

Tending Ants (Hymenoptera: Formicidae) Regulate *Dalbulus quinquenotatus* (Homoptera: Cicadellidae) Population Dynamics

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ABSTRACT Population dynamics of colonies of the myrmecophilous leafhopper *Dalbulus quinquenotatus* DeLong & Nault were recorded in the laboratory in the presence and absence of the tending ant, *Formica fusca* (L.). These experiments used colonies of leafhoppers started with five male and five female adults on a single *Tripsacum dactyloides* L. plant. The first experiment consisted of eight leafhopper colonies, four with tending ants and four without. The second experiment used 16 leafhopper colonies, eight with tending ants and eight without, with four of each of these ant treatments also with *Nabis americanoferus* Carayon predators. The numbers of young nymphs, older nymphs, and adult leafhoppers, along with host plant condition were recorded every 2-3 d for 62 d for both experiments. Nontended leafhopper colonies exploded and overwhelmed their host plants, killing them in an average of 39.0 d, resulting in the extirpation of those leafhopper colonies. Ants maintained leafhopper colonies by regulating population dynamics, with colonies of leafhoppers tended by ants being significantly smaller ($P < 0.02$) and developing from egg to adult significantly slower ($P < 0.001$) than colonies of nontended leafhoppers. Ant-tended leafhopper colonies did not overwhelm their host plants during either experiment, as the ants removed excess honeydew and leafhopper exuvia, thus maintaining a constant supply of honeydew. Ants were observed protecting leafhoppers from nabid predators, although this protection did not significantly influence leafhopper population size or length of egg to adult development.

KEY WORDS *Formica*, leafhoppers, ant-homopteran interaction, mutualism, myrmecophile

MUTUALISTIC RELATIONSHIPS BETWEEN ants and homopterans have been studied extensively, revealing benefits such as constant food sources for the ants, and protection from predation or parasitism, transportation, maintenance of host plant quality, or increased survival for the homopterans (Way 1963, Burns 1973, Wood 1977, Fritz 1982). A number of studies cited by Way (1963) have reported a lack of tending ants increases the mortality or decreases the fecundity of some myrmecophilous homopterans.

One leafhopper (Homoptera: Cicadellidae) species that has been shown to associate with ants is the fivespotted gamagrass leafhopper, *Dalbulus quinquenotatus* DeLong and Nault (Nault et al. 1983, Larsen et al. 1991). This leafhopper has an obligate mutualistic association with ants in the field (Nault et al. 1983, Triplehorn and Nault 1985, Moya-Raygoza and Nault 2000). Previous studies have shown the escape and honeydew excretion behaviors of this leafhopper differs from its nonmyrmecophilous congeners; it is sedentary and gregarious and produces copious amounts of honeydew compared with other *Dalbulus* species (Larsen et al. 1992a).

In Central America and Mexico, *D. quinquenotatus* lives on gamagrasses (*Tripsacum* spp.), perennial rel-

atives of corn, *Zea mays* L. (Nault 1985, Nault 1990). In the laboratory, this leafhopper may be successfully reared on either *Tripsacum* or *Zea* without ants (Nault and Madden 1985, Todd et al. 1990). However, corn seedlings used in rearing the leafhoppers must be replenished every few days as the leafhopper populations rapidly increase and overwhelm this host. Because leafhoppers must have access to a constant source of nourishment, the death of their host plants inevitably results in the extirpation of populations.

Previous observations in the field (K.J.L., unpublished data; Moya-Raygoza and Nault 2000) suggested that populations of *D. quinquenotatus* tended by ants did not increase as rapidly or overwhelm field-grown *Tripsacum* plants as did laboratory-reared populations. We hypothesized three possible mechanisms may be involved in regulating *D. quinquenotatus* populations in the field. First, predation by natural enemies such as spiders or damsel bugs (Hemiptera: Nabidae) may reduce the rate of population growth of leafhoppers. Second, tending ants may improve host plant condition by cleaning excess honeydew from the plants, thus providing a healthier host that can tolerate increased herbivore pressure. Third, ants may be regulating population size of the leafhoppers by removing excess individuals. The objective of this study was to quantify the effects of tending ants and predators on the population growth of *D. quinquenotatus* leafhoppers. Our goal is to identify which mechanism may be

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influencing the long-term survival of colonies of *D. quinquenotatus* on their *Tripsacum* hosts. We confirm some of the results of Moya-Raygoza and Nault (2000), showing tending ants regulate population dynamics of *D. quinquenotatus*. However, this study is the first to show ant attendance affects the length of egg to adult development of *D. quinquenotatus*.

