Can interaction coefficients be determined from census data? Testing two estimation methods with Negev Desert rodents

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Two approaches based on regression models are proposed to estimate competition from census data. The "static" approach is based on censuses of population sizes among species at one point in time over many sites. The "dynamic" approach relies on a time series of species abundance data to examine whether per capita changes in one species are associated with the abundance of other species. We estimated competition interactions in a Negev rodent community consisting of 10 species using both approaches, basing on 8 years (16 half-year periods) of observations. The static approach revealed significant competitive interactions in four of 45 pairs of species, whereas the dynamic approach did so in the same four plus two more pairs. For each species pair, both approaches revealed significant negative interactions in only 1-4 of 16 seasons. The static approach provided nearly symmetric estimations of competition, whereas estimations of dynamic approach were asymmetric. Moreover, estimations of the two approaches did not coincide in time. Cases of negative interactions recorded by the static approach were more frequent at peak and increase phases of population density dynamics, whereas those recorded by the dynamic approach were more frequent at peak and decline phases. Results of field removal experiments with Mus musculus and Gerbillus dasyurus supported predictions of dynamic but not static approaches. We hypothesized that in harsh and fluctuating desert environments that disrupt equilibrium, the dynamic approach indicates true (exploitation) competition, whereas the static approach reflects negative interspecific spatial association (interference).

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Competition holds a central place in ecological and evolutionary theory and particularly in community ecology (Southwood 1987). Competition was considered to be the main process structuring a community, according to the concept of limiting similarity (MacArthur and Levins 1967, MacArthur 1970, May and MacArthur 1972). Even though this concept has been strongly criticized (Rosenzweig 1974, Roughgarden 1976, Turelli 1978) and in fact is no longer a dominant paradigm in ecology, the theories that are replacing it (Roughgarden 1976, Rosenzweig 1979, 1987, 1991, 1995, Pimm and Rosenzweig 1981, Rosenzweig and Abramsky 1986) still rely on interspecific competition as a main motive force. Until now, the role of interspecific competition is under stormy discussion with full spectrum of opinions, from accepting competition as the determinant of the geographic distribution of species, the composition of regional species pools and the coexistence of species in local communities (Brown et al. 2000), to considering the role of competition in the organization of communities as a hypothesis without strong evidence (Stone et al. 2000). Moreover, since Levins (1968) introduced the concept of the community matrix and MacArthur (1972) proposed a model of "diffuse competition", theoretical studies revealed the substantial role of indirect effects and higher

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order interactions in community structuring (Vandermeer 1970, 1972, May 1972, 1974, Gilpin and Case 1976, Pomerantz and Gilpin 1979, Stone and Roberts 1991, Wilson 1992, Shipley 1993, Billick and Case 1994). These studies only gave insight into how communities might be structured and need to be verified by the study of natural communities (Armstrong 1982).

However, data on competition in natural communities are sparse. The direct mode of collecting such data, i.e. by field removal experiments, produced a number of examples of pair-wise interspecific competitive interactions occurring in natural conditions (see Connell 1983, Schoener 1983, Gurevitch et al. 1992 for reviews). Nevertheless, this approach is limited by the practical impossibility of performing experimental studies on each pair of species in a community. For example, even in a simple case of a community consisting of five species, it is necessary to perform 20 experimental treatments with some minimal number of replicates each to estimate a community matrix. It would be benefitial, therefore, to apply a technique for the estimation of competition from field census data. These estimations should be unbiased to avoid misunderstanding of the role of interspecific competition in determining patterns of abundance and distribution among species (Morris et al. 2000).

The first approach to measuring competition coefficients in the field was introduced by MacArthur and Levins (1967). The main idea of this approach was that two species compete in proportion to their overlap in resource use. Thus, the degree of niche overlap can be used as a measure of competition. However, it was shown that the results obtained by this technique are extremely sensitive to the assumptions about the shape of the resource utilization curves (Abrams 1975). This approach was developed by Schoener (1974a) to account for the availabilities of different resource types in the environment. Spiller (1986) demonstrated that application of Schoener formula provided better agreeexperimental data than that of ment with MacArthur-Levins. Nevertheless, the overlap technique was considered to be too inaccurate upon which to rely (Rosenzweig et al. 1984).

Two different approaches based on regression models were later proposed to estimate competition from census data. The first one ("static approach"), proposed by Schoener (1974b), is based on the Lotka-Volterra competition equation

$$dN_1/dt = r_1 N_1 [1 - N_1/K_1 - (\alpha_{21}N_2)/K_1]$$

where N_1 is the population size of species 1, N_2 is the population size of species 2, K_1 is the carrying capacity of species 1, K_2 is the carrying capacity of species 2 and α_{21} is the competition coefficient estimating the effect of species 2 on species 1. At equilibrium, the zero isocline can be determined by the equation

$$N_1 = K_1 - \alpha_{21}N_2$$

where N_1 is a function of the independent variables K_1 and N_2 . Thus, sampling from a variety of different points from an equilibrium population in a homogenous environment should produce a data set from which the values of K_1 and α_{21} can be estimated as coefficients of a linear regression.

