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Density-independent habitat distribution caused by density-dependent habitat selection

Georgy Shenbrot,* Boris Krasnov and Sergei Burdelov

Mitrani Department of Desert Ecology, Jacob Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, Sede Boqer Campus, 84990 Midreshet Ben-Gurion and Ramon Science Center, PO Box 194, 80600 Mizpe Ramon, Israel

ABSTRACT

Question: Why does the habitat distribution of some populations not vary with density?

Hypotheses: Two theories predict that each habitat will contain a fixed proportion of a varying population: (1) habitats differ only qualitatively but are identical quantitatively, at constant carrying capacities (prediction of Morris's isodar theory), and (2) habitats differ only quantitatively, carrying capacities are variable, and densities fluctuate around carrying capacities (prediction of our paraisodar model and modification of isodar theory).

Organisms: Wagner gerbil, *Gerbillus dasyurus*.

Field sites: Two areas in the central Negev Desert (Israel), 13 km apart. In one the substrate is loess, in the other it is gravel.

Methods: We estimated gerbil density with mark–recapture techniques on eight sampling grids in each area. We estimated fitness as the ratio of the number of young individuals at the end of the breeding season to the number of females at the beginning of the breeding season. We estimated resource abundance as the amount of seeds in the seed soil bank. We estimated habitat quality as a short-term population reaction to experimental food additions.

Conclusions: Resource abundance differed significantly between habitats, and varied among years in accordance with rainfall. The density of *G. dasyurus* was positively correlated with resource abundance. Per capita fitness was equal between habitats within years, varied among years, and was positively correlated with the amount of rainfall. Food addition, habitat, and season all influenced local density. But there was no synergistic effect between habitat and supplemental food (a quantitative difference). Constant niche breadth in *G. dasyurus* is caused by density-vague dynamics around varying carrying capacities. Habitat distribution thereby appears to be independent of density, even though the gerbils appeared to select habitats in a density-dependent manner.

Keywords: density-dependence, density-independence, fitness, habitat selection theory, isodar theory.

* Address all correspondence to Georgy Shenbrot, Ramon Science Center, Ben-Gurion University of the Negev, PO Box 194, 80600 Mizpe Ramon, Israel. e-mail: shenbrot@bgumail.bgu.ac.il

INTRODUCTION

Individuals of a population usually occupy their best habitat at low density and spread into other habitats only at higher densities. Such a density-dependent increase in habitat breadth (i.e. in the diversity of habitats used) or, conversely, decreased habitat selectivity (referred to as a 'density-dependent habitat distribution') is predicted by the theory of habitat selection (Mayr, 1926; Fretwell and Lucas, 1970; Rosenzweig, 1981, 1989, 1991, 1995). Fretwell and Lucas (1970) assume that habitats differ in the reward they offer to foragers at density k, that individuals are free to move among habitats to maximize their individual fitness, and that per capita fitness is a negative function of population density. At low density, maximum *per capita* fitness is highest in the best habitat and all individuals should concentrate there. As density increases, per capita fitness in the best habitat decreases to the point where some individuals can achieve the same fitness by moving to the next best habitat. At equilibrium, individuals will be distributed among habitats such that average per capita fitness is equal across habitats, a habitat distribution called the ideal-free distribution. Studies of habitat selection in natural populations have confirmed density-dependent habitat selection in many species, but cases of habitat distributions that are independent of density have also, albeit rarely, been reported (e.g. Abramsky *et al.*, 1985; Rosenzweig and Abramsky, 1985; Shenbrot and Rogovin, 1995). For example, the habitat breadth of the small granivorous Wagner gerbil, *Gerbillus dasyurus* (Wagner, 1842), in the central Negev Desert is constant across a range of population densities (Shenbrot and Krasnov, 2000, 2004).

At first glance, a density-independent habitat distribution appears to refute density-dependent habitat selection and one might conclude that *G. dasyurus* is not a density-dependent habitat selector. But density-independent habitat distributions can actually emerge from the process of density-dependent habitat selection (Morris, 1987, 1988, 1990, 2003).

Consider qualitative and quantitative differences between habitats. Qualitative habitat differences (e.g. structure, type of resources, presence of interacting species) reflect differences in efficiency of resource use and are expressed as different rates of decrease in per capita fitness with increased density across habitats (i.e. the relative strengths of density dependence). They lead to slope differences in plots of habitat-specific per capita population growth rate versus population density. The higher the quality of a habitat, the slower fitness decreases with density.

