

The energetic cost of competition: Gerbils as moneychangers

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ABSTRACT

Using behavioural bioassays, we measure the cost of both inter- and intraspecific competition to a foraging gerbil, *Gerbillus allenbyi*. The bioassay is the amount of foraging activity in field enclosures of 2 ha, and the difference between foraging activity in an experimentally manipulated 1-ha subplot compared to the matched, unmanipulated twin hectare next to it. The bioassay depends on assuming that natural selection has fitted the gerbils to assess the comparative values of feeding opportunities and competitive pressures, although these occur in different currencies. The gerbils perform quantitatively and consistently, smoothly adjusting their foraging effort to the combination of disparate opportunities and costs. Measuring their responses as behaviour allowed us to estimate the costs of competition in the currency of energy flow, that is, the rate at which we experimentally add seeds to subplots.

Keywords: arid lands, bioassay, common currency, competition, gerbil, optimal foraging behaviour, sand dunes.

INTRODUCTION

Early students of optimal foraging often tried to work with simplified systems whose individuals needed to consider only energy. Yet all evolutionary ecologists knew that real individuals face a complex world in which they must combine many different sorts of opportunities and challenges – some relating to energy collection, some to reproductive activity, some to acquisition of environmental information and some to defence against predators. Thus, natural selection will have taught the well-adapted animal how to add apples and oranges, and emerge with units of fitness.

The psammophilic gerbils of the Negev should represent good examples of animals facing challenges in multiple currencies. They face a severely seasonal Mediterranean climate with stark year-to-year variability. They must choose among a wide variety of foods. Their sandy habitats vary greatly in vegetative cover and substrate stability. They must allocate the time and place of their foraging to deal with predators and

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competitors alike. The individuals of such species should reveal the extent to which natural selection has succeeded in solving this difficult problem.

In this paper, we present evidence of nature's success. We base our opinion on new experiments with Allenby's gerbil (*Gerbillus allenbyi*), a common, 26 g rodent that lives in stabilized and semi-stabilized sand not too far from the sea coast of Israel and Egypt. It must assess its own local abundance and that of its food, take account of the local abundance of its mammalian and avian competitors, and judge the severity of predation risk from owls and foxes. Based on this information, it must emerge from its burrow at the proper time of day, forage in the appropriate microhabitats for the appropriate amounts of time, and then return to its burrow.

To determine whether these gerbils could solve the common currency problem, we controlled the amounts of inter- and intraspecific competition present in large field enclosures, while simultaneously varying the foraging reward available. The latter depended on the addition of small amounts of millet seed (mixed with large amounts of sand and offered in feeding trays). We found that the gerbils adjusted their foraging behaviour quantitatively – and with a surprising degree of precision – to compensate for changes in experimental seed addition rates and for the presence of a congener, *G. pyramidum*, which we know to be an important competitor.

The approach

By studying the behaviour of the gerbils, we can determine whether they do in fact respond quantitatively and logically to varying circumstances. Moreover, if they do, they will reveal how they compare the two disparate influences of competition and energy on their lives. Finally, if they do, we will be able to express both influences in the common currency of seed addition rate, that is, energy flow.

To measure the energetic costs of interspecific competition, we use a behavioural bioassay based on the ideal free distribution (IFD), a prediction of optimal habitat selection theory. The IFD expects individuals of a species to distribute themselves among different habitats so that no occupied habitat is better for fitness than another. For example, suppose there are two competing species whose names and densities are N_1 and N_2 . Now suppose there are two habitats whose only difference is the value of N_2 . (We control this difference experimentally.) IFD predicts that some individuals in N_1 will move away from the habitat with more N_2 until they balance its excess interspecific competition with the advantage of reduced intraspecific competition.

Furthermore, the response ought to be quantitative. We expect – and our earlier studies with *Gerbillus allenbyi* and its competitor *G. pyramidum* (Abramsky *et al.*, 1991, 1994, 1998) confirm – that *G. allenbyi* will shift its activity to the subplot without the competitor in direct proportion to how many *G. pyramidum* we add. By comparing the numbers of *G. allenbyi* individuals in the two habitats, we learned the number of foragers equivalent to the inter-specific competitor population that we added.

We can also use IFD to measure the value of extra food. In the total absence of N_2 , we can add food to one of the habitats only. IFD predicts that some individuals of N_1 will move into the habitat with extra food, thus increasing its excess intraspecific competition until it offsets the advantage of the extra food. Again, the response should be quantitative: the more food we add, the more N_1 should move into the habitat that contains it.

This method amounts to behavioural titration. The gerbils distribute themselves so as to

neutralize the difference between habitat plots. That will indeed tell us how much extra foraging it takes to neutralize a specific environmental advantage. For example, we might find that 9 units of extra foraging activity balance 4 units of competitor when there are 40 units of gerbil in the habitats. Or we might find that 6 units of seed addition and 40 units of gerbil result in 22 units of extra foraging activity. But how can we combine the two? How can we determine the costs of the competition in seed addition units?

In principle, one could tackle the problem with brute force: repeat the experiments until one discovers just how much seed addition yields 9 units of extra foraging activity in the presence of 40 units of gerbil. Then we would know how much 4 units of competitor are worth to 40 gerbils. However, the following approach is more efficient and takes into consideration the possible non-linear interactions between extra food and extra competition.

We define a carefully matched pair of adjacent enclosed subplots (1 ha each) to serve as the two habitats. We add individuals of *G. allenbyi* and measure the distribution of its activity in the two subplots. We conduct two sets of experiments. In one, we add a varying quantity of seeds to one subplot. In the second, we add both seeds and competitors to one of the subplots.

