. a. allenbyi* in different gate positions (fully open and partially open; (A) and in different gate positions when *G. pyramidum* (GP) was absent or present at the station (B). NS indicates insignificant difference ($p > 0.05$) between GUDs of *G. a. allenbyi* in the presence and absence of *G. pyramidum* (see text).

station might indicate a local effect of *G. pyramidum* on *G. a. allenbyi*. However, we did not find a significant difference in the GUDs of *G. a. allenbyi* in the absence and presence of *G. pyramidum* at the station ($F_{1,28} = 0.012$, $p = 0.914$ and $F_{1,53} = 0.002$, $p = 0.963$ when gate was fully open and partially open, respectively; Fig. 1B). Hence, the presence of *G. pyramidum* at the station did not affect the GUDs of *G. a. allenbyi*.

Discussion

The ecology of *G. a. allenbyi* and *G. pyramidum* has been studied intensively from mainly two different directions – competitive relationship and habitat

selection of interacting populations in enclosed grids, and foraging behavior of the two species on manipulated seed patches in open grids. The field enclosure studies manipulated population density and revealed that density-dependent habitat selection affects how individuals are distributed in space, and that behavioral isolegs indicated of interference competition. At the same time, geographic studies of habitat selection showing that the abundance and diversity of gerbil species are correlated with productivity have pointed to the importance of resource availability. The seed tray studies revealed that temporal partitioning of foraging between the two gerbil species provides the mechanisms of coexistence. The mechanisms are based on daily pulses of seed availability generated by wind action and subsequent depletion by foraging gerbils, coupled with tradeoffs involving interference, foraging speed, and foraging efficiency.

Thus, the gerbil system has elements of both interference and resource competition. The fingerprints of both should be revealed in the foraging behavior of the gerbils. So, it is of interest to examine how competition by *G. pyramidum* affects the patch use behavior of *G. a. allenbyi* and whether any effect is contributed directly by the presence of *G. pyramidum* in resource patches or indirectly by a change in the background environment. This information can be obtained by using manipulated seed patches in enclosed grids, where population densities were controled, and manipulating access of *G. pyramidum* to seed trays. In particular, we were interested in the following questions: (1) Does *G. a. allenbyi* change its patch use when *G. pyramidum* can forage a seed tray? And if it does, (2) Does it happen directly via the presence of *G. pyramidum* at the seed tray's station or indirectly via resource depletion?

In the presence of *G. pyramidum*, *G. a. allenbyi* left significantly lower GUDs when the gate was fully open than when it was partially open. When individuals of *G. a. allenbyi* had exclusive access to a seed tray (i.e., when the gate was partially open), they left behind higher seed densities. This result held both when *G. pyramidum* was present and when it was absent at a station. In other words, the actual presence of *G. pyramidum* at the station did not affect *G. a. allenbyi*'s patch use, but the potential to forage in a seed tray (i.e., when the gate was fully open) did. This is not unreasonable. Kotler *et al.* (1993a) and Ziv *et al.* (1993) have already showed that the species are most active at different times of the night. Thus, in the present experiment, by the time *G. a. allenbyi* foraged in the seed trays, *G. pyramidum* had likely already stopped most of its foraging activity. *G. a. allenbyi*, therefore, must have been responding to the average number of the seeds left behind by *G. pyramidum* in resource patches, rather than directly to the *G. pyramidum* themselves. However, in addition to the differences in the time of activity between the species, the potential threat by *G. pyramidum* was enough to force individuals of *G. a. allenbyi* to reduce the trays to a lower seed density.

Why did individuals of *G. a. allenbyi* leave lower seed densities in the presence of *G. pyramidum*? We suggest four explanations, which are not mutually exclusive and may operate together. Other explanations are possible based on different models and assumptions. However, these four allow us to suggest aspects of gerbil foraging and the ways in which competition may affect the gerbil species.

The first explanation proposes that individuals forage in each patch for a fixed amount of time. This means that foragers treat each patch independently of the other patches. According to this strategy, individuals of *G. a. allenbyi* should leave higher seed densities in undepleted patches (in the absence of *G. pyramidum*) than in seed patches that have already been depleted by *G. pyramidum*. This is because, in both cases, individuals devote a similar amount of time to foraging each patch. This explanation may be true when *G. pyramidum* is prevented from visiting seed trays when present. Several authors (e.g., Iwasa *et al.*, 1981; Stewart-Oaten, 1982; McNair, 1983) have suggested that a fixed-time strategy may be optimal when foragers are incapable of acquiring information or there is no information to be had (but see contrary evidence in Mitchell and Brown, 1990). But gerbils have been shown to tend to equalize GUDs in patches with different initial seed density, i.e., to use a quitting harvest rate when exploiting resource patches rather than a fixed time rule (Garb *et al.*, 1999).

