

Does interspecific competition from congeners cause the scarcity of *Gerbillus henleyi* in productive sandy desert habitats?

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Summary

1. We tested the hypothesis that *Gerbillus henleyi* (de Winton 1903), the smallest species (10 g) of a psammophilic guild in Israel, is scarce on relatively productive dunes of the Israeli desert, due to negative interactions from the common *G. allenbyi* (Thomas 1918) and *G. pyramidum* (Geoffroy 1825).
2. The alternative hypothesis was that scarcity on sand resulted from the size of its naked hind feet, that do not allow efficient locomotion on sand.
3. Despite their naked soles the weight-bearing surface of *G. henleyi* feet carry less mass/area than those of any other species.
4. We measured interaction coefficients with the two common species using field-manipulation experiments in two enclosures.
5. Habitat usage of *G. henleyi* changed from significantly preferring the stabilized sand, when alone, to significantly using the semistabilized dune, when *G. allenbyi* was also present.
6. We also estimated the interaction coefficients and calculated the *G. henleyi*'s isoclines competing with the two common gerbil species using a technique we developed elsewhere.
7. The stability analysis of the isoclines of *G. henleyi* competing with either *G. allenbyi* or with *G. pyramidum* suggests that stable coexistence occurs when *G. henleyi* is relatively scarce while the competitors are common.
8. Interspecific competition from either *G. allenbyi* or *G. pyramidum* accounts for 90–3% reduction in *G. henleyi* density, relative to when it is alone.
9. We concluded that the negative interactions from congeners was the major cause for the scarcity of *G. henleyi* on the relatively rich sand dunes of the Israeli desert.

Key-words: biodiversity, conservation, gerbils, scarce species.

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Introduction

Scarce species cause problems for the community ecologist. Small numbers make experiments troublesome and small numbers add to coefficients of variation, making it difficult even to describe patterns. Consequently, to err on the safe side, the ecologist often ignores the information added to data sets by scarce species, sometimes deleting their very presence from the data points of the communities in which they are found (e.g. Brown 1984, 1995).

It is no wonder that most studies on rare species are descriptive or non-empirical (e.g. Rabinowitz, Cairns & Dillon 1986; Gaston 1994; Kunin & Gaston 1997; Yu & Dobson 2000) and the processes that lead to rarity are hardly studied, except philosophically (but see the work of Rabinowitz *et al.* 1986; Tikka *et al.* 2001; Lloyd *et al.* 2002, below).

Rarity may endanger the future existence of a species. Conversely, protecting it from extinction may require increasing its population. However, combating rarity requires understanding its causes, one of which may be negative species interactions, i.e. competition and predation.

A tiny (10 g) gerbil, *Gerbillus henleyi* (GH), has been scarce since it was first discovered by western science in 1903 (Harrison & Bates 1991). It lives on many kinds of

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sandy substrates and also on loess. It is rare on all of them (Mendelsohn & Yom-Tov 1999). Its rarity is somewhat mysterious, particularly because the sandy areas of deserts are their most productive areas, and because other gerbils in the same deserts are not uncommon (Mendelsohn & Yom-Tov 1999). Wherever it lives, GH co-occurs with one to two larger and much more common gerbil species. We hypothesized that competition with these other common species helps to limit the densities of GH. Our previous studies (e.g. Abramsky, Rosenzweig & Pinshow 1991; Rosenzweig & Abramsky 1997) and our research installations in the Negev Desert, Israel, put us in a favourable position to investigate the role of competition in generating the rarity of GH. Alternatively, GH might not be common on sand because of poor physiological or morphological adaptation to sandy habitats. Specifically, its naked soles might not allow efficient locomotion on sandy substrate.

In 2000–03, we conducted field observations of GH and we looked at the population densities of all three species across the range of sandy soil types available in the Negev. We determined how readily GH ceases foraging in a patch compared to *G. allenbyi* (GA). We assessed the possible role of a major foot-morphology difference in adapting gerbil species to looser sandy substrates more efficiently compared to GH. In addition, we manipulated the populations of its two common congeners, *G. pyramidum* (GP) and GA, and measured the interaction coefficients of those two species on GH. This was conducted in order to evaluate the hypothesis that interactions with one or both of these species continually depress the populations of GH. We argue that the influence of each of the two gerbil species is likely to be the principal cause of GH's rarity.

Methods

BACKGROUND

Here, we provide a short description of our studied system. For more details see Abramsky, Rosenzweig & Pinshow (1991), Abramsky, Rosenzweig & Subach (2000) and Rosenzweig & Abramsky (1997).

FIELD SITES

Our principal field site was the Holot Mashabim Nature Reserve (31°01' N, 34°45' E) in the Halutza region 50 km south of Beer Sheva, Israel. Precipitation falls in winter (annual average 108 mm) and dew forms on approximately 250 nights per year.

GA and GP are common at Holot Mashabim. GA (mean mass = 24 g) and GP (mean mass = 40 g) occur sympatrically in a wide range of sandy habitats in the western Negev Desert. GH also occurs there but is scarce. All three species are nocturnal burrow-dwellers and are primarily granivores (Bar, Abramsky & Gutterman 1984; Shenbrot, Krasnov & Khokhlova 1994; Khokhlova, Degen & Kam 1995).

At Holot Mashabim, we maintain a system of 2-ha rodent enclosures. Each one, surrounded by rodent-proof fencing, measures 100 m × 200 m. The fences are perforated with portals that we can either open or close to all rodent individuals. The enclosures are in sandy areas. The sands of Holot Mashabim comprise two habitat types, as follows, based on mobility of the sand and on the dominant perennial plant species (Danin 1978).

1. *Artemisia monosperma* and *Retama raetam* dominate long-stabilized dunes ('stabilized sand'). In stabilized sand shrub cover is relatively dense, open patches are smaller, an algal crust commonly covers the soil surface and none of the sand is mobile.

2. In contrast, *Artemisia monosperma* and dead remnants of *Stipagrostis scoparia* dominate dunes in the process of being stabilized ('semistabilized' dunes). In semistabilized dunes, perennial vegetation cover is relatively sparse, open patches of sand are relatively common and portions of the dunes are still mobile.

A rodent-proof fence divides each enclosure into a pair of 100 m × 100 m (1 ha) matched subplots. Each subplot has similar proportions of semistabilized dune and stabilized sand.

An auxiliary site, about 20 km from Holot Mashabim, has a third habitat not present at Holot Mashabim. We classified it as 'very stabilized sand' because it has a very thick soil crust. This site has no enclosures.

General methods

SAND-TRACKING

Many foraging theories are couched in terms of population size. As population sizes change, so does optimal foraging behaviour because larger populations put greater pressure on resources.