In the first set of experiments, we measure the responses of *G. allenbyi* to different seed addition rates in the absence of interspecific competition. If the foragers are well-adapted, this will yield a standard curve, F , of AGA response to seed-addition depending on two variables:

- GA , the total gerbil population of *G. allenbyi* in the two subplots combined;
- X , the seed addition rate (to only one of the subplots).

The result leads to Fig. 1a, in which F is the difference in foraging density between the two subplots.

In the second set of experiments, we introduce four individuals of *G. pyramidum* to the same subplot receiving seed addition. Call this the manipulated subplot, m . Its two treatments have opposite effects. Adding seeds enhances its value to foragers; adding the competitors reduces that value. To be well-adapted, the gerbils (*G. allenbyi*) must integrate these treatments and respond. We add seeds as in the first set of experiments and measure the gerbil response as F_m . (Note that the same method can measure the cost of other factors, such as risk of predation or habitat selection. To accomplish these, we would have to introduce one of these factors instead of interspecific competition.)

Now, from the standardized curve that we obtained in step 1, we determine the seed addition rate, X_s , needed – in the absence of interspecific competition – to produce the foraging response, F_m – the difference actually observed between the manipulated and unmanipulated subplots. Of course, $X_s < X_m$ (because m also has interspecific competition). The difference, $(X_m - X_s)$, equals the effect of the interspecific competition, y . Thus, $y = X_m - X_s$ (Fig. 1b). In other words, apples = oranges.

METHODS

Background knowledge about our field system

We have been studying a particular pair of gerbil species, *Gerbillus allenbyi* and *G. pyramidum*, in Israel for 15 years. *Gerbillus allenbyi* (mean mass = 26 g) and *G. pyramidum* (mean mass = 40 g) occur sympatrically in a wide range of sandy habitats in the Western Negev

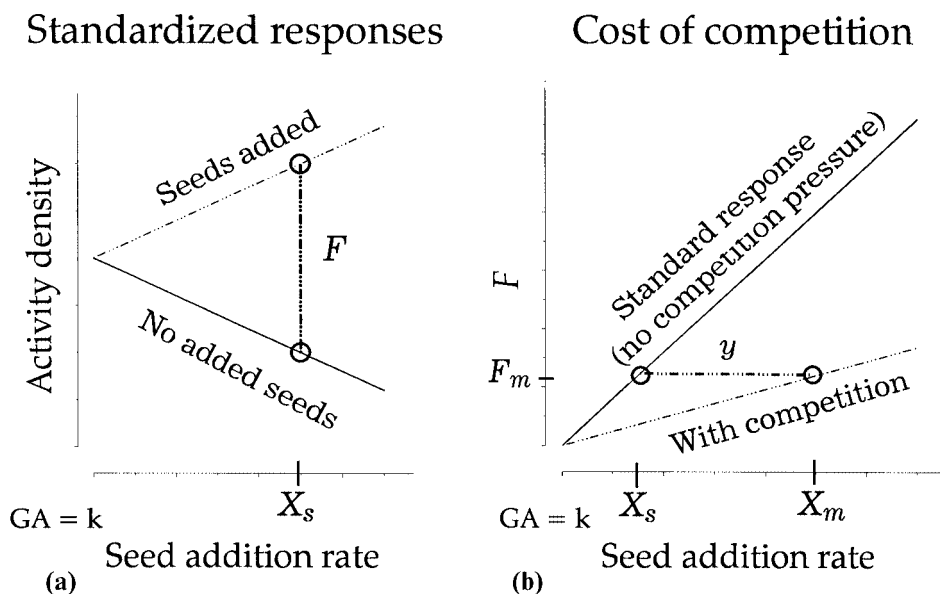


Fig. 1. Measuring the cost of interspecific competition. In (a), we measure a standard curve of response of the gerbils to seed additions at different rates. On a manipulated plot (*m*), we can do the same with seeds and competitors combined (not shown). Of course, gerbils will respond less to a given seed addition if they also face interspecific competition. In (b), we plot the responses against the seed additions. The horizontals are the cost of the competition. For simplicity, we assume that, in this example, density is constant ($GA = k$) and that the curves in (a) are linear. (The technique also works for non-linear curves.)

Desert (Abramsky *et al.*, 1985a). We have studied their population biology (Abramsky, 1984), their diets (Bar *et al.*, 1984), their habitat selection (Rosenzweig and Abramsky, 1985; Abramsky *et al.*, 1985b, 1990), the detailed shape of their competitive and victim isoclines (Abramsky *et al.*, 1991, 1994, 1997), the relationship between productivity and diversity in the communities to which they belong (Abramsky and Rosenzweig, 1984; Abramsky, 1988), their foraging strategies (Abramsky and Pinshow, 1989; Mitchell *et al.*, 1990), and the mechanisms of their co-existence (Kotler *et al.*, 1991, 1993; Ziv *et al.*, 1993). We measured the influence of predation risk on their population dynamics and behaviour (Abramsky *et al.*, 1996, 1997; Rosenzweig *et al.*, 1997). We also measured the magnitude of competition in the presence of risk of predation (Abramsky *et al.*, 1998). Many of these results are summarized in Rosenzweig and Abramsky (1997).

Study site

The study was conducted in enclosures at the Holot Mashabim Nature Reserve (31°01'N, 34°45'E) in the Halutza region 50 km south of Beer Sheva, Israel. Average annual precipitation is 108 mm. Rainfall comes in winter, and dew forms on approximately 250 nights per year.

Sandy areas at the study site comprise two habitat types based on mobility of the sand and on the dominant perennial plant species (Danin, 1978). *Artemisia monosperma* and

dead remnants of *Stipagrostis scoparia* dominate dunes in the process of being stabilized (semi-stabilized dunes). In this habitat type, perennial vegetation cover is relatively sparse, open patches of sand are relatively common, and some portions of the dunes are still mobile. *A. monosperma* and *Retama raetam* dominate long-stabilized dunes (stabilized sand). In this habitat type, shrub cover is relatively dense, open patches are smaller, soil crust is common, and none of the sand is mobile.

