

# The effect of intra- and interspecific aggression on patch residence time in Negev Desert gerbils: a competing risk analysis

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We observed patch-use behavior by two gerbil species in a field setting and investigated how aggression and intrinsic decision-making interact to influence patch residence times. Results were interpreted by using a competing risk analysis model, which uniquely enabled us to estimate the intrinsic patch-leaving decisions independently of external interruptions of foraging bouts by aggression. The experiment was conducted in two 1-ha field enclosures completely surrounded by rodent-proof fences and included allopatric (only *Gerbillus andersoni allenbyi*) and sympatric (*G. a. allenbyi* and *G. pyramidum*) treatments. We predicted that increased food patch quality (i.e., habitat quality) should decrease intrinsic patch-leaving rates and increase rates of aggressive interactions involving the forager feeding in the patch (i.e., the occupant individual). We also anticipated that increasing population density should result in an increase in the rate of aggressive interactions involving the occupant individual. Our results supported the first two predictions, indicating a trade-off between foraging and aggression. However, the third prediction was realized only for *G. a. allenbyi* in allopatry. Furthermore, in allopatry, occupant *G. a. allenbyi* individuals with high competitive ranks were involved in aggressive interactions at lower rates than those with low competitive ranks. However, in sympatry, patch-use behavior of occupant *G. a. allenbyi* individuals was mainly influenced by aggressive behavior of *G. pyramidum*, which did not respond to their competitive rank. Thus, it should pay less for *G. a. allenbyi* to be aggressive in sympatric populations. The observed reduction in intraspecific aggression among individual *G. a. allenbyi* in the presence of *G. pyramidum* supports this assertion. We suggest that this reduction likely weakens the negative effect of intra- and interspecific density on the per capita growth rate of *G. a. allenbyi*. Because this would change the slope of the isocline of *G. a. allenbyi*, it could be an important mechanism promoting coexistence when habitat selection is constrained. *Key words*: aggression, competing risk method, intrinsic decision-making, patch residence time, patch use, survival analysis. [*Behav Ecol* 14:583–591 (2003)]

Understanding community dynamics requires investigating how density-dependent and density-independent processes interact to influence the per capita growth rate of the different populations making up a community (see Fretwell, 1972; Fryxell and Lundberg, 1998). However, measuring per capita growth rates can be difficult, especially under field conditions. Thus, ecologists have developed tools to infer the effects of habitat factors on the per capita growth rate based on the behavioral response of individuals to these factors (see Fretwell, 1972). One of the most prominent examples is the link between habitat quality (e.g., availability of food resources, risk of predation, thermal conditions) and potential growth rate based on patch-use behavior of a forager.

Classical theory (Charnov, 1976) known as the “marginal value theorem” (MVT) states that a forager that experiences diminishing returns as it spends more time foraging, should leave a patch once its net energy gain per time equals the average rate of energy gain over all patches in the entire habitat. Brown (1988) extended MVT by developing a patch-use model that incorporates energetic, predation, and missed opportunity costs. According to his model, the density of food items remaining in a patch after the forager leaves (“giving up density” [GUD]) can be used as proximate measure for the net energy gain at the point of departure.

Measuring GUD is relatively easy in the field. Furthermore, the high concordance of GUD with factors influencing harvest rates (Ziv et al., 1995), energetic costs (Kotler et al., 1993b), predation costs (Kotler et al., 1991, 1993a,c), food characteristics (Kotler et al., 1994), richness of the environment (Brown et al., 1992), and habitat quality (Morris and Davidson, 2000) has made it a popular approach for inferring population level processes.

However, using GUDs can also be problematic. Assumptions underlying MVT are not well tested (Nonacs, 2001) and may be violated (Price and Correll, 2001). Additionally, patch-use behavior can be interrupted by an external event, such as aggression or predation attempts. Because these interruptions are usually not under the control of the forager, they can interfere with the intrinsic decision-making process. If, e.g., the forager feeding in the patch (i.e., the occupant individual) was interrupted by aggression before it could reach its quitting harvest rate, its GUD will be a product of the initial food density alone. In this case, a better habitat (i.e., one with higher food density) would lead to a higher GUD, a pattern that is opposite to the prediction of the MVT framework.

If the frequency of such interruptions is positively correlated with habitat quality, then the analysis will be confounded because high habitat quality may lead to higher rates of aggressive interactions involving the occupant individual, thereby masking the effect of habitat quality on GUD. In such cases, measures of habitat quality vary with the rate of aggressive interactions, which depends on the density of individuals. Thus, measuring GUD might not be suitable for teasing apart the effects of density-dependent and density-independent

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processes on habitat quality, which is necessary for linking patch-use behavior with community dynamics.

Understanding the interplay between aggression and patch-use behavior requires teasing apart giving-up decisions based on forage quality (i.e., intrinsic decisions) from external interruptions of foraging such as aggression. This requires analyzing patch residence times rather than measuring GUD and the use of novel statistical tools. Specifically, patch residence times that were interrupted by external factors also contain information about intrinsic decision-making; we know that the occupant individual did not leave the patch any time before the interruption occurred. Similarly, foraging bouts ended by an intrinsic decision of the occupant individual also contain information about the rate of interruptions. Conventional statistical methods such as ANOVA or linear regression cannot handle information about such unobserved events. Competing risk analysis is one statistical technique designed to extract such information (Kalbfleisch and Prentice, 1980; Lunn and McNeil, 1995) and can therefore be used to distinguish between intrinsic patch-leaving decisions and external interruptions of foraging bouts.

To gain a mechanistic understanding of the competitive interactions between—and coexistence of—two nocturnal desert gerbil species, Allenby's gerbil (*Gerbillus andersoni allenbyi*) and the greater Egyptian sand gerbil (*Gerbillus pyramidum*), we observed patch-use behavior under field conditions and investigated how aggression and intrinsic decision-making interact to influence patch residence times. Results were interpreted by using a competing risk analysis model.

### Natural history

*G. a. allenbyi* (mean mass, 26 g) and *G. pyramidum* (mean mass, 40 g) occur sympatrically over a wide range of sandy areas in the western Negev Desert in Israel (Abramsky et al., 1985). They are solitary burrow dwellers that forage nocturnally primarily for seeds (Bar et al., 1984). Field observations have shown that individual *G. a. allenbyi* and *G. pyramidum* aggressively defend food patches (Ovadia, 1999). Furthermore, intra- and interspecific aggressive interactions occur within and between sexes and always include chasing and attempts at physical contact (Ovadia, 1999).