Crowell and Pimm (1976) expanded this method to take environmental heterogeneity into account. Their technique consisted of two steps: (1) correction of data for habitat variation by eliminating the variance that may be due to environmental heterogeneity using stepwise multiple regression analysis and (2) determining whether the densities of presumed competitors can account for deviations from the habitat regression. The final result of the analysis is expressed in a multiple regression equation

$$N_1 = K_1 + b_1 Z_1 + b_2 Z_2 + \dots + b_i Z_i - \alpha_{21} N_2$$

where N_1 is the population size of species 1, N_2 is the population size of species 2, K_1 is the carrying capacity of species 1, $Z_1...Z_i$ are values of environmental variables 1...i, $b_1...b_i$ are regression coefficients and α_{21} is competition coefficient estimating the effect of species 2 on species 1. Hallett and Pimm (1979) demonstrated that the regression method is robust for relatively small occasional deviations from equilibrium. This method has been applied in several studies of small mammal communities (Dueser and Hallett 1980, Hallett 1982, Hallett et al. 1983).

Modifications of the static approach were proposed by Rosenzweig et al. (1984). Habitat factors are substituted in the regression analysis by their principal components, or habitat factors are initially used as independent variables to remove variation that is attributable to habitat and then the residuals are regressed against one another as an estimate of interspecific interactions.

Comparison of different modifications of the static approach revealed quantitative inconsistency of their results (Rosenzweig et al. 1985). Moreover, it was shown that the relative values of coefficients of interaction of two species were determined by the ratio of their average abundances so that rare species always appeared to have a stronger influence on common ones. It was concluded that such a relationship is a statistical artifact (Rosenzweig et al. 1985). However, these conclusions were criticized (Pimm 1985, Schoener 1985), and the static approach remained in use (Hallett 1991). Recently, Fox and Luo (1996) proposed a procedure of normal standardization of species census data before calculating regression parameters to overcome the artifact mentioned above. They tested it with two rodent species, mouse Pseudomys gracilicaudatus and rat Rattus lutreolus, in coastal heathland of southeastern Australia and demonstrated that after the standardization procedure was applied to the census data, each of the estimated coefficients of interaction matched well the value observed in removal experiment and that the results were consistent with previously published results. This supports the validity of a standardized regression technique. Fox and Luo (1996) also discussed the inconsistency existing among different methods of factoring out habitat effects and recommended the use of competition coefficients calculated from the residual principal component analysis (RPCA) method as the best estimate.

The second approach ("dynamic approach"), proposed by Seifert and Seifert (1976), relies on a time series of species abundance data to examine whether per capita changes in one species are associated with changes in another species. This approach is based on a different model for competition between two species based on the Lotka-Volterra differential equations:

$$N_1(t+1) = N_1(t) \exp\{r[K_1 - N_1(t) - \alpha_{21}N_2(t)]K_1\}$$

or

$$\ln[N_1(t+1)/N_1(t)] = r[K_1 - N_1(t) - \alpha_{21}N_2(t)]/K_1$$

In contrast to the static approach, the above equation does not assume equilibrium conditions and requires a time series of data. If carrying capacities do not vary in time, the equation has the form of a multiple linear regression:

z = a - bx - cy,

where $z = \ln[N_1(t+1)/N_1(t)]$, $x = N_1(t)$, $y = N_2(t)$, a = r, $b = r/K_1$ and $c = r\alpha_{21}/K_1$.

Comparison of competition estimations obtained using static and dynamic approaches with short-term experimental field manipulations of the guild of tidepool fishes showed that the dynamic model predicts interspecific interactions better than the static one (Pfister 1995).

Intensity of interspecific competition can fluctuate in time. Experiments on two species of gerbils revealed that competition varies with density (Abramsky et al. 1991). It was demonstrated that intensity of competition between two rat species estimated by the static approach varied with the phase of the breeding cycle being maximal at breeding phase, moderate at dispersal and minimal at non-breeding phase (Luo et al. 1998). Competition between two desert lizard species was demonstrated during periods of food scarcity but not at other times (Dunham 1980). It has been shown theoretically that some types of competition estimators are density-dependent, whereas others are not (Morris 1999). Theoretically, temporal variation of the intensity of competition should depend on the type of competi-

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tive interactions. In case of behavioral interference, competition should be density-dependent due to increase in probability of between-individual encounters with density growth. In case of exploitative competition, competition coefficient (α) is a constant by definition, but probability to detect it depends on the net effect of competition, which, in turn, should be a linear function of the ratio of density to carrying capacity. If the carrying capacity is a constant, the effect of competition will be density-dependent. However, in a fluctuating environment, the effect of competition will be more resource- than density-dependent.