Instead of measuring the populations of the species, we measured their foraging activities by counting gerbil tracks left in 0.4 m × 0.4 m sand-tracking stations. Each 1-ha subplot had 40 sand-tracking stations arranged in 20 pairs: 10 in semistabilized dune and 10 in stabilized sand. One tracking station per pair was placed under shrubs and the other in the open. We smoothed the stations at sunset and read them at first light. We scored the activity at a station from 0 (no tracks) to 4 (full track coverage). We calculated AGH, AGA and AGP, the activity–densities of GH, GA and GP, respectively, by summing each species' activity–density score in the 40 stations of a hectare.

We believe that foraging activities – rather than raw population sizes – determine foraging strategies. Population size is only an indirect measure of activity; it is activity that results in resource acquisition and therefore activity reflects competitive pressure and the degree of risk (Werner 1991). Through their activity, animals can adaptively balance trade-offs between food and safety (Lima & Dill 1990). Moreover, sampling rodent tracks does not alter natural rodent behaviour (Ziv *et al.* 1993), whereas sampling population sizes may.

We have been using activity densities successfully for 10 years (Abramsky *et al.* 1990, 1991, 2000; Kotler, Brown & Hasson 1991; Rosenzweig & Abramsky 1997). We have shown, for GA and GP, that track coverage is highly correlated with their density (Mitchell *et al.* 1990; Abramsky *et al.* 1991; Ziv *et al.* 1993). It is also true for GH (when alone $AGH = 2.44 GH$, $r = 0.93$, $n = 19$, $P < 0.0001$). Thus, we used activity density in all our analysis and graphs. We converted back to densities only to evaluate the equilibrium densities of GH.

MANIPULATIONS

To estimate interaction coefficients, we introduced various densities of the species into the enclosures. One species was free to travel through the portals that separate the subplots; the other was not.

We inferred the interaction coefficients from the behaviour of the free species. For example, if its activity was higher in the subplot with fewer of the confined species, we interpreted that as a sign of competition. We estimated the value of the competition coefficient by comparing the disparity of the free species' activity in the two subplots to the disparity of the constrained species' activity in the subplots (Appendix I).

We ensured that differences in the free species' activity in the two subplots reflected actual movement between them. We conducted this by setting up additional tracking plots on both sides of the six portals that connected them. These tracking plots reflected the amount of traffic between the subplots. In confirmation of the movement of GH we found significant correlation between the absolute difference in activity between subplots and track density near the portals ($y = 0.51 + 0.61x$, $r = 0.50$, $P = 0.036$, $n = 36$). We have previously checked the technique with GA and GP.

We manipulated the densities of competitors in the enclosures by removing initially introduced individuals and not by adding individuals during the experiment. The reason for this approach was that the addition of individuals would have created a problem, because new naive individuals were introduced into an area already monopolized by the existing experienced individuals which would provide an undesired advantage to the experienced individuals. Changing densities by removing individuals does not provide an advantage to any individuals. The remaining individuals in the enclosures have only to adjust their behaviour to the new density. One may suspect that this technique may lead to a

carry-over effect of density. Our experience, and data collected in the past, shows that the gerbils adjust to the new densities very quickly (in one night: Abramsky *et al.* 1991). In fact, the gerbils were able to compensate for lost activity owing to the presence of a predator within the same night (Abramsky *et al.* 1996). There was no carry-over effect to the next night. Nevertheless, as a precaution we allowed the gerbils 3 nights to habituate to the new density.

GIVING-UP-DENSITIES – GUDS

Brown (1988) developed the method of GUDs to assess how much food an individual was willing to forgo in the field. Leaving more food behind could mean that richer patches are available or further foraging is too risky, or foraging itself is relatively unprofitable compared to some other activity. Careful experimental design and analysis can usually discriminate the alternatives from each other.

We mixed 3 g of millet seeds in 5 L of sand and placed it in a tray in the field at sunset. At sunrise the trays were revisited, tracks of the forager(s) were read and the remaining seeds were sifted from the sand and weighed.

Methods specific to these studies

SURVEY

One of us (YZ) has trapped gerbils once or twice a year since 2000 in five locations in the western Negev about 20 km–35 km from Holot Mashabim. Trapping took place at each location for 4 nights/session in four 1-ha plots.

The dunes of these five places differed considerably in the degree of sand stabilization. Two of them consisted of sand covered by a very thick layer of soil crust (very stabilized sand). They appeared to have relatively low productivity. The other three locations were in stabilized, semistabilized and shifting sand, respectively (Table 1).

GUDS

We introduced eight seed trays to each subplot of both enclosures. Each seed tray was a rectangle of $41 \times 58 \times 4$ cm. In each, we mixed 3 g of millet seeds with 5 L of sand. We put four trays in semistabilized dune and four in stabilized sand. We set out the trays at dusk. At first light, we sieved and collected the remaining seeds of each tray into a different plastic bag. The amount of seeds left in the tray is the GUD.

Table 1. Mean \pm SE of the three gerbil species that are found on sand/ha captured during four trapping sessions, between 2000 and 2003, in the Western Negev in five different locations that differ in the type of the sandy habitat

Location	Sand type	<i>G. allenbyi</i>	<i>G. henleyii</i>	<i>G. pyramidum</i>
1	Very stabilized	7.8 \pm 1.8	4.1 \pm 2.1	0.8 \pm 0.3
2	Very stabilized	2.8 \pm 0.9	4.7 \pm 1.9	0.2 \pm 0.1
3	Stabilized	21.4 \pm 7.3	3.4 \pm 0.8	5.6 \pm 2.8
4	Semistabilized	16.5 \pm 5.3	0.6 \pm 0.4	4.9 \pm 1.4
5	Shifting sand	17.4 \pm 3.9	0.8 \pm 0.4	15.7 \pm 3.9

We also placed 20 seed trays in the very stabilized sand area located 20 km south-west of the enclosures. In this location (designated 1 in Table 1) we measured the foraging efficiencies of gerbils in an area where GH is naturally more common.

MANIPULATIONS

We conducted the manipulation experiments in two 2-ha enclosures. Each night, we treated the two 2-ha enclosures alike, performing the same experiment in each. The fence that divided each enclosure into its matched subplots was perforated by six circular 8.0-mm radius portals. These allowed easy passage of GH, but neither GA nor GP individuals or their juveniles can traverse them. This allowed us to control the densities of the larger species, and thus to manipulate their activity–density.

In each experiment, one subplot contained more potential competitors than the other. We named the subplot with more competitors ‘subplot-*i*’. We named its twin ‘subplot-*j*’.