Previous manipulation experiments show that competition between the two gerbil species is asymmetrical (Abramsky et al., 1990, 1991, 1992, 1994; Ziv et al., 1993). In allopatric populations, both species prefer using the semistabilized dunes habitat (Abramsky et al., 1990) and being active mainly early at night (Ziv et al., 1993). However, in sympatric populations, the larger species, *G. pyramidum*, excludes the smaller and the more efficient forager (Brown et al., 1994), *G. a. allenbyi*, from the habitat they both prefer (Abramsky et al., 1990) and from the activity time that both prefer (Ziv et al., 1993). Thus, ecologists suggested that coexistence between the two species is owing to a trade-off between the dominance of *G. pyramidum* versus the foraging efficiency of *G. a. allenbyi* (Ziv et al., 1993).

### Predictions

In accordance with the large body of information about habitat requirements of the species and in light of the goals of the present study, we predicted for factors with known influence on habitat quality that (1) the intrinsic patch-leaving rate of the occupant individual should be negatively correlated with food patch quality (i.e., habitat quality), and (2) the rate of aggressive interactions involving the occupant individual should be positively correlated with food patch quality. In addition, we predicted that (3) the rate of

aggressive interactions involving the occupant individual should be positively correlated with population density.

The trade-offs between aggression and intrinsic patch-leaving decision may change for a subordinate species in the presence of a dominant competitor. We therefore tested these predictions for *G. a. allenbyi* in allopatry and in sympatry with *G. pyramidum*.

## METHODS

### Study site

The study was undertaken at a site in the Holot Mashabim Nature Reserve (31°01' N, 34°45' E), 35 km south of Beer Sheva, Israel. Sandy areas at the study site can be classified into two habitat types based on mobility of the sand and the dominant perennial plant species. These are semistabilized dunes and stabilized sand (Danin, 1978).

### Experimental plots

The experiment was conducted in two 1-ha plots completely surrounded by rodent-proof fences. Each enclosed plot contained similar proportions of the semistabilized dunes and stabilized sand habitats. Data collected from livetrapping in control plots of the same size over the past 15 years indicate that the average density of *G. a. allenbyi* and *G. pyramidum* is 11 and 2 individuals/ha, respectively (Abramsky Z, unpublished data).

### Experimental design

The experiment consisted of nine rounds, which were divided into two experimental treatments: (1) an allopatric treatment wherein only *G. a. allenbyi* were present in the experimental plots, which was replicated six times (three rounds  $\times$  two plots = six replicates); and (2) a sympatric treatment with both *G. a. allenbyi* and *G. pyramidum* present, which was replicated 12 times (six rounds  $\times$  two plots = 12 replicates) (Table 1).

The experiment was explicitly designed to capture the natural seasonal changes in population densities of the gerbils. In each experimental round, behavioral observations were made at two different population densities. We stocked the enclosures at the beginning of each round with double the natural population density before the round (Table 1) and observed the behavior of the gerbils for 3–4 days. We then removed about 50% of the gerbils from the enclosures and made another set of behavioral observations. All introduced individuals were nonreproductive, and their sex ratio was unity. All behavioral observations were made by using artificial resource patches (seed trays) and thermal imaging cameras (an Infracam and a Radiometer-IR-760, both by Inframetrics).

### Experimental protocol

Gerbil foraging activity is biased by moonlight owing to heightened risk of predation (Kotler et al., 1993b). Thus, each round lasted 3–4 weeks and was scheduled so that behavioral measurements were made on moonless nights. In each round, we used the following protocol. For six consecutive nights, we trapped and removed all the gerbils from the enclosed plots. Gerbils trapped at a nearby site were used to stock the enclosures. We marked each of these individuals by shaving a small distinctive pattern in its fur. The patterns were detectable by the thermal imaging cameras. We then released gerbils in the enclosures and allowed them to habituate to their new surroundings for two nights. During this habituation period, we placed 10 pairs of trays containing a mixture of sand and seeds in each enclosed plot, one of the pair under

a shrub and the other in the open at least 1 m away from the shrub. This spatial scale captures a major part of the behavioral response of the two gerbil species to different predators and/or different levels of predation risk (Kotler et al., 1991, 1992, 1993a,c).

During each of the following three or four nights, we made observations. Each night we randomly selected two out of 10 pairs of trays in each of the two experimental plots. We filled each of these four trays (45 × 60 × 2.5 cm deep) with 5 l of sifted sand, into which we thoroughly mixed 3 g of millet seeds. Because we only had two thermal imaging cameras available, we were able to monitor activity at only one of the two pairs of seed trays in each of the two plots. We stopped the first observation session after 3 h, removed the seed trays, and sifted the sand to recover the remaining millet seeds. After that, we resupplied the trays with seeds and started the second behavioral session for that night.

After three or four nights, we trapped and removed 50% of the gerbils from the experimental plots. We allowed the remaining animals one night to habituate to their new reduced density. We then conducted a second set of behavioral measurements (three or four additional nights) by using the same protocol as for the first set. Finally, at the conclusion of each round, we trapped out all the gerbils and weighed them. Between rounds, gates in the outside fences were opened, so that animal and resource densities could attain similar levels outside and inside the enclosed plots.

**Data processing**

When analyzing 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 had with conspecific and hetero-specific individuals. Additionally, for each aggressive interaction, we identified the dominant individual (the one that won the confrontation) and the subordinate one (the one that lost in the confrontation).

**Aggression**

Gerbils never share a seed tray (Ovadia, 1999). Moreover, each time that two or more gerbils (conspecific or heterospecific individuals) are active around a seed tray, fights immediately take place. Such interactions may last up to 1 min and almost exclusively feature chasing, biting, or butting by the dominant individual (Ovadia, 1999). This is true either when the occupant is the dominant individual or when the occupant is the subordinate individual. Because an aggressive interaction always forces the occupant individual—even if it is the dominant—to leave the patch, the instantaneous rate of patch leaving in response to aggression is also the instantaneous rate of aggressive interactions involving (initiated + received) the occupant individual. To avoid confusion, we use only the latter term in the following text.

**Competitive rank**

We defined competitive rank as the proportion of aggressive interactions won by a given individual (as occupant and intruder) during the entire study. For each aggressive interaction, we determined the winner as the individual that stayed in the vicinity or was the first to return to the food patch.

**Competing risk analysis**

We analyzed our data by using an extension of the Cox proportional hazard model (Cox, 1972) developed by Lunn

**Table 1**

**The numbers of *Gerbillus andersoni allenbyi* and *G. pyramidum* that were introduced into the two enclosed plots at the beginning of each round**

Treatment	Date	Round	Plot	<i>G. andersoni allenbyi</i>	<i>G. pyramidum</i>
Allopatric <sup>a</sup>	3/96	1	1	12	0
	3/96	1	2	12	0
	4/96	2	1	12	0
	4/96	2	2	10	0
	5/96	3	1	16	0
	5/96	3	2	16	0
Sympatric <sup>b</sup>	8/96	4	1	20	4
	8/96	4	2	18	4
	4/97	5	1	4	2
	4/97	5	2	4	2
	5/97	6	1	4	2
	5/97	6	2	4	2
	6/97	7	1	4	2
	6/97	7	2	6	2
	8/97	8	1	12	3
	8/97	8	2	18	4
	9/97	9	1	14	4
	9/97	9	2	14	4

The experiment included two treatments. Allopatric treatment consisted of only *G. a. allenbyi* present in the experimental plots and was replicated six times (three rounds × two plots = six replicates). Sympatric treatment consisted of both *G. a. allenbyi* and *G. pyramidum* present in the experimental plots and was replicated 12 times (six rounds × two plots = 12 replicates).