We applied both static and dynamic approaches to our long-term data on the dynamics of rodent communities of the Central Negev. The aim of this application was to compare the two approaches and to estimate the temporal dynamics of interspecific interactions. Preliminary analysis of collected data indicated necessity of a set of removal experiments to validate the interpretation of these results. We undertook these experiments, and their results are also reported here.

Materials and methods

Study area

We studied the community of rodents in the Ramon erosion cirque and vicinity, Negev Highlands, Israel from 1992 to 2001. The Ramon erosion cirque (30°35'N, 34°45'E, about 200 km² total area) forms the southern boundary of the Negev Highlands. The northern and southern rims of the cirque are 800 m and 510 m a.s.l., respectively, and the lowest point of the cirque bottom is 420 m a.s.l. Summers are hot and winters relatively cold (mean monthly minimum and maximum air temperatures are 33.4°C and 19.8°C in August and 14.8°C and 6.6°C in January, respectively). Rains usually occur from October to March. There is a very sharp decrease in annual rainfall from 91 mm on the cirque north rim to 56 mm in its bottom. This precipitation gradient is also expressed from the west to the east of the Ramon cirque. The coefficient of variation of rainfall is 0.39 (Morin et al. 1998). During the period of our observations, annual rainfall varied from 51 to 162 mm with two peaks, in 1994/1995 and 1997/1998.

The landscape of the Ramon cirque ranges from sand dunes to limestone and sandstone rocks in the rims. Six main habitat types were distinguished within the study area based on rodent species composition (Krasnov et al. 1996): (I) sand dunes under the eastern wall of the cirque with cover of *Calligonum comosum* or *Echiochilon fruticosum* (perennial vegetation cover 7.4%); (II) flat gravel plains of the eastern part of the cirque with sparse vegetation of *Hammada salicornica*, *Anabasis articulata* and *Gymnocarpos decandrum* (cover 5.7%); (III) limestone cliffs of the southern and central parts of the cirque with sparse cover (4.0%) of Zygophyllum dumosum, Helianthemum kahiricum and Reaumuria hirtella and (IV) deep valleys filled by loess with densely vegetated (cover 18.5%) wadis among rocky hills partially covered with loess over the northern rim of the cirque with Anabasis articulata, Atriplex halimus and Artemisia herba-alba; (V) wide wadis among gravel plains of the eastern and central parts of the cirque with dense cover (26.0%) of Retama raetam, Moricandia nitens, Tamarix nilotica and Artemisia monosperma; and (VI) complex of narrow shallow wadis, flat terraces and low loess hills of the western parts of the cirque with Salsola schweinfurthii, Anabasis articulata and Atriplex leucoclada (perennial vegetation cover 6.0%).

Rodent species

Thirteen species formed the community of desert rodents in the Ramon cirque: Dipodidae: Jaculus jaculus (Linnaeus, 1758) (67.0 g); Muridae: Gerbillinae: Gerbillus dasyurus (Wagner, 1842) (21.1 g), Gerbillus gerbillus (Olivier, 1801) (20.1 g), Gerbillus henlevi (de Winton, 1903) (9.8 g), Gerbillus nanus Blanford, 1875 (22.3 g), Meriones crassus Sundevall, 1842 (81.1 g), Psammomys obesus Cretzschmar, 1828 (166 g), Sekeetamys calurus (Thomas, 1892) (52.8 g), Murinae: Acomys cahirinus (Desmarest, 1819) (42.8 g), Acomys russatus (Wagner, 1840) (51.4 g), Mus musculus Linnaeus, 1758 (14.0 g), Rattus rattus Linnaeus, 1758 (76.5 g); Myoxidae: Eliomys melanurus (Wagner, 1839) (49.6 g). Density changes in most rodent species followed fluctuations in the amount of rainfall, with peaks in 1995 and 1998 and troughs in 1993, 1997 and 1999-2000 (Shenbrot and Krasnov 2001).

Four of thirteen rodent species are strict habitat specialists. *G. gerbillus* occurs in sands, *S. calurus* in rocks, and *E. melanurus* and *M. musculus* in dense vegetation of wadi among loess-filled valleys. Two species, *G. dasyurus* and *M. crassus*, are habitat generalists; the former species avoids only sands, whereas the latter avoids rocky habitats. Other species occupy three to five habitat types demonstrating clear habitat preferences. *J. jaculus* and *G. henleyi* prefer flat plains with scarce vegetation, both *Acomys* species favor rocks and *P. obesus* has a preference to loess substrate with dense vegetation. *G. nanus* and *R. rattus* were trapped infrequently and, therefore, we could not determine their habitat preferences (Krasnov et al. 1996; Shenbrot and Krasnov 2001).

