

COMPETITION MEDIATING THE OUTCOME OF A MUTUALISM:
PROTECTIVE SERVICES OF ANTS AS A LIMITING RESOURCE
FOR MEMBRACIDS

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Abstract.—Although competition for mutualists is known to be an influential force in plant-animal interactions, its importance in animal-animal associations is largely unexplored. Here, we demonstrate that phloem-feeding membracids (*Publilia modesta*) compete intraspecifically for the protective services of an ant mutualist (*Formica altipetens*). By experimentally increasing membracid densities in the field, we observed three negative effects due to competition for ants: (1) a 45%–59% reduction in the number of ants tending membracid aggregations, (2) a 63% increase in the abundance of a predatory salticid spider (*Pellenes* sp.), and (3) a 59% reduction in the mean number of membracid nymphs per plant. In total, the loss of protective services due to competition for mutualists translated into a 92% decrease in the production of newly enclosed membracid adults. These findings provide the first experimental demonstration that animal species compete for mutualists. In addition, our work indicates that mutualisms can be strongly influenced by the local biotic neighborhoods in which they occur and thus may be far more variable than previously thought.

Although it is generally accepted that competition can be an important force operating in natural communities (see Connell 1983; Schoener 1983), comparatively few studies have examined the hypothesis that species compete for the services provided by mutualists (Thompson 1982; Rathcke 1983; Waser 1983; Addicott 1985). Most of the research on this topic has involved the possibility that flowering plants compete with each other for the services of animal pollinators (Robertson 1895; Free 1968; Levin and Anderson 1970; Mosquin 1971; Heinrich 1975*a*, 1975*b*; Waser 1978, 1983; Brown and Kodric-Brown 1979; Pleasants 1980; Zimmerman 1980; Kephart 1983; Rathcke 1983, 1988; Campbell 1985*a*, 1985*b*; Campbell and Motten 1985). Additional studies have evaluated the hypothesis that flowering plant species benefit each other through pollinator sharing (Heinrich and Raven 1972; Brown and Kodric-Brown 1979; Waser and Real 1979; Schemske 1981; Rathcke 1983; Rathcke and Lacy 1985).

Few studies have addressed competition for mutualists in nonpollination systems, and no study has experimentally examined the hypothesis that such competition occurs in mutualisms between animal species. Davidson and Morton (1981) present correlative data indicating that two plant species compete for the services of seed-dispersing ants. Buckley (1983) provides experimental data suggesting

that plants bearing extrafloral nectaries compete with membracids for the services of ants. Addicott (1978) and Cushman and Addicott (1989) provide observational and unreplicated experimental data suggesting that aphids compete for the services of ants.

Here, we focus on homopteran-ant associations and argue that the mutualistic services provided by ants to homopterans are crucial resources that can be limiting and form the basis for competition. As a result, the outcome of these mutualistic interactions can be mediated by intra- and interspecific competition. In such insect associations, ants tend phloem-feeding homopterans (primarily aphids, membracids, and scales) and harvest their energy-rich excretions ("honeydew"). Through their tending, ants can provide a range of beneficial services to homopterans, the most frequently cited being protection from natural enemies (Nixon 1951; Way 1963; Buckley 1987).

In this article, we experimentally examine the hypothesis that a homopteran (the membracid *Publilia modesta*) competes intraspecifically for the services provided by an ant mutualist (*Formica altipetens*). Two years of manipulative experiments have already shown that *P. modesta* significantly benefits from being tended by *F. altipetens* (Cushman and Whitham 1989). Here, we assert that the spatial arrangement of homopteran aggregations feeding on neighboring plants strongly influences the strength of the mutualism. We evaluate two conditions that must be met in order to support this contention. First, homopteran aggregations on neighboring plants must reduce the number of ants that each attracts, as might be the case if homopterans on neighboring host plants were tended by the same ant colony. Second, reduction in the number of tending ants must reduce homopteran fitness.