<sup>a</sup> Only *G. a. allenbyi* was present in the plots.

<sup>b</sup> Both species were present in the plots.

and McNeil (1995) to account for competing risks. This model allows estimating the instantaneous patch-leaving rate from the distribution of patch residence times. Patch residence times were characterized by seven environmental factors (time of year, time of night, cumulative foraging time, microhabitat, density of *G. a. allenbyi*, density of *G. pyramidum*, and experimental plot) and two attributes of the occupant individual (sex and competitive rank). We refer to these nine variables below as covariates.

The Cox model assumes the patch-leaving rate  $h(t)$  for observation  $j$  to be as follows:

$$h_j(t) = \lambda(t) \exp\left(\sum_{i=1}^m \beta_i z_{ij}\right) \tag{1}$$

That means the patch-leaving rate consists of an arbitrary baseline rate, which varies over the time spent in the patch  $\lambda(t)$  and is common to all foraging times, and a proportionality coefficient  $\exp(\sum_{i=1}^m \beta_i z_{ij})$ , which depends on the values of the  $m$  covariates  $z_{1j}$  to  $z_{mj}$  attributed to observation  $j$ . Patch residence times are used to estimate the regression coefficients  $\beta_i$ . The term involving the covariates is independent of time. Thus, the patch-leaving rates of different foraging bouts are proportional to each other during a foraging bout and they differ only by the proportionality coefficient.

Gerbils left the seed tray either for reasons unknown to the observer or because of an aggressive interaction with another individual. Because the latter was always observed, we assumed that aggression and intrinsic decision-making were the only two patch-leaving causes. This distinction enabled us to test for the effects of the covariates on the following two instantaneous rates: (1) the instantaneous rate at which the occupant individual leaves the patch owing to an intrinsic decision (i.e., intrinsic patch-leaving rate), and (2) the instantaneous

**Table 2**  
**Data augmentation for the competing risk analysis**

Observation	Foraging time	Censor	Patch-leaving cause	Covariates
$j$	$t_j$	1	$\delta_j$	$(z_{1j}, z_{2j}, \dots, z_{mj}),$ $\delta_j(z_{1j}, z_{2j}, \dots, z_{mj})$
$j$ (rep)	$t_j$	0	$1 - \delta_j$	$(z_{1j}, z_{2j}, \dots, z_{mj}),$ $(1 - \delta_j)(z_{1j}, z_{2j}, \dots, z_{mj})$

Each observation (row) is counted twice, once as exact time for the observed patch-leaving cause and once as censored observation for the alternative cause. The table shows the duplication process for one observation. For intrinsic decision-making,  $\delta_j = 0$  and for aggression  $\delta_j = 1$ . After the method of Lunn and McNeil (1995).

rate of aggressive interactions involving the occupant individual (i.e., the instantaneous rate at which the occupant individual leaves the patch in response to aggression).

A characteristic feature of survival analysis is that it allows information about unobserved events to be incorporated. If an event of interest does not occur in the period of observation, it is treated as a censored observation. To distinguish between the two patch-leaving rates, we treated each observed patch residence time as an exact time for the observed patch-leaving cause and as a censored observation for the alternative patch-leaving cause. Specifically, a foraging bout terminated by an intrinsic decision was counted as an exact time for estimating the intrinsic patch-leaving rate and as a censored observation for estimating the rate of aggressive interactions involving the occupant individual and vice versa.

To tease apart the effect of the covariates on the two patch-leaving rates, a second set of covariates was created by multiplying the original covariate values by  $\delta_j$ , where  $\delta_j = 0$  if foraging time  $j$  is ended by an intrinsic decision of the occupant individual, and  $\delta_j = 1$  if an aggressive interaction ended the foraging bout. The data augmentation described above is summarized in Table 2, after Lunn and McNeil (1995).

Introducing the new set of covariates ( $\delta_j[z_1, z_2, \dots, z_m]$ ) means that two sets of regression coefficients ( $\beta_1, \beta_2, \dots, \beta_m$  and  $\gamma_1, \gamma_2, \dots, \gamma_m$ ) are estimated for the patch-leaving rate  $\lambda(t)\exp[\sum_{i=1}^m(\beta_i z_{ij} + \gamma_i \delta_j z_{ij})]$ . That is, for intrinsic decision-making (leaving cause 1,  $\delta_j = 0$ ), the patch-leaving rate becomes  $\lambda(t)\exp[\sum_{i=1}^m \beta_i z_{ij}]$ , and for aggression (leaving cause 2,  $\delta_j = 1$ ), it is  $\lambda(t)\exp[\sum_{i=1}^m(\beta_i + \gamma_i)z_{ij}]$ . The regression coefficient  $\beta_i$  therefore indicates how the intrinsic patch-leaving rate depends on the value of the covariate  $z_i$ , and its counterpart  $\gamma_i$  shows whether this covariate has a different effect on the rate of aggressive interactions involving the occupant individual. It is noteworthy that the effect of the covariate  $i$  on the rate of aggressive interactions involving the occupant individual be given not by  $\gamma_i$  but rather  $\gamma_i + \beta_i$ .

This analysis is based on maximizing the partial likelihood (Cox, 1975). The maximizing function has distributional properties similar to the conventional maximum-likelihood function. This allows the construction of confidence intervals around the estimated regression coefficients and testing the hypothesis that they differ from zero (Hosmer and Lemeshow, 1999). The likelihood ratio is asymptotically  $\chi^2$  distributed with  $m - 2$  degrees of freedom (where  $m$  is the number of parameters, i.e., regression coefficients in the model), which allows testing the adequacy of the entire model. Including the distinction between aggression and intrinsic decision as a covariate, we have nine covariates in the allopatric and 10 in the sympatric treatment. The doubling of the covariates to account for each leaving cause leads therefore to 16 and 18

degrees of freedom for the sympatric and allopatric treatment, respectively.

To avoid pseudoreplication and to account for possible correlation between foraging bouts of the same individual, we used a robust jackknife variance estimator grouped by observations per individual (Lin and Wei, 1989). Specifically, this technique removed all observations per individual randomly rather than individual observations to calculate the variance of the maximum-likelihood estimator.

We tested the proportionality assumption (described above) for each covariate using Schoenfeld residuals (Schoenfeld, 1982). Variables that did not meet the proportionality assumption were used as stratification factors (a standard procedure for the Cox model; Hosmer and Lemeshow, 1999). This means that they were included in the statistical model, but we could not test for their effect on the patch-leaving rates.

