Harvest rates and foraging strategies in Negev Desert gerbils

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We examined the foraging strategy and quantified the foraging traits of two nocturnal rodent species, Allenby's gerbil (*Gerbillus allenbyi*) and the greater Egyptian sand gerbil (*Gerbillus pyramidum*). In the laboratory, both species used two distinct foraging strategies: either they immediately consumed seeds found in a patch (seed tray); or they collected and delivered the seeds to their nest box for later consumption. Moreover, we found a transition in foraging strategy among individual *G. allenbyi* under laboratory conditions; they all began by consuming the seeds on the tray and, after 7 days on average, switched to the collecting strategy. By contrast, in the field both species used only one foraging strategy; they collected and delivered the seeds to their burrow or to surface caches for later consumption. Furthermore, *G. allenbyi* and *G. pyramidum* collected seeds at significantly higher rates in the field than in the laboratory because the seed encounter rates for both species were higher in the field. This suggests that in natural conditions, probably involving predation risk and competitive pressure, gerbils must respond in two ways: (1) they must choose a foraging strategy that reduces predation risk by minimizing time spent feeding outside their burrows; and (2) they must forage more efficiently. In the field, seed handling time of the larger species, *G. pyramidum,* was shorter than that of the smaller one, *G. allenbyi*. This difference may give *G. pyramidum* an advantage when resource levels are high and when most of a forager's time is spent handling seeds rather than searching for more seeds. Additionally, our field study showed that the seed encounter rate of *G. allenbyi* was higher than that of *G. pyramidum*. This difference may give *G. allenbyi* an advantage when resource levels are low and when searching occupies most of the forager's time. The different advantages that each species has over the other, under different conditions, may well be factors promoting their coexistence over a wide range of resource densities. *Key words:* coexistence, encounter rate, foraging strategy, functional response, handling time, harvest rate. *[Behav Ecol 12:219–226 (2001)]*

I t is becoming increasingly accepted that behavior can play an important role in determining the structure and the function of complex ecological communities (e.g., Fryxell and Lundberg, 1998; Hassell and May, 1985; Sutherland, 1996). One fundamental and essential behavior for all animals is foraging. Indeed, foraging theory was developed about 30 years ago to understand community structure and function, and since then numerous aspects of foraging behavior have been investigated (Emlen, 1966; MacArthur and Pianka, 1966; Perry and Pianka, 1997; Stephens and Krebs, 1986). Two major focuses of foraging theory are foraging strategies (e.g., patch quitting rules and diet selection) and foraging traits (e.g., handling time, encounter rate and nutritional demands) (Stephens and Krebs, 1986).

In many cases, an individual can use a wide range of foraging strategies. Moreover, an individual may switch its foraging strategy in response to environmental changes. Such adaptive foraging behavior is very important because it can affect population persistence (Henein et al., 1998), interactions between species (Hambäck and Ekerholm, 1997; Holt, 1984; Holt and Kotler, 1987; Werner, 1992; Werner and Hall, 1989), and stability of the system (Fryxell, 1997; Schmitz et al., 1997).

Foraging traits, such as handling time and encounter rate, are the basic elements of any foraging model that describes the interaction between a consumer and its resources (Holling, 1959). Measuring foraging traits of different species allows comparison between different patch use and diet selection strategies (Brown and Mitchell, 1989). Moreover, interspecific differences in foraging traits and consequently in harvest rate, may be the basis for the coexistence between species in a community (e.g., Armstrong and McGehee, 1980; Brown, 1989; Kotler and Brown, 1988; Vincent et al., 1996; Waltman, 1983). For example, coexistence between species might be due to differences in their harvest rates while foraging on different substrates (Hughes et al., 1995; Price and Heinz, 1984), at different resource densities (Brown, 1989), or under different levels of predation risk (Kotler et al., 1994).

In order to understand the behavioral mechanisms that promote coexistence between two nocturnal gerbil species, Allenby's gerbil (*Gerbillus allenbyi*) and the greater Egyptian sand gerbil (*Gerbillus pyramidum*), we studied their foraging strategies and quantified their foraging traits under different environmental conditions: a laboratory and a field setting. The foraging strategies on which we focused were: (1) immediate feeding in a patch (on-patch consumption), and (2) collecting in a patch and caching the food for later consumption. The foraging traits were seed handling time and seed encounter rate.

Natural history

G. allenbyi and *G. pyramidum* occur sympatrically in a wide range of sandy habitats in the Western Negev Desert (Abramsky et al., 1985a). The smaller species, *G. allenbyi* (mean mass = 26 g), occurs mostly in stabilized sands and semi-stabilized dunes with relatively dense vegetation cover (Abramsky et al., 1985b). The larger species, *G. pyramidum* (mean mass = 40

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g), occurs mostly in shifting and semi-stabilized dunes with more sparse vegetation cover (Abramsky et al., 1985b). The two gerbil species are similar in their general ecology; they are both solitary burrow dwellers that forage nocturnally for seeds, which constitute large proportions of their diets (Bar et al., 1984). Although individual *G. allenbyi* and *G. pyramidum* do not have cheek pouches, they carry seeds in their mouth and deliver them to surface caches or to their burrows for later consumption (Ovadia, 1999). Individuals of both species typically block their burrow entrance with sand (Ovadia, 1999). We assume that this behavior may reduce predation risk by snakes and protect stored seeds from theft. Direct observations have shown that individual *G. allenbyi* and *G. pyramidum* aggressively defend food sources, and these aggressive interactions include chases and attempts at physical contact (Ovadia, 1999).

