

Foraging and community consequences of seed size for coexisting Negev Desert granivores

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We examined the effects of seed size on patch use and diet selection for three co-existing Negev Desert granivores: Allenby's gerbil (*Gerbillus allenbyi*), greater Egyptian sand gerbil (*Gerbillus pyramidum*), and crested lark (*Galerida cristata*). We manipulated size and spatial distribution of seeds in experimental food patches and quantified foraging behavior by measuring giving-up densities (GUDs: the amount of food remaining in a resource patch following exploitation by a forager). In one experiment, we presented small (<1.4 mm in diameter cracked wheat), medium (2.0–3.3 mm), and large (>3.4 mm) seeds in separate trays; in a second, we presented small and medium seeds separately and mixed together. Gerbils had a higher handling time efficiency on smaller seeds, but a much higher encounter probability on larger seeds (20 times higher on large than medium seeds, and 2–5 times higher on medium than small seeds). This led gerbils to have significantly lower GUDs on larger seeds than smaller seeds and to harvest a higher proportion of the larger seeds. When presented with rich and poor patches, *G. allenbyi* tended to equalize GUDs in both patches, indicating a quitting harvest rate rule for patch exploitation. In contrast, larks appeared to use a fixed time rule for patch exploitation. For larks, seed size did not influence encounter probabilities, and they showed no seed-size selectivity. Still, larks had higher handling efficiencies on smaller than larger seeds, and consequently had a significantly lower GUD on small than medium seeds. Despite large differences between the gerbils and larks in their foraging, our results do not support species coexistence via seed-size partitioning: the larks had much higher GUDs than the gerbils on all seed sizes. Nonetheless, seed size, seed abundance, seed distribution and the animal's patch use behavior all played major roles in determining gerbils' and larks' diet selectivities and GUDs.

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Diet selection is central to an animal's ecology. Diet influences niche breadth, niche overlap with potential competitors, and the magnitude of competition (Elton 1927, Gause 1934, MacArthur and Levins 1967, MacArthur 1968, Roughgarden 1974). Diet selection influences the growth rate of individuals (Ritchie 1988), reproductive output and survivorship (Ritchie 1990), population dynamics (Belovsky 1984), and the intensity and outcome of species interactions (Rosenzweig 1966, Belovsky 1986).

Foraging theory (Stephens and Krebs 1986) predicts that preference for a food item should be based on the energetic yield of the food item per unit of handling time (Pulliam 1974). Prey size is among the most obvious factors affecting energetic yield per unit of handling time. Larger prey generally contain more energy and are often easier to find, but they may require longer handling times (e.g., Grant 1986). Hence, the size of both predator and prey should help to determine the optimal prey size to a predator.

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When food occurs in depletable resource patches, the amount of a food type included in a forager's diet depends on its patch use behavior, food abundance, encounter probability, and the food's energetic value (Brown and Mitchell 1989, Brown and Morgan 1995). Patch use behavior can determine which food patches are acceptable, and the thoroughness with which each is exploited. The types and abundances of foods, the occurrence of different food types in the same or distinct patches, and the forager's behavior in response to the particular distribution and abundance of food types determine its diet selectivity and thoroughness of patch exploitation.

Patch use and diet selection can have consequences for species interactions. For example, animals that feed opportunistically on patchily distributed prey may inflict short-term apparent competition on co-occurring prey. This is the expected outcome providing the forager exploits patches according to a quitting harvest rate rule (Holt and Kotler 1987). For the predators, diet selection provides a frequent mechanism of species coexistence (Schoener 1986). Coexistence among close competitors is possible providing each species has a food type on which it is more efficient than any of its competitors (Kotler and Brown 1988). The most efficient species on a food type can depress the food's abundance below the point at which less efficient species can forage profitably.

Desert granivores (rodents, ants and birds) are one guild for which coexistence via diet selection and food size partitioning has been proposed (Rosenzweig and Sterner 1970, Brown and Lieberman 1973, Brown 1975, Mares and Williams 1977, Brown et al. 1979). Seed size partitioning has been documented for harvester ants (Davidson 1977, 1978, Brown et al. 1979) and for sparrows (Pulliam and Enders 1971, Pulliam 1975, 1980). Larger species eat larger sized seeds. With regards to rodents, however, most evidence suggests that co-occurring species that differ in body size collect similarly sized seeds (Lemen and Rosenzweig 1978, M'Closkey 1983, Price 1983, Price and Brown 1983, Reichman 1975, Stamp and Ohmart 1978). Recently, Yom-Tov (1991) has examined morphological characteristics of co-occurring species of desert rodents in the Negev Desert, Israel. He found that the lengths of cheek tooth rows in co-occurring species are less similar to each other than expected at random. From this, he suggested that these rodents may partition seeds according to seed size.

