


Samson et al. (1992) analyzed 10 yr of ant and rodent data (1977–1987) from the Chihuahuan Desert site and found no evidence for either competition or facilitation between these taxa based on density responses to removals of either taxon. Their analyses of the plant community suggested a trade-off between exploitative competition for seeds during the summer compensated by rodent facilitation of winter plants preferred by ants.

Because of the importance of this system as an example of complex interactions, we analyzed an additional 5 yr of data (1988–1992) from this site for potential interactions between granivorous ants and rodents. The original rodents and ant removal treatments now have been continually maintained for 15 yr. In addition, a new set of removal treatments was initiated in 1988 (Heske et al. 1994). Because the long-term manipulation of the rodent community has produced significant changes in the plant communities among the original treatments that are not yet apparent in these new experimental plots (Brown and Heske 1990, Heske et al. 1994), we can compare ant numbers on the new (1988) and old (1977) experimental treatment plots to evaluate the possibility of indirect effects of rodents on ants through vegetation changes and habitat selection.

**Methods and Results**

The study site, containing 24, 50 × 50 m experimental plots, is located on the Cave Creek Bajada (bajada = an alluvial fan) near Portal, Arizona. See Brown and Munger (1985) and Davidson et al. (1985) for details of the study site, plots, experimental manipulations, and sampling methods.
For the present purposes, it is sufficient to focus on three experimental treatments: all rodents removed, all kangaroo rats (*Dipodomys*, three species) removed, and all granivorous ants removed. In the original experiments, begun in 1977 and continued to the present, there were two replicated plots of each treatment and two unmanipulated control plots. In 1988, two additional replicates of each of the above treatments (including controls) were initiated. This report is based on analyses of data collected from February 1988 through September 1992. Rodents have been censused at monthly intervals and numbers of ant colonies were counted once each year during peak activity after the beginning of summer rains. The data were analyzed using repeated-measures analysis of variance, using plots as replicates. We also examined the initial densities of ant colonies and rodent individuals on the experimental and control plots before the treatments were initiated.

We examined the response of both all rodents and just the small granivorous rodent species to the removal of ants. In both the 1977 and 1988 treatments, there was a trend toward higher rodent density on plots where ants had been removed, but the differences were not significant (Table 1). Because small granivorous rodents (which include all species in the genera Chaetodipus, Perognathus, Peromyscus, Reithrodontomys, and Baiomys) had substantial densities only on plots where kangaroo rats had been removed (Brown and Munger 1985, Heske et al. 1994), we controlled for the effects of kangaroo rats by comparing small granivore numbers on the two plots where both kangaroo rats and ants had been removed with the two plots where only kangaroo rats had been excluded. There was a nonsignificant trend of higher rodent densities on the 1977 ant removal plots but not on the 1988 plots (Table 1).

We restricted our analyses of ant responses to rodent removal to the three most common species of seed harvesters, *Pogonomyrmex desertorum*, *Pheidole xerophila*, and *Pheidole rugulosa* (called *Pheidole sitarchesis* in earlier papers). There were about twice as many colonies of *Pogonomyrmex desertorum* and *Pheidole rugulosa* on rodent removal plots than on control or kangaroo rat removal plots for both 1977 and 1988 treatments, but neither of these differences was significant (Table 1). *Pheidole xerophila* showed no consistent trend with respect to the treatments (Table 1).

Analysis of worker numbers for each species was similar to that of colonies, and is not presented. In addition, before the initiation of the treatments, there were either no differences in the abundances of rodents and ants among plots, or abundances were greater on control than removal plots. Thus, initial differences between plots cannot account for the above trends.

Table 1 show that both *Pheidole rugulosa* and *Pogonomyrmex desertorum* attained their highest densities on rodent removal plots. The major difference between the 1977 and 1988 rodent removal treatments is the dramatic increase in grass cover on the 1977 removal plots (Brown and Heske 1990). To investigate the response of ants to grass cover independent of the presence or absence of rodents, we calculated Spearman rank correlation coefficients between mean number of colonies and percentage of grass cover for grass data collected in both 1989 and 1992 for all plots at our site that were not ant removal treatments (*N* = 14 plots). Because ant data were collected annually during the 5-yr period but grass cover was measured only in 1989 and 1992, we made three sets of correlations: (1) only 1989 ant and grass data, (2) only 1992 ant and grass data, and (3) mean ant colonies for 1988 through 1992 and mean grass cover (1989 grass cover + 1992 grass cover)/2.