Plots

We conducted the experiment in two 2-ha enclosures. Each is a rectangle of 100 × 200 m. The fencing was made of 6-mm mesh hardware cloth, buried 40 cm below the soil surface and extending 60 cm above the ground. Atop both sides of the fence we placed a 15-cm wide ribbon of aluminium flashing to prevent rodents from climbing over.

Using fences exactly like those that surround an enclosure, we divided each enclosure into a pair of 1-ha matched subplots. Each 1-ha subplot has similar proportions of semi-stabilized dune and stabilized sand habitats and it shares with its twin a 100-m common fence. We perforated the common fence with six gates (diameter 19.7 mm) that allowed easy passage of individuals of *G. allenbyi* only. Individuals of *G. pyramidum*, which are larger, cannot go through these gates. We also perforated outside fences with gates that were either open or closed to all individuals. In previous experiments, in the absence of *G. pyramidum*, *G. allenbyi* had distributed its foraging activity equally between the subplots of each pair (Abramsky *et al.*, 1991, 1994, 1996, 1998). Nevertheless, to be certain of the functional similarity of each enclosure's subplots in the current experiments, we repeated the study of the distribution of *G. allenbyi* in the absence of both *G. pyramidum* and seeds.

Gerbils

For the experiment, we first closed outside gates and removed all gerbils from the two enclosures over 3–5 days. *Gerbillus allenbyi* (GA) and *G. pyramidum* (GP) were specifically marked by amputating the hind outside right toe (GA) or outside left toe (GP). Individuals were kept in the laboratory for a maximum of 10 (GA) or 25 (GP) days. We simultaneously introduced 40 individuals of *G. allenbyi* to one enclosure and 50 individuals to the other. Two weeks later, we introduced four *G. pyramidum* individuals to one subplot of each of the two enclosures. When the experiment was terminated, we opened the outside gates in the fences, allowing free access to both species.

We set the densities of *G. allenbyi* to resemble natural densities at the time of the experiments. Densities of *G. pyramidum* were higher than natural densities at that time.

Protocol

We conducted the following 3-week experimental test in each enclosure:

- Introduce 40 or 50 *G. allenbyi*.
- Wait 15 nights (for habituation).
- Measure the activity of the gerbils (see below) for five nights.
- Prebait 24 seed trays in subplots 1a and 2a with 1 g of millet seeds for one night.

- Measure the activity of *G. allenbyi* during four additional nights after adding 9, 7, 5 or 3 g of millet seeds mixed in 2 litres of sand, in each of the 24 trays. (The rate of seeds added in a given night was pre-determined randomly.)
- Introduce four *G. pyramidum* individuals to subplots 1a and 2a and allow one night of habituation.
- Measure rodent activity for two nights without adding seeds.
- Prebait the trays again.
- During the last four nights of the experiment, measure gerbil activity after again adding 9, 7, 5 or 3 g of millet seeds mixed in 2 litres of sand in each tray.
- Open peripheral gates.

Sand-tracking

We measured foraging activity by counting gerbil tracks left in 0.4×0.4 m sand-tracking stations. The score given to a site ranged from 0 (no tracks) through 1 (1/4 track coverage), 2 (1/2 track coverage), 3 (3/4 track coverage), to a score of 4 (full track coverage). Each 1-ha subplot had 40 sand-tracking stations arranged in 20 pairs, 10 in semi-stabilized dune and 10 in stabilized sand. One tracking station per pair was placed under shrub and the other in the open.

We smoothed the stations at sunset and read them 2 h later. Our measure of foraging activity, derived from summing the activity-density score in the 40 stations of a hectare, is *AGA*, the activity-density of *G. allenbyi*, and *AGP*, the activity-density of *G. pyramidum*.

We also established tracking plots on both sides of the six gates in the common fence of each enclosure. These detected movement near the common fence and reflected the amount of traffic between the subplots.

A methodological word about activity density: Although most foraging theories are couched in terms of population size, activity data should actually be more relevant than raw population size itself in determining foraging strategies. Activity is related to resource acquisition and therefore reflects competitive pressure and the degree of risk (Werner, 1991). Through their activity, animals can adaptively balance trade-offs between food and safety (Lima and Dill, 1990; Werner and Anholt, 1996). Furthermore, sampling their tracks does not interfere with natural rodent behaviour in any way.

We have been using activity densities successfully for 10 years (Abramsky and Pinshow, 1989; Abramsky *et al.*, 1990, 1991, 1992, 1994, 1996, 1997; Mitchell *et al.*, 1990; Kotler *et al.*, 1991, 1993; Rosenzweig *et al.*, 1997). We have confirmed repeatedly the prediction that the gerbils follow ideal free distributions (IFD) (Fretwell and Lucas, 1970; Fretwell, 1972) using activity densities (Abramsky *et al.*, 1991, 1992, 1994, 1996, 1997, 1998; Rosenzweig *et al.*, 1997). We have also shown that track coverage is highly and significantly correlated with population size (Abramsky and Pinshow, 1989; Mitchell *et al.*, 1990; Abramsky *et al.*, 1991, 1994, 1997, 1998; Ziv *et al.*, 1993).

Time-frame

We carried out our experiments during September and October 1998. We restricted our experiments to phases of the moon when there was little or no moonlight, because the activity of gerbils decreases significantly during hours with considerable moonlight (Kotler, 1984).