The second explanation is based on the time and energy costs that a forager experiences when traveling between patches. Brown (1988) suggested that a forager should leave a patch when its harvest rate equals its metabolic, predation and MOC. Therefore, increasing costs while traveling between patches (i.e., affecting marginal value of energy and therefore predation costs) should decrease overall time spent traveling and increase the time a forager spends in each patch. Hence, when time and/or energy of traveling between patches increases, a forager leaves a lower GUD of resource in a patch. If so, *G. pyramidum* may have affected *G. a. allenbyi* both directly and indirectly. The direct effect may arise if individuals of *G. a. allenbyi* suffered from interference by *G. pyramidum* when traveling between patches, thus increasing travel costs from one patch to another. The indirect effect may arise if individuals of *G. a. allenbyi* need more time and/or energy to find available seed patches in an environment where resources – including those in seed trays – have been depleted by *G. pyramidum*. In this case, overall increased travel costs due to the existence of *G. pyramidum* may result in a lower GUD for *G. a. allenbyi*.

Third, differences in the effective richness of the environment (i.e., seeds and harvest rates available to *G. a. allenbyi*) may cause differences in GUDs. In a richer environment, foragers experience lower marginal values of energy and should leave a patch at a higher GUD. Individuals of *G. a. allenbyi*, which tend to be active after *G. pyramidum* individuals stop foraging (Ziv *et al.*, 1993),

encounter a poorer environment due to the depletion of the patches by *G. pyramidum* (Kotler *et al.*, 1993). They therefore will have, on average, higher marginal values of energy and lower GUDs. But, when *G. pyramidum* is excluded from seed trays, *G. a. allenbyi* will find more rich patches and experience a richer environment, which, in turn, will result in a higher GUD.

The fourth explanation suggests that higher patch-use values for *G. a. allenbyi* when gates were closed may result from under-utilization of seed trays due to Bayesian sampling in a highly variable environment. Valone and Brown (1989) showed that the Merriam's kangaroo rat, the Arizona pocket mouse, and the round-tail ground squirrel under-utilized rich patches in a highly variable environment. Gerbils when presented with rich and poor resource patches also tended to underexploit the rich patch (Garb *et al.*, 1999). When presented with a rich patch near a poor one, animals did not quite equalize the two neighboring seed patches, but left higher seed density in the richer one. This under-utilization of the rich tray could result from a Bayesian patch assessment strategy (for detailed explanation see Valone and Brown, 1989). In our study, seed trays that *G. pyramidum* did not have access to should have been richer than average and hence under-utilized. Seed trays that *G. pyramidum* did have access to may have been poorer than average (although they are more likely to have been of average value or nearer to value since both they and patches outside of trays have been foraged by *G. pyramidum*) and hence over-utilized. In contrast, when *G. pyramidum* was absent, the gate setting did nothing to affect the value of a tray when compared to the average patch.

In most cases (75% or more), individuals of *G. a. allenbyi* reduced seed trays to a lower seed density when both species had similar opportunity (i.e., both were present at the station and the gate was fully open). This indicates that *G. a. allenbyi* had the ability to reduce the seed level to a lower seed density than did *G. pyramidum*. Indeed, previous studies (Kotler *et al.*, 1993a; Brown *et al.*, 1994) showed that of the two species, *G. a. allenbyi* had the ability to reduce seed resources to a lower level than *G. pyramidum*. This better ability to reduce seed resources to a lower level is, in fact, the competitive advantage of *G. a. allenbyi* over the competitive dominance of *G. pyramidum*. However, in contrast to the high amount of seeds foraged by *G. a. allenbyi* when gate was partially open, only what was left by *G. pyramidum* was available to *G. a. allenbyi* after *G. pyramidum* stopped foraging when gate was fully open. The presence of *G. pyramidum*, therefore, caused *G. a. allenbyi* to have lower energy gain, both because it had fewer seeds to start with and because it wasted additional costs by exploiting seeds at low density.

Overall, Ziv *et al.* (1993) showed that via interference competition *G. pyramidum* forces *G. a. allenbyi* to forage both later in the night and in the less preferred habitat type. Here we suggest that foraging behavior of *G. pyramidum* increases the costs of *G. a. allenbyi* while foraging and may cause *G. a.*

allenbyi to consume fewer seeds. This may result in a lower net energy gain. At the same time, *G. pyramidum* reduces the richness of the environment as seen by *G. a. allenbyi*, and so reduces *G. a. allenbyi*'s marginal value of energy, cost of predation, and GUD in patches. Therefore, competition from *G. pyramidum* occurs both by interference, in which *G. a. allenbyi* is forced to be active in the late part of the night, and exploitation via resource depletion by *G. pyramidum* in the early part of the night. The lower GUDs displayed by *G. a. allenbyi* in the presence of *G. pyramidum* and the lower quitting harvest rates (i.e., benefit of foraging) associated with them (Kotler and Brown, 1990) constitute the cost of coexistence to *G. a. allenbyi*.

Acknowledgements

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