The number of *Pheidole rugulosa* colonies per plot was positively correlated with percentage of grass cover in all three sets of correlations (1989 only: *r* = 0.44, *P* = .06; 1992 only: *r* = 0.38, *P* = .09; mean 1988–1992: *r* = 0.55, *P* = .02; all one-tailed tests). In contrast, neither *Pheidole xerophila* nor *Pogonomyrmex desertorum* colony density showed any significant correlations with grass cover (all *P* values > .2).

**Discussion**

The most notable result was the positive correlation between the number of colonies of one ant species, *Pheidole rugulosa*, and the percentage of grass cover on the experimental plots. This implies an indirect effect between rodents and this species of ant similar to the interactions between kangaroo rats and some species of rodents and between rodents and birds at this site (Thompson et al. 1991, Heske et al. 1994).

Our results are similar to those reported by Davidson et al. (1985; see also Samson et al. 1992). Although the response of rodents to ant removal was again not statistically significant (Galindo 1986, Samson et al. 1992; this study), the consistency of the direction of the response indicates that it may still be biologically meaningful, especially since the small number of replicates at our site results in extremely low statistical power. Note, for instance, that although small granivorous rodents were over twice as abundant on the 1977 plots without ants, these differences were not statistically different (Table 1).

The response of ants was inconsistent among plots and treatments, and did not reveal any strong direct interactions (see also Samson et al. 1992). The apparent response of *Pheidole rugulosa* to rodent removals can be entirely explained by the correlation of this species with grass cover.
TABLE 1. Mean number of rodents or ant colonies per 50 × 50 m plot in the Chihuahuan Desert in response to experimental treatments and results of repeated-measures ANOVA testing for treatment effects. Treatments are as follows: C = control, -A = ant removal, -D = Dipodomys removal, -D-A = Dipodomys and ant removal, -R = all rodents removed. Year refers to initiation of treatment. N = 2 plots for each treatment; df for rodents = 1, 2; df for ants = 2, 3.

<table>
<thead>
<tr>
<th>Response group</th>
<th>Year</th>
<th>Treatment</th>
<th>Mean</th>
<th>F</th>
<th>P</th>
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<tr>
<td>All rodents</td>
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<td>C</td>
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<tr>
<td></td>
<td></td>
<td>-A</td>
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<td>0.07</td>
<td>.81</td>
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<td>1988</td>
<td>C</td>
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<td></td>
<td>.36</td>
</tr>
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<td></td>
<td></td>
<td>-A</td>
<td>5.5</td>
<td>1.42</td>
<td>.36</td>
</tr>
<tr>
<td>Small rodent granivores</td>
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<td>-D</td>
<td>1.8</td>
<td></td>
<td>.11</td>
</tr>
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<td></td>
<td></td>
<td>-D-A</td>
<td>3.7</td>
<td>8.0</td>
<td>.11</td>
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<tr>
<td></td>
<td>1988</td>
<td>-D</td>
<td>2.8</td>
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<td>.4</td>
</tr>
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<td></td>
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<td>-D-A</td>
<td>2.3</td>
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<td><em>Pogonomyrmex desertorum</em></td>
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<td></td>
<td>-R</td>
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<td>-D</td>
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<td>-R</td>
<td>7.9</td>
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<td>C</td>
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<td></td>
<td>-R</td>
<td>7.3</td>
<td>1.10</td>
<td>.44</td>
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</table>

We have no explanation for the apparent increase in number of active *Pheidole xerophila* workers in response to rodent removal, observed from 1977 to 1983 but not observed in either the original or new manipulations since 1988. The lower numbers of *Pogonomyrmex desertorum* colonies on rodent removal plots from 1977 to 1983 can perhaps be attributed to initial differences in abundance of these ants that existed before rodents were removed (Davidson et al. 1985: Fig. 6).

The interactions between rodents and ants in the Chihuahuan Desert is more complex than reported for the Sonoran Desert (Brown and Davidson 1977). After 15 yr of maintaining the experimental regimes, the data indicate that the major interactions between these taxa are indirectly mediated through vegetation (Samson et al. 1992, this study) rather than through direct competition for seed resources. This finding adds to the growing list of studies documenting the importance of indirect effects in ecological communities (e.g., Strauss 1991).