Seed trays

We introduced 24 trays to one subplot of each enclosure (1a and 2a). Each seed tray was circular with a diameter of 30 cm; each contained 2 litres of sand. Trays were distributed evenly in the entire subplot, but never closer than 1 m to a tracking plot. We introduced the appropriate amount of seeds to the trays before sunset, and mixed them thoroughly with 2 litres of sand. Gerbils found and removed most of the seeds from the trays during the first 2 h of the night.

When adding seeds to the system, we must be careful to minimize change to the energy status of individual gerbils. Changes in energy status add to the residual variance and make conclusions more difficult to achieve. Yet, we were adding relatively small amounts of seeds (see Discussion), less than the gerbils' daily energetic requirements (see later). Moreover, this source of superfluous variation is only one of many sources of variation (such as travel cost) that form an integral part of field experiments. So far, despite them, we have been able to tease signal from noise, even when the signal was somewhat weak (e.g. Rosenzweig and Abramsky, 1985, 1986, 1997; Abramsky *et al.*, 1990, 1991, 1994, 1997; Rosenzweig *et al.*, 1997).

RESULTS

In the absence of seeds and G. pyramidum, G. allenbyi treats the two subplots of each enclosure equally

Let AGA_i be activity in one subplot (i), and let AGA_j be activity in the adjacent subplot (j). If the gerbils treat the two subplots equally, the points (AGA_i, AGA_j) should fall along a straight line with slope 1 and intercept 0. Indeed, Bartlett's best fit regression of AGA_i versus AGA_j yielded a line very close to that predicted. The slope is not significantly different from unity ($P > 0.90$) and the intercept is not significantly ($P > 0.90$) different from zero (Fig. 2). This agrees with the results of all our previous studies (see Abramsky *et al.*, 1994, 1998; Rosenzweig and Abramsky, 1998, for references).

When seeds were added to one of a pair of subplots, G. allenbyi increased their activity in that subplot relative to the other (Fig. 3)

As expected of well-adapted foragers, they did so quantitatively, in proportion to the rate of seed addition.

In the presence of unilateral seed addition, AGA may also have increased slightly on the subplot without seed addition, but the increase was not significant. In any case, we have not predicted the nature of such change on the unenriched subplot.

G. allenbyi acted as if G. pyramidum were a competitor when G. pyramidum was added to one of a pair of subplots

In all four cases, the activity of *G. allenbyi* in the subplot without *G. pyramidum* was higher than its activity in the subplot with *G. pyramidum* (paired t -test = 7.14; $P < 0.006$). We used the activity data to estimate the competitive interaction coefficient of *G. pyramidum* on *G. allenbyi*. The mean coefficient was -0.78 . (Sample calculation: In one experiment, AGA was 41 on the side without *G. pyramidum* and 15 on the side with them. *Gerbillus pyramidum*

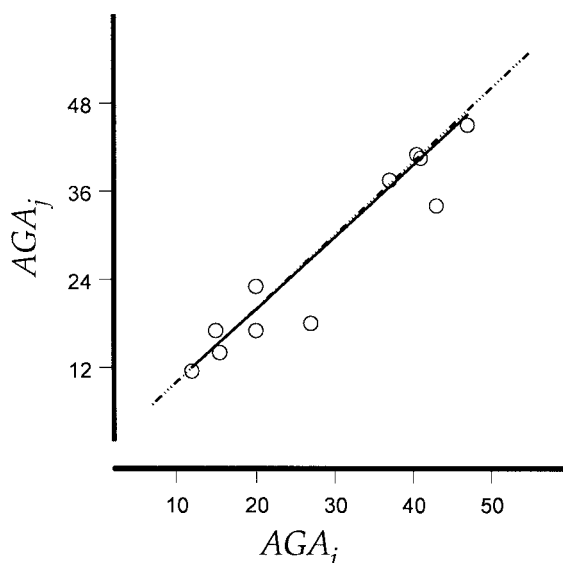


Fig. 2. In the absence of *G. pyramidum*, *G. allenbyi* distribute their foraging activity equally between the two subplots (*i* and *j*) of each pair. This confirms that they quickly achieve an ideal free distribution, because each one of the subplots was situated to duplicate the habitat proportions of its twin. The dashed line is the reference line, $y = x$. The solid line is the robust least trimmed squares regression.

G. allenbyi alone

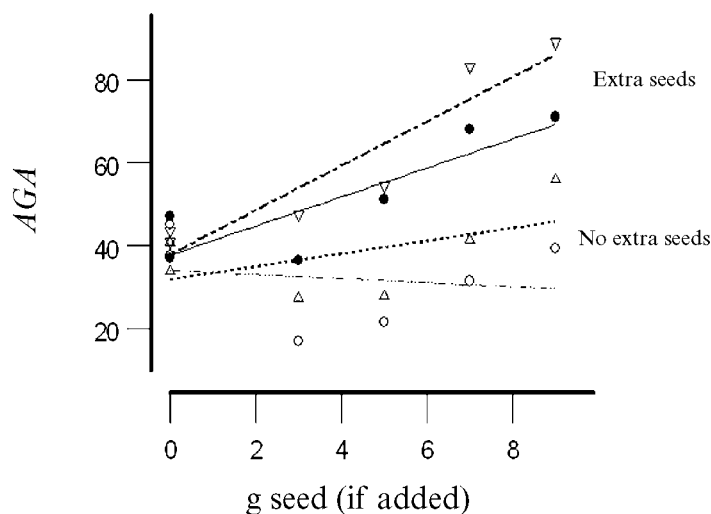


Fig. 3. The activity of *G. allenbyi*, when alone, in the two subplots of each enclosure as a function of different seed addition rates. Note that, in the subplots where seeds were added, the increase in activity was significant. Also, the increase was higher in the enclosure with 50 *G. allenbyi* individuals (triangles) than in the one with 40 individuals (circles).

generated $AGP = 31$ on its side. Thus an estimate of $a_{i,j}$ is $(15-41)/31 = -0.84$.) Abramsky *et al.* (1991, 1992, 1997) arrived at a similar estimate of this competition coefficient, that is, -0.86 . The estimate of Abramsky *et al.* (1998) is also similar. Note that sometimes these estimates come from reading tracks after the entire night and sometimes after only the first 2 h of the night. Nevertheless, the results are similar to, and consistent with, each other.

