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Inter-specific competitors reduce inter-gender competition in Negev Desert gerbils

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Abstract We examined gender-dependent competitive interactions between two nocturnal desert gerbil species, *Gerbillus andersoni allenbyi* and *G. pyramidum*, by a field manipulation experiment. The study was done in two 1-ha enclosed plots and included allopatric (only *G. a. allenbyi*) and sympatric (both species together) treatments. Seed trays and thermal imaging cameras were used to observe the gerbils' foraging activities and aggressive interactions. We found that the negative effect of the competitively dominant species, *G. pyramidum*, on time spent in seed trays, and ability to control these artificial food patches, was stronger on male than on female *G. a. allenbyi*. Consequently, the aggression of male *G. a. allenbyi* towards female *G. a. allenbyi* was markedly reduced, indicating that the dominant species mediated competition between the genders of the subordinate species. Furthermore, this interference-mediated indirect effect was associated with a decrease in the body mass of male *G. a. allenbyi* and an increase in the survival of female *G. a. allenbyi*. We suggest that both the reduction in intra-specific aggression and the positive effect on female survival can potentially stabilize competitive interactions and promote coexistence in this small mammal community.

Keywords Aggression · Indirect effects · Interference competition · Structured populations

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Introduction

Competition plays an important role in structuring ecological communities (Connell 1983; Schoener 1983; Goldberg and Barton 1992; Gurevitch et al. 1992). Proponents of classic views of competitive interactions do not deny that individuals of different sex, size or developmental stage can compete differently and contribute differently to population dynamics (Connell 1983; Schoener 1983). However, they do assume that such fine-scale details can be safely abstracted, and that average competitive effects can be used to obtain accurate generalizations of population and community dynamics. In contrast, the structured-populations approach recognizes that intra-specific variation can strongly affect the dynamics of a single population (Caswell 1989; Tuljapurkar and Caswell 1996), predator-prey interactions (Werner and Gilliam 1984) and competing populations (Cushing and Li 1992; Werner 1994; Takenaka et al. 1997).

The structured-populations approach classifies individuals according to their age, sex, size, or developmental stage, and community dynamics are derived from an analysis of dynamics occurring at these scales (Caswell 1989; Tuljapurkar and Caswell 1996). Applied to competition, this approach might elucidate complex competitive interactions among classes, and possibly also a variety of indirect effects. Most studies investigating indirect effects have focused on interactions among populations rather than among classes within a population (Menge 1995; Abrams et al. 1996). In this study, we investigated the potential of a positive indirect effect between two competing species to be mediated by a reduction in interference competition between males and females within one species.

We conducted manipulation experiments in the field to test for structural differences in competitive effects between and within genders of two desert gerbil species, *Gerbillus andersoni allenbyi* and *G. pyramidum*. Specifically, we examined how the presence of the competi-

tively dominant species, *G. pyramidum*, changes the strength and/or intensity of aggressive interactions between males and females of the subordinate species *G. a. allenbyi*. In addition, we tested for the consequent effects of such interference-mediated indirect interactions on the body mass and the survival of the gerbils.

Materials and methods

Study species

Gerbillus andersoni allenbyi and *G. pyramidum* occur sympatrically over a wide range of sandy areas in the western Negev Desert in Israel (Abramsky et al. 1985a). The smaller species, *G. a. allenbyi* (mean mass = 26 g), occurs mostly in stabilized sand dunes with relatively dense vegetation cover (Abramsky et al. 1985b). The larger species, *G. pyramidum* (mean mass = 40 g), occurs mostly in shifting and semi-stabilized sand dunes with sparser vegetation cover (Abramsky et al. 1985b). The species are similar in their general ecology. They are both solitary burrow dwellers that forage nocturnally for seeds, which constitute much of their diets (Bar et al. 1984). Individual *G. a. allenbyi* and *G. pyramidum* aggressively defend artificial food patches (Ovadia 1999). Furthermore, intra- and inter-specific aggressive interactions occur between genders and always include chasing and attempts at physical contact (Ovadia 1999).

Study site and experimental design

We conducted this study in two 1-ha enclosures, completely surrounded by rodent-proof fencing, located in a

sandy area within the Holot Mashabim Nature Reserve (31°01'N, 34°45'E), 35 km south of Beer Sheva, Israel [for a more detailed description of the enclosures see Abramsky et al. (1990)]. The sandy areas in the study site can be classified into two clear habitat types, semi-stabilized and stabilized sand dunes, based on mobility of the sand and the dominant perennial plant species (Danin 1978). Each enclosure contained similar representations of each habitat type (Abramsky et al. 1990).