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FINDING CONFIDENCE LIMITS ON POPULATION GROWTH RATES: THREE REAL EXAMPLES REVISED

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Comparisons of estimated population growth rates to specific values (e.g., Lande 1988) or among species (e.g., Sarukhán and Gadgil 1974), populations (e.g., Martínez-Ramos et al. 1988), censuses (Bierzychudek 1982), or artificial conditions (e.g., Bridgham 1988) underlie the conclusions of many ecological, evolutionary, management, and conservation studies. Despite the practical and scientific interest of estimating population growth rates, however, confidence limits are rarely assigned to such estimated rates (see Caswell 1989, Alvarez-Buylla and Slatkin 1991). This may be in part because methods available depend on elaborate, computer-intensive procedures.

The mean and standard error of the population growth rate may be approximated using a Taylor’s series expansion (Daley 1979), and assuming a particular type of sampling distribution for the population rate one may use this analytic estimate to assign confidence limits. In a previous study (Alvarez-Buylla and Slatkin 1993) we used idealized examples to test the performance of this analytic approach and demonstrated that it provides reliable confidence limits for a wide range of ideal examples, provided coefficients of variation of demographic estimates are below 50%. To illustrate and test the results obtained from the ideal examples using real biological data, we selected three studies in which population growth rates are compared: to a particular value (Northern Spotted Owl example, Lande 1988), among different populations (Astrocaryum mexicanum palm, Martínez-Ramos et al. 1988), or among different years and populations (jack-in-the-pulpit herb, Bierzychudek 1982). We use the same Monte Carlo approach (sometimes called parametric bootstrap) developed in Alvarez-Buylla and Slatkin (1993) to test the analytic approximation for these three real examples and to estimate confidence limits for the population growth rates obtained in them, and we use such estimates to revise the ecological conclusions reached in each study. In the palm and herb examples the new conclusions contrast with those reached by the original studies.

\textbf{Methods and Materials}

Population growth rates were estimated with matrix projection models that relate the numbers of individuals in a particular age or stage category at time \( t \) (denoted by vector \( n_t \)) to that at time \( t + 1 \):

\[
N_{t+1} = AN_t, \tag{1}
\]

where \( A \) is the matrix of vital rates and its entries, \( a_{ij} \), determine the contribution of each individual in stage \( i \) to stage \( j \) in the next time step. For large \( t \) the constant population growth rate \( (\lambda = 1 \text{ or } > 1) \) will be equal to \( \lambda \), which is the largest positive eigenvalue of \( A \) (Caswell 1989). The elements of \( A \) are estimated from population studies (\( \hat{a}_{ij} \)) and each estimate, \( \bar{a}_{ij} \), is the sum of the actual value \( a_{ij} \) plus an unknown term, \( \epsilon_{ij} \), which is a random variable that represents the error made in estimating each \( a_{ij} \). If the standard errors of the estimates of the \( \hat{a}_{ij} \) are assumed to be small, and the estimates of the \( a_{ij} \) are not biased (hence \( E(\epsilon_{ij}) = 0 \)) it is possible to approximate \( \lambda \) by making a Taylor’s series expansion. For a particular data set, we denote the estimate of \( \lambda \) by \( \hat{\lambda} \) and approximate this \( \hat{\lambda} \) by means of a Taylor’s series expansion (Alvarez-Buylla and Slatkin 1991):

\[
E(\hat{\lambda}) \approx \lambda(a_{ij}); \tag{2}
\]

\[
\text{Var}(\hat{\lambda}) \approx \sum_i \sum_j \text{var}(\hat{a}_{ij}) \left( \frac{\partial \lambda}{\partial a_{ij}} \right)^2 + \sum_i \sum_j \sum_{i' \neq i} \sum_{j' \neq j} \text{cov}(\hat{a}_{ij}, \hat{a}_{i'j'}) \left( \frac{\partial \lambda}{\partial a_{ij}} \right) \left( \frac{\partial \lambda}{\partial a_{i'j'}} \right). \tag{3}
\]

Note that the notation here is slightly different from that in Alvarez-Buylla and Slatkin (1991 and 1993), but the analytic formulae are equivalent in the three

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