When *G. pyramidum* was present on, and a variable amount of seeds were added to, one subplot of a pair, *G. allenbyi* used that subplot in proportion to the amount of seeds added

As the amount of seeds in the treatment increased, the gerbils responded smoothly and quantitatively in both series of experiments (i.e. with 40 or 50 *G. allenbyi* individuals). Without the addition of seeds, the subplot without *G. pyramidum* had more *AGA*; the foragers were avoiding the interspecific competition. With 9 g seed added per tray, this more than compensated for the extra competition, and reached a higher *AGA* than in the subplot with neither extra food nor the second gerbil species. About halfway in between, the plusses and minuses balanced, and *AGA* was about the same on both sides (Fig. 4).

Note that in the enclosure with 40 *G. allenbyi* individuals, the two regression lines cross at a seed addition rate of about 4.4 g of seed per tray, whereas in the enclosure with 50

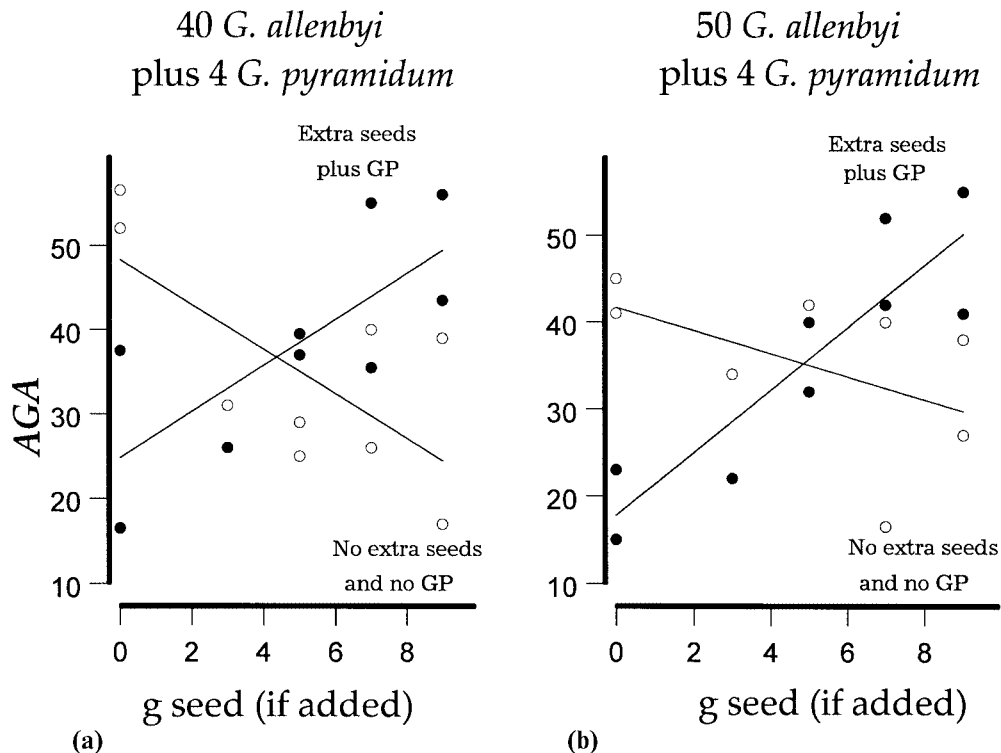


Fig. 4. The activity of *G. allenbyi* in the two subplots of experiments with 40 or 50 individuals. Seeds were actually added only to the subplot with four *G. pyramidum* (GP), but its twin subplot (without seeds or GP) is also shown at that level of seed addition.

G. allenbyi individuals, the crossover occurs at a seed addition rate of about 4.9 g of seed per tray. This small difference appears to have little significance.

DISCUSSION

The smooth quantitative responses of gerbil activity evident in Figs 3 and 4 already suggest the sophistication of the results of natural selection. As we experimentally altered their opportunities and difficulties in our field enclosures, individuals of *Gerbillus allenbyi* gradually changed the balance of their foraging activity. Hence, we can now use the model we explained in the Introduction (Fig. 1) to estimate the costs of interspecific competition in the currency of seed addition rates.

Recall that F is the AGA response of *G. allenbyi* to seed addition. We measured F in the presence and absence of *G. pyramidum* and plotted the results separately. Figure 5 shows the results for the experiments with 40 and 50 *G. allenbyi* individuals.

In each figure, the horizontal distances between the regression lines measure the rate of seed addition required to compensate for the four *G. pyramidum*. This distance is roughly 4.5 g. So, the competition generated by the four *G. pyramidum* individuals costs about 4.5 g of seeds per tray. Note that the lines in both figures are not significantly different from