Gerbils

Before beginning the manipulations, we closed all portals and live-trapped gerbils and removed all gerbils from the two enclosures for 3–5 days. We trapped until no more tracks were evident in the sand. We used only naive gerbils in our experiments. Naive gerbils minimized the chance that a single individual had an advantage over another by virtue of its past experience in an enclosure.

Trapped individuals were removed to our laboratory. Individuals of GA and GP were obtained readily near or at Holot Mashabim. We trapped individuals of GH 20 km SW of the enclosures in the very stabilized sand habitat. This area was adjacent to the site where we studied the GUDs of all species.

After we had collected enough animals to satisfy the experimental requirements of a particular treatment, we introduced them simultaneously into the appropriate enclosures. The experimental densities of GA and GP resembled their natural densities at the time of the experiments. However, the experimental density of GH was much higher than that found on sand dunes.

TIME-FRAME

We conducted our experiments during the summers of 2002 and 2003. 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).

The research in 2002 was divided into three sessions, each lasting 4–6 weeks, as follows.

1. First session: to study the foraging densities of different populations of GH by itself to check whether the subplots of each pair were well matched. If they were,

GH activity density in subplot *i* would be the same as that in subplot *j* no matter how many GH were in the whole plot. It would also confirm that competition was resolved through habitat selection. Also, to measure the habitat preference of GH for semistabilized dunes vs. stabilized sand.

2. Second session: to measure the competitive effect of GA on GH. If there was one, GH activity–density should be higher in the subplot with the lower activity–density of GA; and to test the density dependence of the interaction coefficient by varying the gerbil densities during the session and to measure the habitat preference of GH for semistabilized dunes.

3. Third session: to measure the competitive effect of GA on GH with two GP in all subplots and also to measure the habitat preference of GH for semistabilized dunes.

The research in 2003 was divided into two sessions, each lasting 4–6 weeks as follows.

1. First session: to measure the GUDs of GA and GH in the enclosures and in the very stabilized sand area.

2. Second session: to measure the competitive effect of GP on GH.

PROTOCOL

Session 2002–1: are subplots well matched?

1. Introduce 26 GH to each enclosure.
2. Wait 4 nights (for habituation).
3. Measure the activity densities of the gerbils for 2 nights.
4. Remove six individuals from each enclosure. Allow 3 nights for habituation and then measure activity densities for 2 nights.
5. Remove six more individuals of GH from each enclosure. Allow 3 nights for habituation and then measure activity for 2 nights.

Session 2002–2: to measure the interaction coefficients of GA on GH

1. Introduce 30 and 10 individuals of GH to enclosures 1 and 2, respectively. Introduce 20 and 10 individuals of GA to subplots *i* and *j*, respectively, of each enclosure and allow 4 nights for habituation.
2. Measure the activity densities of GH and GA in each of the four subplots for 4 nights.
3. Remove three individuals of GA from each subplot. Allow 3 nights for habituation. Measure activity densities of the two species during the next 3 nights.
4. Repeat stage 3 twice, reducing GA each time.

Session 2002–3: to measure the interaction coefficients of GA on GH in the presence of small numbers of GP

This experiment is identical to session 2002–2 except that two GP were present in all subplots during the session and we reduced GA densities only twice.

Session 2003-1: to measure the GUDs of GH and GA

1. Introduce 16 and 10 GH to subplots *i* of enclosures 1 and 2, respectively, and introduce 14 and 24 GA to subplots 1*j* and 2*j*, respectively.
2. Allow 4 nights for habituation.
3. During the next 3 nights measure GUDs in eight seed trays/subplot.
4. Measure GUDs with 20 additional seed trays in the very stabilized habitat (location 1 in Table 1).

Session 2003-2: to measure the interaction coefficients of GP on GH

1. Introduce 30 and 10 individuals of GH to enclosures 1 and 2, respectively. Introduce five and two individuals of GP to subplots *i* and *j*, respectively, of each enclosure.
2. Allow 4 nights for habituation.
3. Measure rodent activity densities for 4 nights.
4. Remove one GP from each subplot and allow 3 nights for habituation.
5. Measure rodent activity densities for 4 nights.
6. Repeat stage 4 twice, reducing GP each time.

MEASUREMENT OF THE HIND-FOOT TRACK AREA

We measured the track area of the hind feet of seven individuals of GH, three individuals of GA, three of GP, four individuals of *Meriones crassus* (MC) and one individual of *M. sacramenti* (MS). We recorded the body mass of each individual rodent and then placed it by itself for a few minutes in a 1 m² arena, the bottom of which was covered with 2 cm of sand. Using a digital camera, we photographed three hind-foot tracks of each individual. We measured track area using ImageJ software.

To obtain species averages, we first calculated the mean track area of each individual, then the mean track area and body mass of each species.

Results

FIRST SESSION, 2002: THE FORAGING OF
G. HENLEYI BY ITSELF

In the absence of any experimental treatment, GH used the two subplots (*i* and *j*) of each enclosure similarly (Fig. 1). The hypothesis of equal use amounts to a prediction of the regression line describing the relationship of activity in subplot *j* as a function of that in subplot *i*. This line should have a slope of 1.0 and an intercept of zero. Indeed, the slope of this line (0.76) is not significantly different from 1.00 ($P > 0.05$) and its intercept (2.98) is not significantly different from zero ($P > 0.05$) (note that there was enough power in the data to observe a significant difference from a slope of zero, which we did: $P < 0.005$). Because GH used the subplots similarly, we could conduct the rest of our experiments knowing that we had succeeded in our attempt to match the subplots of each pair.

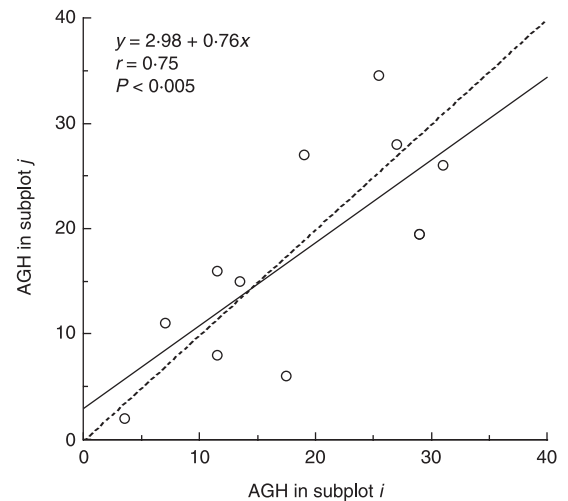


Fig. 1. The activity density of *G. henleyi* (AGH) in subplot *i* was similar to that of subplot *j*. The slope is not significantly different from 1 and the intercept is not significantly different from zero.