The experiment consisted of an allopatric (only *G. a. allenbyi*) and a sympatric (both species together) treatment and was carried out from spring to autumn for 2 consecutive years (Table 1). Several studies have shown that population densities of the gerbils in the area vary greatly within and between years (e.g. Brown et al. 1994). Therefore, we designed the experiments to embrace these natural seasonal changes in gerbil densities. Moreover, at the beginning of the experiments, the natural density of *G. pyramidum* was very low, to the extent that we could not trap even a single individual in our study site. Accordingly, we first did the allopatric treatment and then followed it with the sympatric one only after enough *G. pyramidum* individuals were found in the study site. As a result, our experimental treatments were confounded with time. This issue will be dealt with in the Discussion.

The experiment consisted of nine sequences (Table 1). At the beginning of each sequence, we stocked the enclosures with double the natural densities of gerbils and made behavioural observations for 3–4 days. We then removed about 50% of the gerbils and made another set of observations under conditions mimicking the natural ones. We determined the natural population densities of gerbils prior to each sequence by trapping for 3–4 days in at least two 1-ha plots of unfenced area

Table 1 The numbers of *Gerbillus andersoni allenbyi* and *G. pyramidum* that were introduced into experimental enclosures during nine experimental sequences (see text for details). The allopatric and sympatric treatments were replicated 6 and 12 times, respectively. Variation in population size among sequences represents the

natural seasonal changes in gerbil densities. The few cases of within-sequence variation in population size between plots were caused by death and/or escape of stocked animals. All introduced individuals were non-reproductive adults and their sex ratio was 1:1

	Date	Sequence	Plot	<i>G. a. allenbyi</i>	<i>G. pyramidum</i>
Allopatric treatment (only <i>G. a. allenbyi</i>)	March 1996	1	1	12	0
	March 1996	1	2	12	0
	April 1996	2	1	12	0
	April 1996	2	2	10	0
	May 1996	3	1	16	0
	May 1996	3	2	16	0
Sympatric treatment (both species together)	August 1996	4	1	20	4
	August 1996	4	2	18	4
	April 1997	5	1	4	2
	April 1997	5	2	4	2
	May 1997	6	1	4	2
	May 1997	6	2	4	2
	June 1997	7	1	4	2
	June 1997	7	2	6	2
	August 1997	8	1	12	3
	August 1997	8	2	18	4
	September 1997	9	1	14	4
	September 1997	9	2	14	4

located at our study site. The few cases of within-sequence variation in population size between enclosures were caused by death and/or escape of stocked animals (Table 1). All introduced individuals were non-reproductive and the sex ratio was 1:1.

Gerbil foraging activity is markedly reduced by moonlight due to a heightened risk of predation (Kotler et al. 1993a, 1994). Therefore, we planned each experimental sequence to last 3–4 weeks so that behavioural observations were made on moonless nights (i.e. during the time between the quarter moons and the new moon) and used seed trays identical to those used by Kotler et al. (1993a) and two thermal imaging cameras (an Infracam and a Radiometer-IR-760; Inframetrics).

During each experimental sequence we used the following protocol. For six consecutive nights, we trapped and removed gerbils from the enclosed plots. Our own field experience in the research area taught us that trapping so intensively assured removal of all the gerbils from any given enclosure. Gerbils trapped at a nearby site were used to restock the enclosures with double the natural population densities. Thus, all the introduced gerbils were naïve to the experimental enclosures. We marked the captured animals distinctively by shaving different patterns in small areas of their dorsal and lateral fur. These patterns were detectable by the thermal imaging cameras and visually identifiable. We then released the gerbils in the enclosures and allowed them to habituate to their new surroundings for two nights. Previous studies have shown that after one to two nights of habituation, gerbils distribute themselves equally between two adjacent plots that share a permeable fence (e.g. Abramsky et al. 1991, 1992, 1994), suggesting that the habituation period was sufficient to reach an ideal free distribution. During the habituation period, we randomly placed ten pairs of seed trays containing a mixture of sand and seeds in each enclosure; one of the pair under a shrub and the other in the open at least 1 m from the nearest shrub. This spatial scale captures a major part of the behavioural response of the two gerbil species to different predators and/or different levels of predation risk (Kotler et al. 1991, 1992, 1993b). The positions of these ten pairs of seed trays were fixed throughout the experimental sequence.

During each of the following three to four nights we made observations on two randomly chosen pairs (out of ten possible) of seed trays in each of the two experimental plots. We filled each tray (45×60×2.5 cm deep) with 5 l sifted sand into which we thoroughly mixed 3 g millet seeds. The remaining eight pairs of seed trays were left empty. Using the two thermal imaging cameras, we monitored activity at only one of the two pairs of charged seed trays in each plot. We stopped the first observation session after 3 h, removed the seed trays, and sifted the sand to recover the remaining millet seeds. Next, we recharged the trays with seeds and began a second session of observations. By doing two sequential sets of observations during the night we could test for temporal changes in activity patterns and patch-use

behaviour as reported in previous studies on these gerbils (Kotler et al. 1993c; Ziv et al. 1993).