Quantitative differences, on the other hand, reflect differences in productivity and lead to concomitant differences in maximum fitness. They appear as differences in the intercept in a plot of habitat-specific per capita population growth rate versus population density.

Qualitative and quantitative differences in habitats can be determined by habitat isodars (Morris, 1987, 1988). A habitat isodar is a line plotted in density space. Each point represents an actual density in habitat 1 and the simultaneous density in habitat 2. Provided that there is an ideal-free distribution, at every point of an isodar average fitness of individuals in one habitat equals that of individuals in any other habitat used (otherwise well-adapted individuals would move from the habitat offering lower fitness to the one offering higher fitness). If the isodar's slope differs from 1, there are qualitative habitat differences (by definition). If the isodar's intercept differs from 0, there are quantitative differences (by definition).

Several models of population regulation can be distinguished by recognizing the several combinations of qualitative and quantitative habitat differences that might exist (Morris, 1988):

- Habitats may differ only quantitatively, in which case their respective fitness functions will be parallel to one another and the isodar will possess a positive intercept and slope equal to 1.
- Habitats may differ only qualitatively, in which case their isodar slope will be greater than 1 and its intercept will equal 0.
- One habitat may be both qualitatively better and quantitatively better, in which case the isodar's intercept will be positive and its slope greater than 1.

A zero intercept in a linear isodar corresponds to constant niche width (density-independent distribution) because the proportion in each habitat is constant. However, the foragers in such a system achieve the constant proportion by density-dependent habitat selection. Isodars predict, therefore, constant proportional use of habitats only when habitats are quantitatively equal and qualitatively different.

Shenbrot and Krasnov (2000) expanded isodar theory to include environmental gradients with temporally variable carrying capacities ('paraisodars'). A paraisodar is a line plotted in density space (densities in different habitats at time 1 plotted against densities in the same habitats at time 2) at every point of which the fitness of individuals is constant for each time period. A density-independent habitat distribution (constant habitat breadth) results in a linear paraisodar with zero intercept. The intercept of a paraisodar will equal zero if habitats along a gradient differ only qualitatively. But if habitats differ quantitatively, the intercept would equal $a = (fk_2/\gamma p)((\varphi_1/k_1) - (\varphi_2/k_2))$, where γ and φ are scaling constants, p is per capita demand on resources, k_1 and k_2 are relative resource abundances at time 1 and time 2 respectively, and φ_1 and φ_2 are average per capita fitnesses at time 1 and time 2 respectively. Consequently, $a = 0$ if $\varphi_1/k_1 = \varphi_2/k_2$, and thus $\varphi = ck$, where c is a constant. Thus, the paraisodar models predict that constant habitat breadth will also be observed when seasonal fitness changes in quantitatively different habitats are proportional to shifts in resource abundance.

It is easy to demonstrate that isodars constructed for habitats with variable carrying capacities and fluctuating densities also yield constant niche breadth. Assume that densities can vary around a constant carrying capacity. Thus, in the case of parallel population regulation, analyses of separate subsets collected from periods with similar carrying capacities within a long-term data set will produce a set of isodars with the same slope (equal to 1) and intercepts with various non-zero values. However, the range of observed points along each isodar will be narrow and will shift from low-density ranges on the isodar for periods of low carrying capacity to high-density ranges on the isodar for periods of high carrying capacity. As a result, the analysis of the whole data set will produce a pseudoisodar with zero intercept and slope greater than 1 (Fig. 1), indicating constant habitat breadth. This will be the case, however, only if resource abundances in the two habitats vary proportionally. Such resource variability can be quite common for desert ecosystems where resource abundance is determined by available water. Two habitats may receive a constant proportion of variable rainfall due to their altitudinal positions, or two habitats may obtain the same amount of rainfall but accumulate water with different efficiency due to differences in soil structure. Thus, isodars can predict constant habitat breadth in two cases: (1) if habitats differ only qualitatively but are identical quantitatively at constant carrying capacities, or (2) when habitats differ only quantitatively, carrying capacities are variable, and densities fluctuate.

