Density-dependent habitat selection: evaluation of the isodar method

O. Ovadia and Z. Abramsky


We have tested the performance of the isodar method, in detecting density-dependent habitat selection, underlying modes of community organization, and competitive interaction. For that purpose, we used data obtained from intensive manipulation experiments conducted on two granivorous, desert gerbil species, Gerbillus allenbyi and G. pyramidum. The isodar method detected, in both species, density dependent habitat selection. The isodar method is a good tool to assess differences between habitats, shape and general location of fitness-density graphs. Using the isodar method we discovered new details about the two gerbil species. The G. pyramidum fitness-density graphs are two parallel straight lines. The G. allenbyi fitness-density graphs are two converging straight lines. Isodars estimated for mixed populations agree with the prediction that they should not differ from that calculated for each species in isolation. This point implies that isodars can be used to detect habitat preference of single species even though they exist in a community of competitors. The isodar method was also able to detect the shared preference community organization pattern of the two gerbil species.

We concluded that the isodar method is a useful tool in detecting density-dependent habitat selection and community organization pattern. But we had to conclude that the isodar method is very limited in estimating interspecific competition.

The method was not able to detect interference competition between the two gerbil species although results of manipulation experiments showed that it is the key process in the gerbil system. Also, the isodar method assumes that competition is fixed (density independent). This is a major flaw since all theories of optimal foraging, including density dependent habitat selection, predict that competition coefficients are density dependent. Thus, although the isodar method was able to estimate significant exploitation competition for the two species, we are not sure if it means anything. This is because the estimated isoclines of the two species, using field manipulations, revealed that the isoclines are highly nonlinear and that the magnitude of the interaction, for each density combination, depends on the degree of habitat overlap of the two species. Thus, habitat specific constant interaction coefficients estimated by the isodar method probably mean very little, if anything.

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The theory of density dependent habitat selection was developed by Fretwell and Lucas (1970), and Fretwell (1972). For a single species, Fretwell deduced that, in the absence of strong contest competition, individual animals of a species are better off settling in habitats so that no individual has a higher per capita population growth rate than any other. This is accomplished by individuals distributing themselves unequally in different habitats. More
productive habitats will have more individuals than less productive ones. Fretwell termed such an unequal distribution an Ideal Free Distribution (IFD).

Qualitative and quantitative differences between habitats can be described by fitness-density graphs (Fig. 1). These represent how reproductive fitness varies with changing population densities within each habitat. But, for some organisms, measuring reproductive success is extremely difficult. It may take years, and may be impractical.


Morris (1987) developed the isodar method to detect density dependent habitat selection. Later, he extended the isodar method to also detect community organization (Morris 1988) and the characteristics of inter-specific competition (Morris 1989).

In this paper we test the performance of the isodar method (Morris 1987, 1988, 1989, 1990), in detecting density dependent habitat selection, in revealing the mode of community organization, and in estimating exploitation and interference competitive interaction. For this purpose, we use data obtained from a set of manipulation experiments, conducted on two granivorous desert gerbil species. These experiments were designed to understand processes of habitat selection and competition. In this work, we will use these data to evaluate the performance of the isodar method.

Methods

The isodar method

An isodar is a line of equal fitness (Morris 1988) in a state space of population densities of a species in two habitats. If densities in habitats 1 and 2 are adjusted such that average fitness in both habitats is similar, and decreases with increasing density, the isodar will correctly reveal the underlying pattern of density-dependent habitat use.

The equation of an isodar for one species, A, is (Morris 1989):

\[ N_{A1} = C + bN_{A2} \]  

(1)

\( N_{A1} \) and \( N_{A2} \) are the densities of species A in habitats 1 and 2. The isodar intercept \( (C) \) indicates the quantitative differences in fitness between the two habitats, and the isodar slope \( (b) \) indicates the qualitative difference in fitness between the two habitats. For example, an isodar with a slope not significantly different from 1, and an intercept significantly different from zero suggests parallel fitness-density lines (Morris 1988). The isodar intercept reflects the distance between the two parallel fitness-density lines.

The isodar method has also been extended to treat community structure and interspecific competition (Morris 1987, 1988, 1989, 1990).