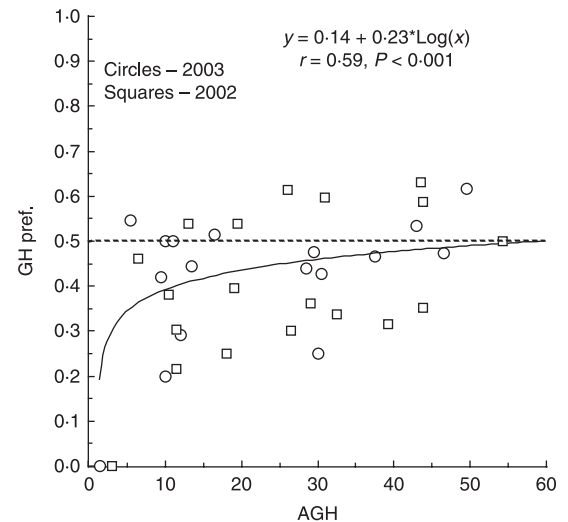


Fig. 2. When alone and in low density *G. henleyi* preferred the stabilized sand habitat type. At intermediate and high densities of *G. henleyi* it equally utilized the two habitat types. The relationship is similar in both summers. The horizontal broken line represents equal selectivity (habitat preference is expressed as the ratio of AGH in semistabilized to total AGH).

Within subplots, GH showed a small preference for the stabilized sand habitat compared to the semistabilized dune. Its preference was evident only when its population was low. As we increased its population, GH utilized the two habitat types similarly (Fig. 2). At the assemblage of densities we used in this experiment, 59.5% ($\pm 0.5\%$) of GH activity occurred in the stabilized sand habitat (Fig. 3). This average differed significantly from 50% ($t = 2.56$, $n = 19$, $P = 0.02$).

We also collected some data in 2003 during periods when GH was unaccompanied in the enclosures (Fig. 2). Then, also when rare, GH showed a small preference for the stabilized sand.

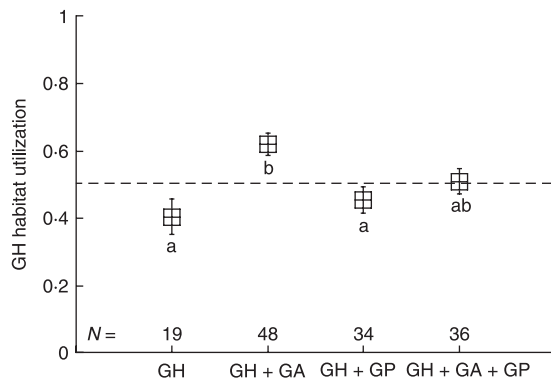


Fig. 3. Mean (\pm SE) habitat utilization of *G. henleyi* (GH) when alone, with *G. allenbyi* (GA), with *G. pyramidum* (GP) and with both. The horizontal broken line represents equal selectivity. *N* represents sample size. Means with different letters are significantly different (Bonferroni *post hoc* test, $P < 0.05$) (habitat utilization is expressed as the ratio of AGH in semistabilized to total AGH).

SECOND SESSION, 2002: HABITAT USE OF *G. HENLEYI* IN THE PRESENCE OF *G. ALLENBYI*

GA reversed the habitat preference of GH. Rather than prefer the stabilized sand, it used the semistabilized dune more. Sixty-two per cent ($\pm 3\%$) of GH activity occurred in the semistabilized dune habitat. This average percentage differed significantly from 50% (Fig. 3) ($t = 3.61, n = 48, P = 0.001$).

GA has a negative effect on the activity of GH. Instead of using subplots equally, as they do in the absence of GA, GH favours the subplot with fewer GA. The relative magnitude of the difference in their activity in the two subplots allowed us to estimate the interaction coefficient of GA on GH (Appendix I).

The interaction coefficients were negative, very strongly so when GA activity density was low, less so over intermediate and higher GA densities (Fig. 4a). The average negative coefficients at intermediate and high GA activity densities (-0.268) was significantly lower than zero ($t = 3.36, n = 32, P < 0.002$). Negative interaction coefficients suggested strongly that GA competed with GH.

During this same session we were also able to measure the habitat preference of GA. It used the two habitats about equally ($53\% \pm 3\%$).

SECOND SESSION, 2003: HABITAT USE OF *G. HENLEYI* IN THE PRESENCE OF *G. PYRAMIDUM*

In the presence of GP, 45% ($\pm 4\%$) of GH activity occurred in the stabilized sand habitat (Fig. 3). This percentage did not differ significantly from 50% ($t = 1.3, n = 34, P = 0.20$). It was also not significantly different ($P > 0.05$) from the 40.5% ($\pm 5\%$) value we obtained from experiments performed when GH was alone.

Despite the fact that GP had no effect on the habitat use of GH it did interact significantly with GH. This was evident in the patterns of GH activity distribution.

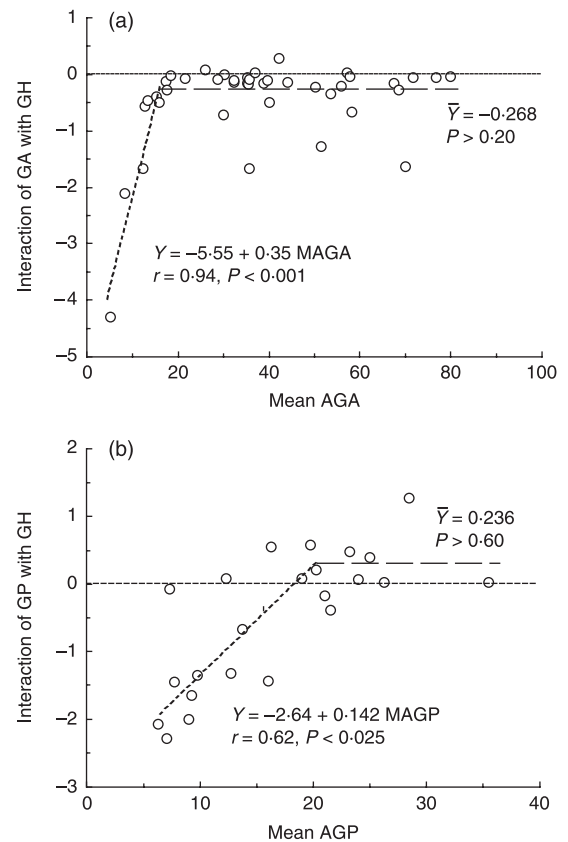


Fig. 4. The interaction coefficients (Appendix I) of (a) *G. allenbyi* (GA) and (b) *G. pyramidum* (GP) with *G. henleyi* (GH), as the function of their mean activity densities.