Data collection

Rodents were trapped on 24 permanent 1-ha grids that were chosen to represent main substrate and vegetation gradients. The regular sampling of the grid system took

place twice a year from July 1993 to February 2001, once in winter (January-February) and once in summer (July-August). Each grid was subdivided into 25 plots of 20 m by 20 m, whose centers were marked with numbered wire flags. Each grid was sampled during three days using Sherman folded live-traps baited with millet seeds and placed near the center of each plot $(5 \times 5$ stations with intervals of 20 m between stations). The number of traps per plot varied from 1 to 3 depending on rodent density so that the number of traps per grid was at least twice the number of rodents to prevent trap competition. The initial number of traps placed on a grid was determined based on the results of the previous trapping session and was adjusted accordingly with the results of the first trapping night of the current session. Jerboas, not trapped in live-traps in summer, were caught with a net at night using a search-light. P. obesus, also not trapped in Sherman live-traps, were observed in the morning using a binoculars, and their burrows were mapped. They were trapped with Havahart two-door cage traps, model 1025, (two traps per burrow system) using fresh leaves of Atriplex halimus or succulent stems of Anabasis articulata as bait. Each trapped animal was sexed, weighed, marked by toe clipping and released.

A 0.5 kg soil sample was taken from the center of each plot for laboratory texture analysis. The angle of the slope of each plot was measured with the Suunto Clinometer PM5/360PC. The number of shrubs (by species) in each plot was counted in a circle of 5 m in radius. To determine vegetation cover and volume by height layers within each plot, the height and diameter of the crown of the shrubs (up to 30 shrubs of each species in the grid) were measured. The abundance of annuals was evaluated by counting all annuals on 0.25 m² sample plots (4 random samples in each plot). Nineteen parameters were used in the subsequent analysis. Descriptions of soil and shrub structure were made at the beginning of the study (with re-description in a few cases when plots were changed as a result of the severe winter flood). Descriptions of annual vegetation were made each year just after the end of the winter trapping session. Summer annual plant abundance was not estimated because the plants are naturally preserved from winter vegetation up to the end of summer.

In total, 3187 individuals were captured (5620 registrations).

Estimation of interaction coefficients

Static estimations of competition were based on 16 data sets, one for each trapping session. Each data set consisted of two types of data, relative densities of rodent species and habitat measurements. Each plot (trap-station) was considered as a datum point or locality. The total number of captures over three trapping nights in each session were used as a relative measure of density for a given species in a locality. Before analyses, data on relative rodent densities were standardized and values of habitat variables were log-transformed to normalize them. The data subset consisting of the values of habitat variables was subjected to principal component analysis (PCA), and scores of the principal component axes were obtained for each plot. The PCA extracted five factors with eigenvalues greater than one, and these five factors were used as independent variables in the regression analyses. On the first step, stepwise multiple linear regressions (with 2.00 as F-toenter value) were estimated for each species with relative normalized density of a species as dependent variable and PCA scores as independent variables, and residuals were calculated. On the second step, a simple linear regression was estimated for each pair of species with a relative normalized density of the first species as dependent variable and residuals obtained on the first step for the second species as an independent variable. Statistically significant negative values of a regression slope were considered as estimations of competitive interactions. The actual number of species recorded during one trapping session varied from 8 to 10. Thus, the real number of analyzed potential interactions was 56 in summer 1993, summer 1997 and winter 2000, 72 in winter 1994, summer 1994, winter 1996, winter 1997, winter 1998 and summer 2000, and 90 in winter 1995, summer 1995, summer 1996, summer 1998, winter 1999, summer 1999 and winter 2001.

Dynamic estimations of competition were based on 15 data sets, one for each pair of trapping sessions. Each data set consisted of relative densities of rodent species for each locality in two consecutive trapping sessions. The total number of captured individuals over three trapping nights in each session was used as a measure of density for a given species in a locality. Parameters of a multiple linear regression, z = a + bx + bx*cy* (where $z = \ln\{[N_i(t+1) + 1]/[N_i(t) + 1]\}, x = N_i(t),$ $y = N_i(t)$, a = r, $b = r/K_1$ and $c = r\alpha_{21}/K_1$, were calculated for each species, *i*, with each of its potential competitors, *j*. Localities with $N_i(t) = N_i(t+1) = 0$ were omitted from analyses. The values of c/b ratio in the cases of statistically significant negative c values were considered as estimations of competitive interactions. Analyses of potential interactions can have a sense in the cases when a potential competitor was recorded during the trapping session t and a target species was recorded during both trapping sessions, t and t + 1. Thus, the real number of analyzed potential interactions was 49 in summer 1997, 56 in summer 1993 and winter 2000, 57 in winter 1997, 64 in winter 1994, 72 in summer 1994, winter 1996, winter 1998 and summer 2000, 73 in summer 1999, 81 in summer 1995 and summer 1996, and 90 in winter 1995, summer 1998 and winter 1999.

