

Intra- and interspecific competition for mutualists: ants as a limited and limiting resource for aphids

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Summary. We present two years of experimental and descriptive data which support the hypothesis that fireweed aphids (*Aphis varians*) compete with intra- and interspecific aphid neighbors for the services of ant mutualists (*Formica fusca* and *F. cinerea*). Specifically, we have shown that ants are a *limited* and *limiting* resource for a tended aphid species. First, the presence of heavily aphid-infested fireweed shoots significantly reduced the number of ants tending neighboring conspecific populations on fireweed. Second, the presence of ant-tended aphids (*Cinara* sp.) on Engelmann spruce significantly reduced the number of ants tending neighboring aphid populations on fireweed. Third, the number of ants, and not just the presence of ants, had a significant effect on the fitness of fireweed aphids. Aphid populations tended by three or more *F. cinerea* exhibited significantly higher probabilities of persisting and growing through time than colonies tended by one or two ants. Aphid populations tended by *F. fusca* had a significantly higher probability of growing when tended by three or more ants only if they had declined in size during the previous week.

Key words: *Aphis varians* – *Cinara* sp. – Competition for mutualists – *Formica cinerea* – *Formica fusca* – Homopteran-ant associations – Mutualism

Mutualism involves interaction between species in which there is a net increase in the fitness of participating individuals (Boucher et al. 1982). This increase in fitness arises through the acquisition of resources or services that can be limiting and thus form the basis for competition (Rathcke 1983; Waser 1983; Addicott 1985). For example, flowering plants may compete for pollinators (Waser 1978; Kephart 1983; Campbell 1985), seed plants may compete for dispersers (Davidson and Morton 1981; Beattie 1985), and homopterans may compete for tending ants (Addicott 1978b).

Here, we examine the hypothesis that neighboring homopteran aggregations compete with each other for the services of ant mutualists. In such mutualistic associations, ant species harvest the sugary waste excretions (“honey-

dew”) of phloem-feeding homopterans. In return, 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).

Three conditions must be met in order to document that homopterans compete for ant mutualists: 1) the presence of tending ants must increase the fitness of homopterans (i.e., there must be evidence of a mutualism); 2) neighboring homopteran aggregations must reduce the number of ants that each attracts (i.e., tending ants must be a *limited* resource for homopterans); and 3) the number of tending ants, and not just the presence of ants, must have a significant impact on the fitness of homopterans (i.e., ants must be a *limiting* resource).

Throughout this paper, we make a distinction between tending ants as a *limited* and *limiting* resource for homopterans. Such a distinction emphasizes the previously neglected two-fold nature of competition for mutualists; that is, ants may be limited but not limiting or ants may be limiting but not limited. For example, if neighboring homopteran aggregations reduce the number of tending ants that each attracts, but reduced tending levels do not adversely impact homopteran fitness, then competition will not occur. Conversely, if reduced tending levels decrease homopteran fitness, but neighboring homopteran aggregations do not influence each other's tending levels, then competition will also not occur.

Only Addicott (1978b) has previously evaluated the competition-for-mutualist hypothesis in homopteran-ant associations. He showed that the longevity of aphid aggregations (*Aphis varians*) on fireweed (*Epilobium angustifolium*) significantly decreased with increasing proximity to neighboring shrubs occupied by three aphid species (including *A. varians*). Thus, Addicott (1978b) provided correlative evidence indicating that tending ants are a limited and limiting resource for this aphid species (conditions 2 and 3). In two other papers, he presented direct and indirect evidence that tending ants benefit *A. varians* populations (Addicott 1978a, 1979; condition 1).

In this paper, we provide an experimental evaluation of the hypothesis that ants are a limited resource for *Aphis varians* (condition 2) and more rigorously address the relationship between ant tend level and the fitness of *Aphis varians* (condition 3). Our findings strongly suggest that intraspecific and interspecific competition for mutualists does occur in this system. We conclude that, under appro-

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appropriate spatial arrangements, competition for mutualists can be an important force structuring homopteran assemblages.