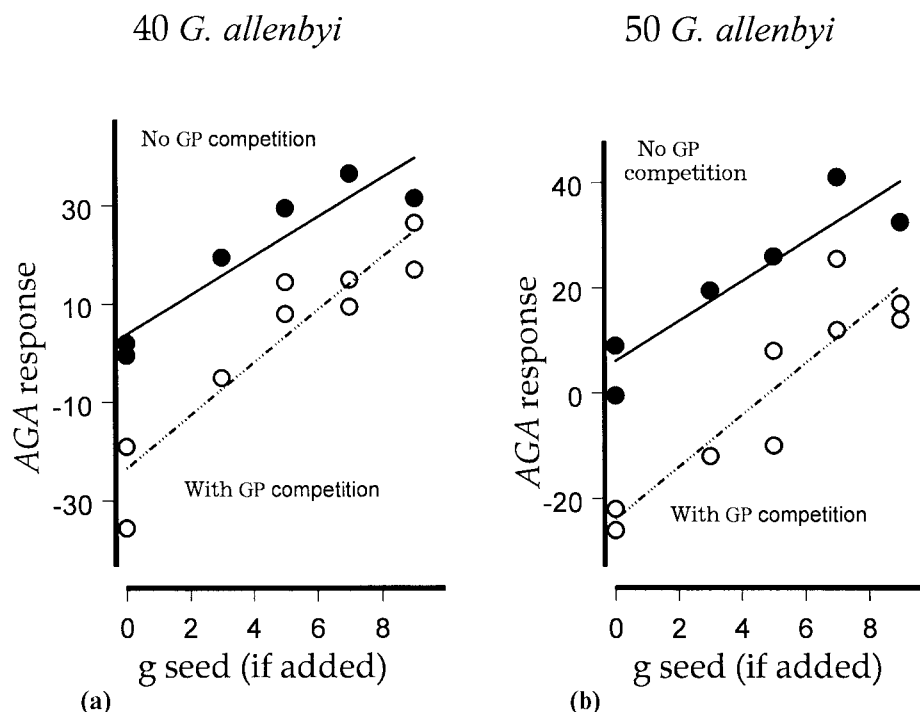


Fig. 5. The difference in *G. allenbyi* activity between the two subplots of the enclosure (F from Fig. 1) when seeds were added in the presence and absence of *G. pyramidum* (GP). The upper regression line is the standard curve mentioned in the text and Fig. 1a. Any horizontal line connecting the regression lines gives y , the cost of the interspecific competition. Results with (a) 40 and (b) 50 *G. allenbyi* individuals.

parallel. Parallel lines mean that, regardless of the addition rate, it takes the same increase to compensate for the addition of the four *G. pyramidum*.

We can also express the equality in terms of activity densities. With 40 *G. allenbyi*, the 5 g addition rates were accompanied by *AGP* values of 21 and 44 (mean = 32.5). With 50 *G. allenbyi*, the 5 g addition rates were accompanied by *AGP* values of 23 and 56 (mean = 39.5). The 5 g rates are quite close to the rate for neutralization of competition (~ 4.5 g). Thus we can conclude that 4.5 g of seeds per tray is equivalent to an *AGP* of about 35.

Now we turn to the cost of the intraspecific competition. This is a little more complicated to measure because we have not yet been able to perform the ideal experiment. (It would involve a set-up in which some *G. allenbyi* could move between the subplots and some could not.) Nevertheless, we have the data that will allow us to infer the cost from the experiments performed without any interspecific competition (i.e. no GP).

First, we imagine an experiment we did not actually perform – adding seeds equally to both subplots of a pair. From all our studies (including Fig. 2 of this paper), we can confidently suppose that the gerbils would treat the two plots equally and subdivide *AGA* evenly between them. Now we compare this with what we did do – add seeds to one side only. The result was always a higher *AGA* on the side with seeds. For example, when we added seeds at the rate of 5 g – in the presence of 50 *G. allenbyi* – *AGA* equalled 54 in the hectare with extra seeds and only 28 in that without them. The total *AGA* of 82 would have been equally shared by the two subplots if we had added seeds at the rate of 2.5 g in each of them instead of 5 g in only one. Thus, *AGA* would have been 41 per hectare in our experiment. The difference between 54 and 41 (i.e. 13) represents the *AGA* value drawn to the side with all the extra seeds. We did this by assuming that we moved 2.5 g of added seed from one side to the other.

These considerations lead us to our estimate of cost. In the case just reviewed, seed additions of 2.5 g per tray paid for an *AGA* of 13. We show all eight results in Fig. 6. Note the striking similarity of the results for 50 and 40 *G. allenbyi*. This makes us confident in the quality of information supplied by the gerbils. It also shows the increase in *AGA* response as seed addition rises. However, it argues for the significance of the decline in *AGA* response from addition rates of 3.5 g to 4.5 g. We do not yet understand the reason for that decline.

We can check the consistency of our results by comparing estimates of the competition coefficient derived from different methods, that is, energetic analysis versus changes of activity. As noted above, the latter yields an estimate of -0.78 . The energetic estimates are similar. With 50 *G. allenbyi*, about 4.9 g per tray neutralizes four *G. pyramidum*. These four gerbils generated mean activity densities of *AGP* = 39.5. So, 8.1 *AGP* is neutralized by 1 g. Meanwhile, 2.5 g per tray neutralizes an *AGA* of 13. So, 5.2 *AGA* is neutralized by 1 g. The ratio 5.2/8.1 is the estimated competition coefficient, that is, -0.64 . Using the same sort of calculation, we estimated the coefficient with 40 *G. allenbyi*; it is approximately -0.80 .

All our estimates depend on us not pushing experimental conditions beyond the bounds of nature. In this regard, we worried most about the effect of seed additions. We added, to each 1-ha subplot of each enclosure, 1.7 kg of seeds during October. In a desert, that would seem to be a great deal; however, it is actually not so extreme.