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Field removal experiments

Two experiments were conducted in the upper part of Nizzana loess valley in January-June and July-December 1997 to test for the effect of G. dasyurus on M. musculus. Four 1-ha grids, each of 25 trap-stations with 20 m distance between stations and three traps per station, were established in each case. Two grids were assigned as experimental and two as control (control grids were the same in both experiments). Trapping sessions were conducted monthly, for three consecutive nights. In each experiment, the first session was general trapping prior to the removal of G. dasyurus from the experimental grids, and the next five monthly sessions were removal sessions. Removed animals were released at least 500 m from the trapping area. Distribution of trapped individuals among trap-stations was not normal; thus, to test the effect of removal, we used nonparametric Mann-Whitney U-test. The trap-stations were arranged in a regular manner, so sampling cannot be considered as a random. To avoid the statistical problem arising from the non-random sampling, we performed bootstrap estimation of the Mann-Whitney U-test. We used Monte Carlo simulations for a random resampling (of the same as original sample size), with replacement, from our original data. The U-statistic was calculated on this "bootstrapped subsample," and recorded. The process was repeated for 200 replications. Finally, the standard errors and confidence limits of the bootstrapped U-statistic were tabulated.

Results

Estimation of interaction coefficients

Static estimations of competition produced significant values for four of 45 species pairs. Within these four pairs, interaction coefficients were significant for one of 16 sessions in the pair G. dasyurus-M. crassus (summer 1995) and G. gerbillus-G. henlevi (winter 2000), for three of 16 sessions in the pair G. dasyurus-M. musculus (winter 1995, summer 1995, winter 1999) and for four of 16 sessions in the pair G. gerbillus-M. crassus (summer 1994, winter 1995, summer 1995, summer 1998). In most cases, estimated values were symmetrical (Table 1). The values were asymmetrical in two cases only: there were significant influences of M. crassus on G. dasyurus and on G. gerbillus in summer 1995 but not vice versa. For four species pairs with at least one significant estimation value, significant interactions were observed at higher combined densities of both species than non-significant ones (Median test; $\chi^2 =$ 5.3396, df = 1, P = 0.021). Analysis of distribution of interaction estimates by the phases of density dynamics (for four species pairs within which interactions were recorded) demonstrated that cases of significant interac-

Table 1. Estir 5 – winter 199	nations of con 99, 6 – winter	mpetition coefficier 2000.	ats using the static	approach. All valı	ues are negativ	'e (\pm SE). 1 – sum	ımer 1994, 2 -	- winter 1995, 3 -	summer 1995, 4	– summer 1998,
	J. jaculus	G. dasyurus	G. gerbillus	G. henleyi	S. calurus	M. crassus	P. obesus	M. musculus	A. cahirinus	A. russatus
J. jaculus G. dasyurus	I	I	1 1	1 1	1 1	$\stackrel{-}{0.116} \pm 0.013^3$	1 1	$\stackrel{-}{0.109} \pm 0.013^2 \ 0.291 \pm 0.014^3$	1 1	1 1
G. gerbillus	I	I		0.195 ± 0.015^6	I	$\begin{array}{c} 0.113 \pm 0.014^1 \\ 0.133 \pm 0.015^2 \\ 0.147 \pm 0.014^3 \end{array}$	I	0.216 ± 0.013^{5}	I	Ι
G. henleyi	I	I	0.138 ± 0.013^{6}		I	0.115 ± 0.014^4	I	I	I	I
s. calurus M. crassus	1 1	$\stackrel{-}{0.116} \pm 0.013^3$	$\begin{array}{c} -\\ 0.087\pm 0.013^1\\ 0.102\pm 0.013^2\\ 0.022\pm 0.013^2\end{array}$	1 1	I	I	1 1	1 1	1 1	1 1
D observe	ļ	I	0.122 ± 0.013 0.103 ± 0.013^4	I	l	ļ		I	I	I
M. musculus		$\begin{array}{c} 0.114 \pm 0.013^2 \\ 0.320 \pm 0.015^3 \end{array}$					I			
A. cahirinus A. russatus	1 1	0.214 ± 0.013^{5}	1 1	1 1	1 1	1 1	1 1	1 1	I	I

tions were most frequent (50% cases) at peak phase, less frequent (25%) at increase phase and rare at decline and low-density phases (by 6.3% cases at each of two phases). Observed distribution of cases of significant interactions differed significantly from random ($\chi^2 = 10.1111$, df = 3, P < 0.0176).