To meet the proportionality assumption for a maximum number of variables, we introduced three time strata following the method described by Harrell and Lee (1986). This allowed the baseline patch-leaving rate to vary among the following three time intervals: (1) less than 1 min since the forager entered the patch, (2) between 1–2 min and (3) more than 2 min.

### From statistics to biology

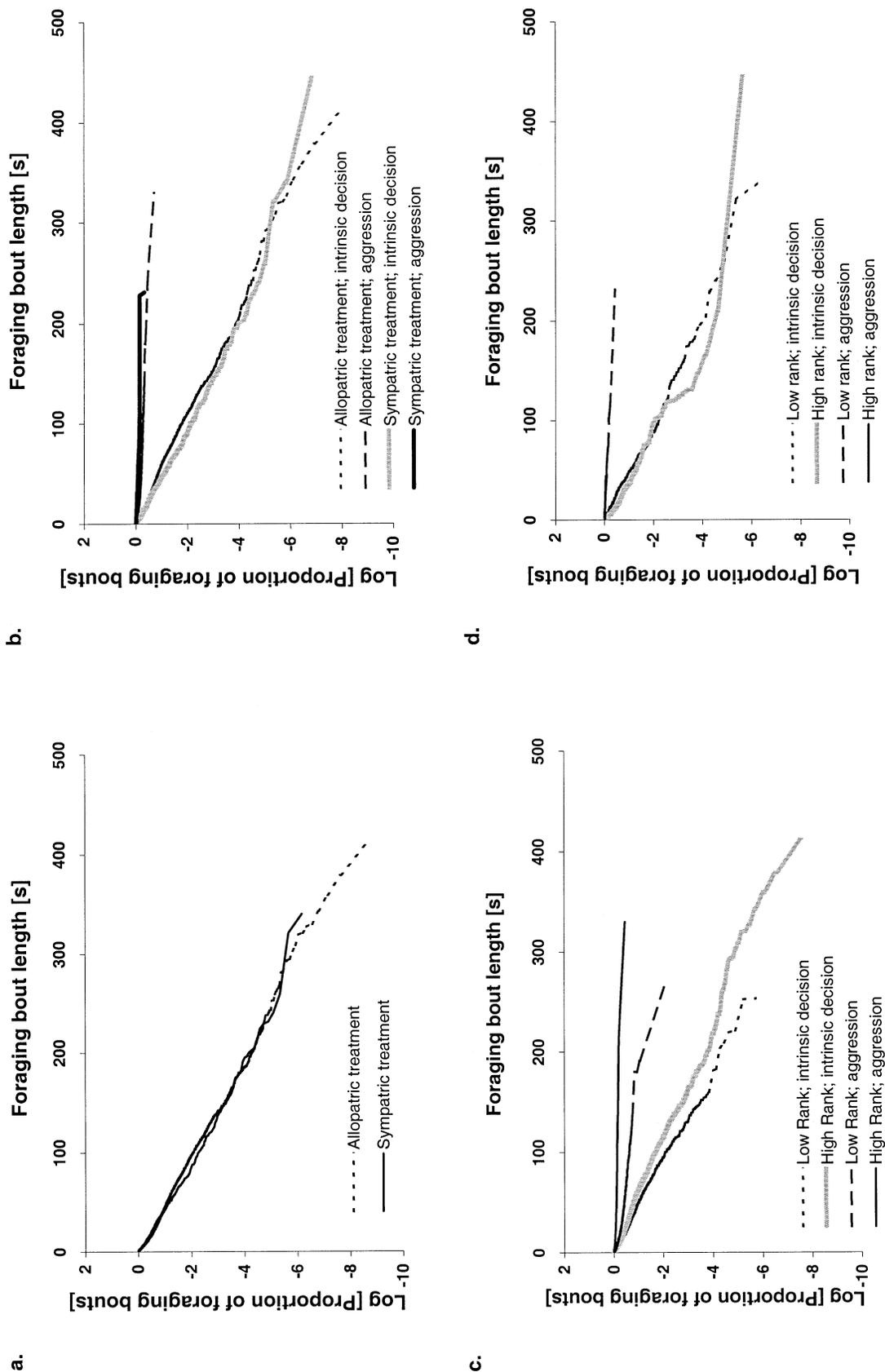
If a covariate ( $z_i$ ) is positively correlated with the food patch quality, one would expect to observe, for high covariate values, a low intrinsic patch-leaving rate and a high rate of aggressive interactions involving the occupant individual. In that case, the regression coefficient  $\beta_i$  would be negative and its counterpart  $\gamma_i$  be positive. Conversely, if  $\gamma_i$  does not show an opposite sign or if  $\beta_i$  does not differ from zero, it is likely that the patch residence times are influenced through aggression. If  $\gamma_i$  does not differ from zero, the covariate causes the same effects on both the intrinsic patch-leaving rate and the rate of aggressive interactions involving the occupant individual. This suggests that foragers behave to avoid aggression. If the regression coefficients for both covariates show the same sign and are significant the ability to avoid aggression is constrained.

## RESULTS

### *Gerbillus andersoni allenbyi*

Patch-use behavior of each individual gerbil can be characterized by a sequence of foraging bouts of varying length. To illustrate the type of information that can be extracted from the distribution of patch residence times, we first examined the data in the aggregate (i.e., no distinction between aggression and intrinsic decision-making). Specifically, we used the Kaplan-Meier method, described in detail elsewhere (Kalbfleisch and Prentice, 1980), to plot the patch-leaving curves of *G. a. allenbyi* (Figure 1a). A constant patch-leaving rate would lead to an exponential decrease in the proportion of foraging bouts (y-axis) lasting at least until the time given by the x-axis. When plotted on a logarithmic scale, one would therefore get a linear curve with a slope equal to the patch-leaving rate. The general patch-leaving curves of *G. a. allenbyi* were linear (Figure 1a; Kolmogorov-Smirnov test,  $p = .98$  and  $p = .18$  for allopatric and sympatric treatment, respectively) and their slopes (i.e., patch-leaving rates) did not vary between the allopatric and the sympatric treatment (Figure 1a;  $p = .19$ ).