At the end of the first set of behavioural measurements (after three to four nights), we trapped and removed about 50% of the gerbils from the experimental plots (i.e. brought the system to natural population densities), weighed and then released these animals at their original site of capture. We allowed the remaining animals one night to habituate to their new, reduced density and then made a second set of behavioural measurements over three to four nights using the same protocol as for the first set. Finally, upon completion of the second set of measurements, we trapped all the gerbils to identify surviving individuals and to measure their body mass. Thereafter, we released the animals at the site of their original capture. Between sequences, gates in the outside fences were opened, so that animal and resource densities could attain similar levels inside to outside the enclosed plots.

Data analyses

When analysing the videotapes, we recorded the identity of each individual that used the seed trays, the time each individual spent in a patch, and the number of aggressive interactions each individual experienced with con- and hetero-specific individuals. In addition, for each aggressive interaction, we identified the “aggressor” (the dominant individual) and the “target” of aggression (the subordinate individual). In post-hoc analysis, we found that variables such as habitat (semi-stabilized dunes vs. stabilized sand), micro-habitat (bush vs. open), time during the night (first vs. second session of observations per night), days during the sequence and density reduction within the sequence had no effects on the patterns presented in this paper. In other words, a parsimonious analysis does not require including these variables, and therefore in each experimental sequence, we treated these variables in the aggregate by estimating mean responses per plot.

Calculating behavioural components

Per capita time in patch

We calculated the per capita time spent in artificial food patches for each of four categories, male *G. a. allenbyi*, female *G. a. allenbyi*, male *G. pyramidum* and female *G. pyramidum*, for each sequence and for each of the two enclosures as the ratio of time spent in seed trays by a particular category and number of individuals in that category.

Patch occupation

During each sequence we ran 12–16 observation sessions for each of the two enclosures [2 sets×3 (or 4)

nights×2 sessions]. We never observed gerbils sharing a seed tray. Each seed tray was used mainly (~80% of the time) by a single individual and was often defended even when completely void of seeds. We calculated the artificial food patch occupation parameter as follows. We first analysed each session separately by summing the total foraging time for each of the four categories of species by gender (see above). We then counted the number of sessions in which the individual (in each category) controlled a seed tray (spent over all more time in a seed tray) for the entire sequence. Finally, we calculated the proportion of artificial food patch occupation as the ratio of number of sessions in which the seed trays were controlled by a particular category and total number of sessions during the entire sequence.

Per capita rate of aggression

We classified aggressive interactions according to the identity of the aggressor and the target using the same four categories of species by gender. We then calculated the per capita rate of aggression for each of the possible aggressor–target pairs as: (total number of confrontations between aggressor and target)/(total number of individual targets in the plot×total time these targets spent in food patches).

Estimating fitness components

Instantaneous rate of change in body mass

We calculated the instantaneous rate of change in body mass for each surviving gerbil as the log ratio of final and initial body mass [$\ln(\text{Final}_{\text{mass}}/\text{Initial}_{\text{mass}})$] divided by number of days [Time (days)] from stocking to removal. Small desert mammals have high mass specific metabolic rates (reviewed by Degen 1996), and thus even during a relatively short period of time, such as 10–12 days, one may observe changes in body mass associated with growth. Gerbils in captivity consume, on average, 3 g seeds per day. Therefore, changes in gut content may result in changes of 10–20% in body mass. Although we could not discern the relative contribution of these two possible factors leading to change in body mass, we assumed that body mass reflects the overall body condition of the individual gerbils.

Instantaneous mortality rate

We calculated the instantaneous mortality rate of gerbils as the negative log of the final and initial densities [$-\ln(\text{Final}_{\text{density}}/\text{Initial}_{\text{density}})$] divided by number of days from stocking to removal [Time (days)].

Statistical tests

We used repeated-measures ANOVA to test for the effect of intra- and inter-specific population densities (between subject factors), and gender (repeated factor/within subject factor) on per capita time in patch, patch occupation, rate of change in body mass, and mortality rate of the gerbils. By using gender as a repeated factor we could: (1) account for possible dependency between males and females within each enclosure, and (2) contrast their responses in a single analysis (for more details on using variables other than time as a repeated factor see von Ende (2001)). The variables “per capita time in patch”, “instantaneous rate of change in body mass” and “instantaneous mortality rate” were normally distributed and thus did not require any transformations. The variable “patch occupation” was arcsine-square root transformed. The assumption of homogeneity of the variances was met in all analyses. Data presented in the text and figures with respect to all variables are mean values±95% confidence limit intervals that were estimated using a bootstrap procedure (Manly 1997).