We tested the two alternative hypotheses explaining density-independent distribution of *G. dasyurus* between two habitats in the central Negev. The first hypothesis predicts different

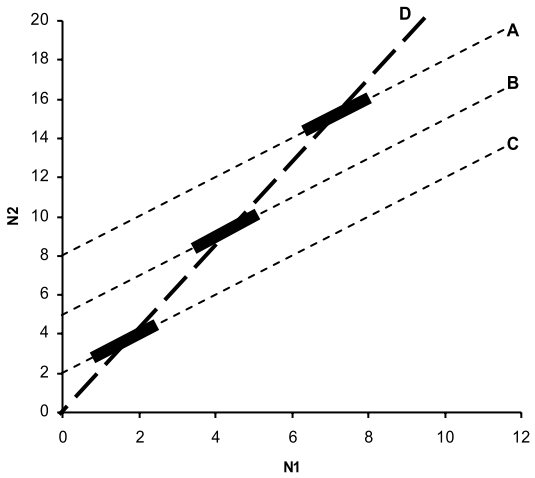

Fig. 1. Habitat isodars corresponding to the model of parallel population regulation at high (A), medium (B), and low (C) resource abundance and resulting perennial 'pseudoisodar' (D). Thick segments indicate limits of density variation within each period.

habitat qualities and spatially and temporally constant resource abundances. The alternative hypothesis predicts equal habitat quality, but spatially and temporally variable resource abundances and resource-dependent changes in fitness and/or density. We begin by testing whether fitnesses in different habitats are equal, to validate the ideal-free distribution assumption. Next, we analyse spatial (between habitats) and temporal (between seasons) variation in habitat quality and resource abundances using observations and field experiments. Finally, we analyse how fitness and density are related to temporal variation in resource abundance.

MATERIALS AND METHODS

Four 1-ha (100×100 m) grids were established at two sites 13 km apart representing two different habitat types (eight grids in total). At each site, the grids were spaced out along dry riverbeds at irregular intervals of 300–700 m. The first site, Wadi Ramon (30°36′N, 34°50′E, 500 m elevation), is a wide, dry riverbed on a gravel plain with moderate cover (18.5%) of *Retama raetam*, *Moricandia nitens*, *Tamarix nilotica*, and *Artemisia monosperma*. The second site, Wadi Nizzana (30°35′N, 34°41′E, 780 m elevation), is a dry riverbed in a deep valley in rocky hills. The wadi is filled with loess and covered by denser vegetation (26.0% cover), predominately *Anabasis articulata*, *Atriplex halimus*, and *Artemisia herba-alba*.

We recorded rainfall during rainy seasons at the two study sites every 30 min using a Watch Dog Data Logger with Compact Rain Gauge (Model 120, Spectrum Technologies Inc.). Data were stored in the memory of a station and downloaded monthly. For retrospective analysis, we used data on rodent density dynamics collected at the above two sites in 1993–2000 as a part of a more extensive monitoring programme (Shenbrot and Krasnov, 2000, 2004). Data on rainfall for this period were recorded using the Weather Monitor IITM weather station (Davis Instruments Corp.) placed in Mizpe Ramon (4 km from Wadi Ramon and 10.5 km from Wadi Nizzana).

We sampled the grids from January 2001 to August 2003, once in winter (January–February, before the beginning of breeding) and once in summer (July–August, after the end of breeding). Each grid was subdivided into 25 plots of 20×20 m, with their centres marked by numbered steel stakes. Each grid was sampled for 3 days with 50 Sherman folding live-traps placed near the centre of each plot (5×5 stations with two traps per station, with intervals of 20 m between stations). We used millet seeds as bait. We chose a 3-day survey period because preliminary results for 6- to 8-day samples demonstrated that 80–85% of all individuals were recorded during the first three nights. Each additional trapping night added no more than 2–7% of the individuals (Shenbrot and Krasnov, 2004). Each trapped *G. dasyurus* was sexed, weighed, marked subcutaneously with a Trovan® ID-100 implantable micro-transponder, and released. For subsequent individual identification, we used an Allflex® ISO compatible RFID portable reader for passive electronic identification of transponders. We estimated the density of *G. dasyurus* as the minimum number of individuals known to be alive. Other rodent species occurred on the trapping grids: *Gerbillus henleyi*, *Meriones crassus*, *Psammomys obesus*, *Acomys cahirinus*, and *Jaculus jaculus* at both sites; *Acomys russatus* in Wadi Ramon; and *Eliomys melanurus* and *Mus musculus* in Wadi Nizzana. We did not analyse the influence of these species on habitat selection of *G. dasyurus* because we showed earlier (Shenbrot and Krasnov, 2002) that *G. dasyurus* interacts with two other species, *G. henleyi* and *M. musculus*, but that these interactions are asymmetrical: *G. dasyurus* influences their distribution and density but is not influenced by them.