We next distinguished between the two patch-leaving causes. This distinction produced two different patch-leaving curves for each treatment (Figure 1b). The lower two patch-leaving curves correspond to patch residence times terminated by an intrinsic decision (their slopes are the intrinsic patch-leaving rates). The upper lines correspond to patch



**Figure 1** Patch-leaving curves of *Gerbillus andersoni allenbyi* estimated by using the Kaplan-Meier method (Kalbfleisch and Prentice, 1980). The y-axis indicates the natural logarithm of the expected proportion of foraging bouts lasting until the time given by the x-axis. (a) General patch-leaving curves (i.e., there is no distinction between intrinsic patch-leaving decisions and those caused by aggression). There is no difference in the general patch-leaving rates between the allopatriotic and the sympatric treatment. (b) Patch-leaving curves separated by patch leaving cause (i.e., aggression or intrinsic decisions). In sympatry, occupant *G. a. allenbyi* individuals are involved in aggressive interactions at a lower rate than in allopatry, but their intrinsic patch-leaving rates tend to be higher in sympatry. These opposing effects cause the general patch-leaving curves to be similar in both treatments. Patch-leaving curves in allopatry (c) and sympatry (d) separated by competitive rank. High competitive rank refers to individuals that won 50% of the aggressive interactions or more during the entire study, and low competitive rank to those that won less than 50% of the interactions. In allopatry, occupant individuals with high competitive ranks are involved in aggressive interactions at a lower rate than those with low competitive ranks. However, in sympatry this pattern is not evident.

Table 3

Results of the competing risk analysis for *Gerbillus andersoni allenbyi* in allopatry, adjusted for nonproportionality of cumulative foraging time and time of night

Covariate	Intrinsic patch-leaving rate		Rate of aggressive interactions	
	Regression coefficient ( $\beta$ )	$p$	Regression coefficient ( $\gamma$ )	$p$
Time of year	-0.0073	.082	0.0356	<.001
Microhabitat <sup>a</sup>	-0.1861	<b>.048</b>	0.0790	.600
<i>G. andersoni allenbyi</i> density	0.0150	.140	0.1097	<.001
Plot	0.2751	<b>.003</b>	1.2144	.057
Sex <sup>b</sup>	-0.3158	<b>.022</b>	0.5066	.160
Competitive rank	-0.0523	.620	-0.9913	<b>.003</b>

Bold type indicates significant effects; df = 16,  $p < .001$ , likelihood ratio test.

<sup>a</sup> Open = 0, bush = 1.

<sup>b</sup> Male = 0, female = 1.

residence times terminated by an aggressive interaction (their slopes are the rates of aggressive interactions involving the occupant individual). Because aggressive interactions were less frequent than were intrinsic decisions, patch-leaving curves for aggression did not decrease as steeply as those for intrinsic decision-making (Figure 1b). Our analysis showed that the rate of aggressive interactions involving occupant *G. a. allenbyi* individuals was significantly higher in the allopatric than in the sympatric treatment ( $p < .01$ ). The intrinsic patch-leaving rate of individual *G. a. allenbyi* tended to be higher in the sympatric than in the allopatric treatment; however, this difference was not significant ( $p = .19$ ).

Below, we describe the effects of the covariates (environmental factors and attributes of the foraging individual) on the intrinsic patch-leaving rate of occupant *G. a. allenbyi* individuals and on the rate of aggressive interactions in which they were involved.

#### Time of year

The experiment was conducted from early spring (March) to early fall (September) in two consecutive years. In allopatry, there was an increase over the year in the rate of aggressive interactions involving occupant *G. a. allenbyi* individuals ( $p < .01$ ; Table 3); however, we could not detect a significant effect on the intrinsic patch-leaving rates ( $p = .08$ ; Table 3). In sympatry, neither intrinsic patch-leaving rate nor rate of aggressive interactions changed significantly over the year ( $p = .06$  and  $p = .08$ , respectively; Table 4).

#### Time of night

The covariate "time of night" indicated whether an observation was made during the first or second of the two consecutive observation sessions per night. This covariate was used as stratification variable for the allopatric treatment because it did not meet the proportionality requirement. During the sympatric treatment, the intrinsic patch-leaving rate of occupant *G. a. allenbyi* individuals was higher in the second session of the night ( $p = .02$ ; Table 4), but there was no significant effect on the rate of aggressive interactions in which they were involved ( $p = .27$ ; Table 4).

#### Cumulative foraging time

In allopatry, the covariate "cumulative foraging time" (i.e., the total length of time that a given seed tray was foraged on

Table 4

Results of the competing risk analysis for *Gerbillus andersoni allenbyi* in sympatry

Covariate	Intrinsic patch-leaving rate		Rate of aggressive interactions	
	Regression coefficient ( $\beta$ )	$p$	Regression coefficient ( $\gamma$ )	$p$
Time of year	-0.0022367	.062	-0.0099215	.080
Time of night <sup>a</sup>	0.2337481	<b>.022</b>	-0.6952566	.270
Cumulative foraging time	0.0000454	.600	-0.0006680	<b>.004</b>
Microhabitat <sup>b</sup>	-0.0358940	.610	0.2598718	.400
<i>G. andersoni allenbyi</i> density	0.0759467	<b>.001</b>	0.0215323	.870
<i>G. pyramidum</i> density	-0.2345450	<b>.020</b>	0.3643247	.330
Plot	-0.5349098	<.001	2.1498448	<.001
Sex <sup>c</sup>	0.0200937	.900	-0.1729670	.780
Competitive rank	0.2595066	.064	-0.2537656	.720

Bold type indicates significant effects; df = 18,  $p < .001$ , likelihood ratio test.

<sup>a</sup> First session = 0, second session = 1.

<sup>b</sup> Open = 0, bush = 1.

<sup>c</sup> Male = 0, female = 1.

since placement in the field) did not meet the proportionality assumption and was therefore used as a stratification variable. In sympatry, we observed a significant reduction in the rate of aggressive interactions involving occupant *G. a. allenbyi* individuals with an increase in the cumulative foraging time ( $p < .01$ ; Table 4), but we could not detect any effect on their intrinsic patch-leaving rate ( $p = .60$ ; Table 4).

#### Microhabitat

In allopatry, individual *G. a. allenbyi* had a lower intrinsic patch-leaving rate in seed trays located under bushes than those in the open ( $p < .05$ ; Table 3). However, in sympatry this effect was not significant ( $p = .61$ ; Table 4). There was no significant effect of microhabitat on the rate of aggressive interactions involving occupant *G. a. allenbyi* individuals during both the allopatric ( $p = .60$ ; Table 3) and sympatric treatment ( $p = .40$ ; Table 4).

#### Conspecific and heterospecific densities

In sympatry, intraspecific density had a positive effect on the intrinsic patch-leaving rate of individual *G. a. allenbyi* ( $p < .01$ ; Table 4). However, in allopatry this effect was not detected ( $p = .14$ ; Table 3). The opposite was true for the rate of aggressive interactions. In allopatry, there was a positive effect of intraspecific density on the rate of aggressive interactions involving occupant *G. a. allenbyi* individuals ( $p < .01$ ; Table 3). However, in sympatry this effect was not evident ( $p = .87$ ; Table 4). The density of *G. pyramidum* had a negative effect on the intrinsic patch-leaving rate of occupant *G. a. allenbyi* individuals ( $p = .02$ ; Table 4), but we could not detect any effect on the rate of aggressive interactions in which they were involved ( $p = .33$ ; Table 4).