The effect of the three major predators, owls, snakes, and foxes, on the behavior of *G. allenbyi* and *G. pyramidum* was investigated intensively. In the presence of owls, both species forage less and avoid the open microhabitat (Abramsky et al., 1996; Kotler et al., 1991, 1992). In contrast, when snakes are present both are active mainly in the open microhabitat (Kotler et al., 1992, 1993a,c). Finally, in the presence of foxes, the two gerbil species reduce their foraging activity, but there is no difference in foraging effort between under-bush and open microhabitats (Ovadia, 1999). Synthesizing the above results reveals that predation risk is not creating an axis of environmental heterogeneity along which the two gerbil species may coexist (Brown et al., 1994b; Kotler et al., 1994).

Field experiments have shown that individual *G. allenbyi* and *G. pyramidum* compete strongly with each other (Abramsky and Pinshow, 1989; Abramsky et al., 1991, 1992, 1994; Mitchell et al., 1990). The larger species, *G. pyramidum,* excludes the more efficient forager (Brown et al., 1994a; Kotler et al., 1993b), *G. allenbyi,* from the best habitat (Abramsky et al., 1990; Ziv et al., 1993) and from the early part of the night (Kotler et al., 1993d; Ziv et al., 1993). Thus, ecologists suggested that coexistence between the two species is due to a trade-off between the dominance of *G. pyramidum* versus the foraging efficiency of *G. allenbyi* (Kotler et al., 1993d; Ziv et al., 1993). Here, we define foraging efficiency as the ratio of harvest rate to foraging costs (see Brown, 1988).

Testing for species-specific foraging traits that may mediate coexistence, Kotler and Brown (1990) measured the harvest rate of *G. pyramidum* and *G. allenbyi*. However, their study was done under laboratory conditions and they did not consider the potential use of more than one foraging strategy: specifically (1) immediate feeding in a patch; and (2) collecting in a patch and caching the food for later consumption. It is possible that each foraging strategy may be associated with specific foraging traits. Therefore, the quantification of the frequency of each strategy in the population and the detection of strategy-specific foraging traits may have important implications regarding the coexistence of the two gerbil species. Furthermore, we believe that extrapolating foraging data obtained in the laboratory to animals under natural conditions may be problematic and therefore we suggest that laboratory studies be complemented with field studies. In this study we measured the strategy-specific foraging traits of gerbils under both laboratory conditions and in the field.

Predictions

In accordance with the natural history of the species and in light of the goals of the present study, we predicted that:
- In the field gerbils will use mainly the collecting and caching strategy which minimizes exposure to predators.
- Gerbils will face diminishing returns in their resource in-

take as a result of the seed distribution and depletion and the cost associated with harvesting.
- The harvest rates of gerbils in the field will be higher than those in the laboratory, because gerbils should compensate for the additional costs that they experience when foraging in the presence of their competitors and predators.
- Foraging traits will differ between the two gerbil species, both under laboratory conditions and in the field. The larger species, *G. pyramidum,* which is active during the first part of the night when resource density is high (Kotler et al., 1993d; Ziv et al., 1993), will have shorter handling times. The smaller species, *G. allenbyi,* the more efficient forager (Brown et al., 1994a), will have higher seed encounter rates.

METHODS

Measuring foraging traits

Holling (1959) developed the first equations describing foraging behavior as a function of handling time and encounter rate (Holling's disc equation). However, using the Holling's disc equation for experimental data may be problematic because it models feeding rate at unchanging resource density, and most experiments allow depletion of the resource by the consumer (e.g., Carter et al., 1984; Collins et al., 1981; Livdahl, 1979; McArdle and Lawton, 1979; Thompson, 1975, 1978). An integrated form of the Holling's disc equation, the random predator equation, has been developed for modeling the functional response of consumers experiencing diminishing returns in their resource intake as a result of the resource depletion (Rogers, 1972; Royama, 1971). The linearized form of this equation (Rogers, 1972), has been recommended (Southwood, 1978), and used in many empirical studies (e.g., Carter et al., 1984; Collins et al., 1981; Thompson, 1975).

Kotler and Brown (1990) suggested a similar integrated linearized form for estimating encounter rate (a, in units of s^{-1}) and handling time (h, in units of s/g) of gerbils foraging on depletable seed patches, from their total foraging time and the amount of food they harvested in a patch:

$$t = \left(\frac{1}{a}\right) \times \ln\left(\frac{N_0}{N_f}\right) + h \times (N_0 - N_f) \tag{1}$$

where t (in s) is the total time spent foraging in patch, N_f (in g) is the mass of food remaining in patch and N_0 (in g) is the initial mass of food on patch. The first term on the right side of the equation describes time spent searching for food and the second term describes the time spent handling encountered food items.

