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AN EXPERIMENTAL STUDY OF DIFFUSE COMPETITION IN HARVESTER ANTS

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In a recent summary of the literature on field experimental studies of competition, Schoener (1983) found evidence for exploitative and/or interference competition (at approximately equal frequencies) in 90% of the more than 150 studies examined and in 76% of the species included in these studies. Despite this overwhelming evidence for the pervasive importance of both forms of competition in natural communities, there is as yet no experimental support for the existence of *diffuse competition,* broadly defined by MacArthur (1972, p. 45) as "competition by a constellation of species." Treating species' interactions with multiple competitors in a simple additive way, MacArthur concluded that, unless niche overlaps were simultaneously reduced, individual species would invariably be disadvantaged by increases in the number of coexisting species. In contrast, nonmanipulative empirical studies have suggested that particular species may be either restricted (Terborgh 1971; Pianka 1974) or facilitated (Lawlor 1979; Davidson 1980) by the effects of diffuse competition.

Which of these two outcomes occurs should be determined by the relative magnitudes of direct and indirect pathways of interspecific interaction (Levine 1976; Lawlor 1979). For example, consider two coexisting competitors, A and B, to which species C, a competitor of both species, is added (fig. 1). Species C will both directly inhibit B and indirectly facilitate this species by suppressing A. In the absence of higher-order interactions (e.g., Case and Bender 1981), the net effect of C on B should equal the arithmetic sum of these direct and indirect interactions.

Here I test earlier predictions (Davidson 1980) about the relative magnitudes of direct and indirect pathways of interaction among three species of Chihuahuan Desert harvester ants. *Pogonomyrmex rugosus* (mean worker body length = 9.2 mm), *Po. desertorum* (7.0 mm), and *Pheidole xerophila* (2.3 mm) commonly coexist in the relatively homogeneous desert scrub habitat on the Cave Creek alluvial plain of the Chiricahua Mountains, approximately 6.5 km east of Portal (Cochise Co.), Arizona. All three species have relatively generalized and somewhat overlapping diets. Data from both nonmanipulative and experimental studies suggest that populations of desert harvester ants commonly may be regulated by

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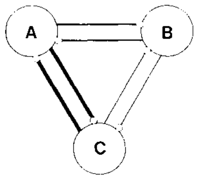

FIG. 1.—Competition among 3 hypothetical species of consumers (modified after Levine [1976]). Line width is directly proportional to intensity of competitive interaction. Although the pairwise interaction between species C and B is competitive, C actually increases the population growth rate of B by suppressing that of A.

their food supply and by the abundances of competing species (Davidson et al. 1985; reviewed in Davidson et al. 1980).

Because the worker body sizes of these ants are highly correlated with the sizes of seeds used (Davidson 1977), interspecific resource competition is likely to be most intense between species most similar in body size. *Pogonomyrmex desertorum* and *Po. rugosus* differ relatively little in size, and strong interference interactions, which are readily observed between these species, give rise to regular interspecific nest spacing and significantly lower-than-expected spatial overlap between foraging workers of the two congeners (Davidson 1977). Approximately 80% of interactions on census baits are resolved in favor of the larger species (Davidson 1980). Although *Po. desertorum* workers are more than three times the size of *Ph. xerophila* and specialize to some extent on different size classes of seeds, they collect many of the same seed species. These two harvester ants are thought to interact by exploitative competition that is reciprocal and of similar intensity for both species (Davidson 1980). Finally, *Po. rugosus* and *Ph. xerophila* differ in body size by a factor of 4. Dietary overlap between these two species is low and concentrated in resource classes characterized by small seeds that are clustered densely in fruiting heads. While the larger *Po. rugosus* workers gather whole fruiting heads early in the fruiting season, they do not collect the isolated small seeds dispersed from these heads. In contrast, *Pheidole* workers are too small to gather fruiting heads, but forage extensively on isolated small seeds.

Indirect facilitation, mediated through competitive interactions, may account for patterns in the local distribution and abundance of these three ant species. I (Davidson 1980) estimated the magnitudes of interference and exploitative interactions in this harvester ant community and used the matrix inversion technique of Levine (1976) to predict the net result of direct and indirect pathways of interspecific interaction. I concluded that, by suppressing populations of the intermediate-size *Po. desertorum, Po. rugosus* should have a strong net facilitative effect on *Ph. xerophila.* I predicted and found (1) a negative correlation in the abundances of *Po. rugosus* and *Po. desertorum* ($P < 0.01$); (2) a negative correlation in the densities of *Po. desertorum* and *Ph. xerophila* ($P < 0.05$); and (3) a positive correlation in the abundances of *Po. rugosus* and *Ph. xerophila* ($P < 0.01$) across 23 $\frac{1}{4}$-ha plots, where ants were censused as part of an extensive experimental study. These species abundance patterns are consistent with the interaction structure depicted in figure 1, but experiments are necessary to exclude the alternative hypothesis that the patterns are determined by habitat selection with respect to some subtle, undetected habitat feature. In this paper I report the results of a 5-yr experimental study established to distinguish between the alternative explanations.