Dynamic estimations of competition produced significant values for six of 45 species pairs. Within these six pairs, interaction coefficients were significant for one of 15 sessions in the pair G. dasyurus-M. crassus (summer 1993) and G. henleyi-M. crassus (summer 1995), for two of 15 sessions in the pair G. dasyurus–M. musculus (summer 1995, summer 1997) and G. gerbillus-M. crassus (winter 1994, winter 1996) and for four of 15 sessions in the pair G. dasyurus-G. henleyi (summer 1993, winter 1996, summer 1998, winter 1999) and G. gerbillus-G. henleyi (summer 1995, summer 1998, winter 1999, summer 1999). In all cases estimated values were asymmetrical (Table 2). Within six species pairs for which interactions were recorded, there was no significant difference in densities between cases of significant and non-significant interactions (Median test: $\chi^2 = 0.1884$, df = 1, P = 0.366). Analysis of distribution of interaction estimates by phases of density dynamics (for six species pairs within which interactions were recorded) demonstrated that cases of significant interactions were most frequent (41.7% cases) at peak density, less frequent (29.2%) at decline phase, rare (2.1.3% cases) at low-density phase and absent at increase phase. Observed distribution of interactions differed significantly from random ($\chi^2 = 17.6154$, df = 3, P <0.0005).

Significant estimations of competitive interactions with both static and dynamic approaches were recorded for the same pairs of species but at different sessions. The two estimations coincided in the one case only, for the pair *G. dasyurus–M. musculus* in summer 1995. However, even in this case, the static approach produced symmetric estimations, whereas the dynamic approach produced asymmetric ones (really, there were one-directional interactions which are extreme cases of asymmetric interactions). Frequency of coinciding significant estimates did not differ from random in the case of independence of two estimates ($\chi^2 = 0.10012$, P < 0.9918).

Field removal experiments

In both experiments there were significant decreases in density of *G. dasyurus* to the end of experimental treatments (Table 3, Fig. 1). In the first experiment (January–June), removal of *G. dasyurus* was not followed by a significant density increase of *M. musculus*. In the second experiment (July–December), a density decrease of *G. dasyurus* was accompanied by a significant density increase of *M. musculus*. It seems that the

1 adle 2. Esumation	us or competition coer	ncients via regressio	on parameters in th	le Irames o	t the aynamic approa	icn.			
Affecting species	Affected species	Season	Interce	spt	q		c		$\alpha \pm SE$
			$a \pm SE$	Р	$b \pm SE$	Р	$\mathbf{c} \pm \mathbf{SE}$	Р	
G. dasyurus	G. henleyi	Summer 1993	1.024 ± 0.207	0.000	-1.027 ± 0.325	0.003	-0.154 ± 0.045	0.001	0.150 ± 0.015
		Winter 1996	0.652 ± 0.301	0.036	-1.473 ± 0.327	0.000	-0.562 ± 0.252	0.030	0.382 ± 0.082
		Summer 1998	1.528 ± 0.276	0.005	-0.779 ± 0.260	0.005	-0.516 ± 0.145	0.001	0.663 ± 0.038
		Winter 1999	1.299 ± 0.252	0.000	-0.708 ± 0.115	0.000	-0.465 ± 0.083	0.000	0.657 ± 0.010
	M. musculus	Summer 1995	1.168 ± 0.407	0.007	-0.418 ± 0.142	0.005	-0.337 ± 0.116	0.006	0.807 ± 0.016
		Summer 1997	2.359 ± 0.249	0.000	-0.678 ± 0.159	0.001	-0.627 ± 0.093	0.000	0.925 ± 0.015
G. gerbillus	G. henleyi	Summer 1995	1.119 ± 0.213	0.000	-1.753 ± 0.189	0.000	-1.339 ± 0.623	0.035	0.764 ± 0.118
1	·	Summer 1998	1.840 ± 0.103	0.000	-1.307 ± 0.178	0.000	-0.939 ± 0.235	0.001	0.718 ± 0.042
		Winter 1999	1.576 ± 0.168	0.000	-2.408 ± 0.163	0.000	-0.879 ± 0.367	0.019	0.365 ± 0.060
		Summer 1999	1.123 ± 0.275	0.001	-1.362 ± 0.259	0.000	-0.822 ± 0.367	0.030	0.603 ± 0.095
M. crassus	G. dasyurus	Summer 1993	0.906 ± 0.205	0.000	-0.847 ± 0.337	0.015	-0.119 ± 0.048	0.016	0.140 ± 0.016
	G. gerbillus	Winter 1994	0.418 ± 0.169	0.035	-0.694 ± 0.267	0.030	-0.635 ± 0.234	0.024	0.916 ± 0.062
		Winter 1996	1.054 ± 0.298	0.001	-1.014 ± 0.194	0.000	-0.473 ± 0.227	0.043	0.467 ± 0.044
	G. henleyi	Summer 1995	0.754 ± 0.365	0.045	-0.388 ± 0.108	0.001	-0.315 ± 0.106	0.005	0.810 ± 0.012

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density increase of *M. musculus* on the experimental grids was a result of the breeding in situ, because at the end of experiment (November-December) young animals with body mass of 5 to 12 g comprised 31% of captured animals on the experimental grids but were not recorded on control grids (difference was significant, $\phi^2 = 0.08418$, P = 0.0015).