Methods

Our system involves the interactions within and between two co-occurring ant-tended aphid species: *Aphis varians* on fireweed (*Epilobium angustifolium*) and *Cinara* sp. on Engelmann spruce (*Picea engelmannii*). Both species are commonly tended by *Formica fusca* and *F. cinerea* along Spring Creek, Gunnison County, Colorado (2700–2900 m elevation). The climate and vegetation of this region have been described by Addicott (1978c) and Langenheim (1962).

In this paper, we refer to the aphids on a given fireweed shoot as being a population rather than a colony, because the latter specifically refers to descendants of the same colonizing individual. In contrast, the aphids on a given fireweed shoot may be the offspring of more than one colonist and thus should not be referred to as a colony (see Hughes 1963; Addicott 1978c).

1. Ants as a limited resource for fireweed aphids

Intraspecific tests. We performed a manipulative experiment in July of 1984 to assess the impact of large fireweed aphid populations on the number of *F. fusca* tending smaller neighboring populations. We marked 51 aphid-infested shoots at site SC11.5a and 21 infested shoots at nearby site SC22. Four times during days 1 and 2 of this experiment, we counted the number of ants tending aphid populations on the 72 shoots to generate daily mean tending levels (premanipulation period). At the end of day 2, we excluded tending ants from 18 heavily infested fireweed shoots in the neighborhood of the experimental shoots (SC11.5a) by placing removable Tanglefoot barriers around the base of each plant. We placed tape sleeves around the base of each experimental fireweed shoot to eliminate the possibility that Tanglefoot affected host plant quality and to facilitate the removal of Tanglefoot. With ants excluded from these potential aphid competitors, we again monitored tending levels during days 3 and 4 (manipulation period). At the end of day 4, we removed the ant barriers from the 18 infested fireweed shoots and monitored subsequent tending levels during days 5 and 6 (postmanipulation period).

In our analysis of this ant-exclusion experiment, we compared the number of ants tending fireweed aphids through time on control and experimental shoots. We performed a repeated-measure one-way analysis of variance (ANOVA) on the data using the BMDP-2V statistical package (Dixon et al. 1985). Neighbor treatment (presence or absence of the 18 heavily aphid-infested neighbors) was the grouping factor and time was the repeated measure. We present and discuss only the treatment \times time interaction term, as the two main effects (treatment and time) are not relevant to this study [see Winer (1971) and Cushman and Whitham (1989) for further discussion of repeated-measure ANOVAs].

Interspecific tests. We performed manipulative experiments in 1984 and 1986 to assess the impact of spruce aphids (*Cinara* sp.) on the number of *F. fusca* tending neighboring fireweed aphid populations. In the first experiment of 1984,

we marked 89 aphid-infested fireweed shoots at site SC11.5a where they co-occurred with an aphid-infested spruce tree and 29 infested shoots at nearby site SC22 which lacked such a neighbor. Four times during day 1, we monitored the number of ants tending aphids on all 118 shoots to generate daily mean tending levels (premanipulation period). At the end of this day, we prevented ants from tending *Cinara* on spruce by excluding them with a removable Tanglefoot barrier placed around the base of the tree. With ants excluded from potential spruce-aphid competitors, we again monitored ant tending levels on control and experimental fireweed shoots during days 2 and 3 (manipulation period). At the end of day 3, we removed the ant-exclusion barrier, and, on day 4, monitored tending levels on all shoots (postmanipulation period). We repeated this same experiment five days later with two modifications: 1) control shoots were located at site SC11.5b instead of SC22, as they were closer to the experimental shoots (10 m compared to 1 km), and 2) the postmanipulation period lasted for two days rather than one.

We returned to SC11.5a in 1986 and again repeated the manipulation experiment. This time we used 106 aphid-infested experimental fireweed shoots at SC11.5a and 54 control shoots at SC11.5b. In addition, duration of the premanipulation, manipulation, and postmanipulation periods were each two days.