This latter condition involves subtleties that demand further clarification. While numerous studies have used ant-exclusion experiments to demonstrate that homopteran species can benefit from ant tending (see Buckley 1987), the complete exclusion of ants rarely occurs in nature. More realistically, the number of ants tending homopterans varies in space and time in response to numerous factors, including variation in honeydew quality and quantity (Sudd and Sudd 1985), distance of homopterans from servicing ant nests (McEvoy 1979; Sudd 1983; see also Inouye and Taylor 1979), nutritional status of ant colonies (Wilson 1971), and the availability of alternative resources for ants. Inouye and Taylor (1979) clearly demonstrated the importance of ant tending *level* for a herbaceous composite bearing extrafloral nectaries, as predispersal seed predation significantly decreased with increasing numbers of tending ants (see also Messina 1981; Barton 1986). However, only Cushman and Addicott (1989) have examined the effect of such variability on homopteran fitness, and no study has experimentally addressed this topic.

STUDY SITE AND ORGANISMS

The study was conducted at Fern Mountain Ranch (2,700 m elevation), located in Hart Prairie 40 km northwest of Flagstaff, Arizona. *Publilia modesta* is a

sexually reproducing and univoltine homopteran found throughout the western United States (Kopp and Yonke 1973). In northern Arizona, this homopteran feeds on a wide range of herbaceous perennial composites and is most abundant on *Helenium* (= *Dugaldia*) *hoopesii*, which commonly forms asexually derived aggregations (Cassady 1940). In this article, we focus exclusively on membracid-ant interactions occurring on *H. hoopesii*. Adult membracids overwinter in the leaf litter and emerge in the spring to mate. Females lay 20–40 eggs into the leaves and stems of the host plant, and aggregations of nymphs begin to appear in late June. Nymphs are much less mobile than adults and complete their 25–40-d developmental period on the natal plant.

Membracid nymphs and adults are actively tended by four ant species at our study site. Here, we consider only the most abundant ant, *Formica altipetens*, which tends *P. modesta* from May to September. A major predator of membracids at the study area is a salticid spider, *Pellenes* sp. (= *Habronattus*). This generalist predator was frequently observed feeding on membracid nymphs but rarely on the more agile and sclerotized adults. During the summers of 1985–1988, we observed an average of one spider for every five membracid-infested plants. No other natural enemies were commonly observed with *P. modesta* during this study.

METHODS

If competition for ant mutualists is to occur in nature, membracid aggregations must be common and in sufficient proximity to each other that ant services are limited. In 1988, we located and marked all membracid-infested *Helenium* ramets within our 50 × 30-m study plot and determined the distance separating all neighboring pairs.

To address the hypothesis that membracid aggregations on neighboring plants reduce the number of ants that each attracts, we performed two 9-d addition/removal field experiments during July and August of 1987. For days 1–3 of the first experiment, we monitored the number of ants tending 20 randomly selected membracid-infested field plants. Because the foraging behavior of ants can be temporally variable (see Sudd and Franks 1987; J. H. Cushman, personal observation), for all experiments we monitored tending levels four times each day to obtain daily mean tending levels for each infested field plant. At the end of day 3, we randomly assigned infested field plants to control and experimental treatments and added two membracid-infested potted *Helenium* plants 50 cm away from each experimental plant. Each potted plant was infested with from 70 to 100 membracid nymphs. During days 4–6, we monitored the number of ants tending infested field plants as a function of the presence or absence of these potential competitors. At the end of day 6, we removed infested potted plants from the neighborhoods of experimental plants, and on days 7–9 we again monitored the number of ants tending all field plants. This latter removal was done to determine whether tending levels would return to that of the premanipulation period. To eliminate the possibility that differences in microsite and/or host plant

genotype were responsible for the observed results in this first experiment, we reversed treatment and control plants and repeated the 9-d experiment as described above.

In 1988, we experimentally evaluated the effect of potential competitors on the abundance of mutualistic ants, membracids (nymphs, overwintering adults, and newly eclosed adults), and predatory salticid spiders (*Pellenes* sp.). In this experiment, we randomly selected 32 membracid-infested field plants and randomly assigned each plant to a control or experimental treatment. The treatment consisted of placing two infested potted plants 50 cm away from each experimental field plant for 21 d. As before, membracid densities on the potted plants ranged from 70 to 100 per plant. During this period, we monitored the number of nymphs, overwintering adults (second year), newly eclosed adults (first year), and salticid spiders on field plants as a function of the presence or absence of potential competitors.