We used the statistical software Resampling Stats (version 4.0.2; Resampling Stats 1995) to run two-sample randomization tests comparing per capita rates of aggression between allopatric and sympatric populations. Randomization tests are advantageous because they do not require the data to be normally distributed, they can be used for small and unequal sample sizes, and they avoid the risk that unimportant small differences in the data will be exaggerated, e.g. by rank methods (Manly 1997). The data from the two samples were pooled and sampled without replacement to generate two random samples. The absolute difference in the mean between the two samples was then calculated and a distribution of this value was generated by repeating this process 1,000 times. In this test, the null hypothesis (that the two original samples belong to the same population) is rejected if <5% of the randomized samples show an absolute difference in mean equal to, or greater than, the difference between the original samples. The assumption of homogeneity of variance was met in all our analyses. All differences found to be significant in the randomization test were also significant by a group *t*-test or a Kruskal–Wallis test.

To test for possible time (year/month) effects on per capita rate of aggression during the allopatric or sympatric treatments, we did a series of Monte Carlo simulations using the above described randomization procedure. However, this time our null hypothesis was that samples from different years or months belong to the same population. Again, this null hypothesis was rejected if <5% of the randomized samples show an absolute difference in mean equal to or greater than the difference between the original samples.

Results

There was no significant difference in time spent in patches between male and female *G. a. allenbyi* ($F_{1,14}=0.03$, $P=0.875$; Fig. 1). Time spent in patches by individual *G. a. allenbyi* was positively correlated with their population density ($F_{1,14}=9.01$, $P=0.010$). The interaction between this variable and gender was significant ($F_{1,14}=6.57$, $P=0.023$), indicating that the positive effect of intra-specific density was stronger with respect to male than with respect to female *G. a. allenbyi*. The density of *G. pyramidum* had a negative effect on time spent in patches by individual *G. a. allenbyi* ($F_{1,14}=22.31$, $P<0.001$; Fig. 1). Also, the interaction between inter-specific density and gender was significant ($F_{1,14}=11.63$, $P=0.004$), indicating that the negative effect of *G. pyramidum* was stronger with respect to male than with respect to female *G. a. allenbyi* (Fig. 1).

We could not detect significant differences in the time spent in patches between male and female *G. pyramidum* ($F_{1,9}=0.19$, $P=0.670$; Fig. 1). There was no significant effect of intra-specific population density on the time spent in patches by individual *G. pyramidum* ($F_{1,9}=3.48$, $P=0.095$), nor was there a significant interaction between this variable and gender ($F_{1,9}=0.25$, $P=0.626$). In contrast, the time spent in patches by individual *G. pyramidum* was positively correlated with the density of *G. a. allenbyi* ($F_{1,9}=12.39$, $P=0.007$), but the interaction between inter-specific density and gender was not significant ($F_{1,9}=0.30$, $P=0.599$).

There was no significant difference in patch occupation between male and female *G. a. allenbyi* ($F_{1,15}=2.09$, $P=0.169$; Fig. 2) and we did not find a significant effect of intra-specific population density on patch occupation of individual *G. a. allenbyi* ($F_{1,15}=0.73$, $P=0.406$). However, the interaction between this variable and

gender was significant ($F_{1,15}=9.40$, $P=0.008$), indicating that intra-specific density had a positive effect on patch occupation of male, but not female, *G. a. allenbyi*. The density of *G. pyramidum* had a negative effect on patch occupation of individual *G. a. allenbyi* ($F_{1,15}=21.11$, $P<0.001$; Fig. 2). The interaction between inter-specific density and gender was significant ($F_{1,15}=8.29$, $P=0.011$), indicating that the negative effect of *G. pyramidum* was stronger with respect to male than with respect to female *G. a. allenbyi* (Fig. 2).

We did not detect significant differences in patch occupation between male and female *G. pyramidum* ($F_{1,9}=0.01$, $P=0.913$; Fig. 2). There was no significant effect of intra- nor inter-specific population density on patch occupation of individual *G. pyramidum* ($F_{1,9}=0.08$, $P=0.782$ and $F_{1,9}=0.42$, $P=0.532$, respectively) and the interactions between gender, and intra- and inter-specific density were not significant ($F_{1,9}=0.00$, $P=0.999$ and $F_{1,9}=0.00$, $P=0.998$, respectively).