#### Experimental plot

In allopatry, there was a significant difference in the intrinsic patch-leaving rate of individual *G. a. allenbyi* between the two experimental plots ( $p < .01$ ; Table 3). In sympatry, the effect of plot on the intrinsic patch-leaving rate was reversed ( $p < .01$ ; Table 4), and there was also a significant difference in the rate

**Table 5**  
Comparing patch residence times of *Gerbillus andersoni allenbyi* between the allopatric and the sympatric treatment

Covariate	Interaction between treatment and intrinsic patch-leaving rate ( <i>p</i> )	Interaction between treatment and rate of aggressive interactions ( <i>p</i> )
Time of year	.510	<b>.014</b>
Time of night	.170	<b>&lt;.001</b>
Cumulative foraging time	.110	.061
Microhabitat	.320	<b>.002</b>
<i>G. andersoni allenbyi</i> density	.490	<b>.003</b>
Sex	.090	<b>.005</b>
Competitive rank	<b>.023</b>	<b>.049</b>

The interaction of covariate effect and treatment with a pooled data set. Bold type indicates significant effects.

of aggressive interactions involving occupant *G. a. allenbyi* individuals ( $p < .01$ ; Table 4).

#### Sex

In allopatry, female *G. a. allenbyi* had a lower intrinsic patch-leaving rate than did male *G. a. allenbyi*; however, there was no significant difference in the rate of aggressive interactions between the two sexes ( $p = .02$  and  $p = .16$ , respectively; Table 3). In sympatry, this difference in the intrinsic patch-leaving rate between *G. a. allenbyi* sexes disappeared ( $p = .90$ ; Table 4).

#### Competitive rank

In allopatry, the competitive rank of occupant *G. a. allenbyi* individuals had a negative effect on the rate of aggressive interactions in which they were involved ( $p < .01$ ; Table 3). Specifically, the higher the competitive rank of the occupant individuals, the lower the rate of aggressive interactions in which they were involved (Figure 1c). However, in sympatry this pattern was not evident (Figure 1d). There was no significant effect of competitive rank on the intrinsic patch-leaving rate during both the allopatric ( $p = .62$ ; Table 3) and the sympatric treatment ( $p = .06$ ; Table 4).

#### Comparing the two treatments

For each covariate that differed between the allopatric and sympatric treatment, we tested whether the interaction term between covariate and treatment yielded a significant regression coefficient using the pooled data set. The effects of time of year, time of night, microhabitat, *G. a. allenbyi* density, sex, and competitive rank on the rate of aggressive interactions involving occupant *G. a. allenbyi* individuals varied significantly between the two treatments ( $p < .05$  for all variables; Table 5). In contrast, only the effect of competitive rank on the intrinsic patch-leaving rate of *G. a. allenbyi* varied between these treatments ( $p < .02$ ; Table 5).

#### *Gerbillus pyramidum*

We do not have data describing the behavior of *G. pyramidum* in allopatry that can be used as a reference point to its behavior in sympatry. Thus, we describe the results for this species in less detail.

We detected a significant decrease over the year in the intrinsic patch-leaving rate of *G. pyramidum* ( $p < .01$ ; Table 6). Interspecific density had a significant positive effect on the intrinsic patch-leaving rate of *G. pyramidum* ( $p = .04$ ; Table 6). In contrast, intraspecific density had a significant negative

**Table 6**  
Results of the competing risk analysis for *Gerbillus pyramidum* in sympatry

Covariate	Intrinsic patch-leaving rate		Rate of aggressive interactions	
	Regression coefficient ( $\beta$ )	<i>p</i>	Regression coefficient ( $\gamma$ )	<i>p</i>
Time of year	-0.004433	<b>.002</b>	0.0005023	.850
Time of night <sup>a</sup>	0.056317	.490	-0.8823262	<b>.016</b>
Cumulative foraging time	-0.000100	.240	0.0006311	.140
Microhabitat <sup>b</sup>	-0.105972	.300	-0.6659238	<b>.034</b>
<i>G. andersoni allenbyi</i> density	0.051201	<b>.041</b>	0.0971958	.400
<i>G. pyramidum</i> density	-0.381060	<b>.001</b>	0.1622041	.790
Plot	-0.449050	<b>.008</b>	0.5402600	.540
Competitive rank	0.091411	.730	-3.7844632	<b>.022</b>

Bold type indicates significant effects;  $df = 18$ ,  $p < .001$ , likelihood ratio test.

<sup>a</sup> First session = 0, second session = 1.

<sup>b</sup> Open = 0, bush = 1.

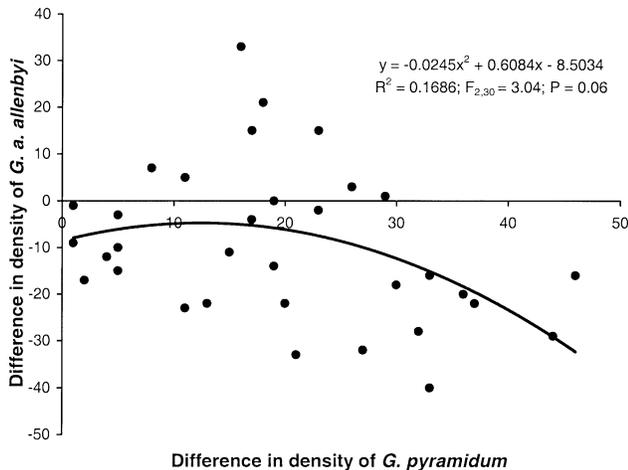
effect on this rate ( $p < .01$ ; Table 6). There was a significant difference in the intrinsic patch-leaving rate of *G. pyramidum* between the two experimental plots ( $p = .01$ ; Table 6).

The rate of aggressive interactions involving occupant *G. pyramidum* individuals was lower in the second session of the night ( $p = .02$ ; Table 6) and in seed trays located under bushes ( $p = .03$ ; Table 6). Occupant *G. pyramidum* individuals with high competitive ranks were involved in aggressive interactions at lower rates than those with low competitive ranks ( $p = .02$ ; Table 6).

## DISCUSSION

We observed patch-use behavior of *G. a. allenbyi* and *G. pyramidum* under field conditions and investigated how aggression and intrinsic decision-making interact to influence their patch residence times. We predicted that increased food patch quality should result in a decrease in the intrinsic patch-leaving rate and an increase in the rate of aggressive interactions involving the occupant individual. All significant effects of covariates with known influence on food patch quality (time of year, time of night, cumulative foraging time, and microhabitat) were consistent with these predictions (Tables 3, 4, and 6), indicating a trade-off between foraging and aggression as we demonstrate below.