Materials and Methods

Leafhoppers. All experiments were performed using populations of laboratory-reared leafhoppers originally collected in Jalisco, Mexico, in 1990. Test colonies of *D. quinquenotatus* leafhoppers were started by placing five female and five male adults in 45.5 by 23 by 45.5-cm screen rearing cages with a single, 5–7 leaf stage eastern gamagrass (*Tripsacum dactyloides* L.) ramet as a host. Plants had an average leaf length of 25 cm and were grown in 10.5-cm-diameter plastic pots. Leafhopper colonies were maintained at 27°C and a photoperiod of 14:10 (L:D) h. Plants were watered every other day, with no new plants added after beginning the study.

Ants. Colonies of the silky ant, *Formica fusca* L., were collected from old fields in Winneshiek County, IA, in September 1995 and 1999. Ant colonies consisting of several hundred workers and at least one queen were housed in modified Giant Ant Farms (Uncle Milton Industries, Culver City, CA). Ant colonies were connected to leafhopper cages via 25-cm lengths of clear Nalgene (Rochester, NY) tubing (9.5 mm i.d.) to allow ants access to colonies of leafhoppers within their cages. Ants would find the leafhoppers within 1 h of connection to the cages and immediately begin soliciting leafhoppers for honeydew.

Experiment 1. To test if tending ants regulate leafhopper population dynamics, eight leafhopper colonies were used. Four cages were used as “no ant” controls, and four cages were connected to ant colonies. The numbers of early (small) instar nymphs, late (large) instar nymphs, and adult leafhoppers, and host plant condition in each cage was recorded every two or three days for 62 d.

Experiment 2. To evaluate the influence of leafhopper predators on ant-tended leafhopper populations, 16 leafhopper colonies were used. Eight “no-ant” control cages and eight “tended” cages were established. On day 14 after the initiation of the study, two adult common damsel bugs, *Nabis americanoferus* Carayon (Hemiptera: Nabidae), were added to four of the “no ant” control cages and four of the “tended” cages. Adult *N. americanoferus* were collected using sweep nets in an alfalfa field, a reconstructed tallgrass prairie, and wooded areas in Winneshiek County, IA, during September 1999. Collected nabids were placed in a screened holding cage with two *T. dactyloides* plants and a mix of potential prey insects as the source for predators needed throughout the study. Additional nabids were taken from this holding cage and added to the leafhopper colony cages as needed. We attempted to keep two nabids in each cage throughout the study. The nabid supply ran out at approximately

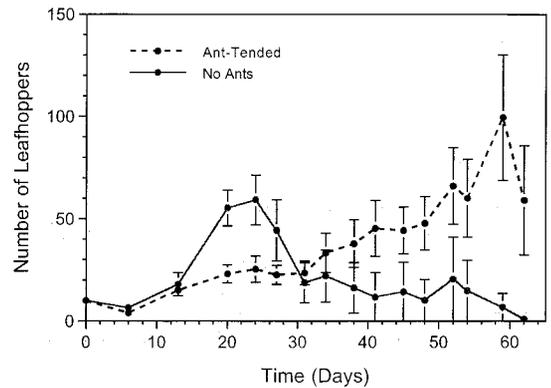


Fig. 1. Size (average \pm SE) of caged populations of *D. quinquenotatus* leafhoppers (both nymphs and adults) over time in the presence and absence of tending ants.

day 40 after which the nabid count decreased as they were killed by ants or died. The numbers of early (small) instar nymphs, late (large) instar nymphs, and adult leafhoppers, numbers of nabids, and host plant condition in each cage was recorded every two or three days for 62 d.

Analysis. The experimental design resulted in two or four treatments with four replicate colonies each. These treatments included the following: (1) leafhopper control with no ants or predators, (2) leafhoppers and ants with no predators, (3) leafhoppers and predators but no ants (experiment 2 only), and (4) leafhoppers with both ants and predators (experiment 2 only). Once a leafhopper population died out following the death of their host plant, that cage was no longer monitored. In experiment 2, the dates of appearance of new adult leafhoppers were used to determine length of egg to adult development.