Gerbils defended seed trays aggressively and we never observed gerbils sharing a seed tray. Moreover, each time two or more gerbils were active around a seed tray, a fight immediately took place. In such fights, the aggressor invariably chased the target for up to 1 min during which it tried to physically harm the retreating gerbil by biting and butting. Such aggression was also observed when the seed trays were completely empty of seeds, suggesting that both measurements, namely per capita time in patch and patch occupation, reflect the dominance hierarchy among individual gerbils. We did not detect any behavioural differences between intra- and inter-specific aggressive interactions, nor did we detect any time (month/year) effect on per capita rate of aggression during the allopatric and sympatric treatments (Monte Carlo simulations, $P>0.300$ for all randomization tests).

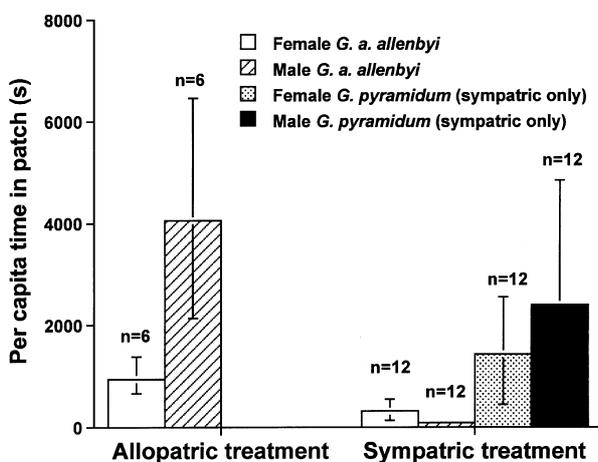


Fig. 1 Per capita time spent in artificial food patches by male and female *Gerbillus andersoni allenbyi* and *G. pyramidum* under conditions of allopatry or sympatry and at controlled population densities (see text for details). Data presented are means \pm 95% confidence limit intervals estimated using a bootstrap procedure

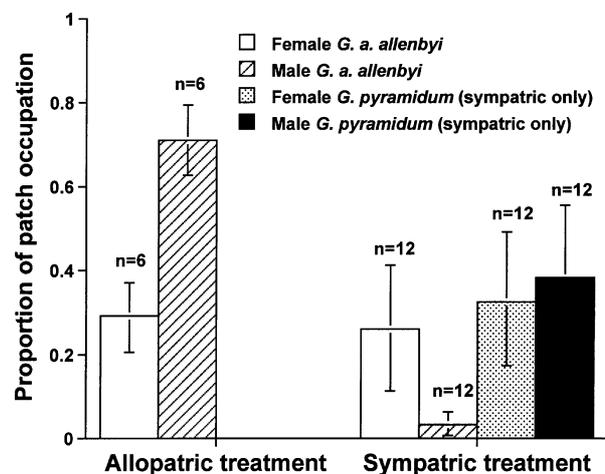


Fig. 2 Artificial food patch occupation of male and female *G. a. allenbyi* and *G. pyramidum* under conditions of allopatry or sympatry and at controlled population densities (see text for details). Data presented are means \pm 95% confidence limit intervals estimated using a bootstrap procedure

In the allopatric treatment, there was no female–female aggression among individual *G. a. allenbyi* (Table 2) and in the sympatric treatment, the rate of these intra-gender interactions was very low (Table 2). In contrast, when *G. a. allenbyi* was alone, the rate of male–male interactions was relatively high (Table 2). But again, in the presence of *G. pyramidum*, these intra-gender interactions were very rare (Table 2).

It is apparent that the dominant species, *G. pyramidum*, mediated competitive effects between genders of the subordinate species, *G. a. allenbyi*. In the sympatric treatment, there was a significant reduction in the aggression of male *G. a. allenbyi* towards female *G. a. allenbyi* (two-sample randomization test, $P=0.020$, Table 2). This is, by definition, a trait-mediated indirect effect. In contrast, there was no significant difference in the aggression of female *G. a. allenbyi* towards male *G. a. allenbyi* between the allopatric and sympatric treatments (Table 2, $P=0.350$).

There was no significant difference between the aggression of female *G. pyramidum* towards male *G. a. allenbyi* and their aggression towards female *G. a. allenbyi* (Table 2, $P=0.632$). Similarly, there was no significant difference between the aggression of male *G. pyramidum* towards male *G. a. allenbyi* and their aggression towards female *G. a. allenbyi* (Table 2, $P=0.566$). We did not observe any aggression of male *G. a. allenbyi* towards male or female *G. pyramidum* (Table 2). In contrast, there was evidence for aggression of female *G. a. allenbyi* towards male and female *G. pyramidum* that did not vary significantly between genders (Table 2, $P=0.885$).

The rate of intra-gender interactions among individual *G. pyramidum* was relatively low (Table 2). However, the aggression of male towards female *G. pyramidum* was significantly stronger than of female towards male (Table 2, $P=0.021$).