All three interspecific experiments were analyzed using similar repeated-measure techniques as discussed above. However, the treatment involved the presence or absence of spruce aphids rather than fireweed aphids.

In both the intra- and interspecific experiments, we had to spatially separate the experimental and control aphid populations so that the two groups were tended by different ant colonies. This separation was necessary because excluding ants from certain aphid-infested plants could strongly influence the behavior of an ant colony toward other neighboring aphid populations, thereby making it difficult to have control and experimental treatments in close proximity to each other.

Due to methodological constraints, our 1984 and 1986 ant-exclusion experiments involve pseudo-replication (sensu Hurlbert 1984), since all experimental “replicates” were subjected to the same manipulation. In the intraspecific experiment, ants were excluded from a group of heavily infested aphid populations and, in the interspecific experiments, ants were excluded from a heavily aphid-infested spruce tree (see the discussion for further elaboration of these problems).

2. Ants as a limiting resource for fireweed aphids

To assess the relationship between ant tending level and aphid fitness, we marked over 4000 fireweed shoots along Spring Creek during the summer of 1977 and recorded the number of aphids and ants on each shoot at 1 week intervals (see Addicott 1978c for further details). In this analysis, we included data for *F. cinerea* as well as *F. fusca*.

We analyzed the descriptive data set with two different procedures. The first involved an analysis of the effects of ant tending on the persistence of aphid populations and the second analysis considered the effects of tending on the growth of aphid populations. Both of these indirect measures of fitness are appropriate, given that there is very little movement of apterous *A. varians* from one fireweed

shoot to another (M.F. Antolin and J.F. Addicott, unpublished work).

For the population-persistence analysis, we classified each *Aphis* population with the following variables: plant height (HEIGHT), aphid population size per plant (DEN), number of tending ants (ANT), and persistence of populations (EXT). Separate analyses were performed for the two ant species, *F. fusca* and *F. cinerea*. HEIGHT was divided into two levels (above and below median plant height). DEN was divided into two levels based on initial population densities (1–20 and 21–90 individuals per population). We included HEIGHT and DEN in the analysis because 1) host quality, as estimated by plant height, affects aphid population growth (J.F. Addicott, unpublished work) and may influence the behavior of ants towards aphids and 2) the probability of extinction is known to be a function of population density (Addicott 1979). ANT was divided into two levels; one to two ants and three or more. Lastly, EXT was categorized into two levels; persistence of two weeks or less and persistence of three weeks or more. We based this division on the assumption that populations that persisted for two weeks or less were extremely unlikely to have produced a mature second generation and colonizing alates, whereas this would be possible after three weeks (J.F. Addicott, unpublished work). In this analysis, each aphid population was used only once.

We used four variables in the second contingency table analysis: aphid density (DEN), number of tending ants (ANT), aphid population growth in the previous week (PREV), and aphid population growth in the current week (GROW). ANT was categorized as discussed above. DEN was divided into four levels; 1–20, 21–90, 91–403, and 404 or more aphids per plant. PREV and GROW were each divided into two levels; populations that declined and those that remained constant or grew. In this analysis, each aphid population could have been used more than once (see below).

We analyzed both descriptive data sets with log-linear contingency table analysis using the BMDP-4F statistical program (Dixon et al. 1985). In the population-persistence analysis (a $2 \times 2 \times 2 \times 2$ table), we were interested in the ANT \times EXT interaction term along with any 3- or 4-way terms that included the ANT \times EXT interaction. In the population-growth analysis (a $4 \times 2 \times 2 \times 2$ table), we focused on the ANT \times GROW interaction along with any 3- or 4-way terms that involved the ANT \times GROW term. If these terms were significant, it would indicate that the probability of an aphid population becoming extinct and the probability of an aphid population growing were both a function of the number of tending ants. Beginning with a fully saturated model, the BMDP-4F program searches for the best model through backward elimination of insignificant interaction terms [at the $P=0.05$ level; see Dixon et al. (1985) for further details].