The study species and their ecology

*Gerbillus allenbyi* and *G. pyramidum* occur sympathetically in a wide range of sandy habitats in the western Negev Desert (Abramsky et al. 1985a). *G. allenbyi*, the smaller of the two (mean mass \( = 26 \) g), occurs mostly in stabilized sand and semistabilized dunes with relatively dense vegetation cover (Abramsky et al. 1985b). *G. pyramidum* (mean mass \( = 40 \) g), occurs in unstabilized and semistabilized dunes with sparse vegetation cover. Both species, however, occur in most sandy regions of the western Negev Desert (Abramsky et al. 1985b). The species are similar in their general ecology; they are both burrow dwellers that forage nocturnally for seeds which constitute large proportions of their diets (Bar et al. 1984).

These two species have been intensively investigated over the last ten years. By manipulating population densities, ecologists found that:

a) competition varies with population density (Abramsky et al. 1990, 1991, 1992, 1994);

b) per capita activity declined as a function of intra- and inter-specific density for each species (Abramsky and Pinshow 1989, Mitchell et al. 1990);

c) the two gerbil species exhibited density dependent habitat selection (Rosenzweig and Abramsky 1985, Abramsky et al. 1990);

d) the distribution of the two gerbil species in areas with two habitat types (semistabilized dune and stabilized sand) follows the predictions of the shared preference community organization model (Abramsky et al. 1990);

e) the shape of the two species isoclines is nonlinear as predicted by the shared preference model (Abramsky et al. 1991, 1992, 1994);

f) the larger *G. pyramidum* physically excludes the smaller and more efficient forager *G. allenbyi* from...
A general description of the manipulation experiments

To estimate the isodars, we used data from experiments that were conducted in the six 1-ha enclosures during three summers (1987, 1988, 1991). Each enclosure received a predetermined density of one or both gerbil species. Habitat use was estimated by measuring the gerbils’ activity in 40 (40 × 40 cm) smoothed sites in each enclosure. Twenty such sites were located in the semistabilized dune and twenty in the stabilized sand. The score given to a site depended on the footprint coverage, and ranged from zero to four. A score of zero was given to a site containing no tracks and a score of four for full track cover. Scores could be assigned to species on the basis of species specific toe clips which were easy to discern in the smooth sand (for more information see Abramsky et al. 1990, 1991, 1993, 1994).

Data reduction

We summed each species’ activity scores over all 40 sand tracking sites. The sum is the total activity density for the species in the plot. In all three experiments, scores of 3 or 4 occurred only in less than 7% of the cases during the entire study and empty sites occurred 30–40% of the time. Thus, we feel that the results represent real relative levels of activity. Abramsky et al. (1990, 1991, 1994) used ANCOVA to show that the effect of temporal replicates on rodent activity, habitat selection, and interspecific interactions, is not significant. Since in this study, we used the data reported earlier (Abramsky et al. 1990, 1991, 1994), we also considered multiple observations within the same enclosure and in the same year as independent of the other observations.

The relationship between activity density and population density

Most studies of nocturnal rodent behavior rely on traps. But traps may affect behavior and distract rodents from their usual activity. Furthermore, once an individual is captured, its activity ceases. Thus, trapping gives only a record of where an animal was at one point of time. In a system where one of the species is larger, faster, dominant, and active mostly during the first part of the night, it may reach traps first and bias the sampling of other species. Such is the case with *G. pyramidum* (Abramsky et al. 1990, 1991, 1992, Ziv et al. 1993). We used the sand tracking technique to avoid biases and inaccuracies of trapping.

Sampling the number of tracks in the sand does not interfere with the rodent’s natural behavior throughout the night. Abramsky and Pinshow (1989), Abramsky et al. (1990, 1991, 1992), and Mitchell et al. (1990) showed that activity data can better assess interactions between the best habitat and from the earlier part of the night (Ziv et al. 1993).

The study site and the enclosures

The data were obtained from studies conducted in the Holot Mashabim Nature Reserve (31°01’N, 34°45’E) situated in the Haluza region 35 km south of Beer Sheva, Israel. Sandy areas in this study region can be classified into two habitat types based on the mobility of the sand and on the dominant perennial plant species. The two habitat types are semistabilized dunes and stabilized sand (Danin 1978). Average annual precipitation at the site is 108 mm. Rainfall is limited to winter, and dew forms on approximately 250 nights per year.