At the beginning of each summer trap session, we collected 20 soil samples from each grid to measure seed abundance. Horizontal seed distribution is heavily influenced by shrub canopies (Guo *et al.*, 1998), so ten samples were collected from randomly selected open places, and ten samples were taken from randomly selected locations under shrub canopies. The vertical distribution of seeds in desert soils is usually also uneven (Guo *et al.*, 1998). *Gerbillus dasyurus* is able to find seeds most effectively in the uppermost (0–3 cm) soil layer (Krasnov *et al.*, 2000). Therefore, we collected soil samples of 400 g from the upper 0–3 cm only. The samples were divided into sub-samples and were analysed by two methods, germination and flotation. Six 50-g sub-samples were placed in small plastic flowerpots and watered for 2 weeks. At the end of the 2-week germination period, all shoots were counted. One 100-g sub-sample was double floated using potassium and then zinc chloride solutions supplemented by sieving to extract and count seeds of different weights (Goodall *et al.*, 1972; Childs and Goodall, 1973). Analysis of the first 50 samples demonstrated a positive correlation between the results provided by the two methods ($r = 0.377$, $P < 0.01$), although absolute values of seed abundance obtained by flotation were approximately eight times higher than those obtained by germination. Because the flotation technique took much longer, we used only the germination technique for the rest of the samples.

Among many different possible estimates of fitness (see review in Benton and Grant, 2000), we chose a measure based on reproductive success: the ratio of the number of young individuals at the end of the breeding season to the number of females at the beginning of the breeding season. We made fitness estimates on all eight sampling grids.

To estimate whether habitats differ qualitatively, quantitatively or both, we measured short-term gerbil reactions to experimental food additions. We organized the food addition experiments as follows: one experimental plot at each site, 250×50 m, with five feeders at 50-m intervals along the long axis in the centre of the plot. Feeders were constructed from cylindrical plastic tubes 10 cm in diameter and 13 cm tall. Each feeder was sealed with an upper cap. Rodents foraged through three entrances made from plastic tubes 10 cm long

and 5 cm in diameter. The tubes were buried so that the upper cap and external entrances were at ground level.

During the first 7 days of an experiment, we left feeders empty and trapped animals using four Sherman live-traps around each feeder and another 30 traps set randomly within the plot. Animals trapped overnight were marked with micro-transponders and released. From the third to seventh nights, we placed a Trovan LID 650 modular decoder near one of the feeders (chosen at random each night) attached to an ANT-611 sensor antenna mounted on the interchangeable cover of the feeder. We did not place traps near feeders when they were equipped with a decoder. Data stored in the decoder were transferred daily to the laboratory computer to identify the animals that had visited feeders during the previous night. On the eighth day, we filled each feeder with 200 g of millet seed. During the next 10 days, we visited the experimental plots at 2-day intervals to add seeds to feeders. After the end of this 10-day feeding period, we emptied feeders of food and again recorded animals for 5 days with the same scheme used during days 3–7 (a feeder was filled with seeds only for the night when it was equipped with a decoder) to estimate any increase in the number of individuals visiting feeders.

RESULTS

During 11 years of observations, the densities of *G. dasyurus* in the two sites were highly correlated ($r = 0.837$, $P < 0.001$). The regression line of density in the loess valley against density in the wadi on gravel plain (Fig. 2) estimated by Model II (major axis) was significant ($P < 0.001$) and its slope was greater than 1 (95% of the estimates of slope were in the range 2.14 to 3.98). Its intercept was not significantly different from zero (95% of the estimates of intercept were in the range −4.38 to 3.76). This regression line conforms to an isodar model of qualitatively different, quantitatively identical habitats (Morris, 1988).

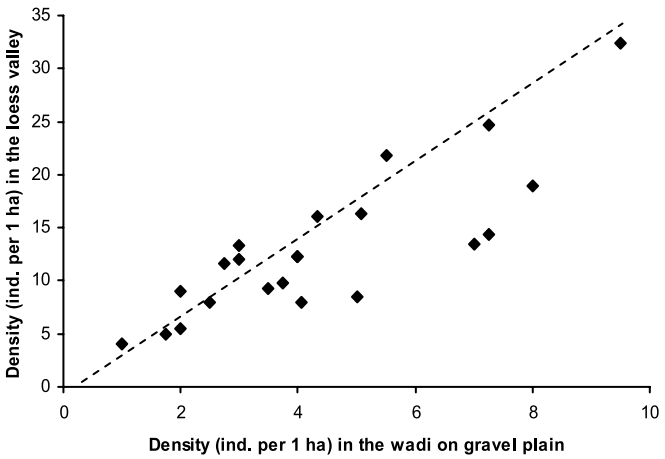

Fig. 2. The relationship between densities of *Gerbillus dasyurus* on sample grids in two habitats during 1993–2003. Data are based on the results of 22 sampling periods (twice a year). For each site, census data were averaged across sampling grids within the habitat and trapping season (three sampling grids in each habitat during 1993–2000 and four sampling grids in each habitat during 2001–2003). The isodar has a zero intercept and a slope exceeding 1.