With one exception (the data set involving newly eclosed adults), we evaluated all data sets presented in this article with repeated-measure ANOVAs using the BMDP-2V statistical package (Dixon et al. 1985). In all cases, we used neighbor treatment (presence or absence of infested potted-plant neighbors) as the grouping factor and time as the repeated measure. In all but one analysis, we present and discuss the treatment-by-time interaction terms (for a brief discussion of repeated-measure analyses and interaction terms, see Cushman and Whitham 1989). In the analysis of the spider abundance data, the treatment-by-time interaction term was not significant, and we thus report the treatment term. We performed square-root transformations on the spider data to stabilize treatment variances for the statistical analyses. We present untransformed data in figure 3C.

RESULTS

At the Fern Mountain study site, membracid aggregations are quite common and naturally occur in close proximity. We found 164 infested ramets in the 50 × 30-m study plot and determined the mean distance separating neighboring infested ramets to be 81.02 ± 3.96 cm (± 1 SE; fig. 1). Figure 1 also illustrates that 30.49% of all infested plants were within 50 cm of a neighboring membracid aggregation. These results suggest that the potted-plant manipulations performed in 1987 and 1988 mimic natural densities and spatial arrangements.

Both experiments in 1987 documented that membracid aggregations on neighboring host plants significantly reduced the number of ants that each attracted (fig. 2; table 1). During the premanipulation periods (days 1–3 of each experiment), tending levels on control and experimental infested plants were not significantly different. However, when infested potted plants were added, the mean number of ants tending membracids on experimental field plants decreased by 45% (fig. 2A) and 52% (fig. 2B) relative to control plants. Specifically, a portion of the ants previously tending membracids on experimental field plants began tending membracids on potted plants (ants do not tend uninfested *Helenium* plants; J. H. Cushman, personal observation). When the potential competitors were removed for the last 3 d of each experiment, the mean number of ants

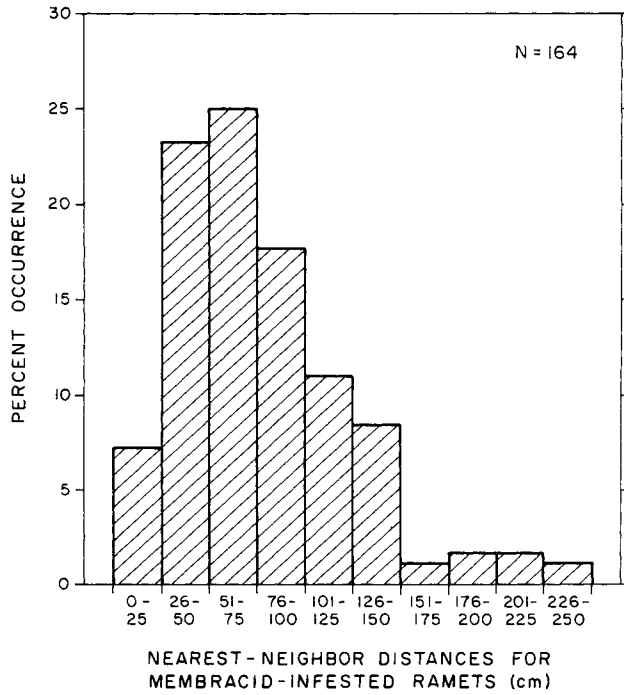


FIG. 1.—The percent occurrence of all nearest-neighbor distances for membracid-infested ramets.

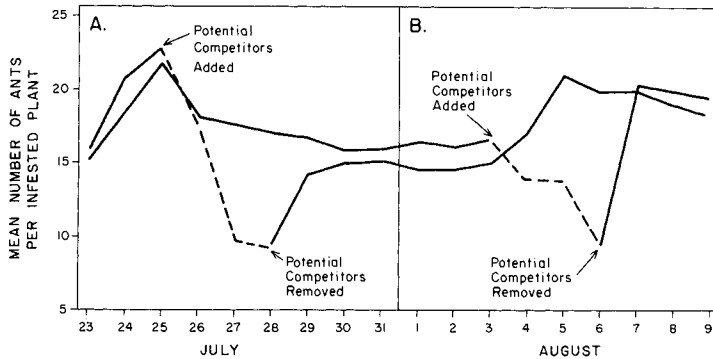


FIG. 2.—The mean number of ants (*Formica altipetens*) tending membracids (*Publilia modesta*) on field plants through time as a function of the presence or absence of neighboring membracid-infested potted plants. A, July 1987; B, August 1987.