The experimental studies were conducted in six 1-ha plots enclosed with rodent-proof fences, during several years (1986–1991). Each 1-ha plot contained similar proportions of the two major habitat types, semistabilized dunes and stabilized sand.

Experimental design

We estimated the isodars using data collected in a set of experiments in which different density combinations of one or two gerbil species were present in the six enclosures (Abramsky et al. 1990, 1991, 1994). These experiments were designed to estimate habitat preference and interspecific competition. The data set we used in the present work to estimate the *G. allenbyi* isodar when *G. pyramidum* was absent, was collected in 1988 and reported in Abramsky et al. (1990). Similarly, we used the data collected in 1991, and reported in Abramsky et al. (1994), to estimate *G. pyramidum* isodar when *G. allenbyi* was absent. To estimate competition coefficients with the isodar method (Morris 1989), we used data collected in 1987 in which both species were present (Abramsky et al. 1990).
these two gerbil species than can data obtained from trapping. Nevertheless, activity of the rodents should be, and is, significantly correlated with density (Abramsky and Pinshow 1989, Abramsky et al. 1990, Mitchell et al. 1990). Thus, we felt quite comfortable in using activity densities instead of real densities to test the performance of the isodar method.

Results

The isodar method shows that the two gerbil species exhibit density-dependent habitat selection

The activity density of each species in the semistabilized dune habitat depends on its activity density in the stabilized sand (Figs 2 and 3). Significant isodars can be interpreted as evidence that the density in each habitat is adjusted such that average fitness in both habitats is about equal and decreases with increasing density (Morris 1989). The significant isodars of both species support the hypothesis that both species are density-dependent habitat selectors. We also found significant (Table 1, 2) isodars when we included the interspecific effect in the regression analysis. These results also support the hypothesis that both species are density-dependent habitat selectors (Morris 1988). Rosenzweig and Abramsky (1985) using census data and the dispersion method and Abramsky et al. (1990) using manipulation experiments have also concluded that both species exhibit density dependent habitat selection.

Table 1. Multiple regression between activity density of G. pyramidum in semistabilized dunes (AGPs) – the dependent variable, and activity density of G. allenbyi in semistabilized dunes (AGAs), activity density of G. allenbyi in stabilized sand (AGAss), and activity density of G. pyramidum in stabilized sand (AGAss) – the independent variables. AGPs = 8.476 – 0.4AGAss + 0.429AGAs + 0.826AGAss

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Table 2. Multiple regression between activity density of G. allenbyi in semistabilized dunes (AGAss) – the dependent variable, and activity density of G. pyramidum in semistabilized dunes (AGPs), activity density of G. pyramidum in stabilized sand (AGPs), and activity density of G. allenbyi in stabilized sand (AGAs) – the independent variables. AGAss = 4.226 – 0.325AGPs + 0.404AGPs + 0.67AGAs

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The isodar method is successful in assessing differences between habitats, shape and general location of fitness-density graphs

The isodar method pointed to the most preferred habitat of the two gerbil species and to the general shape of the fitness density curves. Both gerbil species prefer the semistabilized dune habitat. The isodar intercept of *G. pyramidum* when alone (Fig. 2) is significantly ($t = 4.969, p < 0.000$) greater than zero, and the isodar intercept of *G. allenbyi* when alone (Fig. 3) is also significantly ($t = 2.847, p = 0.008$) greater than zero. The positive intercepts demonstrate that the semistabilized dune habitat can support more individuals of *G. pyramidum* or *G. allenbyi* compared to the stabilized sand habitat.

For *G. pyramidum* the two habitat types are qualitatively similar. The isodar slope of *G. pyramidum* when alone (1.016), is not significantly different from one ($t = 0.144, p > 0.50$; Fig. 2). An isodar with slope equal to one and an intercept greater than zero reveals parallel fitness-density lines (Morris 1988). Thus, for *G. pyramidum* the change in fitness reward with its density is equal in both habitats.