In the presence of GP, GH did not usually use subplots equally, but the deviation from equal use varied depending on GP density. At low GP densities, GH favoured the subplot with fewer GP. At high GP densities, GH favoured slightly the subplot with more GP. At intermediate GP densities GH used the subplots about equally, regardless of the presence of GP.

The interaction coefficients (Appendix I) of GP on GH were negative, very strongly so when GP density was low (Fig. 4b), but they diminished (in absolute value) over intermediate GP densities (activity values about 20). At high GP densities, the coefficients tended to be positive (0.236), although not significantly different from zero ($t = 1.71, n = 10, P = 0.12$). Negative interaction coefficients suggested strongly that GP competed with GH. Positive interaction coefficients suggest that GP may be a GH mutualist.

THIRD SESSION, 2002: THE FORAGING OF *G. HENLEYI* IN THE PRESENCE OF BOTH *G. PYRAMIDUM* AND *G. ALLENBYI*

When both GP and GA were present, GH used the semistabilized dune and the stabilized sand almost equally (Fig. 3). It accumulated 51% ($\pm 4\%$) of its activity in the semistabilized dune. This was not significantly different from 50% ($t = 0.22, n = 36, P = 0.83$).

Table 2. Comparisons of mean GUDs of *G. allenbyi* and *G. henleyi*. GUDs represent the amount of millet seeds left after a night of foraging in a standard experiment (see Methods)

	<i>G. allenbyi</i>			<i>G. henleyi</i>			<i>t</i>	<i>P</i>
	Mean	SD	<i>n</i>	Mean	SD	<i>n</i>		
Very stabilized sand	0.21	0.13	9	0.91	0.08	3	8.8	0.000
Stabilized sand	0.14	0.13	16	0.38	0.33	11	2.59	0.016
Semistabilized dune	0.13	0.06	18	0.27	0.19	17	2.97	0.006

The presence of GP significantly ($t = 6.5$, $n = 140$, $P = 0.000$) also changed the habitat usage of GA. Recall that when GP was absent (2002, session 2), GA used the two habitats about equally ($53\% \pm 3\%$). However, in this session (with GP), GA mainly used the stabilized dune ($73\% \pm 3\%$). This result was similar to that obtained earlier (Abramsky *et al.* 1990) when the two common species were together.

The habitat usage of *G. allenbyi* (GAu) and the activity density of GP were significantly correlated (GAu = $0.53 - 0.015$ AGP; $r = -0.51$; $n = 120$; $P < 0.0001$) (GAu is expressed as the ratio of AGA in semistabilized to total AGA).

The habitat usage of *G. allenbyi* (GAu) was not correlated with the activity density of GH (GAu = $0.50 - 0.001$ AGH, $n = 44$, $r = 0.04$, $P = 0.82$), nor was the habitat usage of GP correlated with the activity density of GH (GPu = $0.59 + 0.002$ AGH; $n = 54$; $r = 0.12$; $P = 0.40$).

FIRST SESSION, 2003: FORAGING EFFICIENCY – GUDS

Our question was whether different species have different foraging efficiencies on the same habitat type. Therefore, we were not interested in comparisons of GUDs across habitats and report the three separate *t*-tests.

The GUDs of GH in the set of three habitat types were significantly higher than the GUDs of GA in the same habitat (Table 2).

HIND-FOOT AREA AND BODY MASS

GH has the smallest track area of any species in our study (Fig. 5a). Also, the soles of the hind feet of both GA and GP are heavily furred, whereas those of GH are naked. The fur, when present, enlarges the weight-bearing area of the hind foot. We (as well as many other mammalian ecologists) have long surmised that this area provides support and good footing on sand, especially loose sand – rather like a snowshoe on snow. Perhaps GH's lack of abundance in sandy habitats derives not from biotic interactions but from inadequate foot morphology; this is why we measured hind-foot areas and body masses.

The method we used to measure track area included the imprint of the fur. Therefore our measurements reflected the support that an individual gains from its

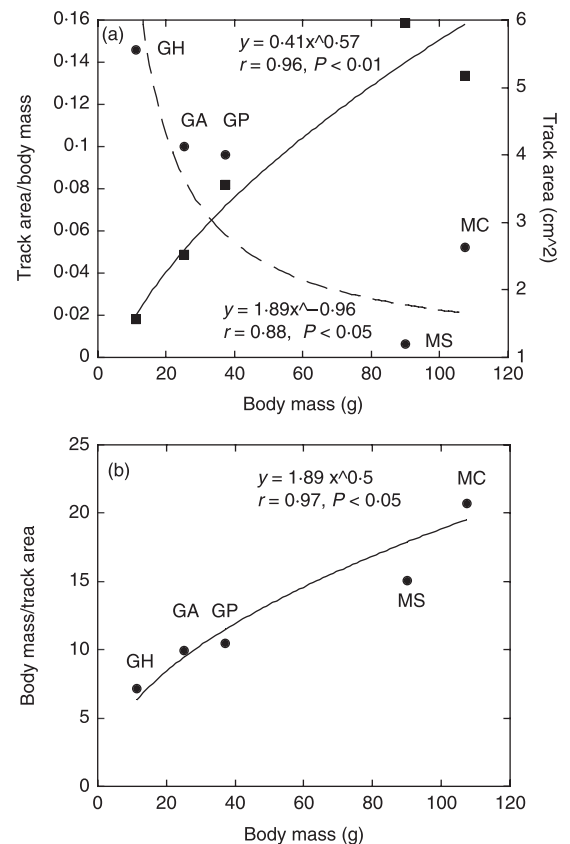


Fig. 5. (a) The area of the track size of the hind foot (circles) and the ratio of track area/body mass (squares) of several species of gerbils. (b) Actual data (circles) relative to the allometric curve of the sand dwelling species (continuous line): GH, *G. henleyi* ($n = 7$); GA, *G. allenbyi* ($n = 3$); GP, *G. pyramidum* ($n = 3$); MS, *Meriones sacramenti* ($n = 4$); MC, *M. crassus* ($n = 1$).

feet when moving about on a loose sandy substrate. This support is measured by the variable 'area per unit body mass' and appears as one of the *y*-axes in Fig. 5a.

Despite their smallness and nakedness, the hind feet of *G. henleyi* provide the greatest support of any of the species we studied. In fact, without exception, the larger a species the more weight it places on each unit of its hind foot area (Fig. 5b). This measure is merely the inverse of that in Fig. 5a; however, it is the ratio used more traditionally by engineers. It also allows us to perform an informative calculation, as follows.