We could not detect significant differences in the instantaneous rate of change in body mass between male

and female *G. a. allenbyi* ($F_{1,14}=0.64$, $P=0.437$; Fig. 3). There was no significant effect of intra-specific population density on the rate of change in body mass ($F_{1,14}=1.80$, $P=0.201$); however, the interaction between this variable and gender was significant ($F_{1,14}=4.48$, $P=0.051$). Indeed, there was a negative correlation between intra-specific population density and the instantaneous rate of change in body mass of female *G. a. allenbyi* ($r=0.61$, $F_{1,16}=9.44$, $P=0.007$), but no such correlation was detected for male *G. a. allenbyi* ($r=0.05$, $F_{1,15}=0.05$, $P=0.831$). The presence of *G. pyramidum* had no significant effect on the rate of change in body mass of individual *G. a. allenbyi* ($F_{1,14}=2.45$, $P=0.140$) and the interaction between inter-specific density and gender was not significant ($F_{1,14}=1.38$, $P=0.259$). However, using a planned comparison test we found that the presence of *G. pyramidum* had a significant negative effect on the body mass of male *G. a. allenbyi* ($F_{1,15}=4.43$, $P=0.053$; Fig. 3).

We could not detect significant differences in the instantaneous rate of change in body mass between male and female *G. pyramidum* ($F_{1,5}=0.85$, $P=0.398$; Fig. 3). There was no significant effect of intra-specific population density on the rate of change in body mass ($F_{1,5}=0.64$, $P=0.459$), nor was there a significant interaction between this variable and gender ($F_{1,5}=0.06$, $P=0.818$). The density of *G. a. allenbyi* had no significant effect on the rate of change in body mass of individual *G. pyramidum* ($F_{1,5}=0.34$, $P=0.583$) and the interaction between inter-specific density and gender was not significant ($F_{1,5}=0.08$, $P=0.792$).

The instantaneous mortality rate of female *G. a. allenbyi* was significantly lower than that of male *G. a. allenbyi* ($F_{1,15}=4.51$, $P=0.050$; Fig. 4). We could not detect significant effects of intra- nor inter-specific population density on the instantaneous mortality rate of individual *G. a. allenbyi* ($F_{1,15}=0.31$, $P=0.586$ and $F_{1,15}=0.48$, $P=0.500$, respectively). The interaction between intra-specific density and gender was not signifi-

Table 2 Per capita rate of aggressive interactions during allopatric and sympatric treatments (see text for details) expressed in units of interactions target⁻¹ h⁻¹. Data presented are mean values and their 95% confidence limit intervals (CLI) estimated using a bootstrap procedure

Aggressor	Target			
	♀ <i>G. a. allenbyi</i>	♂ <i>G. a. allenbyi</i>	♀ <i>G. pyramidum</i>	♂ <i>G. pyramidum</i>
Allopatric treatment				
♀ <i>G. a. allenbyi</i>	0.00 (0.00 < 95% CLI > 0.00)	0.13 (0.04 < 95% CLI > 0.23)		
♂ <i>G. a. allenbyi</i>	3.16 (0.63 < 95% CLI > 6.93)	1.14 (0.11 < 95% CLI > 2.74)		
Sympatric treatment				
♀ <i>G. a. allenbyi</i>	0.02 (0.00 < 95% CLI > 0.05)	0.43 (0.00 < 95% CLI > 0.87)	0.86 (0.00 < 95% CLI > 2.51)	1.84 (0.00 < 95% CLI > 5.27)
♂ <i>G. a. allenbyi</i>	0.01 (0.00 < 95% CLI > 0.29)	0.14 (0.00 < 95% CLI > 0.44)	0.00 (0.00 < 95% CLI > 0.00)	0.00 (0.00 < 95% CLI > 0.00)
♀ <i>G. pyramidum</i>	1.22 (0.19 < 95% CLI > 2.67)	0.36 (0.00 < 95% CLI > 0.71)	0.35 (0.00 < 95% CLI > 1.06)	0.08 (0.00 < 95% CLI > 0.25)
♂ <i>G. pyramidum</i>	0.98 (0.35 < 95% CLI > 1.76)	1.60 (0.30 < 95% CLI > 3.42)	1.13 (0.34 < 95% CLI > 1.98)	0.39 (0.01 < 95% CLI > 0.96)