Kotler and Brown (1990) developed Equation 1 based on the natural history of *G. allenbyi* and *G. pyramidum*. The similar linearized form proposed by Rogers (1972) has been criticized for inaccuracy when tested with a simulated data set (Juliano and Williams, 1987). However, we have used Equation 1 for our experiments because it was developed specifically to fit both the gerbil system and the kind of data we collected during this study.

Field study

The field site was located in the Holot Mashabim Nature Reserve (31°01′ N, 34°45′ E), situated in the Haluza region, 35 km south of Beer Sheva, Israel. Sandy areas at the study site can be classified into two habitat types based on mobility of the sand and on the dominant perennial plant species. The two habitat types are 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.

Table 1

The encounter rate (a) and the handling time (h) of *G. allenbyi* and *G. pyramidum* under laboratory conditions and in the field

Species	Foraging strategy	Encounter rate			Handling time			Model statistics		
		a [s^{-1}]	t_{df}	p	h [s/g]	t_{df}	p	R^2_{df}	F_{df}	p
Laboratory experiment										
G. allenbyi	Feeding in tray	9.4×10^{-4}	$t_{30} = 2.17$	.038	582.9	$t_{30} = 2.49$	.018	$R^2_{32} = 0.97$	$F_{2,30} = 432$	<.001
G. allenbyi	Collecting seeds	1.58×10^{-3}	$t_{21} = 5.67$	<.001	313.05	$t_{21} = 4$	.001	$R^2_{23} = 0.99$	$F_{2,21} = 1275$	<.001
G. pyramidum	Feeding in tray	1.04×10^{-3}	$t_{24} = 1.75$	.094	715.1	$t_{24} = 2.59$	.016	$R^2_{26} = 0.97$	$F_{2,24} = 393$	<.001
G. pyramidum	Collecting seeds	1.92×10^{-3}	$t_{13} = 5.21$	<.001	156.36	$t_{13} = 2.05$	.06	$R^2_{15} = 0.99$	$F_{2,13} = 498$	<.001
Field experiment										
G. allenbyi	Collecting seeds	5.9×10^{-3}	$t_{73} = 3.35$	.001	380.67	$t_{73} = 9.55$	.001	$R^2_{75} = 0.97$	$F_{2,73} = 1026$	<.001
G. pyramidum	Collecting seeds	2.4×10^{-3}	$t_{46} = 4.84$	<.001	154.91	$t_{46} = 2.59$	.013	$R^2_{48} = 0.96$	$F_{2,46} = 517$	<.001

We used one 1-ha plot enclosed with rodent-proof fences to measure the harvest rates of the two gerbil species. The 1-ha plot contained similar proportions of the two major habitat types, semi-stabilized dunes and stabilized sand. Direct observation and sand tracking suggest that these fences did not effect the activity of mammalian predators. Data collected from live trapping in control plots of the same size over the past 15 years indicate that the average density of *G. allenbyi* and *G. pyramidum* is 10.75 ± 1.41 and 2.18 ± 0.51 individuals/ha, respectively (Abramsky Z, unpublished data).

We did two field experiments with each gerbil species. Each experiment lasted 12 nights and was scheduled so that foraging measurements occurred on moonless nights. We used the following experimental protocol. For six consecutive nights, we trapped and removed all the rodents from the enclosed plot. Thereafter, we released six naive gerbils of a single species into the plot and let them habituate to their new surroundings for two nights. During each of the following three nights we ran one to three foraging sessions. We began each foraging session by placing six seed trays ($60 \times 45 \times 2.5$ cm deep) in an open area (≥ 1 m from shrubs). The distance between adjacent seed trays was 1 m. Each seed tray was filled with 3 dm^2 of sifted sand into which 3 g of millet seeds were thoroughly mixed. We videotaped the foraging sessions using two thermal imaging cameras (an Infracam and a Radiometer-IR-760, both by Inframetrics Inc.). We stopped foraging sessions after different time intervals to obtain data spread over the entire range of patch depletion. At the end of each session, we removed the seed trays and sifted the sand to recover the remaining millet seeds. For each session we recorded the total time that gerbils spent foraging in each tray (t in s) and the mass of the seeds remaining in the tray (final mass, or N_f, in g). Because the initial mass (N_0) of seeds on each tray was 3 g, the amount of seeds harvested was the difference between the initial and final masses ($3 - N_f$). At the end of each experiment we opened gates in the fences of the enclosed plot for two weeks so that animal and resource densities could attain similar levels outside and inside the plots.

Data from livetrapping and sand tracking stations suggest that on average an individual *G. allenbyi* or *G. pyramidum* covers a minimum area of 20×20 m per night (Brown et al., 1994a). Furthermore, in most foraging sessions we were able to observe three to six gerbils simultaneously foraging on different seed trays. Thus, we believe that during each experiment almost all individuals in the enclosure contributed to the data set.