In this paper, we experimentally examine the effects of seed size and distribution (foods occurring together or apart) on patch use and diet selection for a community of granivorous vertebrates in the Negev Desert of Israel. Principal species include one bird, crested lark (*Galerida cristata*), and two rodents, Allenby's gerbil (*Gerbillus allenbyi*) and greater Egyptian gerbil (*G. pyramidum*). And, we look for community conse-

quences of diet selection and patch use on depletable resources that differ in size.

Optimal patch use strategies

Consider diet selectivity in the context of patch use. Intensity of patch use measures foraging efficiency on different-sized seeds, estimates relative encounter probabilities and handling time, and determines diet selectivity on different food items. In food patches where the forager experiences diminishing returns (harvest rate declines with time spent exploiting the resource patch), an optimal forager exploiting a risky environment should exploit a patch until its harvest rate, H , in the patch falls to equal the sum of its energetic, C , predation, P , and missed opportunity costs, MOC , of foraging (Brown 1988, 1992):

$$H = C + P + MOC \quad (1)$$

The density of resources at which eq. (1) is satisfied and the forager leaves the resource patch is its giving-up density (GUD; Brown 1988). The lower the GUD, the more efficient the forager (Brown 1989). In support of the theory for desert rodents, GUDs change appropriately in response to factors influencing harvest rates (Ziv et al. 1995), energetic costs (Kotler et al. 1993a), predation costs (Brown et al. 1988, Kotler et al. 1991, 1993b, 1994), and the richness of the environment (Brown et al. 1992).

The optimal patch use model in eq. (1) assumes that the forager has a fairly accurate estimate of its expected harvest rate. This allows the forager to use a quitting harvest rate rule (Valone and Brown 1989) and devote more effort to patches with high initial resource abundances or low foraging costs. A food item in a rich patch is more likely to be harvested than one in a poor patch. Foragers that cannot satisfactorily measure harvest rates should instead devote a fixed amount of search time to each patch (Iwasa et al. 1981). In this situation, the density of a food type remaining after patch exploitation will be proportional to its initial abundance.

Estimating selectivities: foods co-occurring in patches

We estimated selectivities of gerbils and larks for seeds of various sizes using Manly's index (Manly 1974), as modified for depletable resources (Chesson 1983):

$$S = \ln(N_1/R_1)/(\ln(N_1/R_1) + \ln(N_2/R_2)) \quad (2)$$

where S equals the selectivity for prey type 1, N_1 and N_2 are giving-up densities for prey types 1 and 2, respectively, and R_1 and R_2 are the initial abundances of prey in the resource patch. Manly's index gives values between 0 and 1, where $S = 1$ indicates an absence of prey 2 from the diet and $S = 0$ indicates an absence of prey 1; $S = 0.5$ indicates no selectivity for either prey. In what follows, N_1 will always refer to the smaller of the seed sizes being compared, so a value of S significantly greater than 0.5 indicates a disproportionate consumption of the smaller seed.

Manly's index is quite general, but two special cases pertain when food types co-occur in patches (Brown and Morgan 1995). First, foragers may have unequal encounter probabilities for the two food types, but otherwise feed opportunistically. In this situation, $S = a_1/(a_1 + a_2)$ where a_1 and a_2 are the encounter probabilities on foods 1 and 2, respectively. Furthermore, S does not change with intensity of patch exploitation. Second, foragers may be expanding specialists (Heller 1980, Brown and Mitchell 1989) and select only the preferred prey type when this food's abundance is sufficiently high, but switch to an opportunistic tactic as this food becomes depleted. Here, selectivity is the encounter probability with one prey type weighted by the amount of time spent searching for that prey type divided by the sum of encounter probabilities for both prey types, weighted by the amounts of search time on each. A consequence of expanding specialization is that selectivity changes with the degree of patch depletion. Selectivity for the preferred prey, S , decreases with the intensity of patch exploitation.