Our population-growth analysis (Table 3a and b) may involve a minor amount of pseudo-replication. Specifically, because we used a survey method of data collection (analogous to sampling with replacement), any one aphid population may have been repeatedly sampled during the course of a summer, depending on how long it persisted. However, if we have pseudo-replicated, the effects of this violation are minimal because, for each observation, we included aphid population density and previous population growth in our analysis.

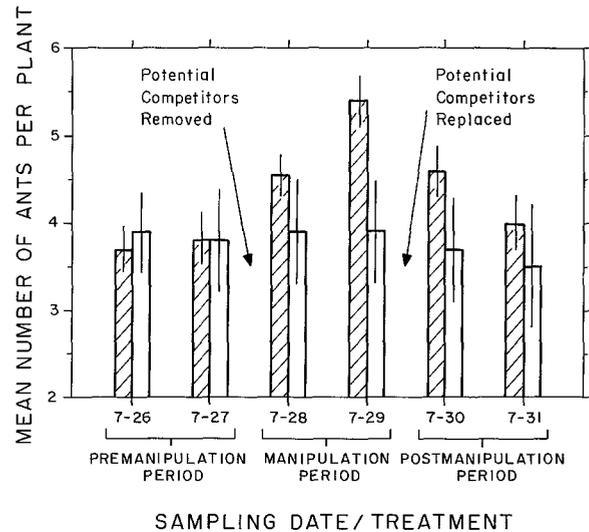


Fig. 1. The mean number of tending ants (*Formica fusca*) per aphid-infested fireweed shoot through time for control (open bars) and experimental treatment areas (shaded bars) in 1984. The arrows indicate the period when ants were prevented from tending neighboring conspecific aphids on fireweed. Vertical bars illustrate ± 1 standard error

Table 1. Repeated-measure ANOVAs performed on the number of ants tending aphids on fireweed through time

EXPERIMENT/ YEAR/SOURCE	SS	DF	MS	F	P
Intraspecific Experiment					
1984: Treatment \times Time	29.6	5	5.9	5.2	0.0001
Error	396.4	350	1.1		
Interspecific Experiments					
1984: Experiment 1					
Treatment \times Time	119.9	3	40.0	14.0	<0.0001
Error	941.1	330	2.9		
1984: Experiment 2					
Treatment \times Time	35.3	4	8.8	4.1	0.0027
Error	942.1	440	2.1		
1986: Treatment \times Time					
Error	55.1	5	11.6	15.8	<0.0001
Error	580.2	790	0.7		

Results

1. *Ants as a limited resource for fireweed aphids*

If ants were a limited resource for fireweed aphids, the number of ants tending experimental *Aphis* populations should increase when ants were prevented from tending neighboring fireweed and spruce aphids. Conversely, tending levels of *Aphis* populations should decrease when ants were again allowed to tend these neighboring aphids. Throughout the four-to-six day experiments, tending levels of control *Aphis* populations should remain fairly constant, exhibiting minor variation due to fluctuations in ambient air temperature.

Intraspecific tests. Results from the 1984 experiment indicated that the presence of heavily aphid-infested fireweed shoots significantly reduced the number of *F. fusca* tending

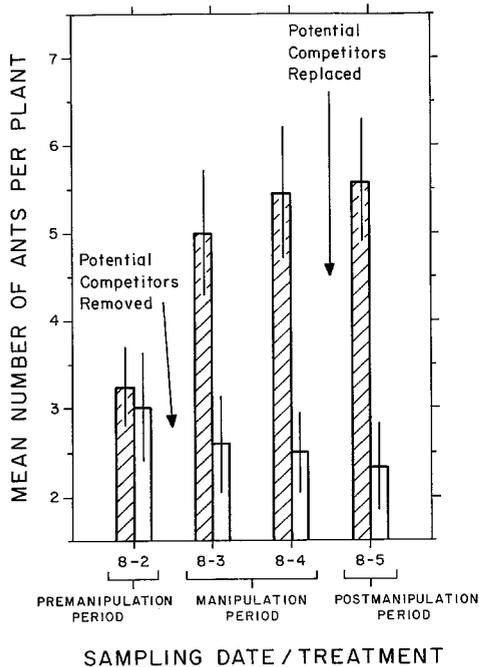


Fig. 2. The mean number of tending ants (*Formica fusca*) per aphid-infested fireweed shoot through time for control (open bars) and experimental treatment areas (shaded bars) in 1984 (Experiment 1). The arrows indicate the periods when ants were prevented from tending neighboring *Cinara* sp. on Engelmann spruce. Vertical bars illustrate ± 1 standard error