For *G. allenbyi* the stabilized sand habitat is qualitatively better than the semistabilized dune habitat. The isodar slope of *G. allenbyi* when alone (0.756) is significantly ($t = 2.56, p < 0.05$) less than one (Fig. 3). An isodar with slope significantly less than one and an intercept significantly greater than zero corresponds to convergent fitness-density lines (Morris 1988). For *G. allenbyi* the change in fitness reward with density in the stabilized sand habitat is smaller than in the semistabilized dune habitat. Hence, for *G. allenbyi* the stabilized sand habitat is qualitatively better than the semistabilized dune habitat.

Morris (1987) suggested a simple test to determine whether the relationship between fitness and density is linear or nonlinear. The relationship can be assessed by comparison of paired regressions over (at least) three density treatments. If the function is linear, sequential paired regressions should produce equal slopes. If it is concave downward, increased overall population density will result in density regressions of significantly lower slopes. The opposite will be true of convex functions (Morris 1987).

We applied this test to our gerbil species. We sorted the activity density of both species for each habitat in each of the six enclosures and selected for the semistabilized dune; low, medium, and high activity density values. Then, we regressed separately for each species the lowest and medium values of activity density in the semistabilized dune versus the paired activity density in the stabilized sand. We repeated this procedure for the medium and highest values, and made two sequential regressions. Each regression consisted of 12 points, and it represented one of the species in the two habitats for two levels of density.

For *G. allenbyi*, the slopes of the two sequential regressions were not significantly different ($Y_1 = 12.8 + 0.64X, r = 0.61, p = 0.06$; and $Y_2 = 5.4 + 0.64X: r = 0.85, p = 0.002$). For *G. pyramidum* the two slopes were also not significantly different ($Y_1 = 4.6 + 1.06X, r = 0.83, p = 0.001$; and $Y_2 = 18.1 + 1.01X, r = 0.49, p = 0.10$). These results suggest that for both gerbil species the fitness-density lines are linear.

Experimental field studies conducted by Abramsky and Pinshow (1989) and Abramsky et al. (1990) have shown that indeed the two gerbil species (*G. allenbyi* and *G. pyramidum*), when alone, and in relatively low density, prefer the semistabilized dune habitat. Thus, the field experiments confirmed the results of the isodar analysis.

The isodar method detects the community organization of the two gerbil species

Abramsky et al. (1990) have shown experimentally that in areas with two habitat types, semistabilized dune and stabilized sand, the distribution of the two gerbil species follows the predictions of the shared preference community organization model. At low densities, both species prefer to utilize the same habitat, i.e. the semistabilized dune. As their intraspecific populations increase, their habitat selection changes. Both shift to using the second habitat. A few individuals of *G. pyramidum* change the preference of *G. allenbyi*, from the semistabilized dune to an apparent preference for the stabilized sand. The reverse interspecific effect is not as strong. *G. pyramidum* does not prefer the stabilized sand: even in the presence of high densities of both species it uses both habitats (Abramsky et al. 1990).

The isodar intercept of *G. pyramidum* when alone (Fig. 2) is significantly ($t = 4.969, p < 0.000$) greater than zero, and the isodar intercept of *G. allenbyi* when alone (Fig. 3) is also significantly ($t = 2.847, p = 0.008$) greater than zero. The positive intercepts demonstrate that both gerbil species prefer the semistabilized dune habitat. In a two-habitat system, if both gerbil species prefer the same habitat type, the distributions of the two gerbils follow the predictions of the shared preference model (Abramsky et al. 1990). Thus, the isodar method also detects the shared preference community organization pattern.