Estimating harvest rate parameters: foods apart

When different food types occur in separate patches, GUDs can be used to compare the forager's relative preferences (energy per unit of handling time) and encounter probabilities for the different food types. Consider two food types, 1 and 2, which occur in different patches and which differ in size. Harvest rate on a food type can be described by Holling's (1959) disc equation (as is the case for gerbils; Kotler and Brown 1990):

$$Q_i = a_i e_i N_i / (1 + a_i N_i h_i) \quad (3)$$

where Q_i is harvest rate (joules), a_i is the encounter probability on food i (per time), e_i is the energetic value of food i (joules/gram), N_i is the abundance of food i (grams), and h_i is the handling time on food i (time/mass). Since optimal foragers should equalize quitting harvest rates across patches, we can use GUDs to investigate encounter probabilities and handling times

of two foods by setting Holling's disc equation for one food type equal to the disc equation of the other food type (Thorson 1995):

$$a_1 e_1 N_1 (1 + a_1 h_1 N_1) = k = a_2 e_2 N_2 (1 + a_2 h_2 N_2) \quad (4)$$

where k is the forager's quitting harvest rate and N_i is the forager's GUD on food i . Solving for N_2 , taking the reciprocal of N_2 , and setting e_1 and e_2 equal (in our experiments, seeds in experimental patches differ only by size and therefore have the same energetic value on a per gram basis) yields:

$$1/N_2 = a_2(h_1 - h_2) + (a_2/a_1)1/N_1 \quad (5)$$

(Thorson 1995).

Eq. (5) predicts a linear relationship between the reciprocals of N_1 and N_2 . If the y -intercept of this relationship is positive (or negative) then the forager has a higher (or lower) handling time (per gram) on food 1. If the slope of the relationship is less (or greater) than 1 then the forager has a higher (or lower) encounter probability on food 1 (Thorson 1995).

Community consequences of patch use and diet selection

Patch use behavior and diet selection of a forager can have community consequence for both its competitors and its foods. Diet selection can provide a mechanism of species coexistence. Two species can coexist via resource partitioning providing each has a food type at which it is more efficient than its competitors (Kotler and Brown 1988). This can arise when food types differ in crypticity, size, digestibility, nutrient content, toxins, etc., and species differ in their abilities to detect, capture, or digest the different food types (Kotler and Brown 1999). Evidence for such a mechanism can be obtained by placing the food types of interest in different food patches and comparing the GUD of each competitor on each food type. When food types only vary in size then coexistence requires tradeoffs in food-type specific encounter probabilities and/or handling times.

A forager's patch use behavior can result in apparent competition among its foods when the forager uses a fixed quitting harvest rate patch use strategy. Adding a second food to a patch increases the forager's harvest on the first food because increasing the initial density of either food type in a patch improves patch quality and encourages a forager to remain longer in order to deplete food densities to its quitting harvest rate. This $(-, -)$ interaction between the two food types mediated by the behavior of their shared predator is short-term apparent competition (Holt and Kotler 1987). Short-

term apparent competition can be tested for by comparing GUDs for each food type when they occur apart and when they occur together in patches (e.g., kangaroo rat, *Dipodomys merriami*, Brown and Mitchell 1989; fox squirrel, *Sciurus niger*, Brown and Morgan 1995).

Methods

We conducted experiments at Be'er Asluj in the Holot Mashabim Nature Reserve, northwestern Negev Desert, Israel. The site contains mosaics of semi-stabilized and stabilized sand dunes. The dominant perennial plant species are *Artemisia monosperma* and *Retama raetam* (Abramsky et al. 1985). Rodent species on the sandy habitats include *Gerbillus allenbyi* (Allenby's gerbil, 25 g), *G. pyramidum* (greater Egyptian sand gerbil, 39 g), *G. henleyi* (pygmy gerbil, 11 g), Buxton's jird (*Meriones sacramenti* 120 g) and common jerboa (*Jaculus jaculus*, 50–70 g; Abramsky et al. 1990). All are nocturnal, burrow-dwelling, and either primarily or somewhat granivorous (Bar et al. 1984). The most common granivorous bird on the study site, and the only bird known to forage from our food patches, was *Galerida cristata* (crested lark, 39 g). Its diet includes seeds, insects, fruit and some herbage (Shkedy and Safriel 1991, Shkedy 1992).

Within the semi-stabilized and stabilized sand habitats, we established two 2.56-ha grids. Each contained 81 stations arranged 9×9 with 20-m spacing between stations. We used aluminum seed trays ($45 \times 60 \times 2.5$ cm deep) filled with sifted sand and cracked wheat seeds of various sizes depending on the experiment. Three trays were placed at grid stations located at the intersection of evenly numbered rows and columns. This placement required 16 triplets of trays per grid with 40-m spacing between stations with trays. To place the trays of a triplet close together (control for C, P, and MOC at a station) and to avoid spatial biases in triplet orientation, we arranged the trays of a station as a three-pointed star radiating from a central point. Data collection consisted of stocking trays with the appropriate seeds, allowing animals to forage in trays, identifying the forager species in each tray based on tracks, recovering the remaining seeds, cleaning and weighing seeds to obtain the GUD, and recharging trays with new seeds. The GUD was credited to the one or several species whose tracks were visible in the tray.