TABLE 1
 REPEATED-MEASURE ANOVA TABLES FOR THE 1987 AND 1988 EXPERIMENTS

| Experiment/Source | Sum of Squares | df | Mean Square | <i>F</i> | <i>P</i> |
|-------------------|----------------|-----|-------------|----------|----------|
| 1987 experiment: | | | | | |
| July: | | | | | |
| Treatment × time | 514.86 | 8 | 64.36 | 3.32 | .002 |
| Error | 2,794.46 | 144 | 19.41 | | |
| August: | | | | | |
| Treatment × time | 873.39 | 8 | 109.17 | 8.03 | <.0001 |
| Error | 1,950.75 | 144 | 13.55 | | |
| 1988 experiment: | | | | | |
| Ants: | | | | | |
| Treatment × time | 1,456.31 | 6 | 242.72 | 7.32 | <.0001 |
| Error | 5,971.57 | 180 | 33.18 | | |
| Spiders: | | | | | |
| Treatment only | 2.26 | 1 | 2.26 | 11.56 | .002 |
| Error | 5.86 | 30 | .20 | | |
| Nymphs: | | | | | |
| Treatment × time | 123,316.94 | 3 | 61,010.69 | 4.51 | .005 |
| Error | 821,099.50 | 90 | 9,123.33 | | |
| Adults*: | | | | | |
| Treatment × time | 8.21 | 3 | 2.74 | .96 | .414 |
| Error | 255.93 | 90 | 2.84 | | |

* Second-year adults.

tending membracids on experimental plants increased by 39% (fig. 2A) and 53% (fig. 2B) relative to controls. This increase resulted from tending ants' being forced off membracid-infested potted plants and subsequently returning to membracids on experimental field plants. The similar outcomes of the first (fig. 2A) and second (fig. 2B) experiments demonstrate that, if variation in microsite and/or host plant genotype influences the behavior of ants toward membracids, such effects are small relative to the treatment effects.

In just 21 d, a 19.5% increase in the number of membracid-infested plants in our study area resulted in a 59% decrease in the mean number of tending ants per membracid-infested plant relative to controls (fig. 3A; table 1). We judged the experimental increases in membracid densities (through the addition of infested potted plants) to be realistic, as they were within the normal range of fluctuations observed in the field during 1985–1988 (J. H. Cushman, personal observation).

Associated with the reduction in ant tending levels, we observed a 63% increase in the mean number of predatory salticid spiders per membracid-infested plant relative to controls (fig. 3B; table 1). This increase occurred rapidly, unlike other response variables from the 1988 experiment (ants, nymphs, and adults), and the treatment-by-time interaction term was not significant ($P = .17$).

Corresponding to a decrease in tending levels and an increase in spiders, we observed a dramatic decline in the abundance of membracid nymphs and production of newly eclosed adults. The changes in abundance of protective ants and predatory spiders were associated with a 59% decrease in the mean number of membracid nymphs per plant (fig. 3C; table 1). The significant decrease in nymphs

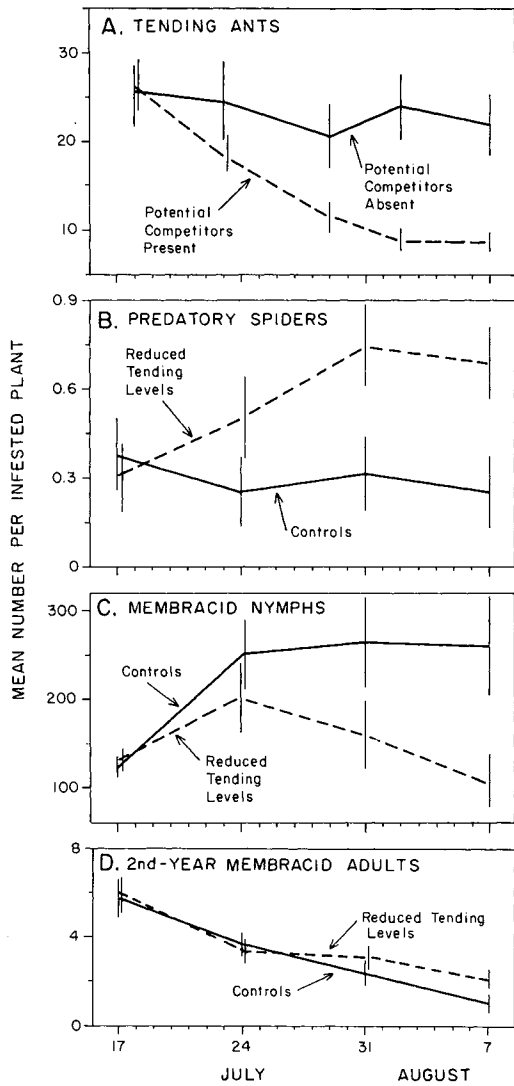


FIG. 3.—The effect of reduced number of tending ants (A) on the mean number of predatory salticid spiders (*Pellenes* sp.) per membracid-infested plant through time (B), the mean number of membracid nymphs per plant through time (C), and the mean number of overwintering adults per plant through time (D).