METHODS

In July 1978, I initiated experiments at the site of the original analysis of exploitative and interference interactions. A detailed description of this Chihuahuan Desert locality can be found in Davidson (1980). Prior to establishment of experimental treatments, colonies of *Pogonomyrmex desertorum* and *Pheidole xerophila* were censused to a distance of 12 m from each of four *Po. rugosus* colonies located within the $\frac{1}{4}$-ha study plot. Workers of *Po. rugosus* commonly forage over distances as great as 15 m, and circular quadrats centered at nest entrances and 12 m in radius surrounded the areas most strongly influenced by colony foraging. Two *Po. rugosus* colonies, chosen at random from the four, were removed with repeated local application of an insecticide (AMDRO, Allied Chemical Corporation) to this species' nest mounds and foraging columns. The remaining two colonies served as unmanipulated controls. Thereafter, ants were censused once annually on the four plots during July and August when summer rains stimulated high levels of ant activity and nest excavation made colonies most conspicuous. Nest entrances within 0.5 m of one another were assumed to represent the same colony, while those separated by distances greater than this somewhat arbitrary threshold were scored as belonging to different colonies (see Brown et al. [1979] for justification).

Repeated Measures ANOVA (Biomedical Computer Programs, BMDP2V) was used to calculate whether trends in the densities of colonies differed through time on treatment and control plots. Directions of changes in species' densities were determined graphically.

RESULTS

Colony densities exhibited significantly different trends through time on experimental and control plots for both *Pogonomyrmex desertorum* and *Pheidole xerophila* ($P < 0.04$ and 0.03, respectively, in Repeated Measures ANOVA). These differences are largely attributable to an increase in populations of *Po. desertorum* on *Po. rugosus* removal plots (1978–1980) and a subsequent decline in densities of *Ph. xerophila* (predominantly after 1980) in relation to populations of conspecifics on control plots (figs. 2*a* and 2*b*, respectively).

DISCUSSION

Over the 5-yr term of these experiments, ant populations changed in accordance with predictions. Densities of *Pogonomyrmex desertorum* colonies increased differentially on plots from which its interference competitor, *Po. rugosus,* had been removed. On these same plots, *Pheidole xerophila,* the hypothesized ex-

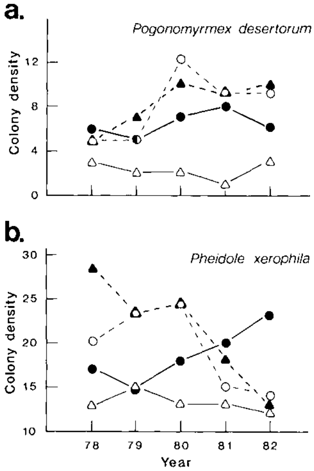

FIG. 2.—Colony densities of harvester ants: *a*, *Pogonomyrmex desertorum* and *b*, *Pheidole xerophila* on ~ 452 m^2 circular plots centered on *Po. rugosus* colonies which are extant (solid lines = control plots) or were removed in July 1978 (dotted lines).

ploitative competitor of *Po. desertorum*, later showed the anticipated population decline in relation to colony densities on control plots. The ordering of these two events supports the hypothesis that the beneficial effect of *Po. rugosus* on *Ph. xerophila* is mediated through the suppression of *Po. desertorum*.