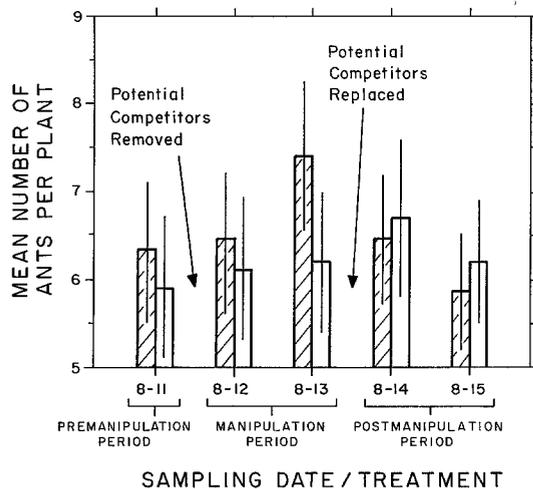


Fig. 3. The mean number of tending ants (*Formica fusca*) per aphid-infested fireweed shoot through time for control (open bars) and experimental treatment areas (shaded bars) in 1984 (Experiment 2). The arrows indicate the period when ants were prevented from tending neighboring *Cinara* sp. on Engelmann spruce. Vertical bars illustrate ± 1 standard error

other aphid-infested shoots (Fig. 1; Table 1). When ants were excluded from the 18 heavily infested shoots, the mean number of ants tending 51 neighboring infested shoots increased by 42% whereas mean tending levels on control shoots remained relatively constant. When we removed the barriers and allowed ants to again tend the heavily infested shoots, mean tending levels of the neighboring experimental shoots decreased by 25% whereas tending levels on control shoots decreased slightly.

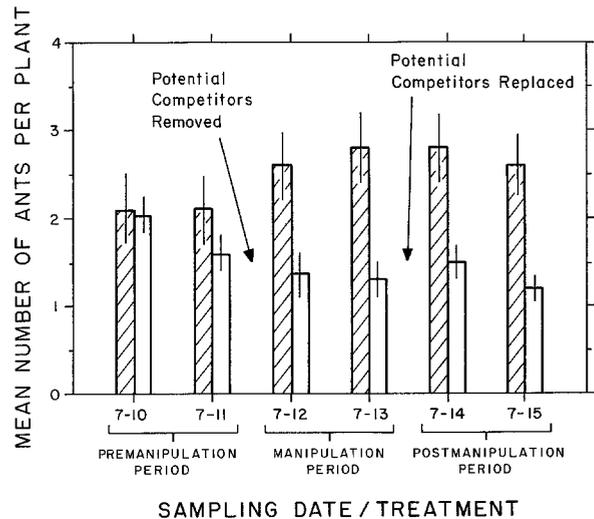


Fig. 4. The mean number of tending ants (*Formica fusca*) per aphid-infested fireweed shoot through time for control (open bars) and experimental treatment areas (shaded bars) in 1986. The arrows indicate the period when ants were prevented from tending neighboring *Cinara* sp. on Engelmann spruce. Vertical bars illustrate ± 1 standard error

Interspecific tests. Results from two experiments in 1984 and one in 1986 document that the presence of an aphid-infested spruce tree significantly influenced the number of *F. fusca* tending neighboring fireweed aphid populations through time (Figs. 2, 3 and 4; Table 1). In the first experiment of 1984, the mean number of ants tending experimental fireweed populations increased by 68% when ants were excluded from tending aphids on the spruce tree, whereas tending levels actually decreased by 16% on the nearby control populations (Fig. 2). When we removed the ant barrier on the spruce, the number of ants tending experimental aphid populations did not decline as predicted but continued to increase.