on experimental host plants translated into a 92% decrease in the mean number of newly eclosed adults produced per plant relative to controls (fig. 4; Mann-Whitney *U*-test, $P < .0005$).

We were unable to detect an effect of reduced numbers of ants on the abundance of overwintering adults (fig. 3D; table 1). Although these second-year adults do not directly benefit from being tended by ants, they benefit from tending indirectly because their offspring are positively influenced by ants (figs. 3, 4).

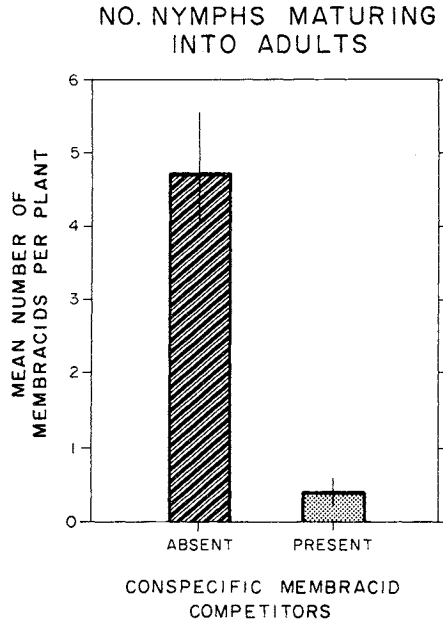


FIG. 4.—The mean number of membracid nymphs (*Publilia modesta*) maturing into adults on field plants after 21 d of the presence or absence of experimentally added membracid competitors.

This same result was also found for *Publilia modesta* when ants were completely excluded (Cushman and Whitham 1989).

DISCUSSION

We have provided the first experimental support for the hypothesis that animals compete for the protective services of mutualists. Membracid aggregations on neighboring host plants occur in close proximity and, as a result, reduce the number of ants that each attracts. This reduction is, in turn, associated with an increased abundance of predators and a decreased abundance of membracid nymphs and newly eclosed adults. These results demonstrate that competition can mediate the dynamics of an animal mutualism. In addition, this study departs from previous research on homopteran-ant interactions by performing ant-reduction experiments, rather than less realistic ant-exclusion experiments (i.e., focusing on the relationship between ant tending *level* and homopteran fitness; see also Messina 1981).

Fate of Competing Membracids

As a result of membracid competition, ants were reduced in abundance (fig. 3A), salticid spiders increased (fig. 3B), and rates of predation presumably increased for membracid nymphs. Field observations from 1985 to 1988 offer support for this contention; we observed 38 events in which salticid spiders preyed

on membracid nymphs and, in over 85% of these cases, ants were either absent or, more commonly, in low abundance. When tending levels were reduced, nymphs also fed less, exhibited increased movement on the host plant, and sometimes even left the host, although this latter behavior occurred very infrequently (J. H. Cushman, personal observation). Thus, we hypothesize that the major service provided by ants to membracid nymphs is protection from predators and that this service is reduced by competition. Ants may also benefit nymphs by increasing feeding rates and reducing emigration, but these services appear to be less important.

For the ant-reduction experiment in 1988, the abundance of membracid nymphs decreased by 59% compared to controls, whereas the abundance of newly eclosed adults decreased by 92%. If the source of new adults (i.e., nymphs) decreased by an average of 59% on experimental plants relative to controls, one would expect to observe a similar decrease in the production of new adults. The substantial difference (59% vs. 92%) is probably caused by the emigration and spider-related deaths of newly eclosed adults on experimental plants. Second-year adults did not respond in the same way. Presumably, this results because second-year adults have greater mobility and more heavily sclerotized exoskeletons than newly eclosed first-year adults (see Cushman and Whitham 1989).