Area grows as the square of a body's linear size, whereas mass grows as its cube. Hence, the ratio of mass/area (*y*) should increase allometrically as L^2/L^3 with mass

(x). All species, therefore, that lie on the same line $y = cx * 0.5$ share the same allometric relationship.

We calculated the allometric constant, c , for each species as:

$$c = y/(x * 0.5).$$

We then calculated the mean c -value for the group of five species as the allometric constant of this group of gerbil species. The result was 1.885. We plotted this allometric equation in Fig. 5b to give us a reference against which to compare the species. Those with y -values below the line exceeded the allometric expectation and were better adapted for sand than the group average. Those above it were not as well adapted for locomotion on sand. Both GA and GH have hind-foot areas very near the allometric expectation. GP lies well below it, indicating a better than expected adaptation to loose sand. However, the small sample size did not allow definitive conclusions regarding this species.

Despite the fact that GH has small naked feet, it would appear to be at no disadvantage on sand compared to the other species of its subfamily.

ESTIMATING THE ISOCLINE OF GH COMPETING WITH GA

The coefficient values plotted in Fig. 4a provide the slopes of the GH isocline. We integrated the equations of those slopes to estimate its shape. When integrated, the equation over the left portion of the figure yields:

$$AGH = C_1 - 5.55AGA + 0.175AGA * 2 \quad \text{eqn 1}$$

where C_1 is the constant of integration and $AGA < 18$.

The equation over the horizontal right portion has integral

$$AGH = -0.268AGA + C_2 \quad \text{eqn 2}$$

(where $AGA > 18$); so the slope of the GH isocline should begin at its steepest over its intersection with the AGH axis (at $AGA = 0$), become gentler and reach a constant value of -0.268 beyond $AGA = 18$. Because no interaction term was significant, plugging different constants into eqns 1 and 2 will yield a parallel family of isoclines.

ESTIMATING THE ISOCLINE OF GH COMPETING WITH GP

The coefficient values plotted in Fig. 4b provided the slopes of the GH isocline in this space. We integrated the equations of those slopes to estimate its shape. When integrated, the equation over the left portion of the figure yielded:

$$AGH = C_3 - 2.64AGP + 0.071AGP * 2 \quad \text{eqn 3}$$

where C_3 is the constant of integration and $AGP < 19$.

The equation over the horizontal right portion has integral

$$AGH = 0.236AGP + C_4 \quad \text{eqn 4}$$

where $AGP > 19$. As before, the slope of the GH isocline should begin at its steepest over its intersection with the AGH axis (at $AGP = 0$), become gentler and reach a constant value of $+0.236$ beyond $AGP = 19$. Because no interaction term was significant, plugging different constants into eqns 3 and 4 will yield a parallel family of isoclines.

Discussion

In Israel, GH is scarce wherever it is found and in all habitat types (Abramsky, Brand & Rosenzweig 1985). Pebbly and rocky habitats in Israel have few rodents of any species. In a peak year 4.7 individuals of GH were found on 1 ha of sand, 4.0 on gravel and 2.4 in wadis (Mendelsohn & Yom-Tov 1999). GH is scarce in the very stable sandy habitat (Table 1). It is even more scarce in the much richer, less stable sandy habitat (Table 1). One hectare of semistabilized dune or stabilized sand contains approximately 0.6–3.4 individuals of GH and a hectare of shifting sand has < 1 individual. In other regions of the Middle East GH is also relatively rare and occurs mainly in different types of sandy habitats (Shenbrot *et al.* 1994). All the other gerbil species are also scarce on loess and on very stabilized sand. But why should GH be scarce in other sandy habitats?

Such scarcity is especially surprising, for two reasons:

1. GH (10 g) is much smaller than GA (24 g) or GP (40 g), its two common sand-dwelling congeners. During the summer, a typical hectare of semistabilized or stabilized sand dune carries 10.82 individuals of GA and 2.41 individuals of GP. (Rosenzweig & Abramsky 1997). Judging from its smaller size, one might expect a hectare of sand dune to carry many more GH. If we transform the biomass of the larger species into an equivalent biomass of GH, we can calculate that a hectare of mixed stabilized sand and semistabilized dune (approximately 50/50, like the control plots and the enclosures) ought to carry 27.68 individuals of GH, not the one or two individuals that it actually has. $[(2.41 * 40 * 0.75 + 10.82 * 24 * 0.75)/10 * 0.75 = 27.68]$.
2. Sandy habitats are the desert's most productive. Sand conserves the meagre precipitation of a desert more efficiently than any other soil type, soaking it up like a sponge and allowing very little to run off. Moreover, the higher productivities of the sands are well reflected by the abundances of the other gerbils. Nevertheless, GH is rare there.

The soles of GH's hind feet lack fur. Fur on the feet, present in most sand-dwelling gerbils, increases hind-foot surface area and might allow easier locomotion on sand, but this morphological difference fails to help explain the scarcity of GH. Our comparisons of track size and biomasses among different species of gerbils showed that despite their naked soles, the weight-bearing surface of GH feet carry less mass/area than those of any other species (Fig. 5a). GH feet also fit the allometric curve of the sand-dwelling species (Fig. 5b). Hence, GH

appears to be as well adapted as the others for locomotion on sand. Thus, we are able to reject the hypothesis of poor morphological adaptation to sand.

We were much more successful with the competition hypothesis. To test it, we used our large rodent-proof field enclosures in the Negev. As can be seen, we concluded that competition from GA and GP is largely responsible for GH's scarcity in sandy habitats.

THE *G. ALLENBYI* AND *G. PYRAMIDUM* ZERO ISOCLINES

G. allenbyi

We did not conduct the manipulation experiments that would have revealed the shape of the GA isocline in GH–GA space. Nevertheless, we observed that GH did not change the habitat usage of GA. This suggests that GH has no competitive effect on GA. This hypothesis is bolstered by our finding that GUDs of GA are less than those of GH in all sandy habitats, therefore we will draw the GA isocline as a straight line perpendicular to the GA axis of the space. The intercept of the GA isocline occurs at the steady-state density of GA in the presence of GP. Rosenzweig & Abramsky (1997), their Fig. 11) showed that to be $AGA = 40$.

G. pyramidum

We did not conduct the manipulation experiments that would have revealed the shape of the GP isocline in GH–GP space. Nevertheless, we observed that GH did not change the habitat selection of GP. This result suggests that the competitive effect of GH on GP is very small if it exists at all. Thus, the GP zero isocline should be perpendicular (or nearly perpendicular) to its own axis. It will intersect that axis at a point determined by the competition between it and GA. Rosenzweig & Abramsky (1997), their Fig. 12 showed that to be $AGP = 19$.