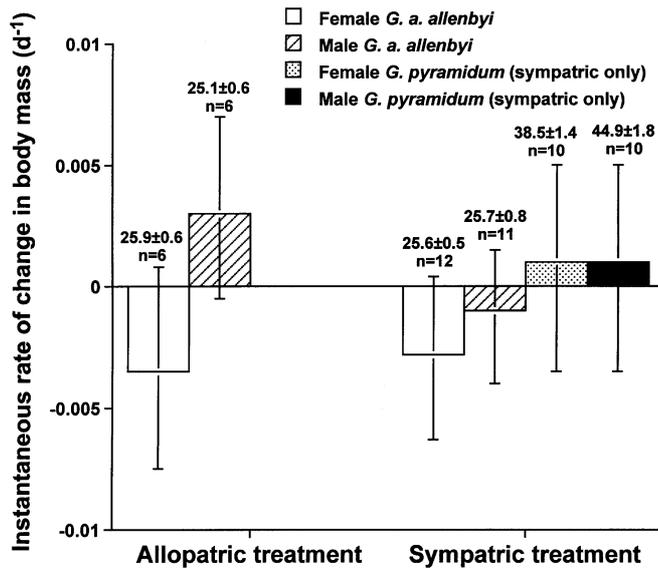


Fig. 3 The instantaneous rate of change in body mass of male and female *G. a. allenbyi* and *G. pyramidum* under conditions of allopatry or sympatry and at controlled population densities (see text for details). Numbers above bars are mean body mass ± 1 SE and sample size, n . Data presented are means $\pm 95\%$ confidence limit intervals estimated using a bootstrap procedure. $d^{-1} \text{ Day}^{-1}$

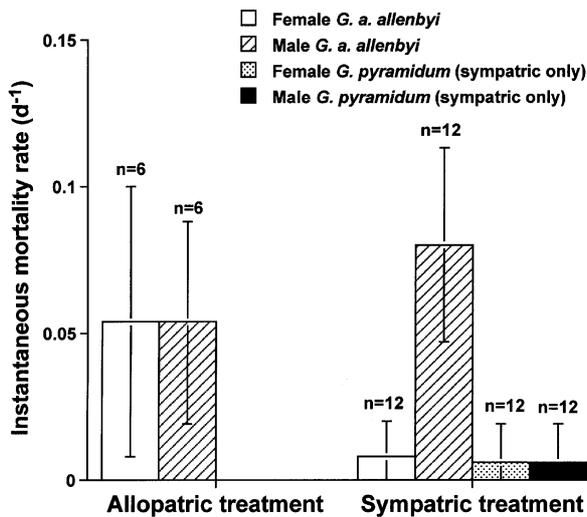


Fig. 4 The instantaneous mortality rate of male and female *G. a. allenbyi* and *G. pyramidum* under conditions of allopatry or sympatry and at controlled population densities (see text for details). Data presented are means $\pm 95\%$ confidence limit intervals estimated using a bootstrap procedure

cant ($F_{1,15} = 3.49$, $P = 0.080$). However, there was a significant interaction between inter-specific density and gender ($F_{1,15} = 4.80$, $P = 0.045$). Indeed, in the presence of *G. pyramidum*, there was a decrease in the instantaneous mortality rate of female *G. a. allenbyi*, but an increase in the instantaneous mortality rate of male *G. a. allenbyi* (Fig. 4).

We found no significant differences in the instantaneous mortality rate between male and female *G. pyra-*

midum ($F_{1,9} = 0.20$, $P = 0.669$; Fig. 4) and no significant effects of intra- nor inter-specific population density on instantaneous mortality rate of individual *G. pyramidum* ($F_{1,9} = 0.09$, $P = 0.774$ and $F_{1,9} = 0.39$, $P = 0.549$, respectively). Finally, the interactions between intra- and inter-specific density, and gender were not significant ($F_{1,9} = 0.00$, $P = 0.994$ and $F_{1,9} = 0.06$, $P = 0.809$, respectively).

Discussion

We used a field manipulation experiment and direct observations to test for structural differences in competitive effects within and between genders of two desert gerbil species. The negative effect of the dominant species, *G. pyramidum*, on time spent in seed trays and ability to control these artificial food patches was stronger with respect to males than with respect to females of the subordinate species *G. a. allenbyi*. Consequently, there was a substantial reduction in the aggression of male *G. a. allenbyi* towards female *G. a. allenbyi*. We interpret this to mean that the dominant species mediated competitive effects between genders of the subordinate species. Moreover, this interference-mediated indirect effect was associated with a decrease in the body mass of male *G. a. allenbyi* and an increase in the survival of female *G. a. allenbyi*.