Experiment 1: foods apart

We designed experiment 1 to yield data for gerbils only. We collected seed tray data for gerbils on seven consecutive days from 6 January through 12 January 1995. We provisioned seed trays late each evening and col-

lected data the following morning. At each station, each tray contained approximately 3 g of either small (< 1.41 mm), medium ($3.36 \text{ mm} > x > 2.0$ mm), or large (> 3.36 mm) "seeds" (whole or cracked wheat), with each tray containing a different seed size. These seed size classes were created by sieving wheat using mesh screens of standardized sizes. We measured out seeds using a 4.3-ml scoop. This yielded 3.02 g (s.e. = 0.0977, $n = 20$) for the small seeds, 3.08 g (s.e. = 0.0985) for the medium seeds, and 3.27 g (s.e. = 0.116) for the large seeds. We rotated treatments among trays each night. *G. allenbyi* and *G. pyramidum* were the primary foragers in trays. Many of the comparisons we wanted to make required that all the GUDs in the three seed trays at a station on a given day be credited to a single species. This rarely happened for *G. pyramidum*, lowering our ability to compare between the two gerbil species in diet selectivity and GUDs (see Discussion).

Experiment 2: foods together and foods apart

We measured GUDs from 30 July through 2 August and from 4 August through 7 August 1995. We collected seed tray data both in the early morning (nocturnal foraging by gerbils) and the late evening (diurnal foraging by larks) of each day, recharging seed trays with fresh seeds each time. We placed three trays at each station, one containing 3 g of small seeds, one containing 3 g of medium seeds, and one containing 3 g of small and 3 g of medium seeds mixed together. Data from mixed seed size trays were used to test for short-term apparent competition and to measure selectivities. Experiment 2 yielded data principally for *G. allenbyi* and *G. cristata*. *G. pyramidum* was at low abundance and rarely foraged from trays.

Results

The effect of seed size on encounter rates and handling time: seeds apart

We examined how encounter rates and handling times changed with seed size. To do so, we regressed (type II) the reciprocal of the GUDs on medium versus small seeds (both experiments) or large versus medium seeds (experiment 1 only) using data from trays containing only a single seed size. We used data from those stations at which a single species was credited with both of the GUDs. From eq. (5), negative (or positive) y -intercepts indicate that smaller seeds offer more (or less) food per unit of handling time. A slope greater (or less) than 1 indicates that the forager has a higher (or lower) encounter probability on larger seeds.

For *G. allenbyi* in the first experiment, the y -intercept did not differ from 0 when comparing medium versus

small seeds, but was significantly negative for large versus medium seeds. In addition, the slopes of both regressions were significantly greater than 1. Similarly, in the second experiment, *G. allenbyi* when foraging on medium versus small seeds had a significantly negative intercept and a slope significantly greater than 1 (Table 1). For *G. allenbyi*, handling time per unit of energy decreased with seed size, and encounter probability increased with seed size.

For *G. cristata* foraging on medium versus small seeds, the y -intercept was significantly negative, and the slope did not differ from 1 (Table 1). In this range, handling time (per gram) decreases with seed size (like the gerbil), and encounter probability does not vary with seed size.

Selectivity and resource abundance: foods together

We used data from the second experiment to test whether selectivities changed with resource densities in accord with an expanding specialist diet strategy. We regressed selectivity for small seeds when foods co-occurred in patches against the sum of seeds remaining in the two patches where small and medium seeds occurred apart (this provides a measure of patch use intensity that is independent of the data used to compute S). Selectivities of either species did not change with GUDs (for *G. allenbyi* slope of 0.012, s.e. = 0.011; for *G. cristata* slope of 0.010, s.e. = 0.027). Both species appeared to harvest seeds opportunistically when two seed sizes co-occurred within food patches.

