



Reply to Galindo

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control (13 vs. 11) and in 1974 the treatment plot of replicate 2 was 250% higher than its control plot (7 vs. 2). Because of the lack of pre-treatment data it is not possible to know if these differences represent a response to the treatments. The treatment grids had slightly higher numbers of rodents throughout the experiment, but the differences were very small. The average differences between treatments and controls were 1.2 (23%) and 0.61 (15%) individuals in replicates 1 and 2, respectively. Most small-mammal research projects have much less similarity between control plots. For example, Thompson (1982) working with plots of similar size and with a similar species (*Dipodomys merriami*) in the Mojave Desert reported differences of 0.54 (16%), 0.74 (19%), 0.85 (35%), 1.28 (39%), 1.39 (57%), and 2.14 (88%) individuals per plot in pairwise comparisons among four plots before any treatment had been applied.

So, is there actually a 20% difference between treatments and controls? If the censuses are averaged, the mean numbers of individuals present in treatments and controls, respectively, are 6.5 and 5.2 for the first replicate and 4.6 and 4.0 for the second replicate. These differences represent a 25% and a 15% difference (not increase) that is equivalent to an average of only one rodent individual divided among four species!

I conclude that the experiments in the Sonoran Desert do not show any density response of rodents to the removal of ants. In fact, the amount of replication would have to be greatly increased to differentiate between inherent variability of plots and small responses to treatments.

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REPLY TO GALINDO¹

James H. Brown² and Diane W. Davidson³

We agree with Galindo's main point that we erred in applying the Wilcoxon matched-pairs signed-ranks test to repeated samples of the same experimental plots in our original papers (Brown and Davidson 1977, Brown et al. 1979). We also admit that any rigorous reanalysis of the data probably will not sustain with a high level of statistical confidence our conclusion that rodents increased on plots from which ants had been removed. Like most other field experiments that were

conducted before 1980 on vertebrates, the rodent and ant experiments at issue here suffered from limited replication, and the statistical analyses incorrectly used repeated measures of the same plots ("pseudoreplication"; see Hurlbert 1984). Since becoming aware of these problems, we have tried to use greater replication and more rigorous statistical analyses (such as repeated measures ANOVA) in our subsequent work (e.g., Munger and Brown 1981, Davidson et al. 1984, 1985, Brown and Munger 1985, Brown et al. 1985).

Other points raised by Galindo require clarification. First, Galindo points out that our reanalysis of the number of ant colonies on rodent removal and control plots using repeated measures ANOVA (Davidson et al. 1984) showed a significant increase in the number of colonies in the absence of rodents only for ants of the genus *Pheidole*. This is correct and completely con-

sistent with results that we had reported earlier. Our most reliable estimate of ant foraging was the number of active colony entrances, and life histories of the species on our plots suggest that *Pheidole* are the only granivorous ants that regularly increase the number of nest entrances in response to relatively short-term changes in food abundance such as would have been caused by removing rodents. We have emphasized repeatedly that the response of ants to rodent removal was primarily due to an increase in activity of *Pheidole* colonies, and this has been documented independently by Bryant et al. (1976).

Second, there are two reasons why the repeated censuses of rodents on the two pairs of ant removal and control plots might not represent independent samples. One is that these are time series data, so the number of rodents counted in any given census may not have been independent of the numbers counted in previous censuses. Although theoretically this could be a serious problem, we do not think it was an important source of error in this experiment. There were very similar long-term fluctuations in rodent numbers on all plots (see Galindo 1986: fig. 1). This suggests that temporal trends in the rodents counted on each plot reflected primarily fluctuations in the large rodent population that inhabited the entire region surrounding the study area. The differences between plots in the numbers of individuals counted in the same census period probably reflected short-term adjustments in the small number of individual rodents temporarily foraging in these local patches. Recent analyses of rodent population dynamics on experimental plots (Zeng Z. and J. Brown, *personal observation*) suggest that individual animals can rapidly shift their home ranges and modify their foraging behavior to take advantage of changes in available food resources. The other reason why the repeated censuses might not represent independent samples is that the pairs of plots may not have been identical to start with, so that repeated comparisons of ant removal and control plots may simply have indicated an inherent difference in the attractiveness of these plots to foraging rodents rather than an effect of removing ants. We cannot completely exclude this possibility. We made every effort to choose indistinguishable patches of habitat and we assigned treatments at random, but we made no pretreatment censuses because funding did not permit the repeated sampling that would have been necessary to obtain reliable estimates of initial densities. The first rodent census cannot be used to estimate the baseline number of rodents using the plots before ants were removed, as Galindo suggests, because >4 mo had elapsed since the initiation of ant removal, providing ample opportunity for the presence or absence of ants to influence the availability of food for rodents before the first census. Nei-