Laboratory study

We captured six individuals of each gerbil species at the field study site and brought them to the laboratory. We built six

0.7×3 m adjacent arenas. We placed a nest box on one side of the arena and a metal seed tray ($60 \times 45 \times 2.5$ cm) on the other. Using one species at a time, we introduced one animal into each of the six adjacent arenas and allowed them 2 days for habituation. For the next several nights, we conducted on average 12 foraging sessions. At the beginning of each foraging session, we introduced a single seed tray into each arena. Again, each seed tray contained 3 dm^2 of sifted sand into which 3 g of millet seeds were thoroughly mixed. By direct observation and using six stopwatches, we measured the time that each of the six gerbils spent foraging for seeds. We stopped the foraging sessions after various time intervals to obtain data spread over the entire range of patch depletion, removed the seed trays, and sifted the sand to recover the remaining millet seeds. The data from a session consisted of the time spent foraging by a gerbil within its seed tray, the mass of the seeds that it collected or consumed, and the final mass of seeds left in its tray.

RESULTS

Foraging strategies: laboratory and field studies

A notable finding of the laboratory experiments was that both species had two distinct foraging strategies: either they consumed seeds immediately on the tray, or they collected and delivered the seeds to their nest box for later consumption (Figure 1 and Table 1). Moreover, we found a transition in foraging strategy among individual *G. allenbyi*; they all began with the on-tray consumption strategy and after a few days switched to the collecting strategy (Figure 2). Such pattern was not found among individual *G. pyramidum*.

By contrast, in the field both species used only one foraging strategy: They collected and delivered the seeds to their burrow or to surface caches for later consumption (Figure 3 and Table 1). In a separate field experiment, a similar pattern was found. Gerbils ate seeds in the patch in less than 1% of the foraging bouts, and in 99% they collected and delivered seeds to their burrows or to surface caches for later consumption (Ovadia, 1999).

Harvest rates: laboratory study

We used Equation 1 to do a multiple regression analyses and found that under laboratory conditions the harvest-rate curves of the two gerbil species fit a type II functional response as described by Holling (1959) (see Figure 1 and Table 1). The slopes of the harvest rate curves decrease as the time spent foraging increases (Figure 1), implying that gerbils experience diminishing returns from their harvest as they spend more time foraging (Charnov, 1976).

Figure 1
Seeds harvested [g] as a function of time spent foraging in a patch [s] by *G. allenbyi* and *G. pyramidum* for each of the two foraging strategies that they used under laboratory conditions. The two foraging strategies are feeding in a patch and collecting seeds for later consumption. The lines were fitted to the data by multiple linear regression with Equation 1 as the model.
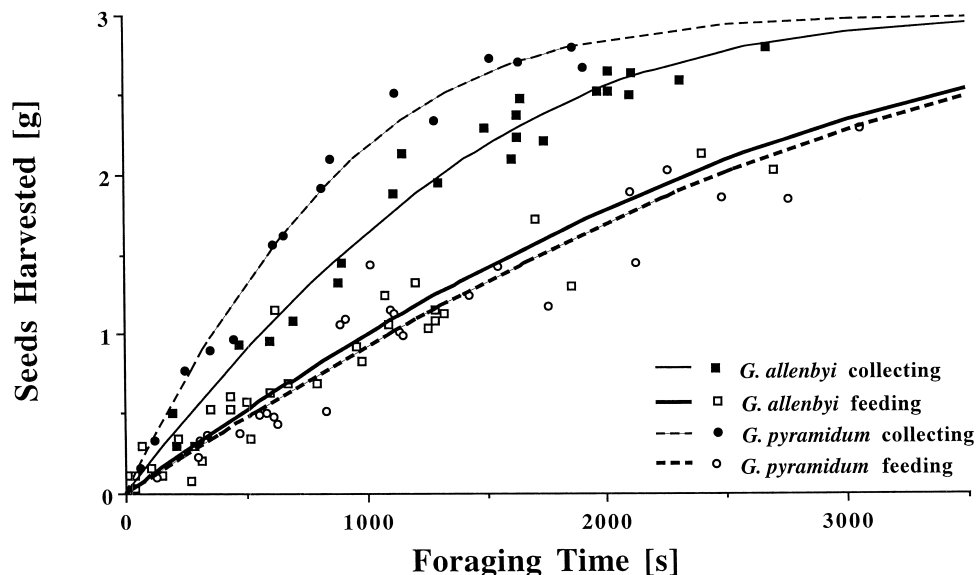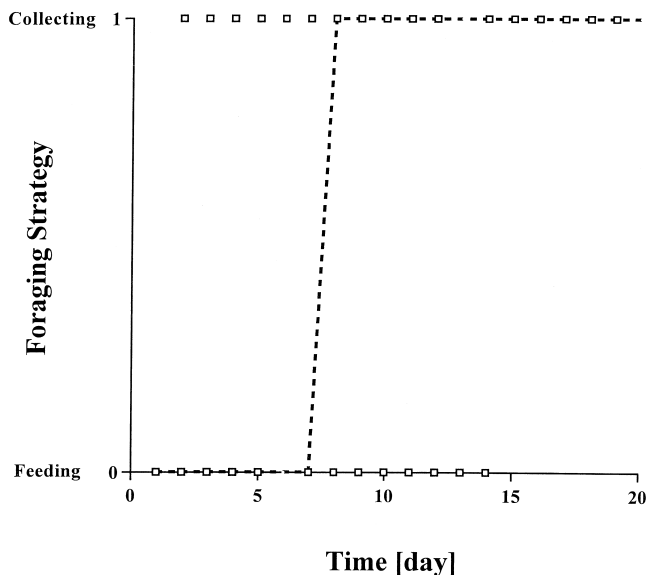