Effect of seed size on selectivity: foods together

For opportunistic foragers, selectivities different from 0.5 indicate unequal encounter probabilities. In particu-

lar, based on the differences in encounter probability revealed when seed types were apart, *G. allenbyi* foraging opportunistically should have a selectivity for small seeds that is less than 0.5, and *G. cristata* should have a selectivity for small seeds that does not differ from 0.5. When seed types co-occurred in patches, *Gerbillus allenbyi* had a selectivity of 0.316 (s.e. = 0.012), which was significantly less than 0.5 ($t_{183} = 15.462, p < 0.001$), indicating an encounter bias towards larger seeds. In contrast, *Galerida cristata* had a selectivity of 0.494 (s.e. = 0.018), which did not differ from 0.5 ($t_{102} = 0.328, n.s.$).

Community consequences of patch use and seed size selection

Mechanisms of species coexistence

We now compare the GUDs themselves to examine community consequences of seed size selection. The following analyses use the logarithmic transformation of GUD as the dependent variable from trays containing only a single seed size (Figs 1, 2). Logarithmic transformations are commonly used on GUD data because of the non-linear relationship between harvest rate and seed density (Kotler and Brown 1990).

In the first experiment, the gerbils' GUDs declined significantly with seed size ($F_{2,470} = 9.35, p < 0.01$ for a model containing date, grid, seed size, station nested within grid, and the interactions of date by seed size and grid by seed size). An a posteriori Tukey test revealed significant differences in GUDs for all three pairwise comparisons, with lowest GUDs occurring on the large size and highest GUDs on the small size. In the second experiment, with only medium and small seeds to choose from, GUDs of *G. allenbyi* were lowest on the medium-sized seeds ($F_{1,304} = 229, p < 0.001$). De-

Table 1. Coefficients (standard errors) for the regression equations for the reciprocals of the giving-up densities for seed types occurring separately. ($1/N_2 = B_0 + B_1 N_1$). From eq. (5), the y -intercept represents the product of the encounter rate on the larger-sized seeds times the difference of the handling times. A significantly negative intercept indicates a preference for smaller seeds. The slope represents the ratio of the encounter rates of the larger to the smaller seed size. t -tests on intercepts (B_0) test for differences from 0; t -tests on slopes (B_1) test for differences from 1.

Species	B_0	t	B_1	t
<i>Gerbillus allenbyi</i>				
Experiment 1:				
	Medium versus small ($n = 135$) -0.085 (0.214)	0.397	1.822 (0.183)	4.491***
	Large versus medium ($n = 141$) -19.40 (3.97)	4.887***	19.10 (1.92)	9.330***
Experiment 2:				
	Medium versus small ($n = 179$) -1.78 (0.279)	6.380***	5.069 (0.396)	10.275***
<i>Galerida cristata</i>				
Experiment 2:				
	Medium versus small ($n = 92$) -0.116 (0.052)	2.231*	1.158 (0.106)	1.491

* $p < 0.05$, *** $p < 0.001$.

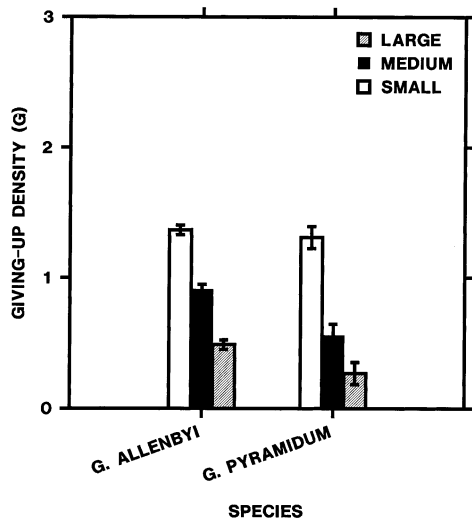


Fig. 1. Giving-up densities (GUDs) in grams of seeds (\pm s.e.) for *Gerbillus allenbyi* and *G. pyramidum* in the first experiment on small, medium, and large seeds. *G. allenbyi* has its lowest GUD on the large seeds.

spite a handling time advantage on smaller versus larger seeds, the large increase in encounter probability with seed size makes the gerbils more efficient foragers on large than small seeds.

The crested larks in the second experiment had a significantly lower GUD on small versus medium seeds ($F_{1,190} = 12.6$, $p < 0.001$). The handling time advantage that larks enjoy on small seeds was sufficient to make the larks more efficient foragers on small seeds.

In light of the above results, diet selection can provide a mechanism of species coexistence if the crested lark had lower GUDs than Allenby's gerbil on small seeds, and if Allenby's gerbil had lower GUDs than crested lark on the larger seeds. However, gerbils had significantly lower GUDs than larks regardless of seeds size ($F_{1,42} = 78.1$, $p < 0.001$).