According to Morris (1988: Table 1), shared preference community organization should yield isodars, of both species, with slopes equal to one. The slope of the isodar of *G. pyramidum*, the dominant species (Abramsky et al. 1990), agrees with the prediction of Morris (1988) for the shared preference community organization model (Fig. 2). However, the slope (0.756) of the isodar of *G. allenbyi* does not agree with that prediction. It is significantly ($t = 2.56, p = 0.01 < p < 0.05$) less than one (Fig. 3). Here we have a conflict, the isodar intercepts clearly suggests shared preference organization but the isodar slope of *G. allenbyi* does not support shared preference organization.
Morris (pers. comm.) suggested that the isodar slope of *G. allenbyi* could imply that it switches its preference from semistabilized dune habitat to stabilized sand habitat, at high density, as predicted by the shared preference model and the centrifugal model (Rosenzweig and Abramsky 1986). This could not be the case here since the *G. allenbyi* isodar was estimated when it was alone. In this case, the habitat preference of *G. allenbyi* changes gradually from preferring the semistabilized dune, at low densities, to using both habitats equally, at high densities (Abramsky et al. 1990: Figs 1c, 2c). Only when *G. pyramidum* is present *G. allenbyi* switches its habitat preference, at high densities, from semistabilized dune to apparent preference of the stabilized sand (Abramsky et al. 1990). Thus, our field results do not support the definition of community structures as reflected by the slopes of the isodars and summarized in Morris (1988: Table 1). However, as mentioned above, the isodar method is able to point correctly to the shared habitat preference exhibited by the gerbils.

The isodar method revealed the existence of competition, but not the existence of interference competition between the two gerbil species

Morris (1989) extended the isodar method to estimate interspecific competition coefficients:

$$N_{A1} + \alpha N_{B1} = C + \beta(N_{A2} + \beta N_{B2}) = \text{species A isodar.}$$

$$N_{B1} + \alpha ' N_{A1} = C' + \beta ' (N_{B2} + \beta ' N_{A2}) = \text{species B isodar.}$$

Where $\alpha$ is the average exploitation coefficient of species B on species A in habitat 1 and $\beta$ is the same coefficient in habitat 2. $\alpha '$ and $\beta '$ are the respective coefficients of species A on B in the two habitats.

The results of the isodar method point to the existence of competition between the two gerbil species. The resultant significant equation from the multiple regression of the activity density of *G. pyramidum* in the semistabilized dune habitat (dependent variable) against the activity densities of both species in both habitats (Table 1) is:

$$AGPs = 8.476 - 0.4AGAss + 0.429AGAs + 0.826AGPs$$

Where AGPs is the activity density of *G. pyramidum* in semistabilized dunes, and AGPs is the activity density of *G. pyramidum* in stabilized sand. AGAss and AGAs are the respective activity densities of *G. allenbyi* in the two habitats. The average exploitative competition coefficient of *G. allenbyi* on *G. pyramidum* in the semistabilized dune habitat is equal to $-0.4$. The activity density of *G. allenbyi* in the semistabilized dune habitat reduces the activity density of *G. pyramidum* in that habitat. The average exploitative competition coefficient of *G. allenbyi* on *G. pyramidum* in the stabilized sand habitat is equal to $0.429/0.826 = 0.52$. As a consequence of the competition of *G. allenbyi* on *G. pyramidum* in the stabilized sand the activity density of *G. pyramidum* increased in the semistabilized dune habitat. An increase in *G. allenbyi* density in the stabilized sand habitat turns it to less attractive habitat of *G. pyramidum*.

The equation from the multiple regression of the activity density of *G. allenbyi* in the semistabilized dune habitat (dependent variable) against the activity densities of both species in both habitats (Table 2) is:

$$AGAss = 4.226 - 0.325AGPs + 0.67AGAs + 0.404AGPs$$

The average exploitative competition coefficient of *G. pyramidum* on *G. allenbyi* in the semistabilized dune habitat is equal to $-0.325$. The activity density of *G. pyramidum* in the semistabilized dune habitat reduces the activity density of *G. allenbyi* in that habitat. The average exploitative competition coefficient of *G. pyramidum* on *G. allenbyi* in the stabilized sand habitat is equal to $0.404/0.67 = 0.6$.

Note that estimated exploitation competition coefficients of the two species are similar and that the dominance of *G. pyramidum* over *G. allenbyi*, that was found in manipulation experiments (Ziv et al. 1993), is not detectable. Also, the competitive interactions in the two habitats are not equal; competition in the stabilized sand is more intense than in the semistabilized dune. Since the semistabilized dune is the preferred habitat of the two species, we would have expected to observe the most intense interactions in this habitat.