We did analyses of covariance to test for the effect of foraging strategy on harvest rates of the two gerbil species. We treated time spent foraging in a patch as the dependent variable, $\ln(N_0/N_f)$ and (N_0-N_f) as covariates, and foraging strategy as an independent categorical variable. The effect of foraging strategy on the harvest rates of *G. allenbyi* and *G. pyramidum* was highly significant ($F = 33.75$; df = 1,52; $p < .001$ and $F = 45.29$; df = 1,38; $p < .001$, respectively), with both species harvesting faster when collecting the seeds for later consumption. These differences may be due to differences in seed handling time, seed encounter rate, or both. The mul-

tiple regression analyses provided the values of seed encounter rate and seed handling time for each species (Figure 4a,b and Table 1). For both species, seed handling time was shorter and seed encounter rate was higher when collecting seeds than when consuming seeds in the tray (Figure 4a,b and Table 1). To test whether these differences are significant, we added the interaction terms between foraging strategy and the covariates into our models. The interaction between the foraging strategy and seed handling time of *G. allenbyi* and *G. pyramidum* was not significant ($F = 0.997$; df = 1,50; $p = .323$ and $F = 0.849$; df = 1,36; $p = .363$, respectively). Hence, neither species had significantly different seed handling times when using different foraging strategies (Figure 4b and Table 1). The interaction between the foraging strategy and seed encounter rate of *G. allenbyi* and *G. pyramidum* also was not significant ($F = 0.322$; df = 1,50; $p = .573$ and $F = 0.927$; df = 1,36; $p = .342$, respectively). It follows that neither species had significantly different seed encounter rates when using different foraging strategies (Figure 4a and Table 1). We could not relate the differences in harvest rates between the two foraging strategies to seed encounter rate or to seed handling time in either species.

We did not find significant differences in harvest rates between the two species when they consumed seeds in the tray ($F = 2.08$; df = 1,55; $p = .155$). However, when they collected seeds for later consumption, we were able to detect significant interspecific differences; *G. pyramidum* harvested seeds at a higher rate than *G. allenbyi* ($F = 50.12$; df = 1,35; $p < .001$). We could not relate this interspecific effect to differences in seed handling time (Figure 4b and Table 1) or in seed encounter rate (Figure 4a and Table 1) between the two gerbil species ($F = 0.608$; df = 1,33; $p = .441$ and $F = 0.353$; df = 1,33; $p = .557$, respectively). Instead, these differences may be the result of the combined effect of seed handling time and seed encounter rate.

Figure 2
The transition in foraging strategy found among individual *G. allenbyi* under laboratory conditions. All individuals begun by consuming the seeds on the tray and, after 7 days on average, switched to the collecting strategy. The line was fitted using a simple logistic regression with maximum likelihood estimation: Strategy = $\exp(B0 + B1 \times \text{Time})/[1 + \exp(B0 + B1 \times \text{Time})]$ The coefficients and their 95% confidence limit intervals are: B0 = -1.495 ($-2.50 < B0 > -0.49$); B1 = 0.198 ($0.07 < B1 > 0.33$).