We also detected a significant response of ants when the experiment was repeated six days later (Fig. 3). Tending levels for experimental populations increased by 17% when ants were excluded from spruce aphids and decreased by 21% when the ant barrier on the spruce was removed.

In 1986, we also detected a significant negative effect of spruce aphids on the number of *F. fusca* tending neighboring fireweed aphids (Fig. 4). Mean tending levels of experimental populations increased by 32% when ants were excluded from the spruce aphids and decreased by 7% when the barrier was removed. Tending levels for control populations gradually decreased by 40% during the six-day experiment, presumably due to the overcast weather that characterized this period (J.H. Cushman, unpublished work).

2. Ants as a limiting resource for fireweed aphids

Here, we present two lines of evidence which indicate that tending ants are a limiting resource for aphid populations. First, results from the population-persistence analysis indicated that the number of *F. cinerea* initially tending *A. varians* populations was associated with the probability of extinction of the populations (ANT \times EXT interaction term; likelihood-ratio $\chi^2 = 3.63$, $df = 1$, $P = 0.0568$; Table 2a). While none of the 3- and 4-way interaction terms

Table 2a, b. The probability that *Aphis varians* populations feeding on fireweed persisted three or more weeks as a function of the number of tending ants, initial aphid population density, and plant height; a) aphids tended by *Formica cinerea* and b) aphids tended by *Formica fusca*. Sample sizes are in parentheses

a *Formica cinerea*

Ants	Plant Height			
	Below Median		Above Median	
	Initial Population Size		Initial Population Size	
	1-20	21-90	1-20	21-90
1-2	0.782 (101)	0.918 (98)	0.735 (117)	0.943 (105)
3+	0.833 (42)	0.960 (125)	0.830 (53)	0.943 (128)

b *Formica fusca*

Ants	Plant Height			
	Below Median		Above Median	
	Initial Population Density		Initial Population Density	
	1-20	21-90	1-20	21-90
1-2	0.779 (181)	0.927 (317)	0.771 (170)	0.917 (288)
3+	0.727 (11)	0.977 (86)	0.813 (16)	0.964 (111)

involving ANT × EXT were significant, we did detect a significant association between the size of aphid populations and the probability of extinction (DEN × EXT interaction term; likelihood-ratio $X^2 = 47.17$, $df = 1$, $P < 0.0001$). This analysis also revealed that the number of *F. fusca* tending fireweed aphids was associated with probability of extinction (ANT × EXT interaction term; likelihood-ratio $X^2 = 4.08$, $df = 1$, $P = 0.0433$; Table 2b). As with *F. cinerea*, there

were no significant 3- and 4-way interaction terms, but there was strong density dependence (DEN × EXT interaction term; likelihood-ratio $X^2 = 49.6$, $df = 1$, $P < 0.0001$). Thus, aphid populations tended by either ant species had a greater probability of persisting three or more weeks when they were tended by three or more ants rather than one or two ants.

Results from the population-growth analysis showed that the number of *F. cinerea* tending *A. varians* populations was associated with their probabilities of declining (ANT × GROW interaction term; likelihood ratio $X^2 = 6.85$, $df = 1$, $P = 0.0089$). Aphid populations tended by three or more *F. cinerea* were far less likely to decline in size than populations tended by one to two ants (Table 3a).

The growth response of aphid populations tended by *F. fusca* was more complex. Aphid populations tended by three or more *F. fusca* were less likely to decline in size than populations tended by one to two ants, but this result was dependent on the previous history of growth for the populations (Table 3b). Having more ants was most beneficial to aphid populations when they had declined in size during the previous week, and less influential for aphid populations that did not decline in size during the previous week. This effect is shown statistically by the fact that the ANT × GROW interaction term was significant only in the context of the 3-way term ANT × GROW × PREV (likelihood-ratio $X^2 = 6.41$, $df = 1$, $P = 0.0114$).