The slopes and the intercepts of two species isodars when exploitative competition exists should be equivalent to these expected for a single species in allopatry (Morris 1989). If the isodars are not the same, one can conclude that they were changed by some form of species-dependent interaction besides exploitation, like interference competition (Morris 1989). The isodar slope (0.826) and intercept (8.48) of *G. pyramidum* competing with *G. allenbyi* do not differ significantly from the isodar slope (1.02) and intercept (6.66) of *G. pyramidum* when alone (the 95% confidence limits are 0.794–1.24, and 3.97–9.34 respectively).

The isodar slope (0.67) and intercept (4.23) of *G. allenbyi* competing with *G. pyramidum* do not differ significantly from the isodar slope (0.756) and intercept (8.00) of *G. allenbyi* when alone (the 95% confidence limits are 0.56–0.95, and 2.24–13.7 respectively).

Although at this stage we could not find evidence for interference competition using the isodar method, we tried to detect the interference using an additional regression analysis suggested by Morris (1989). When evidence for interference and exploitative competition between the two species exists, the two isodar equations are modified to include the effect of interference competition (Morris 1989):

for species A:
Table 3. Multiple regression between activity density of *G. pyramidum* in semistabilized dunes (AGAss) – the dependent variable, and activity density of *G. allenbyi* in semistabilized dunes (AGPs), activity density of *G. pyramidum* in stabilized sand (AGAss), activity density of *G. allenbyi* in stabilized sand (AGPs), and the interaction between activity density of *G. pyramidum* in stabilized sand to activity density of *G. allenbyi* in stabilized sand (AGPs × AGAss) – the independent variables. AGPs = 0.431 + 0.399AGAss + 0.833AGPs + 0.431AGAs – 0.001AGPs × AGAss.

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\[ N_{A1} + \alpha N_{B1} + \gamma (N_{A1}N_{B1}) = C + b(N_{A2} + \beta N_{B2} + \varepsilon(N_{A2}N_{B2})) \]  

for species B:

\[ N_{B1} + \alpha' N_{A1} + \gamma' (N_{B1}N_{A1}) = C' + b'(N_{B2} + \beta' N_{A2} + \varepsilon'(N_{B2}N_{A2})) \]

Where \( \gamma \) and \( \varepsilon \) are scaling constants reflecting the interference of species B on species A in habitats 1 and 2 respectively. \( \gamma' \) and \( \varepsilon' \) are the respective effects of species A on B in the two habitats.

There are some difficulties using eqs (4) and (5) to detect interference competition between any pair of species including the two gerbil species. The interaction between the two species in the semistabilized dune habitat confounds an independent variable with the dependent variable (activity density of *G. pyramidum* or *G. allenbyi* in the semistabilized dune habitat) and the interaction between the two species in the stabilized sand habitat may result in multicollinearity among the independent variables (Morris 1989). To overcome these problems we ran two multiple regressions for each species. In each, we included only the intraspecific activity densities and one of the interaction terms, as suggested by Morris (1989). In all four multiple regressions the interaction terms between both species’ activity densities in the two habitats were not significant (Tables 3, 4, 5, 6).

Using the isodars, we could not find any evidence for interference competition between the two gerbil species in the two habitats. However, manipulation experiments have shown (Ziv et al. 1993) that interference competition is a key factor in the coexistence of the two species. *G. pyramidum*, the dominant species, excludes *G. allenbyi* from the preferred time of activity and the preferred habitat. *G. allenbyi* can still make a living using the less preferred habitat and time of activity (Ziv et al. 1993).

Since independent manipulation experiments (Ziv et al. 1993) showed that interference is a key factor in the distribution of the two gerbil species we must conclude that the isodar method could not detect the interference competition between the two gerbil species.