In the sandy habitats of the Negev desert of Israel, as in many other desert ecosystems, most seeds are produced in the spring and are slowly depleted over the course of the summer. Our experiment was conducted from early spring (March) to early fall (September) in two consecutive years. During that period of the year, seed trays should gain importance over time. We therefore predicted that from spring to summer to fall, there would be a decrease in the intrinsic patch-leaving rate and an increase in the rate of aggressive interactions involving the occupant individual. The first prediction was realized for *G. pyramidum* in sympatry and the second for *G. a. allenbyi* in allopatry. Therefore, our data are partially consistent with the results of Brown et al. (1994), indicating a rapid decrease in the GUD of both gerbil species during that period of the year.



**Figure 2**

Effect of density differences of *Gerbillus pyramidum* on density differences of *G. andersoni allenbyi* between two adjacent plots, separated by a fence permeable for only *G. a. allenbyi* (data was taken from Abramsky et al., 1991). Because all differences on the x-axis are positive, positive y-values indicate positive association between the two species. The data show positive values at intermediate differences of *G. pyramidum*. The line shows a fit of a quadratic function.

Time of night could also influence food patch quality and, hence, patch-leaving behavior. Manipulation experiments have shown that both of our gerbil species prefer being active during the early part of the night (Ziv et al., 1993). This suggests that the value of seed trays should decrease during the night. We thus predicted that as the night wore on, there should be an increase in the intrinsic patch-leaving rate and a decrease in the rate of aggressive interactions involving the occupant individual. Both predictions were realized during the sympatric treatment, in which we observed an increase over the night hours in the intrinsic patch-leaving rate of *G. a. allenbyi* and a decrease in the rate of aggressive interactions involving occupant *G. pyramidum* individuals.

Cumulative foraging time, the total length of time that a given seed tray has been foraged on since placement in the field, is a measure of patch depletion. Therefore, one would expect to find, as our data indicated for *G. a. allenbyi* in sympatry, a reduction in the rate of aggressive interactions involving the occupant individual with an increase in cumulative foraging time.

Kotler et al. (1993b) found lower GUD for seed trays under bushes. Similarly, we found that in allopatry, the intrinsic patch-leaving rate of *G. a. allenbyi* was lower in seed trays located under bushes than those in the open. But in contrast to our expectations, we observed a reduction in the aggressive interactions involving occupant *G. pyramidum* individuals in seed trays located under bushes. We suggest that this be mainly owing to interspecific aggression avoidance behavior by *G. a. allenbyi*. However, because we do not have data describing the behavior of *G. pyramidum* in allopatry, we could not verify this point.

We anticipated that increasing population density should result in an increase in the rate of aggressive interactions involving the occupant individual. We found that this occurred only for *G. a. allenbyi* in allopatry. In sympatry, on the other hand, intraspecific density caused an increase in the intrinsic patch-leaving rate of occupant *G. a. allenbyi* individuals, but had no effect on the rate of aggressive interactions in which they were involved. Therefore, we suggest that, in the presence of *G. pyramidum*, intraspecific aggression among individual *G. a. allenbyi* becomes less important to their patch-use behavior.

Furthermore, when we compared the two treatments, we found that the rate of aggressive interactions involving occupant *G. a. allenbyi* individuals was lower in the sympatric than in the allopatric treatment (Figure 1b). In addition, in sympatry, more than 86% of the aggressive interactions involving occupant *G. a. allenbyi* individuals were interspecific ones (Ovadia, 1999). We thus interpret this to mean that the presence of *G. pyramidum* suppresses the aggression by *G. a. allenbyi*. This reduction in intraspecific aggression might be important for community dynamics and equilibria because it decreases both intra- and interspecific per capita effects on *G. a. allenbyi* and could therefore decrease the slope of its isocline. Habitat selection theory shows that such changes in the slope of the isocline could promote species coexistence (see Rosenzweig, 1991).

An overview of the covariate by treatment interactions indicated that almost all significant differences between allopatric and sympatric treatments included only the rate of aggressive interaction involving occupant *G. a. allenbyi* individuals (Table 5). This implies that in sympatric populations, patch-use behavior of *G. a. allenbyi* is mainly controlled by interspecific aggression. Our results are in accord with previous studies showing that this interference competition is the basis for spatial (Abramsky et al., 1990) and temporal (Ziv et al., 1993) activity segregation patterns, which promote the coexistence of these two gerbil species.

In allopatry, occupant *G. a. allenbyi* individuals with high competitive ranks were involved in aggressive interactions at a lower rate than those with low competitive ranks (Figure 1c). A similar pattern was detected for *G. pyramidum* in sympatry. There are two possible explanations for this relationship between aggression and competitive rank. The first is that surrounding individuals avoid the high-ranking occupant individual. The second is that our measure of competitive rank, proportion of aggressive interactions won by a given individual as occupant and intruder was negatively correlated with the total number of aggressive interactions involving that individual. Because we could not detect such negative correlation, we are confident that our findings indicate a response by the surrounding individuals.

This link between competitive rank and the rate of aggressive interactions could provide a possible explanation for the observed suppression in intraspecific aggression among individual *G. a. allenbyi* in sympatry. The fact that in sympatric populations, the competitive rank of occupant *G. a. allenbyi* individuals had no influence on the rate of aggressive interactions in which they were involved suggests that the *G. pyramidum* did not respond to the competitive rank of occupant *G. a. allenbyi* individuals. This lack of response might reduce the benefit individual *G. a. allenbyi* could gain from being aggressive, which in turn should have a negative effect on their tendency to initiate an aggressive interaction.

In an earlier study of habitat selection in these gerbils, Abramsky et al. (1990) found that habitat preference of *G. a. allenbyi* (defined as proportion of its activity in the preferred habitat) was negatively correlated with intra- and interspecific population densities, but positively correlated with the interaction term of these densities. The reason for this interaction was unclear, but our results provide an explanation. An increased density of the competitively dominant species, *G. pyramidum*, has a direct negative effect on the activity of *G. a. allenbyi* in the preferred habitat. However, it also has a subtle indirect positive effect because it suppresses intraspecific aggression of the competitively subordinate species. As we discussed earlier, this suppression may have a stabilizing effect on this small mammal community.

Abramsky et al. (1991) studied the competition of *G. pyramidum* on *G. a. allenbyi* in exactly the same experimental

system. They used species-specific gates to allow the free movement of only *G. a. allenbyi* between two 1-ha adjacent plots. They then measured equilibrium density of *G. a. allenbyi* for a wide range of experimentally controlled density differences of *G. pyramidum*. Their study showed that the per capita strength of interspecific competition by *G. pyramidum* on *G. a. allenbyi* changed with population density as predicted by habitat selection theory. However, a plot of the density differences of *G. a. allenbyi* against those of *G. pyramidum* reveals that most positive associations between these two species occurred at intermediate density differences of *G. pyramidum* (Figure 2). This pattern is not predicted by habitat selection theory, but can be explained using our results. Increasing density of *G. pyramidum* increased interspecific and decreased intraspecific aggressive interactions involving *G. a. allenbyi*. It is therefore conceivable that, at certain differences in density of *G. pyramidum*, the adverse effect of higher density of *G. pyramidum* through interspecific aggression was outweighed by the suppression of intraspecific aggression. This was most likely to occur at intermediate density differences of *G. pyramidum* because small differences might not alter the behavior of *G. a. allenbyi* and because large differences are likely to compensate for the decrease in intraspecific aggression.