We added far less seeds than estimates of seed production or seed in the soil banks in deserts (80–1480 $\text{kg} \cdot \text{ha}^{-1}$; Brown *et al.*, 1979). Our 1.7 kg is also much smaller than the amounts reported for deserts by Price and Reichman (1987), Childs and Goodall (1973), Nelson and Chew (1977) and Parmenter and MacMahon (1983). We also added less than

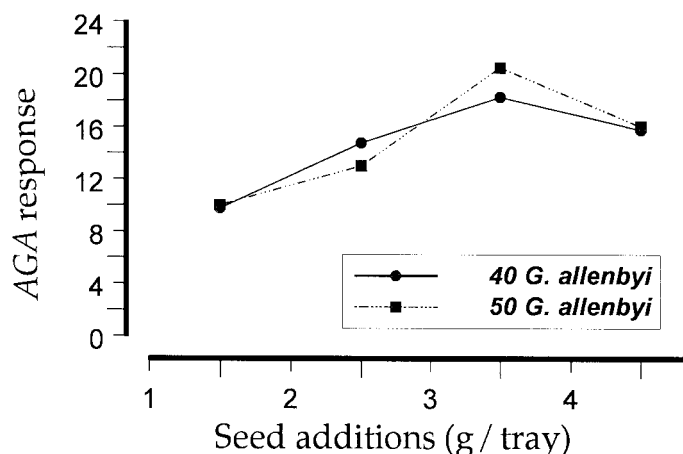
G. allenbyi alone

Fig. 6. The intraspecific response of *G. allenbyi* to seed additions. The cost of the response is the amount of seed added it took to get it. It is thus the cost of intraspecific *G. allenbyi* competition.

the seeds found in the seed bank ($380 \text{ kg} \cdot \text{ha}^{-1}$) or in the seed rain ($167 \text{ kg} \cdot \text{ha}^{-1}$) of the Mojave Desert (Price and Joyner, 1997). Moreover, Thompson *et al.* (1991) added more than ten times as much as we did ($19.2 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{month}^{-1}$) while working with granivores in the Chihuahua Desert.

We also considered whether seeds were accumulating in our experimental enclosures. This seems most unlikely. Even ignoring other seed-eaters like ants, the gerbils in our studies needed more seeds than we ever supplied. Each enclosure contained 40 or 50 *G. allenbyi* and four *G. pyramidum*. Each gerbil needs about 3–4 g of seeds per day for basic requirements. That amounts to $132\text{--}162 \text{ g} \cdot \text{day}^{-1}$ for the entire population in a 2-ha enclosure. During the 19-day experiment, that totals 2.5–3.1 kg – more than we provided.

Several studies showed that animals can respond behaviourally to the trade-off between food and safety, both qualitatively and quantitatively (e.g. Pitcher *et al.*, 1988; Abrahams and Dill, 1989; Nonacs and Dill, 1990; Todd and Cowie, 1990; Hughes and Ward, 1993; Kotler and Blaustein, 1995). In this study, we extend this approach to measuring the comparison that foragers must make between competition and food.

Our results suggest that gerbil behaviour is anything but random. It adjusts quantitatively to the environmental variations we cause in its enclosures. The adjustments make qualitative sense if we assume that natural selection has indeed shaped the behavioural responses of these animals. Of course, we cannot say that they make quantitative sense, because we ourselves lack the sophisticated ability to combine elements of disparate units and emerge with units in a common currency. But the gerbils act as if they do know how to do it.

We believe that one can use behavioural titration experiments such as ours to measure many biotic interactions. In fact, we are presently doing just this. We have already measured the energetic cost of interference competition as well as the temporal habitat partitioning

reported by Ziv *et al.* (1993) and Kotler *et al.* (1993). And we are at work on habitat selection and risk of predation, too. In the end, we hope that the behavioural bioassays we conduct on the gerbils will enable us to reduce the various dynamic influences on fitness to the common currency of energy. Perhaps, one day, international bankers will consult mice when they want to know the value of a dollar.

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REFERENCES

- Abrahams, M.V. and Dill, L.M. 1989. A determination of the energetic equivalence of the risk of predation. *Ecology*, **70**: 999–1007.
- Abramsky, Z. 1984. Population biology of *Gerbillus allenbyi*. *Mammalia*, **48**: 197–206.
- Abramsky, Z. 1988. The role of habitat and productivity in structuring desert rodent communities. *Oikos*, **52**: 107–114.
- Abramsky, Z. and Pinshow, B. 1989. Changes in foraging effort in two gerbil species correlate with habitat type and intra- and interspecific activity. *Oikos*, **56**: 43–53.
- Abramsky, Z. and Rosenzweig, M.L. 1984. Tilman's predicted productivity–diversity relationship shown by desert rodents. *Nature*, **309**: 150–151.
- Abramsky, Z., Brand, S. and Rosenzweig, M.L. 1985a. Geographical ecology of gerbilline rodents in sand dune habitats of Israel. *J. Biogeogr.*, **12**: 363–372.
- Abramsky, Z., Rosenzweig, M.L. and Brand, S. 1985b. Habitat selection in Israel desert rodents: Comparison of a traditional and new method of analysis. *Oikos*, **45**: 79–88.
- Abramsky, Z., Rosenzweig, M.L., Pinshow, B., Brown, J.S., Kotler, B.P. and Mitchell, W.A. 1990. Habitat selection: An experimental field test with two gerbil species. *Ecology*, **71**: 2358–2369.
- Abramsky, Z., Rosenzweig, M.L. and Pinshow, B. 1991. The shape of a gerbil isocline using principles of optimal habitat selection. *Ecology*, **72**: 329–340.
- Abramsky, Z., Rosenzweig, M.L. and Subach, A. 1992. The shape of a gerbil isocline: An experimental field study. *Oikos*, **63**: 193–199.
- Abramsky, Z., Ovadia, O. and Rosenzweig, M.L. 1994. The shape of a *Gerbillus pyramidum*, (Rodentia: Gerbillinae) isocline: An experimental field study. *Oikos*, **69**: 318–326.
- Abramsky, Z., Strauss, E., Subach, A. and Kotler, B.P. 1996. The effect of barn owls (*Tyto alba*) on the activity and microhabitat selection of *Gerbillus allenbyi* and *G. pyramidum*. *Oecologia*, **105**: 313–319.
- Abramsky, Z., Rosenzweig, M.L. and Subach, A. 1997. Gerbils under threat of owl predation: Isoclines and isodars. *Oikos*, **78**: 81–90.
- Abramsky, Z., Rosenzweig, M.L. and Subach, A. 1998. Do gerbils care more about competition or about predation? *Oikos*, **83**: 75–84.
- Bar, Y., Abramsky, Z. and Gutterman, Y. 1984. Diet of gerbilline rodents in the Israeli desert. *J. Arid Environ.*, **7**: 371–376.
- Brown, J.H., Reichman, O.J. and Davidson, D.W. 1979. Granivory in desert ecosystems. *Ann. Rev. Ecol. Syst.*, **10**: 201–227.
- Childs, S. and Goodall, D.W. 1973. Seed reserves of desert soils. *United States/International Biological Program Desert Biome Research Memorandum*, **44**: 45–72.
- Danin, A. 1978. Plant species diversity and plant succession in sandy area in the northern Negev. *Flora*, **167**: 409–422.