Discussion

Our results of competition estimates using static and dynamic approaches were inconsistent. Partial inconsistency of estimations by the two approaches was demonstrated earlier in a set of controlled field experiments (Pfister 1995). However in our case, the inconsistency was complete suggesting that the two approaches measured different and independent processes.

It has been shown experimentally that dynamically derived measures of interaction strength better predict effects of one species on another than static ones (Pfister 1995), although these results, among other things, can be explained by the lack of standardization in the static approach (Fox and Luo 1996). Our experiments also demonstrated agreement between results of field experiments and measures of the dynamic approach. Experimental removal of G. dasyurus had no effect on density of M. musculus during the period when the dynamic approach did not indicate interactions, whereas during the period when the dynamic approach indicated significant interactions the experimental removal had pronounced effect. Agreement between results of field experiments and measures of the dynamic approach was demonstrated for one pair of species only and needs additional validation with other cases. However, such additional validation is time- and labor-consuming because (a) competitive interactions are infrequent and (b) field experiments have to be organized in the absence of measures of the dynamic approach that can be obtained post hoc only.

We did not perform specific experimental tests of predictions of the static approach. However, in one case when a field experiment demonstrated competition between G. dasyurus and M. musculus the static approach did not detect it. The question is what the static approach really indicates? Basically, it demonstrates the negative spatial association of two species after removing effects of environmental variables. Such spatial distribution can be the result of current competition or ghost of recently passed competition or just behavioral interference in the absence of exploitative competition.

The use of static approach was validated experimentally in two cases (Schmitt and Holbrook 1990, Fox and Luo 1996). In other cases, however, static regression models demonstrated low consistency with experimental results, sometimes even predicting interactions with a different sign from those in experiments (Abram-

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	B	eginning of experim	nent		End of experiment			
	U	Z	Р	U	Z	Р		
			Experiment	1				
G. dasvurus	1177.5-1235.0	0.127-0.603	0.546-0.899	804.5-1018.5	2.177-3.775	0.0001-0.029		
M. musculus	596.5-669.0	-0.320 - 0.756	0.450-0.749	560.0-672.5	-1.648 - 0.142	0.099-0.887		
Experiment 2								
G. dasvurus	1191.5-1232.0	-0.167 - 0.521	0.602 - 0.867	779.0-956.0	2.288-3.644	0.0002-0.022		
M. musculus	553.0-661.0	-1.743 - 0.285	0.081 - 0.776	313.0-494.0	-2.210 - 4.429	0.00001 - 0.027		

Table 3. Bootstrap estimations of the Mann-Whitney U-test for differences in rodent densities between experimental and control grids.

sky et al. 1986, Pfister 1995). The lack of correspondence between static estimations and experimental results can be explained by the fact that most researchers did not use the standardized protocol developed by Fox and Luo (1996) but also may indicate the non-fulfillment of the basic assumptions of the model. The basic assumption of the static approach is equilibrium of considered populations, and the fallacy of its application may indicate non-equilibrium conditions. In our case, where use of the dynamic approach was validated, inconsistency between two approaches means that the static approach does not indicate competition, possibly as a result of non-equilibrium conditions.

If the dynamic approach indicates current competition, whereas the static approach indicates ghost of recently passed competition, the estimates of these two approaches should be temporally correlated and dynamic indications of interactions have to follow by static indications. However, we recorded only one case when a dynamic indication of competition was followed by a static indication, which did not differ from random coincidence. Thus, in our case, we have no evidence that static estimations can be considered as indications of recently passed competition.

It is also possible that negative spatial association between species indicated by the static approach is the result of behavioral interference in the absence of exploitative competition. If this is a case, estimations provided by the static approach should be density-dependent due to an increase in probability of between-individual encounters with density growth. Our finding that significant estimated interactions were observed at higher densities than non-significant ones can serve as support for hypothesis of the interference nature of estimations obtained with the static approach. The results of Luo et al. (1998) demonstrated that intensity of competition estimated by the static approach varied among phases of the breeding cycle and reached its maximum at the breeding season. This may indicate interference rather than exploitative competition. However, this hypothesis needs to be tested in short-term field removal experiments. An immediate density increase as a response to removal of a potential competitor and a fast return to the pre-manipulation situation after the end of removal would be a validation of the hypothesis.

The nature of competitive interactions in all observed cases can be explained relatively easy as exploitative competition for food resources. The diet of all species that we recorded as involved in competitive interactions consists mainly of seeds. *G. gerbillus* and *G. henleyi* are strictly granivorous (Qumsiyeh 1996, Kam et al. 1997). *G. dasyurus* feeds mainly on seeds with some invertebrates (Degen and Kam 1992, Qumsiyeh 1996). The diet of *Meriones crassus* includes seeds, green plant parts and insects (Harrison and Bates 1991, Kam et al. 1997). *Mus musculus* is omnivorous; in natural arid conditions its diet consists mainly of seeds and insects (Bomford 1987, Tann et al. 1991).