Short-term apparent competition

To test for short-term apparent competition between seed species (sizes) arising from the patch use behavior of the gerbils and larks, we used data from the second experiment. We used a paired t -test of GUDs at a station to compare the GUD on a seed type when it was alone in a patch with when it co-occurred with the other seed type. Lower GUDs on a seed size when the two seed types co-occur is indicative of short-term apparent competition.

G. allenbyi exploited patches in a way that inflicts apparent competition on the two seed sizes (Fig. 2). *G. allenbyi* had significantly lower GUDs on a particular seed type when it co-occurred with the other than when it occurred by itself (small seeds: difference = 0.245 g, $t_{159} = 4.95$, $p < 0.001$; medium seeds: difference = 0.256 g, $t_{159} = 5.42$, $p < 0.001$). That is, gerbils always re-

moved more seeds from richer patches than poorer patches irrespective of the seed sizes they contained because each patch is left at approximately the same GUD. In contrast, there was no evidence for short-term apparent competition when *G. cristata* was the forager (Fig. 2). *G. cristata* had similar GUDs for small-sized seeds in the mixed and separate treatments (difference = -0.031 g, $t_{91} = 0.728$, n.s.) and showed lower GUDs on medium sized seeds when occurring with small-sized seeds than when occurring separately (difference = 0.206 g, $t_{91} = 4.18$, $p < 0.001$). The results suggest a weak short-term (0, -) apparent interaction.

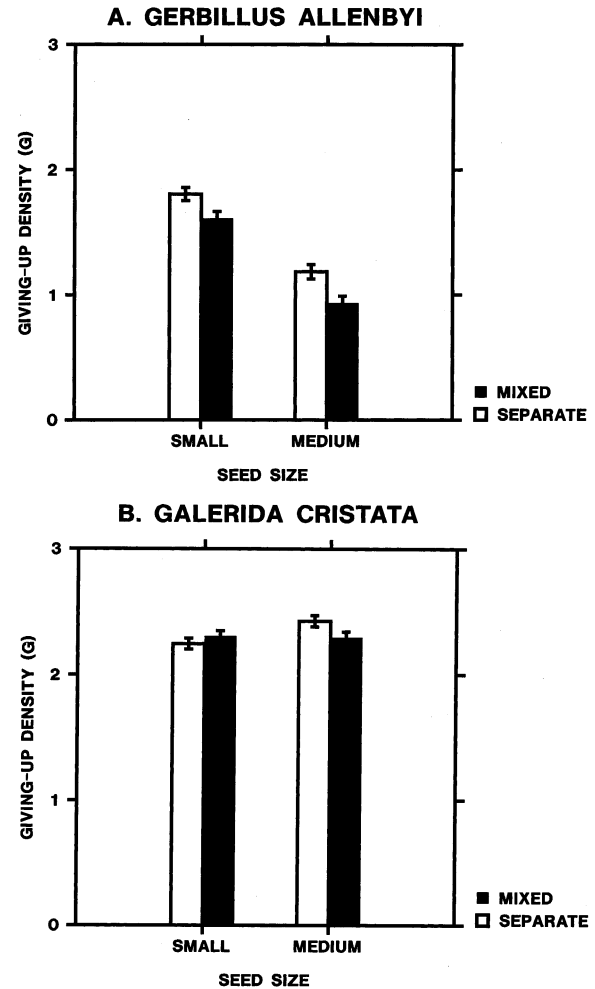


Fig. 2. Giving-up densities (GUDs) in grams of seeds (\pm s.e.) for (A) *Gerbillus allenbyi* and (B) *Galerida cristata* in the second experiment on small and medium seeds occurring in separate seed trays and occurring mixed together in a single tray. *G. allenbyi* always has lower GUDs than *G. cristata* and exploits patches in a manner which leads to short-term apparent competition between the seed types.

Discussion

An animal's diet results from the interplay between the distribution of its foods and its behavioral responses (Brown and Mitchell 1989, Brown and Morgan, 1995, Thorson 1995). Patch use decisions, whether or not different food types co-occur in patches, and dietary decisions based on handling times, energetic value, and encounter probabilities of different food types combine to determine diet. We examined these aspects for granivores in the Negev Desert and addressed some of the possible community consequences.