The idea that a net effect of one species on another may be positive even though the direct effect is negative is not new in ecological theory (Holt 1977, 1984; Yodzis 1988) and was supported by several empirical studies (e.g. Davidson et al. 1984; Wootton 1992). However, in these studies as well in some others the driving forces were density-mediated indirect effects, rather than trait-mediated indirect effects. Trait-mediated indirect effects strongly influence community structure (Werner 1992; Abrams et al. 1996). Empirical studies have shown that trait-mediated indirect effects can change the strength of community-level interactions such as predation (Beckerman et al. 1997) and competition (Werner 1991; Morrison 1999). However, most theoretical and empirical studies dealing with trait-mediated indirect effects involve three or more species from at least two trophic levels (Werner 1992; Abrams et al. 1996). The present study shows that trait-mediated indirect effects can propagate internally within the same trophic level through structural differences in competitive effects. This phenomenon reflects previous observations showing that trait-mediated indirect effects have inter-gender consequences both within and across trophic levels (e.g. Sih and Krupa 1996).

Previous studies have shown that the larger species, *G. pyramidum*, excludes the smaller species, *G. a. allenbyi*, both from the habitat that both species prefer (e.g. Abramsky et al. 1990; Ziv et al. 1993) and from activity hours favoured by both (Kotler et al. 1993c; Ziv et al. 1993). Brown et al. (1994) found that the giving up density of seeds in an artificial patch of *G. a. allenbyi* is

lower than that of *G. pyramidum*. Based on these results, ecologists suggested that coexistence between the two species is based on a trade-off between the dominance of *G. pyramidum* and the foraging efficiency of *G. a. allenbyi* (Kotler et al. 1993c; Ziv et al. 1993; Brown et al. 1994). The present study provides another potential mechanism underlying coexistence between these species. In the presence of *G. pyramidum*, there was a reduction in intra-specific aggression among individual *G. a. allenbyi*. Such suppressed intra-specific aggression is likely to weaken density-dependent effects and thereby influence the shape of the isoclines, a process that can promote coexistence (Rosenzweig 1991). This finding might apply to other systems in which interference competition is a driving force.

For instance, in vertebrates, particularly in the non-breeding season, males will almost always be in competition with females, either exploitatively or by interference (e.g. Alcock 2001). Thus, other animal species which cause a reduction in the abundance or activity of males of the species in question should indirectly benefit females. In some cases, like the one presented here, such indirect effects may outweigh any direct effects. Males often differ in size from females (e.g. in birds and mammals, males are typically larger). Moreover, inter-specific interactions such as interference competition which vary in their strength as a function of body size (Huntingford and Turner 1987) will affect males differently from females. Consequently, even direct inter-specific effects should differ by gender.

Male and female *G. a. allenbyi* do not differ in their body mass between spring and autumn (Abramsky 1984; Brand and Abramsky 1987). This pattern was also evident in our experiment (Fig. 3). In contrast, male *G. pyramidum* are larger than their con-specific females throughout the year (Brand and Abramsky 1987). Indeed, we observed differences of up to 15% in body mass between male and female *G. pyramidum* (Fig. 3). This size polymorphism may be the principal explanation for the observed dominance of male over female *G. pyramidum*.

At a first glance, it seems that in the sympatric treatment, *G. pyramidum* became a substitute aggressor, replacing the aggression of male *G. a. allenbyi* towards female *G. a. allenbyi*. However, examining the data more carefully suggests that these intra- and inter-specific effects are not substitutional. First, in the presence of *G. pyramidum* there was an increase in the survival of female *G. a. allenbyi*. Second, there appeared to be a reciprocal aggressive response of female *G. a. allenbyi* toward *G. pyramidum*. In the allopatric populations, there was almost no aggression of female *G. a. allenbyi* toward conspecific males. We interpret this to mean that among female *G. a. allenbyi*, intra-specific competition is stronger than inter-specific competition. As far as we know this pattern of gender dimorphism in inter-specific competition has never been reported in the literature.

The influence that we attributed to *G. pyramidum* (or interactions involving other variables and *G. pyrami-*

dum) may be caused by some timing effects that we cannot completely rule out. This is because the presence/absence of *G. pyramidum* was confounded with time (Table 1). However, experiments done in the same enclosures over the last 15 years show no evidence for such timing effects (e.g. Abramsky et al. 1990, 1991, 1992, 1994). Furthermore, short- and long-term studies investigating competition have shown that this small mammal community is very stable and that the strength of species interactions does not change over time (e.g. Abramsky et al. 1991, 1992). Indeed, using Monte Carlo simulations we could not detect any effect of time (year or month) on the per capita rate of intra- and inter-specific aggression. We therefore believe that if such timing effects do exist they do not mask our analyses and interpretations.

In conclusion, the present study demonstrates how interference-mediated indirect effects can propagate internally within the same trophic level through structural differences in competitive effects. We suggest that detecting such fine-scale detail can improve our understanding of species interactions and community-level patterns such as coexistence.

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