In experiment 1, unpaired two sample *t*-tests (Zar 1999) were used to analyze for the effects of the presence or absence of ants effects on the average size of each population and length of host plant survival. In experiment 2, two-way analysis of variance (Zar 1999) tests were used to analyze for the effects of the presence or absence of ants and the presence or absence of nabid predators on the overall average size of each population, the length of leafhopper egg to adult development (unbalanced), and the length of host plant survival. Fisher least significant difference (LSD) multiple comparison of means tests were used to indicate significant differences among the four treatments in experiment 2 when appropriate.

Results

Ant Regulation of Leafhopper Populations. In experiment 1, the average population size of *D. quinquenotatus* colonies tended by ants was 38.5 (± 3.0) leafhoppers over the 62-d study (Fig. 1), significantly greater ($t = 3.64$, $df = 5$, $P = 0.015$) than populations averaging 20.6 (± 3.9) leafhoppers which were not tended by ants. Nontended populations peaked on day

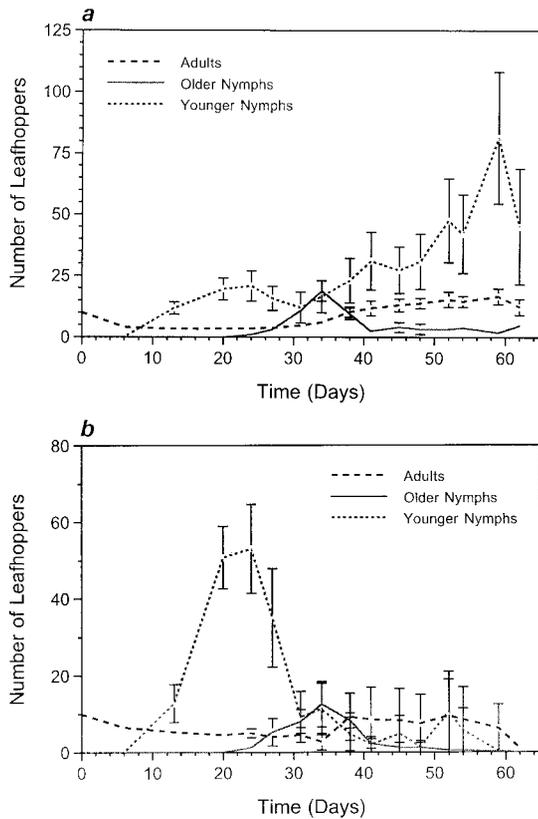


Fig. 2. Number (average \pm SE) of young nymphs, older nymphs, and adults of *D. quinque-notatus* leafhoppers over time in the a. presence and b. absence of tending ants.

24 at an average of 59.25 individuals (Fig. 1), followed by a dramatic population crash in most colonies. Ant-tended populations grew much more gradually, peaking at an average of 99.5 individuals at day 59, giving host plants time to grow and accommodate to larger leafhopper populations.

Ant-tended populations had an initial peak of 20.75 young nymphs on day 24, followed by a peak of larger nymphs on day 34, with adults emerging by about day 36. This was quickly followed by the appearance of more young nymphs (Fig. 2a), beginning the second generation. Nontended leafhopper populations had a much higher initial peak of 53 young nymphs on day

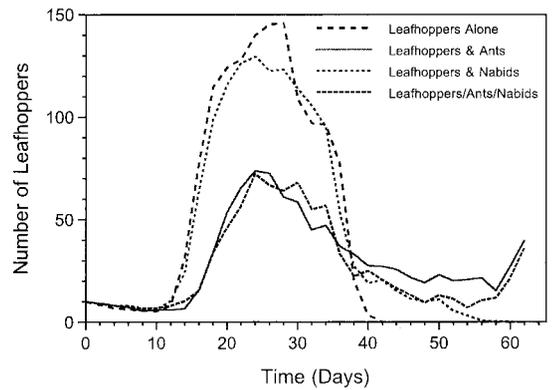


Fig. 3. Average population size of caged *D. quinque-notatus* leafhopper populations (both nymphs and adults) over time in the presence or absence of tending ants and with or without nabid predators.

24, followed by subsequent peaks of older nymphs and adults (Fig. 2b). However, this first generation of nontended leafhoppers was so large it overwhelmed the host plants and led to extirpation of the populations.