Conflicting Pressures on Competing Membracids

Membracids face a trade-off between the negative effects of competition and their dependence on ants. They could reduce or eliminate the effects of competition for ants by increasing the distance between neighboring aggregations. However, *Publilia modesta* does the exact opposite and forms multiple aggregations on host plants near servicing nests (J. H. Cushman, personal observation). Such clumping around ant nests has also been observed by McEvoy (1979) for the congener *Publilia concava*. We suggest that competition for mutualists in this system is an inevitable consequence of the need for membracids to be close to servicing ant nests and their inability to assess the abundance of competitors. If membracids were to feed on plants in areas that were free of closely neighboring membracid aggregations, it is probable that they would not be tended by ants at all. Alternatively, if multiple membracid aggregations feed on hosts near a servicing ant nest, each aggregation will receive at least some attention from mutualistic ants and thus protection from salticid predators.

Given the trade-off between competition and mutualism in this system, membracids may colonize host plants in a manner similar to that proposed by Fretwell and Lucas (1970) and Fretwell (1972). Their model of habitat selection would predict that, as the densities of membracid-infested plants increase in patches close to ant nests (high-quality patches), membracids begin colonizing host plants that are located in patches farther from ant nests (low-quality patches) but that lack as many neighboring membracid-infested plants. In this model, the fitness differences between high- and low-quality patches vanish when reduced tending levels caused by increased distance from servicing ant nests equal the reduced tending levels due to competition for mutualists.

For the Fretwell-Lucas model of habitat selection to be applicable in our sys-

tem, ovipositing membracids must be able to assess accurately both the proximity of host plants to ant nests and the abundance of neighboring membracid aggregations. Our data suggest that *P. modesta* can assess and respond to ant density in a manner similar to that found by Atsatt (1981) for ant-tended lycaenid butterflies, since it forms multiple aggregations on host plants near servicing nests where tending levels are high. Such clumping appears to result from habitat selection rather than differential survival of randomly distributed egg clutches, since we rarely observed membracid nymphs emerging from host plants far from ant nests. However, our observations suggest that *P. modesta* cannot accurately assess the density of neighboring competitors, because membracid eggs are embedded in the stems and leaves of host plants and are not directly visible to ovipositing females. Thus, the Fretwell-Lucas model does not appear to apply to our system, because a crucial assumption is violated.

Another complexity in this system involves the conflicting influence of density on different spatial scales. Previously, we have shown that positive density dependence occurs on the scale of individual membracid aggregations: *P. modesta* individuals in large aggregations acquire 36%–46% more benefit from ant tending than individuals in small aggregations (Cushman and Whitham 1989). McEvoy (1979) and Wood (1982) also found a similar pattern for two other membracid species. In addition, our work here demonstrates that negative density dependence can occur on the scale of the patch because homopteran aggregations on neighboring plants compete for ants. That is, as the density of membracid-infested plants increases in a given patch, the beneficial effects of ants are diluted (see also Addicott 1978; Cushman and Addicott 1989). Thus, in this system, high membracid densities are advantageous on one scale and disadvantageous on another. If these forms of density dependence are consistent in space and time, natural selection should operate to favor female membracids that (1) deposit large egg clutches on individual plants and (2) distribute their eggs so as to (a) minimize the number of neighboring host plants that are already infested with membracids and (b) maximize the number of ants that will tend their offspring (e.g., by choosing high-quality host plants, either because they are close to ant nests or offer superior nutrition; see Cushman 1991). However, as mentioned earlier, it may be difficult for membracids to simultaneously accomplish 2a and 2b.

Relationship between Field Experiments and Nature

Skeptics may argue that our manipulative experiments do not reflect natural circumstances and that competition for mutualists is rare, short-lived, or nonexistent in nature. One potential criticism is that membracid-infested plants do not just suddenly appear, as was the case with our potted-plant additions. However, this system is naturally characterized by sudden pulses in the abundance of membracids; it is common for a host plant to be uninfested one day and then infested with 20–400 membracid nymphs the next day, the magnitude of the pulse being a function of the number and sizes of egg clutches embedded in the plant's leaves and stems. Thus, our sudden addition of membracid-infested plants mimics the pattern of nymph emergence observed in the field.