Harvest rates: field study

We found that in the field the harvest rate curves of the two gerbil species fitted a type II functional response curve (Holling, 1959; see Figure 3 and Table 1). As in the laboratory situation, the slopes of the harvest rate curves decrease as the time spent foraging increases (Figure 3), again suggesting that
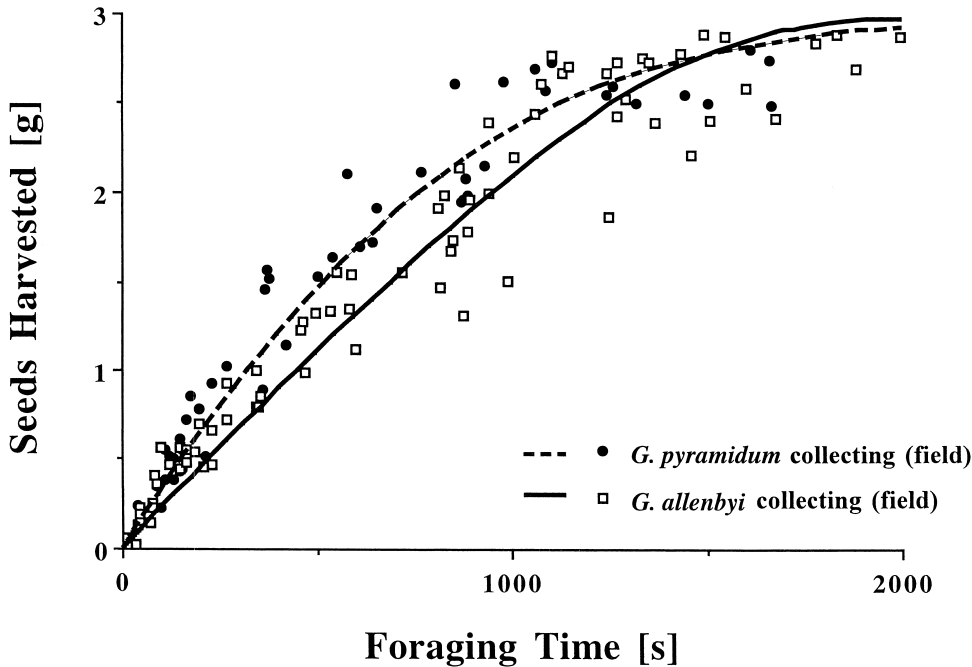
Figure 3
Seeds harvested [g] as a function of time spent foraging in a patch [s] by *G. allenbyi* and *G. pyramidum* in the field. The two gerbil species used only one foraging strategy, they collected and delivered the seeds into their burrow or to surface caches for later consumption. The lines were fitted to the data by multiple linear regression with Equation 1 as the model.
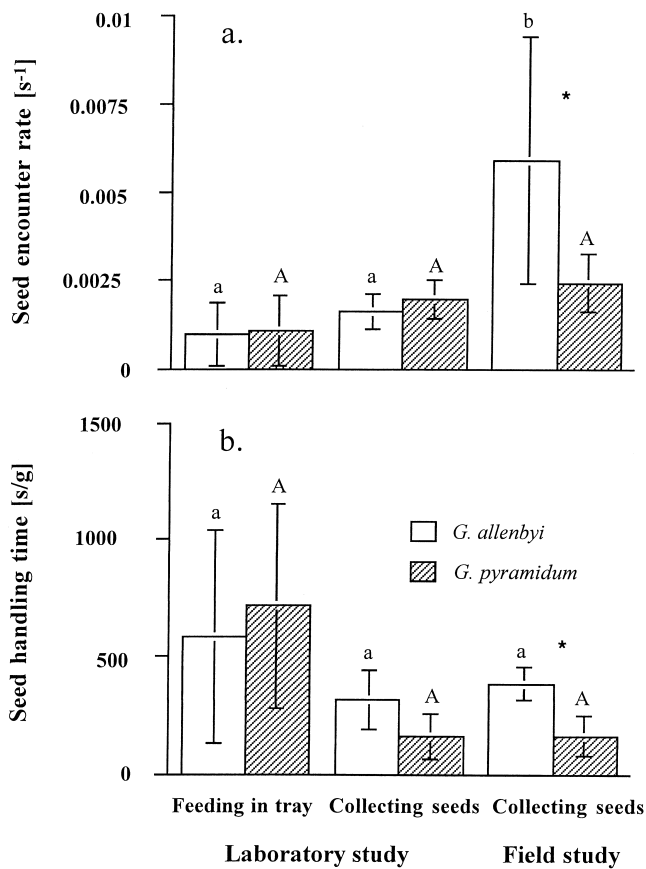

Figure 4
Seed encounter rate (a), and seed handling time (b) of *G. allenbyi* and *G. pyramidum* under laboratory conditions and in the field (with 95% confidence limit intervals). Results that differ statistically, are allocated different letters: lower case, comparison between foraging strategies of *G. allenbyi*; upper case, comparison between foraging strategies of *G. pyramidum*. Asterisks (*) indicate significant difference between species for specific foraging strategy.

gerbils experienced diminishing returns from their harvest as they spend more time foraging (Charnov, 1976).

We found a significant difference in harvest rates between the two species, with *G. pyramidum* harvesting seeds at a higher rate than *G. allenbyi* ($F = 8.625$; df = 1,120; $p = .004$). Seed handling time of *G. pyramidum* (154.91 s/g) was significantly shorter than that of *G. allenbyi* (380.67 s/g) ($F = 6.81$; df = 1,118; $p = .01$; Figure 4b, Table 1). Thus, when both species forage in rich patches, *G. pyramidum* will have an advantage over *G. allenbyi*. Seed encounter rate of *G. allenbyi* (5.9×10^{-3} s^{-1}) was significantly higher than that of *G. pyramidum* (2.4×10^{-3} s^{-1}) ($F = 5.867$; df = 1,118; $p = .017$; Figure 4a and Table 1). Thus, when food density in patches is very low, *G. allenbyi* will have an advantage over *G. pyramidum*.