Our results indicated competitive suppression of all three Gerbillus species (G. gerbillus, G. dasyurus and G. henleyi) by M. crassus. M. crassus may have a competitive advantage over Gerbillus species because it is less dependent on seeds than Gerbillus (Kam et al. 1997). Within genus Gerbillus, G. henleyi was affected by both G. gerbillus and G. dasyurus. Competitive advantage of two the latter species may be explained by their ability to find seeds in deep soil layers, whereas G. henleyi extracts seeds effectively only from surface layer (Krasnov et al. 2000). Suppression of M. musculus by G. dasyurus seems to be a result of competition for invertebrates as water sources rather than competition for seeds. G. dasyurus can tolerate relatively low amounts of free water in its diet (Degen and Kam 1992), whereas M. musculus has high water requirements (Moro and Bradshaw 1999) and a water deficit can limit its breeding success and population levels (Mutze et al. 1991). Our observations on decreased breeding success of M. musculus in the presence of G. dasyurus supports this suggestion.

In most species pairs in which we did not record competitive interactions, such interactions hardly can be expected due to considerable ecological differences between species. However, two *Acomys* species, *A. cahirinus* and *A. russatus*, are believed to be competitors because presence of *A. cahirinus* shifts the activity of *A. russatus* from nocturnal to diurnal (Shkolnik 1971, Kronfeld-Schor et al. 2001). We did not find any indiFig. 1. Densities of rodents (individuals per trap station per 3 nights) on control and experimental grids during the first (A; January–June 1997) and the second (B; July–December 1997) experiments.



cations of negative interactions between these two species neither with dynamic nor with static approaches. It means the absence of both exploitative competition and negative spatial association. Lack of interactions can be the result of low densities of both species. However, in summer the two species demonstrate micro-habitat segregation, whereas in winter both species are insectivorous to a great extent, and behavioral interference resulted in spatio-temporal segregation of them can provide conditions for food resource partitioning that is enough for avoidance of competition (Kronfeld-Schor and Dayan 1999, Jones et al. 2001).

Our estimations based on the dynamic approach suggest that interspecific competition is not a widespread

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phenomenon in the community of Negev desert rodents. About half the time (7 of 15 seasons) competition was absent or at least was too weak to be recorded. Even in seasons when competition was recorded, non-zero elements comprised not more than 3.3% of all off-diagonal elements of the community matrix. One may wonder whether such a small percentage of significant interaction terms differs from chance. It would be true if all species in the community are ecologically similar, and probability of competition is the same for each pair of species. However, the species are ecologically different, and it is possible to expect a priory existence of competition between more similar species and the absence of competition among less similar species. A posteriori analysis of distribution of the significant interaction terms among pairs of species demonstrated highly significant influence of species pair on the frequency of interaction events (ANOVA: $F_{(35,486)} = 3.0059$, P < 0.001 for dynamic approach and $F_{(35,497)} = 2.9163$, P < 0.001 for static approach). Thus, the frequency of interactions differs from chance, at least in the pairs G. dasyurus-M. musculus and G. gerbillus-M. crassus for static estimations and in the pairs G. dasyurus-M. musculus, G. gerbillus-M. crassus, G. dasyurus-G. henleyi and G. gerbillus-G. henleyi for dynamic estimations. The rarity of interspecific competition may be due to the existence of the community in a harsh and unpredictable environment in which population equilibrium is often disrupted (Wiens 1977, Huston 1979), and competition can be detectable only during the periods of drastic resource shortage when density/resource ratio considerably increases. The circumstantial evidence of non-equilibrium conditions indicated the non-adequacy of the static approach in our conditions. If this suggestion is true, a similar pattern should be found in other desert rodent communities. Thus, the results of analyses of the structure and stability of small mammal faunas based on community matrices obtained with the static approach (Hallett 1991) should be revised, at least in desert fauna part.

The usual point of view is that harsh and fluctuating environments disrupt equilibrium and prevent consistent effects of competition (Wiens 1977, Huston 1979). However, theoretical consideration demonstrated that under some conditions it could not be the case (Chesson and Huntly 1997). Moreover, it is not clear how large deviations from equilibrium have to be to prevent competition. Indeed, in our case, competition took place at least in some pairs of species and in some seasons. The results of this competition can explain our earlier observations that in the Negev rodent community densities of co-existing species strictly determined the spatial distribution and population dynamics of at least one species, namely *G. henleyi* (Shenbrot and Krasnov 2001). Acknowledgements – D. Ward and A. A. Degen (Ben-Gurion University of the Negev) discussed results and made helpful comments. We also thank two anonymous reviewers for their helpful comments on the manuscript. Financial support was provided by Israel Ministry of Science, Israel Ministry for New Immigrant Absorption and by seed money grant of Ben-Gurion University of the Negev. This is publication No. 132 of the Ramon Science Center.

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