Estimates of fitness in 2001–2003 in the two habitats demonstrated that there were no differences in fitness between habitats within a given year. But fitness varied significantly among years (Fig. 3, Table 1). Fitness values were 6.1 young per female in 2001, 0.34 in 2002, and 1.8 in 2003. Analysis of data collected in 1994–2000 for both habitats pooled together indicated that fitness varied among years from 0.08 in 1996 to 8.2 in 1995. Thus, fitnesses during the 3 years of this study ranged over most of the variation present during the entire 11 years of our work. In summary, *G. dasyurus* fitnesses varied over time but not space.

Estimates of seed abundances in soil varied significantly both between habitats and between years (Fig. 4, Table 2). Seed abundance in the wadi (gravel plain) was always 40–50% of that in the loess valley. Seed abundance did not differ from 2001 to 2002 but it increased 2- to 2.5-fold in 2003. The density of *G. dasyurus* on each sampling grid was correlated positively with the seed abundance in the soil of that sampling grid ($r = 0.772$, $P < 0.001$; Fig. 5). Nevertheless, the fitness estimates in the grids did not correlate with these seed abundances (for any habitat). However, the fitness estimates for both habitats pooled together for the period 1994–2003 were significantly related to annual rainfall, the surrogate estimator of annual seed production: $y = (0.06 + 0.02)x$; $r = 0.771$; $P < 0.05$ (Fig. 6).

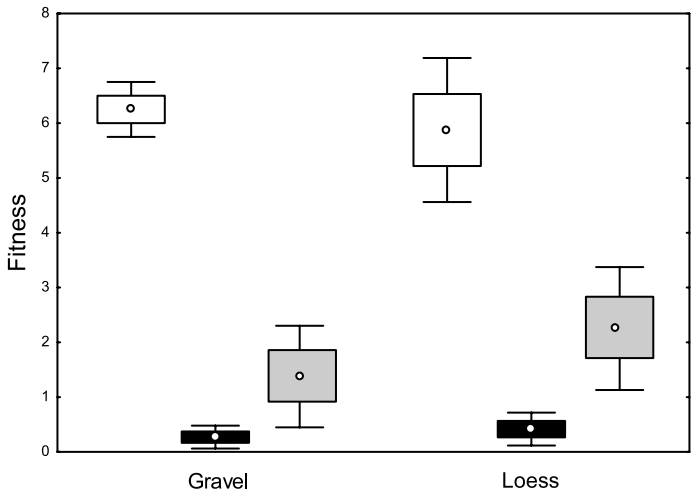

Fig. 3. Variation of fitness of *G. dasyurus* among habitats and years. *Key*: points = mean; boxes = standard deviation; whiskers = standard error; white boxes = 2001; black boxes = 2002; grey boxes = 2003. Fitness differed between years but not habitats.

Table 1. Results of ANOVA of the effect of habitat and year on fitness in *G. dasyurus* (for two habitats and three years)

Effect	d.f.	MS	*F*	*P*
Habitat	1	0.278	0.400	0.5350
Year	2	70.565	101.522	<0.0001
Habitat × year	2	0.789	1.134	0.3436
Error	18	0.695		

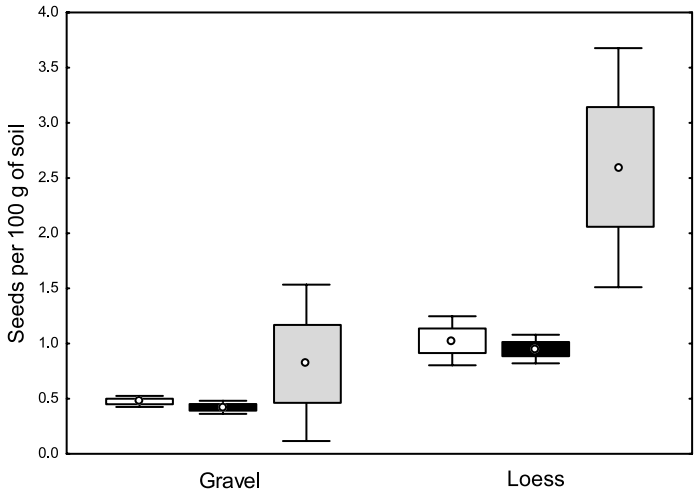

Fig. 4. Variation of seed abundance in soil among habitats and years. *Key*: points = mean; boxes = standard deviation; whiskers = standard error; white boxes = 2001; black boxes = 2002; grey boxes = 2003. Seed abundance varied from year to year but seeds were always more abundant in loess.