Harvest rates: comparison between the laboratory and the field studies

We tested for differences in the harvest rates between the field and the laboratory experiments. The results showed that, when collecting seeds for later consumption, both *G. allenbyi* and *G. pyramidum* harvested seeds at significantly higher rate in the field than under laboratory conditions ($F = 77.045$; df = 1,95; $p < .001$ and $F = 8.04$; df = 1,60; $p = .006$, respectively; Figure 5). We found that for both species, seed handling time was similar and seed encounter rate was higher in the field than in the laboratory (Figure 4a,b and Table 1). For *G. pyramidum,* we did not find significant differences in seed encounter rate between the field and the laboratory ($F = 1.15$; df = 1,58; $p = .288$; Figure 4a). However, seed encounter rate of *G. allenbyi* was significantly higher in the field (5.9×10^{-3} s^{-1}) than in the laboratory (1.58×10^{-3} s^{-1}) ($F = 13.83$; df = 1,93; $p < .001$; Figure 4a).

DISCUSSION

Foraging strategies and foraging traits are two of the major focuses of optimal foraging theory (Stephens and Krebs, 1986). The interaction between each one of them and environmental heterogeneity may have important ramifications
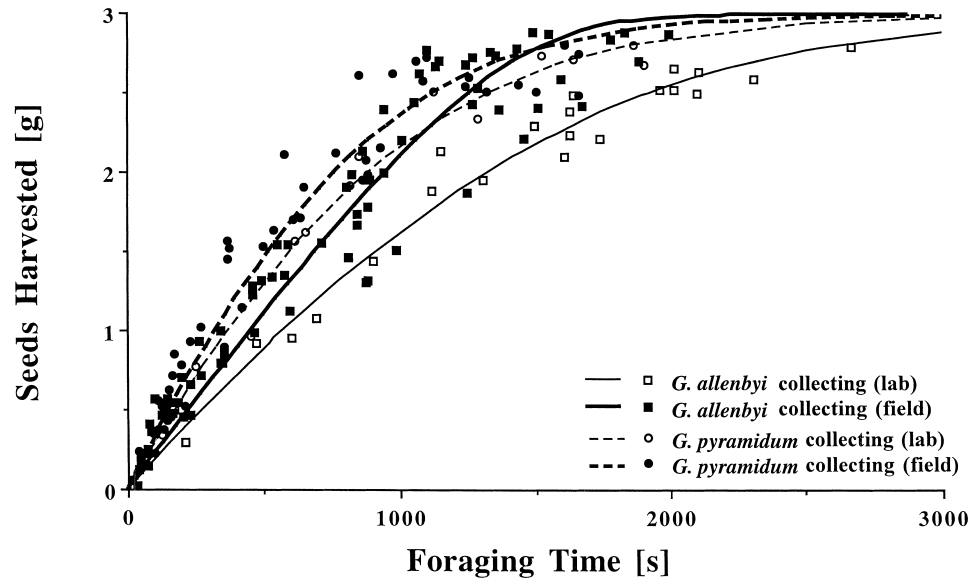
Figure 5
Seeds harvested [g] as a function of time spent foraging in a patch [s] by *G. allenbyi* and *G. pyramidum* for the field and the laboratory study when both species collected and delivered the seeds into their burrow or to surface caches for later consumption. The lines were fitted to the data by multiple linear regression with Equation 1 as the model.

for the understanding of population and community patterns and processes (e.g., Hambäck and Ekerholm, 1997; Henein et al., 1998; Holt and Kotler, 1987; Kotler and Brown, 1988; Werner, 1992).

We found that under laboratory conditions, both *G. allenbyi* and *G. pyramidum* used two distinct foraging strategies; either they immediately consumed seeds on the provided seed trays, or they collected the seeds for later consumption. Additionally, individual *G. allenbyi* began with the on-tray consumption strategy and then switched to the collecting strategy (Figure 2). However, in the field both species used only one foraging strategy. They collected seeds on trays and delivered them to their burrow or to surface caches for later consumption. Why, in the field, do gerbils rarely eat seeds where they find them?

Our preliminary experiments show that in smaller arenas gerbils primarily used the on-tray consumption strategy. This suggests that the distance between a food patch and an individual burrow may affect foraging strategy. During the laboratory study, the distance between the food patch and the nest box did not change, and gerbils used both foraging strategies. Moreover, in each of the four field experiments (two for each species), few individuals located their burrows adjacent to the seed trays (less than 1 m), and none fed on the seed trays. Thus, although distance may be an important factor, it seems that this was not the main factor motivating gerbils in the field to use the collecting strategy exclusively.

Gerbils in the field are subjected to conflicting pressures imposed by abiotic and biotic factors. For example, predation risk may compel gerbils to minimize the time that they spend foraging outside their burrows, while competition may encourage them to stay longer in patches and to defend them from other gerbils. Calculations based on field data have shown that predation risk amounts to 91% of the total foraging cost (Brown et al., 1994b). Moreover, predation risk causes gerbils to reduce their activity (Abramsky et al., 1996; Kotler et al., 1991, 1992, 1993a,c) and, under high predation pressure, the strong competition between the two gerbil species almost disappears (Abramsky et al., 1998). Therefore, it is likely that predation risk has a strong effect on gerbil foraging strategy. Indeed, the results of our field study show that gerbils chose a foraging strategy that reduces predation risk by minimizing the time spent feeding outside their burrows.