Table 4. Multiple regression between activity density of *G. pyramidum* in stabilized sand (AGPs) – the dependent variable, and activity density of *G. allenbyi* in stabilized sand (AGAss), activity density of *G. pyramidum* in semistabilized dunes (AGPs), activity density of *G. allenbyi* in semistabilized dunes (AGAss), and the interaction between activity density of *G. pyramidum* in semistabilized dunes to activity density of *G. allenbyi* in semistabilized dunes (AGPs × AGAss) – the independent variables. AGPs = 0.002 – 0.443AGAss + 0.654AGPs + 0.459AGAss – 0.011AGPs × AGAss.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Coefficient</th>
<th>Std. error</th>
<th>T-value</th>
<th>P (2-tail)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Constant</td>
<td>0.002</td>
<td>1.666</td>
<td>0.001</td>
<td>0.999</td>
</tr>
<tr>
<td>AGAss</td>
<td>-0.443</td>
<td>0.053</td>
<td>-8.327</td>
<td>0.000</td>
</tr>
<tr>
<td>AGPs</td>
<td>0.654</td>
<td>0.085</td>
<td>7.738</td>
<td>0.000</td>
</tr>
<tr>
<td>AGAss</td>
<td>0.459</td>
<td>0.099</td>
<td>4.657</td>
<td>0.000</td>
</tr>
<tr>
<td>AGPs × AGAss</td>
<td>-0.011</td>
<td>0.006</td>
<td>-1.864</td>
<td>0.064</td>
</tr>
<tr>
<td>n = 192</td>
<td></td>
<td></td>
<td>R = 0.736</td>
<td></td>
</tr>
</tbody>
</table>

Table 5. Multiple regression between activity density of *G. allenbyi* in semistabilized dunes (AGAss) – the dependent variable, and activity density of *G. pyramidum* in semistabilized dunes (AGPs), activity density of *G. pyramidum* in stabilized sand (AGAss), activity density of *G. allenbyi* in stabilized sand (AGPs), and the interaction between activity density of *G. pyramidum* in stabilized sand to activity density of *G. allenbyi* in stabilized sand (AGPs × AGAss) – the independent variables. AGAss = 5.108 – 0.519AGPs + 0.255AGPs + 0.61AGAs + 0.011AGPs × AGAss.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Coefficient</th>
<th>Std. error</th>
<th>T-value</th>
<th>P (2-tail)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Constant</td>
<td>5.108</td>
<td>1.372</td>
<td>3.722</td>
<td>0.000</td>
</tr>
<tr>
<td>AGAss</td>
<td>-0.319</td>
<td>0.061</td>
<td>-5.229</td>
<td>0.000</td>
</tr>
<tr>
<td>AGPs</td>
<td>0.255</td>
<td>0.118</td>
<td>2.15</td>
<td>0.033</td>
</tr>
<tr>
<td>AGAs</td>
<td>0.611</td>
<td>0.062</td>
<td>9.846</td>
<td>0.000</td>
</tr>
<tr>
<td>AGPs × AGAs</td>
<td>0.011</td>
<td>0.007</td>
<td>1.664</td>
<td>0.098</td>
</tr>
<tr>
<td>n = 192</td>
<td></td>
<td></td>
<td>R = 0.709</td>
<td></td>
</tr>
</tbody>
</table>

Table 6. Multiple regression between activity density of *G. allenbyi* in stabilized sand (AGAs) – the dependent variable, and activity density of *G. pyramidum* in stabilized sand (AGPs), activity density of *G. pyramidum* in semistabilized dunes (AGPs), activity density of *G. allenbyi* in semistabilized dunes (AGAss), and the interaction between activity density of *G. pyramidum* in semistabilized dunes to activity density of *G. allenbyi* in semistabilized dunes (AGPs × AGAss) – the independent variables. AGAs = 8.684 – 0.61AGPs + 0.213AGPs + 0.543AGAss + 0.011AGPs × AGAss.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Coefficient</th>
<th>Std. error</th>
<th>T-value</th>
<th>P (2-tail)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Constant</td>
<td>8.684</td>
<td>1.852</td>
<td>4.69</td>
<td>0.000</td>
</tr>
<tr>
<td>AGPs</td>
<td>-0.611</td>
<td>0.073</td>
<td>-8.327</td>
<td>0.000</td>
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<tr>
<td>AGPs</td>
<td>0.213</td>
<td>0.113</td>
<td>1.887</td>
<td>0.061</td>
</tr>
<tr>
<td>AGAss</td>
<td>0.543</td>
<td>0.116</td>
<td>4.687</td>
<td>0.000</td>
</tr>
<tr>
<td>AGPs × AGAss</td>
<td>0.011</td>
<td>0.007</td>
<td>1.656</td>
<td>0.099</td>
</tr>
<tr>
<td>n = 192</td>
<td></td>
<td></td>
<td>R = 0.767</td>
<td></td>
</tr>
</tbody>
</table>
The interaction coefficients measured using the isodars are constant within any one specified habitat

The competition coefficients that the isodar method yields are constant within any one specified habitat which limits the isodar method. This limitation is especially true in the gerbil system since both species isoclines are highly non-linear as predicted by the shared preference model (Abramsky et al. 1990, 1991, 1992, 1994).