Table 2. Results of ANOVA of the effect of habitat and year on seed abundance in soil (for two habitats and three years)

Effect	d.f.	MS	*F*	*P*
Habitat	1	5.403	18.578	<0.0001
Year	2	2.629	9.040	0.0004
Habitat × year	2	1.008	3.467	0.0532
Error	18	0.2909		

Analysis of rainfall data demonstrated that separate rainfall events at the two sites were temporally synchronized but differed in rainfall amount. The amount of rainfall of separate rainfall events was correlated between the two sites ($r = 0.637$, $P < 0.001$); the average annual rainfall was 91 mm in Wadi Nizzana and 60 mm in Wadi Ramon.

The number of individuals recorded at and in the vicinity of feeding points increased in all food addition experiments (Fig. 7). The effect of food addition depended on habitat and season (and their interaction). There were no interactions between habitat and food addition or among habitat, season, and food addition (Table 3).

DISCUSSION

The absence of fitness differences between habitats within a year support our hypothesis that the distribution of *G. dasyurus* can be approximated as ideal-free. This phenomenon seemed to operate at a relatively large spatial scale: Our two sites, representing different habitats, were separated by 13 km. If there is an ideal-free distribution in this case, it must occur by a step-wise flow of individuals across a network of adjacent habitat patches in the whole landscape rather than by direct migration between the two sites.

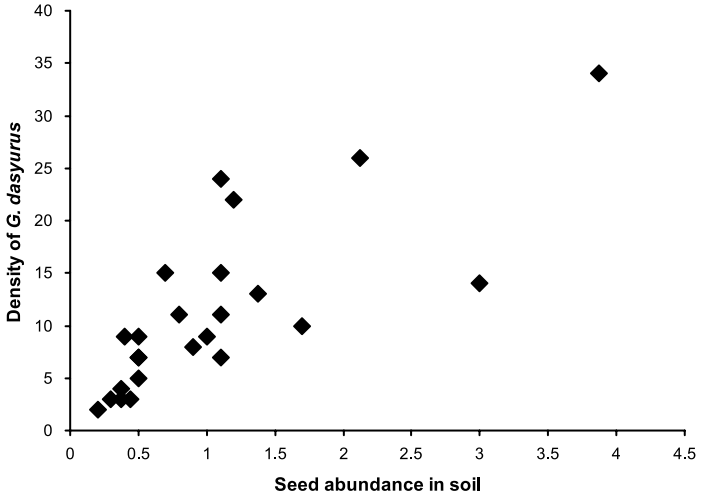

Fig. 5. Density of *G. dasyurus* in sample grids correlates with the seed abundance in soil (years 2001–2003).

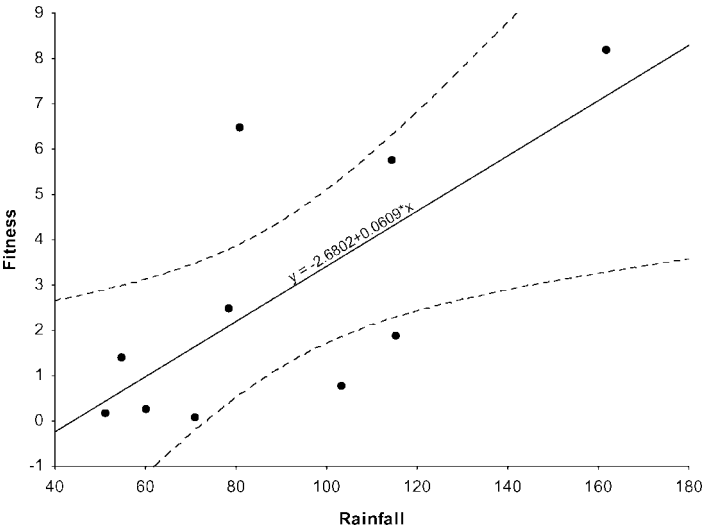

Fig. 6. The fitness of *G. dasyurus* increases with rainfall (years 1993–2003). Dashed lines are 95% confidence intervals.