Discussion

We have presented experimental and observational data which support the hypothesis that fireweed aphids compete with intra- and interspecific neighbors for the services of ant mutualists. First, the presence of heavily aphid-infested fireweed shoots reduced the number of ants tending neighboring aphid populations on fireweed. Second, the presence of ant-tended aphids on Engelmann spruce reduced the

Table 3a, b. The probability that *Aphis varians* populations feeding on fireweed declined as a function of the number of tending ants, population size, and their population growth during the previous week; a) aphids tended by *Formica cinerea* and b) aphids tended by *Formica fusca*. Sample sizes are in parentheses

a *Formica cinerea*

Ants	Previous Population Growth							
	Decline				No Decline			
	Initial Population Size				Initial Population Size			
	1-20	21-90	91-403	404+	1-20	21-90	91-403	404+
1-2	0.591 (66)	0.512 (43)	0.778 (9)	0.667 (3)	0.369 (130)	0.414 (146)	0.481 (52)	0.545 (11)
3+	0.419 (31)	0.426 (68)	0.421 (38)	0.467 (30)	0.350 (60)	0.341 (179)	0.380 (158)	0.473 (131)

b *Formica fusca*

Ants	Previous Population Growth							
	Decline				No Decline			
	Initial Population Size				Initial Population Size			
	1-20	21-90	91-403	404+	1-20	21-90	91-403	404+
1-2	0.700 (130)	0.631 (130)	0.649 (37)	0.700 (10)	0.424 (203)	0.335 (451)	0.508 (181)	0.486 (73)
3+	0.571 (14)	0.554 (56)	0.615 (65)	0.529 (17)	0.375 (8)	0.392 (130)	0.473 (167)	0.596 (109)

number of ants tending neighboring aphid populations on fireweed. Third, the number of ants, and not just the presence of ants, had a significant effect on the fitness of fireweed aphids. Thus, in this study we have shown that ants are a *limited* and *limiting* resource for a homopteran species.

Our study is the first to evaluate experimentally the hypothesis that ants are a limited resource for tended homopterans. Using ant-exclusion experiments, we demonstrated that intra- and interspecific neighbors substantially reduce the number of ants tending fireweed aphids. These experiments also revealed that tending ants commonly exhibit delayed recruitment behavior in response to changes in resource (honeydew) availability. For example, even when our ant-exclusion barrier was removed from the *Cinara*-infested spruce, the number of ants tending experimental *Aphis* populations continued to increase (Fig. 2). We suggest that the one day of postmanipulation was not of sufficient duration to detect the predicted decrease in tending levels.

While many homopteran species benefit from ant tending (Nixon 1951; Way 1963; Addicott 1978a; McEvoy 1979; Fritz 1982; Wood 1982; Bristow 1984; Buckley 1987) and have apparently evolved a variety of morphological and behavioral traits that encourage this association (Way 1963; Blackman 1974; Heie 1980), our study is the first to explicitly consider the relationship between ant tending level and homopteran fitness. Our observational data indicated that fireweed aphids had greater fitness when tended by three or more ants than when tended by one to two ants.

In our system, the relationship between ant tending level and aphid fitness was influenced by the species of tending ant (Table 3). Three or more tending *F. cinerea* significantly reduced the probability that aphid populations declined in size whereas, for *F. fusca*, this was true only in the context of each population's previous history of growth. For this ant species, a higher tending level was most beneficial to aphid populations that had declined in size during the previous week and less influential for populations that did not decline during the previous week. Earlier studies by Addicott (1979), Messina (1981), and Bristow (1984) have also reported that ant species vary in their ability to tend homopterans.