A second potential criticism involves the duration of our 1988 experiment. Sceptics may argue that we have only shown that membracids compete for ants in the short term (3 wk) and such resource limitation disappears with time (within and/or between years). Ants may become more abundant in resource-rich areas that have consistently high membracid densities because they produce or divert a greater number of workers per colony devoted to tending membracids and/or exhibit increased rates of colony establishment and survival. Regardless of the response of ant colonies, we would argue that short-term effects of competition are extremely important for a univoltine insect herbivore inhabiting high-elevation sites characterized by a short growing season. In addition, our field observations suggest that the effects of competition in the short term persist through time. First, membracid abundances fluctuate substantially within and among years (J. H. Cushman, personal observation). Because the longevity of *Formica* colonies in a given area is significantly greater than that of membracid aggregations (see Wilson 1971), it seems unlikely that a spatially and temporally unpredictable resource, such as membracid honeydew, would stimulate a consistent reproductive response in tending ants, such that short-term effects would disappear over time. Second, for short-term effects to be eliminated over time, ant colonies would have to be strongly dependent on membracid honeydew. However, little is known about how dependent ants are on honeydew (see below).

Do Ants Compete for Membracids?

Although we have focused exclusively on the hypothesis that neighboring homopteran aggregations compete for the services of ants, it is also possible that neighboring ant colonies compete for the energy-rich resources (honeydew) of homopterans. Two conditions must be met in order to provide support for this latter possibility: neighboring ant colonies that tend homopterans must compete, and the resource for which ant colonies compete must be, at least in part, homopteran honeydew. In regard to the first condition, an earlier study (Cushman et al. 1988) presented three lines of evidence, each suggesting that neighboring *Formica altipetens* colonies compete: nests of this species are uniformly dispersed, the degree of uniformity increases with nest density, and the distance separating neighboring ant nests increases as their combined sizes increase.

Since the earlier study (Cushman et al. 1988) did not document the resource(s) for which the ant colonies compete, direct evidence for or against the second condition is not available. Although homopteran honeydew constitutes an energy-rich resource, little is known about how dependent ant colonies are on honeydew. However, our observations suggest that honeydew is an important component of this ant species' diet, because it commonly forms satellite nests at the bases of plants that are heavily infested with *P. modesta* (Cushman et al. 1988; Cushman and Whitham 1989). Pierce and Mead (1981) also observed this behavior when *F. altipetens* tended the lycaenid *Glaucopsyche lygdamus* in Colorado. Thus, although we cannot rigorously test the hypothesis that ant colonies compete for the honeydew of membracids, previously published data and preliminary observations are consistent with this contention. In general, hypotheses that

focus on mutualisms from the ant's perspective have been largely ignored by previous studies and warrant further attention (see Beattie 1985; Cushman and Beattie 1991).

Conditional Mutualisms

Numerous factors influence the occurrence and strength of competition in this mutualistic association. First, as shown here and in an earlier study (Cushman and Whitham 1989), the competition is age-specific. Only membracid nymphs directly compete for ant mutualists, whereas the overwintering adults do not. Second, the competition is temporally variable. In 1985, 1987, and 1988, ants had a positive effect on membracid nymphs, but they did not in 1986 (fig. 3C; Cushman and Whitham 1989). Thus, in years when the mutualism breaks down (i.e., 1986), competition does not occur. Finally, because membracid nymphs in large aggregations benefit proportionally more from ant tending than do small aggregations (Cushman and Whitham 1989), the negative effects due to competition for mutualists are density-dependent (on the scale of individual membracid aggregations).

Conditional interactions, such as the competition discussed here, may play a significant role in the population dynamics of mutualistic systems. For example, density dependence (on the scale of the patch) due to competition for mutualists should have a strong stabilizing effect on the dynamics of participating populations (see May 1973, 1981; Addicott 1981; Wolin and Lawlor 1984; Wolin 1985). As the intensity of mutualism declines with increasing density, the tendency of mutualistic populations to increase in size declines (Wolin 1985) and systems return to equilibrium (Addicott 1981).

As several authors have recently discussed, the outcome of species interactions is strongly dependent on the physical and biological settings in which they occur (Morin 1981, 1987; Thompson 1982, 1988; Addicott 1985; Brown et al. 1986; Morin et al. 1988; Cushman and Addicott 1989, and in press; Cushman and Whitham 1989). Here, we have demonstrated that the strength of an insect mutualism is strongly influenced by the spatial arrangement of local biotic neighborhoods. Detection of such complex relationships between competition and mutualism illustrates the need for experimental field studies that explicitly focus on the conditional outcomes of mutualisms and species interactions in general.

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