- Fretwell, S.D. 1972. *Populations in a Seasonal Environment*. Princeton, NJ: Princeton University Press.
- Fretwell, S.D. and Lucas, K.L., Jr. 1970. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta Biotheor.*, **19**: 16–36.
- Hughes, J.J. and Ward, D. 1993. Predation risk and distance to cover affect foraging behavior in Namib Desert gerbils. *Anim. Behav.*, **46**: 1243–1245.
- Kotler, B.P. 1984. Risk of predation and the structure of desert rodents communities. *Ecology*, **65**: 689–701.
- Kotler, B.P. and Blaustein, L. 1995. Titrating food and safety in heterogeneous environments: When the risky patch is of equal value. *Oikos*, **74**: 251–258.
- Kotler, B.P., Brown, J.S. and Hasson, O. 1991. The specter of predation: Factors affecting gerbil foraging behavior and rates of owl predation. *Ecology*, **72**: 2249–2260.
- Kotler, B.P., Brown, J.S. and Subach, A. 1993. Mechanisms of species coexistence of optimal foragers: Temporal partitioning by two species of sand dune gerbils. *Oikos*, **67**: 548–556.
- Lima, S.L. and Dill, L.M. 1990. Behavioral decisions made under the risk of predation: A review and prospectus. *Can. J. Zool.*, **68**: 619–640.
- Mitchell, W.A., Abramsky, Z., Kotler, B.P., Pinshow, B. and Brown, J.S. 1990. The effect of competition on foraging activity in desert rodents: Theory and experiments. *Ecology*, **71**: 844–854.
- Nelson, J.F. and Chew, R.M. 1977. Factors affecting seed reserves in the soils of a Mojave Desert ecosystem, Rock Valley, Nye County, Nevada. *Am. Midl. Nat.*, **97**: 300–320.
- Nonacs, P. and Dill, L.M. 1990. Mortality risk vs. food quality trade-offs in a common currency: Ant patch preferences. *Ecology*, **71**: 1886–1892.
- Parmenter, R.R. and MacMahon, J.A. 1983. Factors determining the abundance and distribution of rodents in a shrub-steppe ecosystem: The role of shrubs. *Oecologia*, **59**: 145–156.
- Pitcher, T.J., Lang, S.H. and Turner, J.A. 1988. A risk-balancing trade off between foraging rewards and predation hazard in shoaling fish. *Behav. Ecol. Sociobiol.*, **22**: 225–228.
- Price, M.V. and Joyner, J.W. 1997. What resources are available to desert granivores: Seed rain or seed bank? *Ecology*, **78**: 764–773.
- Price, M.V. and Reichman, O.J. 1987. Distribution of seeds in Sonoran Desert soils: Implications for heteromyid rodent foraging. *Ecology*, **68**: 1797–1811.
- Rosenzweig, M.L. and Abramsky, Z. 1985. Detecting density-dependent habitat selection. *Am. Nat.*, **126**: 405–417.
- Rosenzweig, M.L. and Abramsky, Z. 1986. Centrifugal community organization. *Oikos*, **46**: 339–348.
- Rosenzweig, M.L. and Abramsky, Z. 1997. Two gerbils of the Negev: A long-term investigation of optimal habitat selection and its consequences. *Evol. Ecol.*, **11**: 733–756.
- Rosenzweig, M.L., Abramsky, Z. and Subach, A. 1997. Safety in numbers: Sophisticated vigilance by Allenby's gerbil. *Proc. Nat. Acad. Sci., USA*, **94**: 5713–5715.
- Thompson, D.B., Brown, J.H. and Spencer, W.D. 1991. Indirect facilitation of granivorous birds by desert rodents: Experimental evidence from foraging patterns. *Ecology*, **72**: 852–863.
- Todd, I.A. and Cowie, R.J. 1990. Measuring the risk of predation in energy currency: Field experiments with blue tits, *Parus caeruleus*. *Anim. Behav.*, **40**: 112–117.
- Werner, E.E. 1991. Nonlethal effects of a predator on competitive interactions between two anuran larvae. *Ecology*, **72**: 1709–1720.
- Werner, E.L. and Anholt, B.R. 1996. Predator-induced behavioral indirect effects: Consequences to competitive interactions in anuran larvae. *Ecology*, **77**: 157–169.
- Ziv, Y., Abramsky, Z., Kotler, B.P. and Subach, A. 1993. Interference competition and temporal and habitat partitioning in two gerbil species. *Oikos*, **55**: 237–246.