We have suggested that the rodents have been reacting to density differences at a surprisingly large scale. One might suppose instead that our results have a simpler explanation – specifically, the following hypothesis (or something quite similar).

Let there be two gerbil populations of one species and let them be largely isolated from each other. Let one of the two populations inhabit a location with much better soil (say loess) than the other (say gravel). As a consequence, let gerbil carrying capacity in loess be about twice as high as in gravel. On account of the weather, which they share, both locations

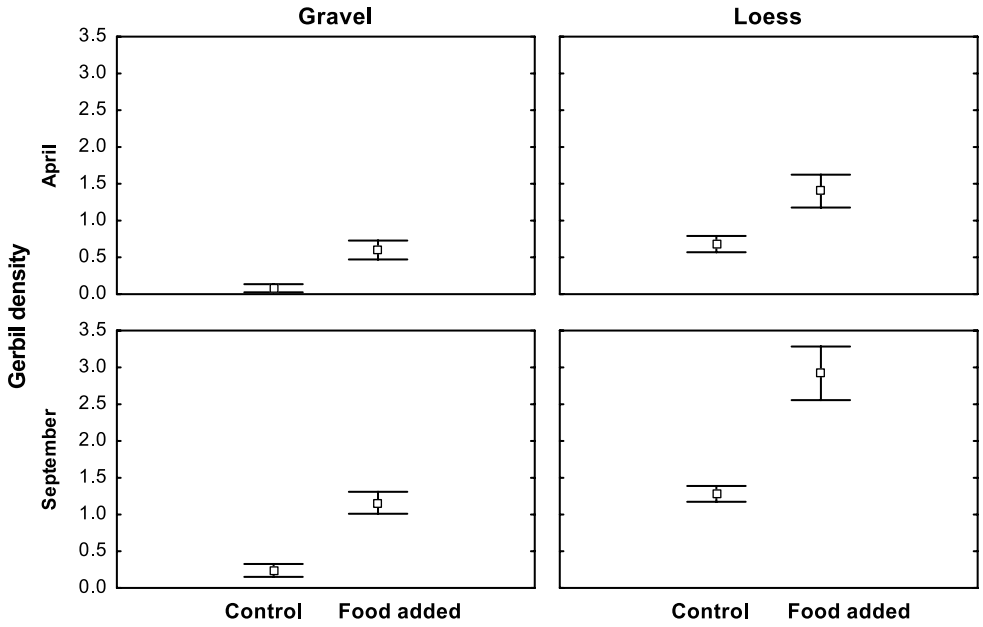

Fig. 7. Influence of experimental food addition on local abundance of *G. dasyurus* depending on site and season. *Key*: points = mean; whiskers = standard error.

Table 3. Results of ANOVA of the effect of food addition, habitat, and season on abundance of *G. dasyurus* (for two habitats and two seasons)

Effect	d.f.	MS	*F*	*P*
Treatment	1	45.125	56.231	<0.0001
Habitat	1	55.125	68.692	<0.0001
Season	1	25.205	31.408	<0.0001
Treatment × habitat	1	2.645	3.296	0.0710
Treatment × season	1	5.445	6.785	0.0099
Habitat × season	1	6.125	7.632	0.0063
Treatment × habitat × season	1	0.845	1.053	0.3061
Error	192	0.803		

show extreme inter-annual variation in resources. Result: gerbil populations will vary a lot as gerbils track their carrying capacities independently in the two locations. But the distribution of gerbils between habitats will be nearly constant.

This scenario would seem to apply to *G. dasyurus* at the two sites that we studied. However, we do not believe that actual carrying capacities will vary with such a high autocorrelation, for the following reason.

The sites are located on the opposite slopes of a low mountain ridge (elevation: 900–950 m) that runs along a southwest to northeast axis. The Nizzana site is located on the northwest slope, whereas the Ramon site is on the south-east slope.

Two types of rain events occur on the ridge: (1) Atlantic cyclones bring relatively regular winter rains from the west-northwest; (2) autumn and spring monsoons bring rain from the south-southeast, but only rarely and irregularly. Because the Ramon site is in the rain shadow of an Atlantic cyclone, a winter rain will produce about half the rain at Ramon as at Nizzana. But when the rain is monsoonal, it is Nizzana that lies in the rain shadow, and Ramon gets more rain. Because the ratio of these two types of rain events varies significantly among years, the correlation of annual amount of rainfall between the two sites is not so high ($r = 0.637$, but not 0.9), and the ratio of carrying capacities also varies unpredictably among years. Thus these temporally synchronized rainfall events can produce temporally correlated fitness changes but not fitness equalization between the two sites.