### Conclusion

As a general pattern, increasing food patch quality results in a decrease in the intrinsic patch-leaving rate and an increase in the rate of aggressive interactions involving the occupant individual, indicating a trade-off between foraging and aggression. Additionally, in allopatry, occupant *G. a. allenbyi* individuals with high competitive ranks were involved in aggressive interactions at a lower rate than those with low competitive ranks. However, in sympatry, this pattern was detected only for *G. pyramidum*. We argue that the fact that in sympatry the other players in the system did not respond to the competitive ranks of occupant *G. a. allenbyi* individuals was fundamental, because it reduced the benefit of being aggressive and thereby reduced the amount of intraspecific aggression in that species. The fact that in sympatric populations the rate of aggressive interactions involving occupant *G. a. allenbyi* individuals was lower than in allopatry and did not increase with an increase in intraspecific density supports this assertion. This is an important finding because it has the potential to help us understand the factors that promote species coexistence.

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### REFERENCES

- Abramsky Z, Brand S, Rosenzweig ML, 1985. Geographical ecology of gerbilline rodents in sand dune habitats of Israel. *J Biogeogr* 12:363–372.
- Abramsky Z, Ovadia O, Rosenzweig ML, 1994. The shape of a *Gerbillus pyramidum* (Rodentia: Gerbillinae) isocline: an experimental field study. *Oikos* 69:318–326.
- Abramsky Z, Rosenzweig ML, Pinshow B, Brown JS, Kotler BP, Mitchell WA, 1990. Habitat selection: an experimental field test with two gerbil species. *Ecology* 71:2358–2369.
- Abramsky Z, Rosenzweig ML, Pinshow P, 1991. The shape of a gerbil isocline measured using principles of optimal habitat selection. *Ecology* 72:329–340.
- Abramsky Z, Rosenzweig ML, Subach A, 1992. The shape of a gerbil isocline: an experimental field study. *Oikos* 63:193–199.
- Bar Y, Abramsky Z, Gutterman Y, 1984. Diet of gerbilline rodents in the Israeli Desert. *J Arid Environ* 7:371–376.
- Brown JS, 1988. Patch use as an indicator of habitat preference, predation risk, and competition. *Behav Ecol Sociobiol* 22:37–34.
- Brown JS, Kotler BP, Mitchell WA, 1994. Foraging theory, patch use, and the structure of a Negev desert granivore community. *Ecology* 75:2286–2300.
- Brown JS, Morgan RA, Dow BD, 1992. Patch use under predation risk. II: a test with fox squirrels, *Sciurus niger*. *Ann Zool Fenn* 29:311–318.
- Charnov EL, 1976. Optimal foraging and the marginal value theorem. *Theor Popul Biol* 9:129–136.
- Cox DR, 1972. Regression models and life tables (with discussion). *J R Stat Soc B* 34:187–220.
- Cox DR, 1975. Partial likelihood. *Biometrika* 62:269–276.
- Danin A, 1978. Plant species diversity and plant succession in a sandy area in the Northern Negev. *Flora* 167:409–422.
- Fretwell SD, 1972. Populations in a seasonal environment. Princeton, New Jersey: Princeton University Press.
- Fryxell JM, Lundberg P, 1998. Individual behavior and community dynamics. New York: Chapman and Hall.
- Harrell F, Lee K, 1986. Verifying assumptions of the proportional hazards model. *Proc 11th Annual SAS User's Group Int* 11:823–828.
- Hosmer DW, Lemeshow S, 1999. Applied survival analysis: regression modeling of time to event data. New York: John Wiley & Sons.
- Kalbfleisch JD, Prentice RL, 1980. The statistical analysis of failure time data. New York: Wiley.
- Kotler BP, Blaustein L, Brown JS, 1992. Predator facilitation: the combined effect of snakes and owls on the foraging behavior of gerbils. *Ann Zool Fenn* 29:199–206.
- Kotler BP, Blaustein L, Dednam H, 1993a. The specter of predation: the effects of vipers on the foraging behavior of two gerbilline rodents. *Israel J Zool* 39:11–21.
- Kotler BP, Brown JS, Hasson O, 1991. Factors affecting gerbil foraging behavior and rates of owl predation. *Ecology* 72:2249–2260.
- Kotler BP, Brown JS, Mitchell WA, 1993b. Environmental factors affecting patch use in two species of gerbilline rodents. *J Mammal* 74:614–620.
- Kotler BP, Brown JS, Slotow RH, Goodfriend WL, Strauss M, 1993c. The influence of snakes on the foraging behavior of gerbils. *Oikos* 67:309–316.
- Kotler BP, Gross JE, Mitchell WA, 1994. Applying patch use in Nubian ibex to measure resource assessment ability, diet selection, indirect interactions between food plants, and predatory risk. *J Wild Manage* 58:300–308.
- Lin DY, Wei LJ, 1989. The robust inference for the Cox proportional hazards model. *J Am Stat Assoc* 84:1074–1079.
- Lunn M, McNeil D, 1995. Applying Cox regression to competing risks. *Biometrics* 51:524–532.
- Morris DW, Davidson DL, 2000. Optimally foraging mice match patch use with habitat differences in fitness. *Ecology* 81:2061–2066.
- Nonacs P, 2001. State dependent behavior and the marginal value theorem. *Behav Ecol* 12:71–83.
- Ovadia O, 1999. Integrating behavioral responses of individual *Gerbillus allenbyi* and *G. pyramidum* (Rodentia: Gerbillinae) with their measured population responses (Ph.D dissertation). Beer-Sheva: Ben-Gurion University of the Negev.
- Price MV, Correll RA, 2001. Depletion of seed patches by Merriam's kangaroo rats: are GUD assumptions met? *Ecol Lett* 4:334–343.
- Rosenzweig ML, 1991. Habitat selection and population interaction: the search for mechanism. *Am Nat* 137:S5–S28.
- Schoenfeld D, 1982. Partial residuals for the proportional hazards regression model. *Biometrika* 69:239–241.
- Ziv Y, Abramsky Z, Kotler BP, Subach A, 1993. Interference competition and temporal and habitat partitioning in two gerbil species. *Oikos* 66:237–246.
- Ziv Y, Kotler BP, Abramsky Z, Rosenzweig ML, 1995. Foraging efficiencies of competing rodents: why do gerbils exhibit shared-preference habitat selection? *Oikos* 73:260–268.