Gerbils and crested larks differ in their patch use strategies and abilities. *Gerbillus allenbyi* tended to equalize GUDs and therefore quitting harvest rates among resource patches that differed in initial prey density. They assess patch quality, direct their efforts to richer resource patches, and appear to use a quitting harvest rate rule for patch exploitation. Factors contributing to patch quality, such as food quality or abundance, will increase patch residence time and therefore the likelihood of a forager consuming a particular food item. The gerbils' keen sense of olfaction may contribute to their ability to assess patch quality. The Sonoran Desert rodents, Merriam's kangaroo rat (*Dipodomys merriami*), Arizona pocket mouse (*Perognathus amplus*), and roundtailed ground squirrel (*Spermophilus tereticaudus*) also share the gerbils' olfactory abilities and appear to use a quitting harvest rate strategy when patch quality varies highly (the pocket mouse and the ground squirrel appear to use fixed time strategies when patch quality varies little) (Valone and Brown 1989).

In contrast to the gerbils, the crested larks, *Galerida cristata*, failed to equalize GUDs across patches of different initial value, at least at the scale examined in our experiments. Patches that began twice as rich before exploitation remained twice as rich after exploitation. This suggests that crested larks cannot assess patch quality accurately. They come close to exhibiting a fixed time strategy and apply equal amounts of search time to each patch irrespective of quality (Iwasa et al. 1981, Valone and Brown 1989). However, they must make some assessments as larks were able to effect slightly lower GUDs on trays with small seeds than medium seeds, despite similar encounter probabilities on small and medium seeds. Like the larks, the Sonoran Desert granivorous birds mourning dove (*Zenaidura macroura*) and Gambel's quail (*Callipepla gambelii*) also used fixed time strategies for patch exploitation (Valone and Brown 1989).

Gerbils and larks also differed markedly in their response to food characteristics. *Gerbillus allenbyi* disproportionately harvested the largest seed size available, and this selectivity remained unchanged over the range of resource densities examined in our experiments. The available data showed that *Gerbillus pyra-*

midum biased its harvest towards larger seeds ($t_0 = 2.38$, $p < 0.05$), and that the two gerbil species did not differ in their selectivities. We attribute the selectivity for larger seeds to the higher encounter probability for larger seeds relative to smaller sized seeds. Encounter probabilities ranged from 2 to nearly 20 times higher for the larger seed relative to a smaller one. This encounter rate advantage for larger seeds was enough to offset the handling time (per unit of energy) advantage that gerbils enjoyed on smaller seeds. This is in contrast to predictions from simple diet models (Puliam 1974) and is due to the encounter rate advantage on larger seeds.

Fox squirrels (*Sciurus niger*) have been similarly studied. When foraging on buried food items that differed only in size (whole versus chopped sunflower seeds), squirrels had lower handling times on smaller food items (higher e/h), higher encounter probabilities on larger food items, lower giving-up densities on larger food items, and greater selectivity for larger food items (Thorson 1995). Like the gerbils, the higher encounter rates on larger food items overcame the handling time advantage that squirrels enjoyed on smaller food items and gave squirrels a higher foraging efficiency on larger seeds.

The squirrels may differ from gerbils in how selectivity varies with resource abundance (Brown and Morgan 1995). When foraging for whole sunflower seeds and granulated peanuts, fox squirrels preferred sunflower seeds to granulated peanuts, but had an encounter probability advantage on peanuts. The selectivity of fox squirrels changed with intensity of patch exploitation, with squirrels showing a partial preference for the peanuts at low resource density (a consequence of the encounter bias, with encounter rate being particularly important when food is rare) and a partial preference for the sunflower seeds at high resource density (a consequence of handling time and an expanding specialist diet strategy). In contrast, the selectivity of the gerbils did not change with resource abundance. Thus, the impact that squirrels have on their foods will vary with food availability. This can promote coexistence of food species. The gerbils, however, always affect the larger food items more.

Crested larks had a slight preference for small seeds over medium-sized seeds. And, they foraged patches with small seeds to lower GUDs than patches with medium seeds. Larks had the same encounter probability on both seed sizes. And, they harvested the same amount of small and medium seeds from patches that contained both seeds mixed together. The small effects of seed size on the larks' diet and patch use may be due to their foraging mode. To visually expose buried seeds, crested larks peck and sweep the soil surface with their beaks. In contrast, gerbils use tactile senses and olfaction when searching for seeds.