COMPETITION OF *G. ALLENBYI* WITH *G. HENLEYI*

Our results provide three types of evidence to show that GA competes with GH, as follows, and which will be discussed in turn.

1. GA shifts the habitat use pattern of GH from stabilized sand to semistabilized sand.
2. In all sandy habitats it has lower GUDs than GH.
3. GH shifts its foraging away from places where GA lives.

In the absence of other gerbil species and at low densities, GH's usage of the stabilized sand significantly exceeded 50% (Fig. 2). This result shows us that GH prefers stabilized sand to semistabilized dune. As its density increases, intraspecific competition obscures the preference. Rules (such as ideal free distribution) take over (Fretwell 1972).

The preference is also obscured when GA is present. In fact, when GA is present GH's usage of semistabi-

lized dune increases significantly to more than 50% (Fig. 3). The functional relationship between GA activity–density and GH's usage of semistabilized dune is: $GH_{ss} = 0.45 + 0.003 AGA$ ($r = 0.43; n = 80; P < 0.005$). When one species is moved away from its preferred habitat by another species, it seems reasonable to conclude that a negative interaction is occurring.

The lower GUDs of GA suggest that it is a more efficient forager than GH. It continues to take food from places that GH abandons. Perhaps it does so because it is less susceptible to predation, or perhaps GA is the more efficient forager, so that depleted patches are worth more to GA than to GH. Whatever the reason, the small size of GH would seem to preclude its defending richer patches from the depredations of GA. Thus it ought to lose any competitive contest with GA.

Certainly, GH acts as if GA causes it problems. If there are GA in a subplot, GH prefers to forage in its twin subplot (Fig. 4a). Provided that natural selection has schooled the GH well, that avoidance of places with GA is a strong proof of the negative competitive effect.

How important is the competitive influence of GA? Can it greatly depress GH densities? We answer this question by using our results to construct zero-isoclines for the interaction between GA and GH.

Because the GA isocline is vertical and that of GH has a negative slope they must cross at a stable equilibrium (Fig. 6a). We know the equilibrium activity density of GA to be 40 AGA. If we know the equilibrium activity density of GH we will be able to draw its zero isocline using eqns 1 and 2. We assumed that the equilibrium density of GH could be calculated from the average densities (Table 1) found on stabilized sand and semistabilized dune during 4 years of study $[(3.4 + 0.6)/2 = 2]$. We converted this number to activity density (4.88) using the relationship between density and activity density ($AGH = 2.44 GH$). Thus, the GH isocline has to cross the GA isocline at ($AGH = 4.88$ and $AGA = 40$). So, we can calculate the C_2 of eqn 2 by evaluating it at $AGA = 40$ and $AGH = 4.88$, which equals 15.6. We can now use eqn 2 to calculate AGH at $AGA = 18$. By inserting this result ($AGH = 10.78$) and $AGA = 18$ to eqn 1 we can calculate ($C_1 = 53.98$).

The AGH isocline we plot in Fig. 6a begins with eqn 1 and changes to eqn 2 at $AGA = 18$.

The equilibrium point in Fig. 6a occurs at $AGA = 40$ and $AGH = 4.88$. It is stable. It shows clearly that the competitive effect of GA on GH in the dunes of the western Negev allows only a very small number of GH to occur there.

COMPETITION OF *G. PYRAMIDUM* WITH *G. HENLEYI*

The zero isoclines of GH and GP must intersect in a stable equilibrium at $AGP = 19$ and $AGH = 4.88$. We solved for C_4 in eqn 4 at $AGP = 19$ and $AGH = 4.88$, which equals 0.4. We used the same values of AGP and AGH to calculate ($C_3 = 29.41$).

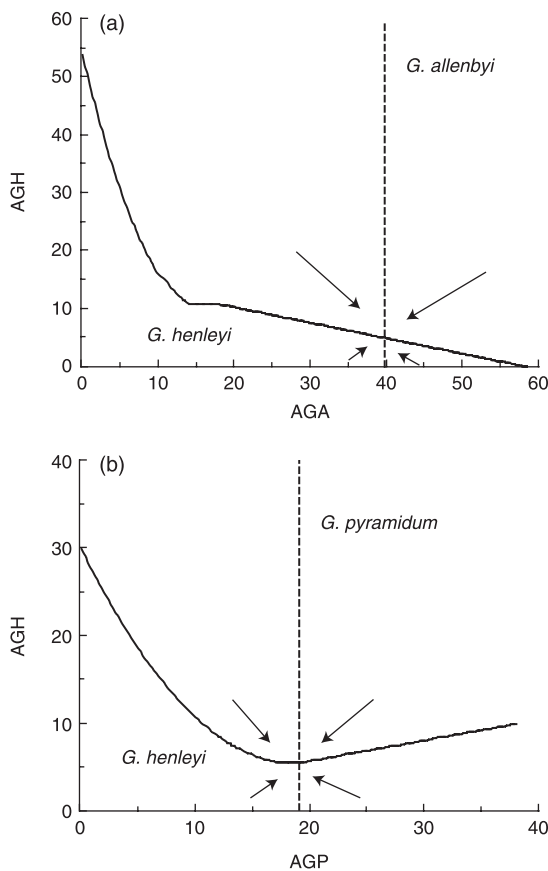


Fig. 6. The zero isoclines of *G. henleyi* and *G. allenbyi* (a) and those of *G. henleyi* and *G. pyramidum* (b) drawn in the state space of activity densities. The horizontal broken lines in (a) and (b) are the isoclines of the competitors while that of the solid line is that of *G. henleyi*. Note that the equilibrium points are stable.

The AGH isocline we plot in Fig. 6b begins with eqn 3 and changes to eqn 4 at $AGP = 19$. The isoclines of GH and GP intersect at $AGH = 4.88$ and $AGP = 19$, leading to a stable equilibrium (Fig. 6b).

How many individuals of GH can live in 1 ha of semistabilized dune and stabilized sand? Recall that zero isoclines cross their axis at the carrying capacity of the habitat. The above calculations lead to two different estimates for K. The intercept with the AGH axis is $53.98 (= 22.2 \text{ GH})$ when competing with GA and $AGH = 29.41 (= 12.1 \text{ GH})$ when competing with GP. Our measurements of activity density and our calculations of the GH isoclines are not error-free. Also, GH isoclines are strongly non-linear and very steep near the K of GH, and thus the errors become magnified. Therefore, K has some error associated with it.