While it is possible that the measured density responses result from interactions mediated through alternative pathways involving neglected species (e.g., the recent caution by Bender et al. [1984]), this seems unlikely here. Other experiments in the immediate proximity of the study reported here show that ant removal has no measurable effect on populations of seed-eating rodents (Davidson et al. 1985). Thus, ant responses to the removal of *Po. rugosus* are not likely to have been related to changes in the density or foraging behavior of rodents, nor of avian granivores, which search for food over extensive areas and do not readily locate small patches where resources are concentrated (Mares and Rosenzweig 1978; Morton, in press). Ant responses are also unlikely to have been mediated through populations of *Phrynosoma* lizards, the primary predators at our site. Individual ant colonies rapidly reduce or cease activity when losing workers to these lizards (Munger 1984), and relatively small and local changes in colony densities are unlikely to lead to significant functional or numerical responses in these widely foraging predators. Finally, it is possible that the dynamics of resource species have influenced the responses of ants to the experimental treatment. If, for example, large-seeded annual plants increased in density when *Po. rugosus* was removed, competitively superior large-seeded annuals may have gradually excluded small-seeded species (e.g., Inouye 1982; Davidson et al. 1984) and reduced the resource base for the small-bodied *Pheidole*. However, extensive overlap in the sizes of seeds taken by *Po. rugosus* and *Po. desertorum* (Davidson 1977) suggests that increased foraging by *Po. desertorum* on *Po. rugosus* removal plots should have compensated for any increase in the densities of large seeds.

It is useful to try to evaluate elements of the model (Davidson 1980) that may have been essential to its success in predicting experimental results. The model assumed that (1) species were present at equilibrium abundances determined by their food supply on the study site; (2) at these abundances, species interactions could be represented by approximately linear functions; (3) measures of dietary overlap, discounted by resource availability, were positively correlated with the intensity of resource competition; and (4) there were no higher-order interactions among the harvester ants. Because species-removal experiments cause a major departure from equilibrium, the experimental design used here imposed a further assumption: (5) that species interactions far from equilibrium were similar to those near equilibrium (Lawlor 1979). It is unlikely that any of these assumptions are precisely true or that, in aggregate, they are unique in predicting the observed outcome of experiments. The utility of the model in specifying the broad outcome of experimental results may rest largely on its incorporation of the strong pairwise interactions between *Po. rugosus* and *Po. desertorum* and between the latter species and *Ph. xerophila.* If this is true, the correspondence between the theory and its test may be most dependent on assumption (3), an assumption that appears to be well supported in other experimental studies of competition (Schoener 1983). Bender et al. (1984) caution that actual mechanistic interspecific interaction coefficients are very difficult to estimate from perturbation experiments and can only be estimated from spatial correlations in species abundances under unusual circumstances. This and the earlier study at the same site suggest, however, that independently derived estimates of interspecific interactions may be useful in predicting both community dynamics in perturbation experiments and patterns in the relative abundance of species in unmanipulated communities.

The analysis of exploitative and interference competition among these ants predicted that competition between *Po. desertorum* and *Ph. xerophila* should be reciprocal, i.e., an increase in either one should harm the other. In conjunction with results reported elsewhere, data from the present study suggest that this might be so. Davidson et al. (1985) documented a significant decline in *Po. desertorum* populations on plots where the activities and/or within-colony worker populations of *Ph. xerophila* had previously increased in response to rodent removal. Reciprocal, or symmetric, competition would be noteworthy in view of its apparent rarity in nature (Connell 1983; Schoener 1983). Unfortunately, however, we cannot exclude an alternative explanation, that rodent removal affected colony densities of *Po. desertorum* primarily by changing the absolute or relative abundances of resource species.

The paucity of well-documented examples of diffuse competition makes it difficult to assess its role in regulating organismal distribution and abundance and in determining patterns of coexistence among competitors. Because such interactions are indirect and mediated sequentially through several species populations, studies longer than the relatively brief term of most field experiments (2–3 yr in Connell [1983] and Schoener [1983]) will likely be necessary to provide a data base adequate for generalization. Results of this study suggest, however, that body-size differences may be good predictors of indirect pathways among closely related and competing species if, as in harvester ants, these differences are well correlated with the intensity of interspecific competition. Thus, it may be worthwhile to look for facilitation of small species by large species in the presence of a competitor of medium body size. Indirect pathways including such unrelated competitors as ants and rodents (possible examples are discussed by Munger and Brown [1981] and Davidson et al. [1984]) are more difficult to anticipate, because these groups differ in many ways that are likely to affect resource competition.

SUMMARY

Experiments carried out over a 5-yr period in the Chihuahuan Desert support the a priori prediction of diffuse competition between two species of harvester ants. Despite dietary overlap between a large species (*Pogonomyrmex rugosus*) and a small species (*Pheidole xerophila*), the large species facilitates the small species indirectly by suppressing populations of an intermediate-size species (*Pogonomyrmex desertorum*). Although similar indirect interactions may occur frequently in natural communities and be predictable on the basis of body size, very long term studies may be necessary to demonstrate their effects experimentally.

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