To test implications of the non-linearity on the utility of isodars, we plotted and evaluated the residuals from the two multiple regressions used to estimate interaction coefficients (Tables 1 and 2). In both cases, the residuals were randomly distributed. Thus, non-linear effects have not masked the estimated interaction coefficients.

Discussion

The theory of density dependent habitat selection relies on qualitative and quantitative differences in fitness between habitats. These differences are the consequence of abiotic and biotic conditions. Different habitat combinations can lead to different community organization and affect the competition between species in the community.


We used the results of intensive manipulation experiments, that were designed to understand habitat selection and interspecific competition of two gerbil species (Abramsky et al. 1990, 1991, 1994), to assess the performance of the isodar method.

We have found that the isodar method discriminates species that are density-dependent habitat selectors. Furthermore, in multi-species communities, isodars can be used to infer density-dependent habitat selection of single species. This is an advantage that can save much of the field work when studying habitat selection in such communities.

To draw the species fitness density graph one needs to know qualitative and quantitative differences between habitats. Isodar method detects such differences using species densities in various habitats. Thus, it eliminates the difficult measurement of reproductive fitness. Using the isodar method we discovered new details about the two gerbil species. The G. pyramidum fitness-density graphs are two parallel linear lines. The G. allenbyi fitness-density graphs are two converging linear lines.

The isodar method detected the community structure of the two gerbil species. The significant positive isodar intercepts of G. pyramidum and G. allenbyi indicate that both species prefer the semistabilized dune habitat. In a two-habitat system, if both gerbil species prefer the same habitat type, the distributions of the two gerbils follow the predictions of the shared preference model (Abramsky et al. 1990).

It was when we examined the ability of the isodar method to detect interspecific interactions that we ran into serious problems.

The method assumes that competition is constant and is not density dependent. This is a serious flaw since all optimal foraging models, including density dependent habitat selection, predict that competition coefficients are density dependent (Abramsky et al. 1994). Indeed, we have measured, using manipulation experiments, the isoclines of the two gerbil species and found that they are density dependent (Abramsky et al. 1991, 1994). In fact, since we were able to estimate the isoclines, we can calculate the competition coefficients for every density combination of the two gerbil species.

The isodar method divides the competition coefficient in two components: exploitation competition and interference competition. The isodar method did not detect interference competition between G. pyramidum and G. allenbyi. Manipulation experiments (Ziv et al. 1993) showed that interference is a key factor determining the spatial and temporal distribution of the two gerbil species. The fact that the isodar method failed to detect the interference in the gerbil system is another serious flaw of the isodar method.

Using the isodar method we were able to estimate exploitation competition coefficients. In fact, we were able to estimate, for both species, two such coefficients, one for each habitat. These competition coefficients are constant within any one specified habitat. What could the meaning of these coefficients be in the real world consisting of a mosaic of stabilized sand and semistabilized dunes? We are not sure. But it is clear to us that in a system where both species always use the two habitat types and that the competition coefficients are density dependent and depend on the degree of habitat overlap, an habitat specific constant competition coefficients could not mean very much.

One may argue that habitat specific constant competition coefficients may have more meaning in a relatively larger landscape consisting of one habitat type. But, the theory of density dependent habitat selection was developed, and we can take advantage of it, only in cases where at least two habitats are present.

Ziv et al. (1993) have shown, experimentally, that one mechanism of coexistence is the cause of two different patterns exhibited by the two gerbil species. The mechanism is the dominance of G. pyramidum and the greater foraging efficiency of G. allenbyi. The patterns are temporal partitioning of foraging activity and shared preference habitat selection. Since both patterns occur simultaneously, one pattern does not obscure the existence of the other and the isodar method should have been able to estimate the competition coefficients based on the habitat distribution.
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References