Above, we calculated an independent estimate of K by transforming the biomass of GP and GA into equivalent biomass of GH ($K = 27.68$). The average of the three carrying capacity estimates $[(22.2 + 27.68 + 12.1)/3] = 20.66$ individuals/ha is probably close to the actual one. Using non-linear fit to the data in Fig. 4 yields a similar average estimate of $K (\pm 1 \text{ individual})$.

The presence of the two common species together does not increase the magnitude of interspecific competition beyond that when they are alone. We did not find a significant difference between the magnitude of competition coefficients in session 2 of 2002 when only GA was with GH, and those of the third session of 2002 when both GP and GA were present with GH (ANCOVA $F = 0.715$, d.f. = 1,38, $P = 0.40$).

The results from the study of foraging efficiencies and the isocline stability analysis probably mean that interspecific competition is responsible for the exclusion of about $(100\% - 2/20.6 * 100) = 90.3\%$ of the population of GH from the sand dunes. Although this number has some variance we believe that this estimated equilibrium density is not too far away from the actual one.

Why is GH scarce in non-sandy habitat types? We assume that these poor habitats probably cannot support high populations of GH even in the absence of competition (Shenbrot *et al.* 1994).

The competitive effect of both gerbil species on GH was similar – strong competitive effect at low competitor densities and weak (GA) or no negative effect (GP) at intermediate and high competitor densities. We suspect that the effect of interspecific competition on GH weakens at high competitor density as at high competitor densities predators direct their foraging efforts to the common and larger competitive species and ignore the smaller GH. At these intermediate and high competitive densities the small GH benefits from both the virtual refuge from the predators, and from the fact that its competitor is busy avoiding the predators. Indeed, we have shown earlier that under risk of predation the competitive effect of GP on GA diminishes (Abramsky *et al.* 2004).

The sum of evidence from other studies, on the role of interspecific competition in scarce species, is conflicting. Rabinowitz *et al.* (1986) conducted several greenhouse de Wit replacement series with seven species of sparse and common grasses. They showed that sparse species are not disadvantaged by interactions with their common neighbours and concluded that the competitive ability of sparse grasses is a mechanism that compensates for the hazards of low density and reduces the probability of local extinction. Lloyd *et al.* (2002) used a within-taxon comparative approach to test for differences in competitive ability between rare and common species in two genera of plants. They concluded that although rare species may have low competitive ability in some cases, it should not be assumed to be the cause for all rare species. Tikka *et al.* (2001) conducted a field experiment in which they were able to show that competition from weeds might be the reason for the rarity of grassland species in central Finland. Our results support the assumption that interspecific competition is the major factor that is responsible for the rarity of GH.

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Appendix I.

ESTIMATING INTERACTION COEFFICIENTS AND ISOCLINES

Isoclines were extensively used in developing the theory that led to understanding interactions between species, such as competition (e.g. MacArthur 1972) and predation (e.g. Rosenzweig & MacArthur 1963). An isocline is a line in a state space on which every point of the state variable in question (or a fixed transformation of it such as its logarithm) has a fixed value of its time derivative. The state space has one axis for the population of each species. Zero isoclines play a large role in predicting what will happen to a set of interacting species.

Suppose there are two habitats, i and j , and two species, 1 and 2, with total densities N_1 and N_2 . Let $N_{1,i}$

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$N_{1,j}$; $N_{2,i}$; and $N_{2,j}$ be the habitat specific densities. If the $N_{2,i}$ individuals in habitat i have the same average fitness as the $N_{2,j}$ individuals in habitat j , then N_2 is said to be at ideal free distribution (IFD) (Fretwell 1972). Barring complications, IFD is the ESS (evolutionary stable strategy), and optimal individuals will try to attain it. Foragers should also approach IFD when they are using habitat patches that differ only in the density of a competitor (Abramsky *et al.* 1991). In this situation, competitors depress the value of a patch and foragers should respond by distributing their foraging between patches in inverse proportion to the competitor's density.

Given a forager seeking an ideal free distribution (IFD) and an experimental pair of matched patches, one can estimate competitive coefficients and isoclines as follows. First introduce some individuals of species 1, allowing them to move freely between patches i and

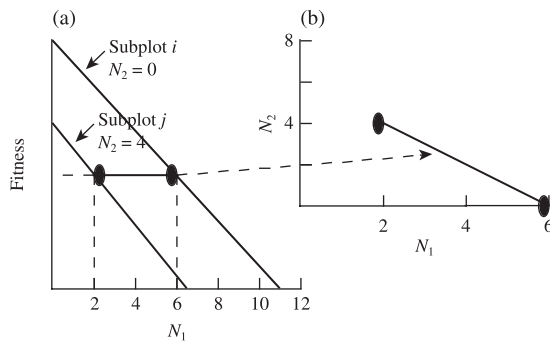


Fig. 7. (a) The relationship between the fitness of species 1 and its population density (N_1) plotted as separate lines for matched patches with different values of N_2 . For simplicity, the figure shows an example with straight lines (although curved ones would do as well). Points at the ends of the thick line constitute an ideal free distribution of N_1 ; its individuals have the same fitness in both patches. (b) The densities of the two species at the IFD of species 1 are transferred to a state space of population densities (N_1, N_2). The line connecting these two points is a linear estimate of the isocline of species 1 because its individuals have the same average fitness at both points of the IFD. The slope of the line estimates $\alpha_{1,2}$, the interaction coefficient of species 2 with species 1.

j. Now show that species 1 moves freely between the two experimental patches and views them as equivalent. Do this by removing species 2 entirely and determining that $N_{1,i} = N_{1,j}$ at various values of N_1 . Next reintroduce the competitor, fixing its densities at $N_{2,i}$ and $N_{2,j}$. For example, set $N_{2,i} = 0$ and $N_{1,j} = 4$ as in Fig. 7a. Measure the distribution attained by species 1. The free densities they reach and the fixed densities of their competitors constitute a set of two points in an (N_1, N_2) state space (Fig. 7b): ($N_{1,i}, N_{2,i}$) and ($N_{1,j}, N_{2,j}$). Because the average fitness of species 1 should be equal in the two subplots [i.e. $d(\ln N_{1,i})/dt = d(\ln N_{1,j})/dt$], the two points should lie on one isocline of species 1. So the line connecting them is a linear estimate of the N_1 isocline in the neighbourhood of the two points. Its slope is negative $\alpha_{1,2}$ ($\alpha_{1,2}$ = the effect of an individual of species 2 on an individual of species 1).

Repeat the last few steps of this procedure many times with various values of N_1 and N_2 . The result will be estimates of $\alpha_{1,2}$ and isocline slopes throughout the state space. Thus, even if $\alpha_{1,2}$ depends on population densities and the isocline is curvilinear, the method will succeed.