Other species of seed-eating birds do show strong size preferences. Sparrows from arid grasslands in Arizona partition seed size according to body size (Pulliam 1975, Pulliam and Mills 1977). The coexisting species have broadly overlapping efficiencies based on handling time and energetic content of the seed (e/h), with highest efficiencies occurring on small seeds ranging from 0.2 to 2.0 mg (Pulliam 1985). Optimal seed size for the three species examined in the laboratory occurred within a 0.4-mg range (0.38 mg to 0.78 mg). In nature, sparrows show much more pronounced seed size partitioning, and include much larger seeds in their diets (Pulliam 1975). This is consistent with Getty and Pulliam's (1993) finding that these sparrows encounter larger seeds more readily than small seeds and direct their search to where seeds are most detectable. Similarly, granivorous birds in an experimental tallgrass prairie community consumed mostly large seeds (Howe and Brown 1999). The discrepancy between preferences for small seeds measured in the laboratory and diets biased towards large seeds measured in other settings is consistent with the encounter probability advantage on large seeds that we found for gerbils.

Our results do not support the hypothesis of species coexistence by seed size selection. In each of our experiments, *G. allenbyi* had the lowest GUD on all available seed sizes. Coexistence must therefore be based on axes of environmental heterogeneity other than seed size (Kotler and Brown 1988, Brown 1989). In the case of the two gerbil species, their coexistence is based on daily renewal of seed resource patches by wind action on the sand dunes and a tradeoff of foraging efficiency at high versus low resource availability driven by interference (Kotler et al. 1993c, Ziv et al. 1993, Brown et al. 1994). Also, both gerbils are more efficient than the crested larks and can forage profitably on the opportunities left behind in resource patches already exploited by the larks (Brown et al. 1997). But how can the larks coexist with the gerbils? Two things may contribute. First, the winds that blow sand and seeds and renew the resource patches occur in the afternoon, and the diurnal larks can exploit the renewing resource patches before the nocturnal gerbils (Brown et al. 1994). Second, larks are more efficient than gerbils and have lower GUDs in non-sandy habitats such as loess and rock (Kotler and Brown 1999). The greater mobility of the larks allow them to simultaneously exploit sandy, loessal, and rocky habitats while *G. allenbyi* and *G. pyramidum* are restricted to sand dunes.

Seed size has consequences for the interaction of the plants whose seeds are eaten by the gerbils and the larks. Gerbils typically exploit seeds distributed in resource patches, and the gerbils' fixed quitting harvest rate rule for patch exploitation leads to short-term apparent competition (Holt and Kotler 1987) on

the seed types that comprise the gerbils' diet. This includes all seed sizes used in our experiments. Therefore, the presence of another seed type by increasing the density of food in a patch thereby increases patch quality, increases the percentage of vulnerable seeds in a patch, and increases mortality on all seed types occurring in the patch. Thus, seed predation by gerbils causes a (-, -) interaction among seed types co-occurring in patches. The result can limit species numbers and determine the characteristics of coexisting species (i.e., species with high reproductive output relative to the rate of predator-induced mortality; Holt 1977). In addition, apparent competition may add to direct density-dependent competitive effects among the plants themselves to further limit population density and species numbers (Holt et al. 1994). Similar effects of apparent competition have been observed in different types of seeds eaten by kangaroo rats (Brown and Mitchell 1989) and fox squirrels (Brown and Morgan 1995) and in gastropods and bivalves consumed by lobsters and whelks (Schmitt 1987). In addition, asymmetrical apparent competition among seed plants consumed by a guild of kangaroo rats has led to the replacement of large-seeded plants by small-seeded plants at a Chihuahua Desert site (Brown and Heske 1990).

Whether short-term apparent competition occurs among sand dune plants in the Negev Desert remains a debatable point. Our data suggest that the answer is yes provided that seed types tend to co-occur in patches and that patches with more than one seed type have higher initial densities of seeds than those with just a single seed type. The richer multi-species seed patches are compared to single species patches, the stronger will be the apparent competitive effect. While multi-species seed patches seem to be common, we do not know how multi-species seed patches compare to single species patches in initial densities.

In summary, over certain ranges of seed size, encounter probabilities and handling times increase with seed size. And, depending upon the magnitude of these effects, diets may be biased towards the preferred food (the one that has the lowest handling time per unit reward) or towards the food which is easiest to find. When foods vary in handling time and encounter probability, diets will also be strongly influenced by whether foods occur separately (encouraging a bias towards the preferred food) or co-occur (encouraging a bias towards the more conspicuous food) within food patches. The taxon of forager matters. For gerbils, diets were always biased towards the more conspicuous, larger seeds. For larks, the diet was biased towards the preferred, smaller seed; but only slightly and only when seed sizes occurred in separate patches. These types of taxa-specific effects may promote coexistence, but not always as was the case of the two gerbil species and the crested lark.

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