While our study has shown that three or more tending ants benefit aphid populations more than one or two ants, such relationships may not hold for all homopteran-ant associations. In addition, future studies that consider ant tending levels as a continuous rather than categorical variable may reveal more complex relationships between tending level and homopteran fitness. For example, while the fitness of homopterans may generally increase with increasing numbers of tending ants, it seems probable that the relationship is characterized by two threshold levels: 1) a minimum tending level required before ants benefit homopterans, and 2) a maximum tending level after which additional ants provide no further benefit.

The ability of a given aphid population to compete for the services of tending ants may be influenced by the quality of its host plant. Such impact could occur if 1) the chemical composition and/or quantity of honeydew produced by aphids varied with changes in host plant quality and 2) ants preferentially tend those colonies producing the most rewarding honeydew. This possibility would be suggested by a significant ANT \times EXT \times HEIGHT interaction term

in the population-persistence analysis. However, we did not detect such an effect for either ant species (*F. cinerea*-likelihood-ratio $X^2=0.01$, $df=1$, $P=0.91$; *F. fusca*-likelihood-ratio $X^2=0.02$, $df=1$, $P=0.89$; Table 2). There are numerous potential explanations for such negative results. First, host plant impact may not occur in this assemblage, either because host plant quality did not vary significantly in the fireweed population we studied or because *F. cinerea* and *F. fusca* were unable to detect variation in the quality or quantity of honeydew produced by *Aphis varians*. Alternatively, host plant quality may influence the *Aphis-Formica* mutualism but our measure of host quality was too crude to detect such effects. Further, even our crude measure of host quality might have revealed significant host impact if our analysis had involved the presence or absence of ants rather than tending level. That is, aphid populations on smaller plants may be more or less likely to be tended by ants, regardless of population density, than taller plants. Clearly, this is a topic that warrants further study.

In the interspecific portion of this study, we were able to assess the impact of *Cinara* sp. on *Aphis varians* but could not evaluate the reverse situation. This was because it was difficult, if not impossible, to determine the size, fitness, or ant tending level of *Cinara* populations, because they inhabited a 25 m tall Engelmann spruce. However, our observations suggest that interactions at the study site were strongly asymmetrical, with *Cinara* attracting ants away from *Aphis* and *Aphis* having very little impact on the number of ants tending *Cinara*. First, the *Cinara* populations attracted more than twice as many ants as did *Aphis* populations. Second, tending ants had to pass directly by the infested fireweed shoots on their way to the spruce aphids (J.H. Cushman, unpublished work), thus suggesting that the latter populations offered greater nutritional rewards to tending ants.

Despite the statistical problems in the analysis of our ant-exclusion experiments, we feel that the results still provide support for the hypothesis that tending ants are a limited resource for fireweed aphids. First, in both years (1984 and 1986) and types of experiment (intra- and interspecific), we detected a strong negative impact of aphid neighbors on the number of ants tending other aphid populations. Second, we duplicated the interspecific experiment within and between years with a similar response of ants. Third, in all four experiments, the number of ants tending neighboring control populations did not vary substantially through time.

As Cushman and Whitham (1989) have recently shown, the intensity and occurrence of mutualistic interactions can be strongly dependent on the physical and biological setting in which they occur. In this paper, we provide further evidence that mutualisms are conditional by documenting that biotic neighborhoods strongly affect a homopteran-ant mutualism. Detection of such complexity illustrates the need for experimental studies that focus on the variability in species interactions and the resulting impact on natural communities.

Acknowledgements. We thank Mike Antolin, Bob Holmes, Kate Shaw, and Felix Sperling for assistance with field work. We are also indebted to Mike Antolin, Jim Brown, Alan Harvey, Bob Holmes, Ralph Preszler, Peter Price, and Tom Whitham for comments on drafts of this manuscript. J.H.C. gratefully acknowledges the support and companionship of Joyce Maschinski throughout

this study. Laboratory space and housing were provided by the Rocky Mountain Biological Laboratory, Crested Butte, Colorado, USA. Lastly, this work has been funded by grants from the Natural Sciences and Engineering Research Council of Canada, the University of Alberta (both to J.F.A.), and the National Science Foundation (to J.H.C.).

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Received August 26, 1988