Another alternative explanation of the gerbil fitnesses is that habitat selection occurs across very small spatial scales [on the order of 100 m (Morris, 1992)], and thus the absence of fitness differences between habitats occurred because site differences were swamped by temporally synchronized events (rainfall).

However, the scale of habitat selection is determined (in part) by dispersal distances, which are believed to be a product of the landscape within which they have evolved (Morris, 1992). Deer mice, *Peromyscus maniculatus*, in a badland–prairie system in southern Alberta have the small foraging ranges (approximately 60 m) and short dispersal distances (~140 m) (Morris, 1992) that might indeed contribute to this alternative. But although in the central Negev *G. dasyurus* has similar foraging ranges [30–90 m (Gromov *et al.*, 2000)] to those of deer mice, its dispersal distances are much longer. We often recorded movements of 300–500 m and once noted a movement of 3 km in one night (personal observation).

Neither of the two alternative explanations seems valid to us. In fact, we believe that density-dependent habitat selection in desert landscapes operates at the relatively large spatial scale indicated by these *G. dasyurus* results.

Resource abundance differed significantly between the two habitats. The volume of seeds in the soil bank in the loess habitat (Wadi Nizzana) was 2 to 2.5 times greater than in the gravel habitat (Wadi Ramon). These differences are higher than differences in rainfall amount between the two sites (1.5 times). One can expect the loess to be better also because it has a higher water capacity than the gravel. Resource abundance did vary from year to year in accord with variation in rainfall.

Precipitation in deserts is generally accepted as the main limiting factor directly determining productivity of plants (Noy-Meir, 1973). Relationships between productivity and rainfall differ among plant life forms and depend on habitat type and the pattern of separate rain events (Southgate *et al.*, 1996). Nevertheless, seed production of desert annual plants is directly correlated with the amount of rainfall (Kadmon, 1993; Gunster, 1994). And there is much evidence that breeding success in rodents is regulated by resource abundance. Examples include offspring survival [*Sciurus vulgaris* (Wauters and Lens, 1995); *Clethrionomys glareolus* (Koskela *et al.*, 1998)], fertility rate and age at maturity [*Peromyscus difficilis* (Galindoleal and Krebs, 1998); *Spermophilus columbianus* (Dobson and Oli, 2001)], and litter size [*Sigmodon hispidus* (Campbell and Slade, 1995)]. In *G. dasyurus*, breeding intensity was found to vary among years according to amount of winter rainfall (Shenbrot *et al.*, 1997).

The density of *G. dasyurus* correlated directly with resource abundance. The two habitats were qualitatively similar (*sensu* Morris, 1988). The qualitative similarity was confirmed by the food addition experiments. Gerbil density increased at feeding sites, but there was no interaction with site (habitat) or season. This indicates that there was no difference between habitats in the efficiency of resource consumption by gerbils.

Modelling of habitat selection in a stochastic setting where habitat quality fluctuates in both time and space showed that in a variable environment, direct application of isodar analysis may give misleading results (Jonzén *et al.*, 2004). However, incorporation of temporal environment variability in isodar analysis showed that it can be used not only as a descriptive technique for habitat selection patterns, but also as a powerful tool for natural history studies, as it was shown for habitat selection of the fat sand rat (*Psammomys obesus*) in the Negev Desert (Shenbrot, 2004). The results of the present study also show that isodar analysis is a powerful exploratory tool that can help to generate hypotheses about the underlying processes.

Both paraisodars (Shenbrot and Krasnov, 2000) and the modified isodar theory that we present here predict that constant habitat breadth should occur in two cases: (1) if habitats differ only qualitatively, or (2) if habitats differ only quantitatively *and* between-season fitness changes are proportional to shifts in resource abundance *and* density is correlated directly with resource abundance. The first model is clearly not supported by our data. The two habitats were quantitatively different and qualitatively identical. The second model, however, is well supported. Our data demonstrated: (a) habitat and year differences in food abundance, (b) a direct correlation between gerbil density and resource abundance, and (c) a significant linear regression with zero-intercept of fitness with rainfall (an indirect estimate of resource abundance). These findings support the hypothesis that a density-independent habitat distribution and consequent constant niche breadth can occur in concert with density-dependent processes of habitat selection.

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