G. allenbyi and *G. pyramidum* harvested seeds at significantly higher rates in the field than in the laboratory (Figure

5). This difference was due to the increased seed encounter rate (Figure 4a and Table 1) and suggests that under natural conditions—which probably include predation risk and competition pressure—gerbils not only change their foraging strategy, but also forage more efficiently. The ability of individuals to adaptively switch their foraging strategy or to change their harvest rates may have substantial implications on both the population and the community levels (e.g., Fryxell, 1997; Hambäck and Ekerholm, 1997; Henein et al., 1998; Holt, 1984; Holt and Kotler, 1987; Schmitz et al., 1997; Werner, 1992).

Kotler and Brown (1990) measured the values of seed handling time and seed encounter rate for the two gerbil species under laboratory conditions. Their estimated seed handling times of *G. allenbyi* and *G. pyramidum* were 939.3 s/g and 534.9 s/g, respectively (Kotler and Brown, 1990). Their estimated seed encounter rates of *G. allenbyi* and *G. pyramidum* were 2.09×10^{-3} s^{-1} and 1.62×10^{-3} s^{-1}, respectively (Kotler and Brown, 1990). Laboratory seed handling time and seed encounter rate measured by Kotler and Brown (1990) were close to the laboratory values we measured for gerbils consuming seeds in trays (Table 1). The arena used by Kotler and Brown in their laboratory study (70×55 cm) was smaller than the arena that we used (70×300 cm). Since our preliminary experiments showed that, in the smaller arenas, gerbils primarily used the on-tray consumption strategy, we suggest that in the Kotler and Brown experiment, gerbils most often fed on the seed trays.

In the field the two species demonstrate a significant difference in harvest rates, with *G. pyramidum* harvesting seeds at a higher rate than *G. allenbyi* (Figure 3). In addition, our field study supports Kotler and Brown's (1990) conclusions regarding seed handling time. *G. pyramidum*'s seed handling time (154.91 s/g) was significantly shorter than that of *G. allenbyi* (380.67 s/g) (Figure 4b and Table 1). This difference may give *G. pyramidum* a foraging advantage over *G. allenbyi* in rich patches: *G. pyramidum* will collect more seeds per unit time. Moreover, we found that in the field, seed encounter rate of *G. allenbyi* (5.9×10^{-3} s^{-1}) was significantly higher than that of *G. pyramidum* (2.4×10^{-3} s^{-1}) (Figure 4a and Table 1). Thus, when patch food density has been lowered, *G. allenbyi* will have an advantage over *G. pyramidum*: it will be able to find and collect more seeds per unit time of search.

Previous studies have shown that the larger species, *G. pyr-*

amidum, excludes the smaller species, *G. allenbyi,* both from the preferred habitat (Abramsky et al., 1990; Ziv et al., 1993) and from favored activity h (Kotler et al., 1993d; Ziv et al., 1993). Brown et al. (1994a) found that the giving up density of *G. allenbyi* is lower than that of *G. pyramidum.* Based on these results, ecologists suggested that coexistence between the two species is based on a trade-off between dominance of *G. pyramidum* and foraging efficiency of *G. allenbyi* (Brown et al., 1994a; Kotler et al., 1993d; Ziv et al., 1993). This trade-off occurs along an axis of environmental heterogeneity comprised of spatial and temporal variability in resource abundance (Ben-Natan, 1999).

Our study demonstrates that the interspecific differences in foraging traits may be sufficient to promote coexistence between the two species. At the beginning of the night, when resource density in patches is high and the forager spends most of its time handling seeds, *G. pyramidum* is more efficient due its shorter handling time. Later in the night, when resource density in patches is low and the forager spends most of its time searching for seeds, *G. allenbyi* is more efficient due to its higher encounter rate. Therefore, we suggest that coexistence between the gerbil species is sustained by several related mechanisms operating along the same axis of environmental heterogeneity.

Vincent et al. (1996) developed a theoretical model to explore how trade-off in conversion efficiency, handling time, and encounter rate effect coexistence between species. One important outcome of this model is that a difference in encounter rate between species may support coexistence over a wide range of environmental heterogeneity. Although Vincent et al. (1996) deal with different situations, our results lend credence to their theoretical study concerning the importance of encounter rate in promoting species coexistence. The relative advantage in encounter rate of the subordinate species, *G. allenbyi,* over *G. pyramidum,* allows it to exploit resource patches that are not profitable for the dominant species. This advantage may permit species coexistence over a wide range of resource densities.

Finally, we showed that there are substantial differences in foraging strategies and foraging traits between laboratory and field experiments. Thus, we suggest that, in order to effectively test foraging theories, laboratory experiments should be run in conjunction with field studies, where animals are exposed to real ecological pressures.

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