ther of these two problems of statistical independence is addressed adequately by reanalyzing the two replicates separately using the Wilcoxon matched-pairs signed-ranks test, as Galindo does. His reanalyses are also based on repeated measurements of pairs of plots and are subject to the same problems in meeting the test's assumption that these measurements represent independent samples.

Third, Galindo points out that the magnitude of the differences in rodent numbers between ant removal and control plots is small (23% and 15% for replicates 1 and 2, respectively). We have emphasized repeatedly that the competitive interaction between rodents and ants is asymmetrical, so that the impact of rodents on ants is much greater than the reciprocal effect. That the magnitude of this effect may be less than some mammalian ecologists report for their "replicate" control plots or that it may be equivalent to only about one individual rodent per plot per census is largely irrelevant. Any significant reduction in foraging by rodents owing to competition from ants is interesting and potentially important. We agree that more extensively replicated experiments are desirable to test more rigorously for such competition and to assess more accurately its magnitude and its effects on desert ecosystems.

Finally, our conclusion that seed-eating desert rodents compete with ants has always rested on several additional lines of mutually consistent but largely independent evidence: (1) both groups of taxa are food limited, as indicated by increases in abundance and species diversity in a geographic gradient of increasing productivity and by temporal variations in population density (rodents) and foraging activity (ants) within local sites that were correlated with fluctuating seed availability; (2) rodents and ants overlapped substantially in diet and in the timing and location of foraging; (3) the two taxa complemented each other in depressing seed resource populations, as shown by much greater accumulation of seeds in the soil on plots where both taxa had been experimentally removed than where only rodents or ants had been excluded; and (4) ants increased on plots where rodents had been experimentally removed. Galindo rightly criticizes the statistical analysis that we used to infer that rodents increased on plots from which ants had been experimentally removed. But even though we can no longer place so much confidence in the analysis of this one experiment, the results are still consistent with our original interpretation. We urge those readers who are interested in these issues to read our original papers. We remain convinced that competitive interactions between distantly related taxa play major roles in the structure, function, and evolution of ecosystems. We believe that our research on granivorous desert rodents and ants

still provides sound justification for calling attention to the importance of these kinds of interactions.

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HOW COMPETITION FOR LIGHT AND NUTRIENTS AFFECTS SIZE VARIABILITY IN *IPOMOEA TRICOLOR* POPULATIONS¹

Jacob Weiner²

Because of the correlation between fitness (i.e., survivorship and fecundity) and size within plant populations, the determinants of size differences are of great interest. One of the ecological factors that affects size variability is competition, also termed interference. A recent review found that plants grown at higher densities showed greater size variability than plants grown at lower densities in 14 out of 16 published experiments (Weiner and Thomas 1986). Little is known about the mechanisms by which competition increases size variability. I advanced the hypotheses that competition for light is "asymmetric" and will increase the variability in plant size over that of noncompetitive situations, whereas competition for nutrients is "two-sided" and will reduce size variability (Weiner 1985). To test these

hypotheses I performed an experiment with the annual vine *Ipomoea tricolor* in which root and shoot competition were separated.

In "asymmetric" (Begon 1984) or "one-sided" competition large individuals are able to obtain more resources than their share (based on relative size) and to suppress the growth of smaller individuals. If plant competition is one-sided, plants grown with competition should show greater size inequality than plants grown without competition in the absence of density-dependent mortality. In two-sided competition, resources are shared equally or in proportion to size. If plant competition is two-sided, competing plants should show the same or lower size variability than noncompeting plants (Weiner and Thomas 1986). Thus, symmetry or asymmetry is a characteristic of among-individual competition that can be observed at the population level.

Materials and Methods

Populations of *Ipomoea tricolor* Cav. var. "Pearly Gates" were grown under four competitive regimes. These were (1) no competition: one individual per container, with one stake, which it climbed; (2) shoot competition only: eight individuals, each in its own container, placed in a closed circle around one stake, which all eight plants climbed; (3) root competition only: eight