In experiment 2, there were significant differences among ant-tended and nontended treatments ($F = 7.78$; $df = 1, 12$; $P = 0.016$) in overall population size. However, in contrast with experiment 1, larger populations of leafhoppers developed in nontended colonies and smaller populations developed in ant-tended colonies (Table 1). As in experiment 1, nontended populations peaked much higher and earlier than ant-tended populations (Fig. 3) and then crashed as host plants died. Ant-tended populations had a more distinct first population peak in experiment 2, and were clearly beginning a second population peak when the experiment was terminated.

Influence of Predators on Ant-Tended Leafhopper Populations. In experiment 2, nabid predators caused a slight reduction in average leafhopper population size (Table 1), although this was not significant ($F = 0.21$; $df = 1, 12$; $P = 0.65$). There was also no significant impact of the ant-predator interaction on average leafhopper population size ($F = 0.001$; $df = 1, 12$; $P = 0.97$).

Egg to Adult Leafhopper Development. A total of 176 leafhoppers developed from egg to adult in experiment 2 among the four treatment combinations.

Table 1. Average (mean \pm SE) size of *D. quinque-notatus* leafhopper colonies, length of leafhopper egg to adult development (in days), and length of survival (in days) of *Tripsacum* host plants, both with and without tending ants or nabid predators over a 62-d monitoring period

Treatment	Leafhopper colony size	Leafhopper egg to adult development (days)	Host plant survival (days)
Leafhoppers alone	46.4 \pm 30.6a	34.37 \pm 0.15a	36.0 \pm 1.4a
Leafhoppers and ants	29.7 \pm 12.7b	38.52 \pm 0.55b	62.0 \pm 0.0b
Leafhoppers and predators	43.4 \pm 30.8a	34.78 \pm 0.27a	54.5 \pm 5.6b
Leafhoppers with ants and predators	27.2 \pm 13.7b	37.67 \pm 0.52b	56.0 \pm 6.0b

Within each column, means followed by the same letter are not significantly different (Fisher's LSD multiple comparison of means test, $\alpha = 0.05$).

When tended by ants, it took these leafhoppers significantly ($F = 100.59$; $df = 1, 172$; $P < 0.001$) longer (≈ 3 d) to develop from egg to adult than when they were not tended by ants (Table 1). Neither the presence of nabid predators ($F = 0.39$; $df = 1, 172$; $P = 0.53$) or the ant-predator interaction ($F = 3.25$; $df = 1, 172$; $P = 0.07$) had a significant influence on duration of egg to adult development.

Leafhopper Host Plant Condition. Leaves of host plants in nontended control cages became covered within 3–4 wk by a sticky mixture of honeydew and exuvia. Mold grew on those leaves later in the study. Host plants in leafhopper cages with tending ants, however, were clean, healthy, and continued to grow throughout the duration of both experiments. In experiment 1, all host plants with tending ants survived the full 62 d of the study, significantly longer ($t = 3.92$, $df = 6$, $P = 0.008$) than the average of 39.0 d the host plants survived in nontended colonies. In experiment 2, host plants with tending ants also survived significantly longer than those from nontended colonies ($F = 10.97$; $df = 1, 12$; $P = 0.006$). However, the presence or absence of predators had no significant impact on host plant survival ($F = 2.27$; $df = 1, 12$; $P = 0.16$), although predator presence did increase average host plant survival over when no tending ants were present (Table 1).

Behavioral Observations. Ants were observed aggressively attacking damsel bugs, approaching and chasing away nabids that came close to tended leafhopper clusters. On several occasions, ants congregated around a nabid, grabbed its legs with their mandibles, and dragged it away from the leafhoppers, sometimes killing it. As a result, nabids had to be replaced frequently in ant-tended colonies until our supply ran out, but were rarely replaced in nontended colonies. We did not observe ants killing leafhoppers or removing them from their colonies.

Discussion

It appears the most important mechanism for regulating *D. quinquenotatus* populations involves tending ants controlling the size and length of development of leafhopper populations. When tended by the ant *F. fusca*, *D. quinquenotatus* populations were smaller. By keeping leafhopper populations smaller, tending ants may be able to ensure continued survival of the colony (Buckley 1987) by avoiding overpopulation of the host plant, ending in the death of the plant and subsequent extirpation of the leafhopper colonies. This study clearly shows the presence of tending ants decreases *D. quinquenotatus* colony size and improves leafhopper host plant quality and survival in a controlled setting. Although we did not observe tending ants killing excess leafhoppers, Moya-Raygoza and Nault (2000) reported this behavior between the tending ant *Formica subsericea* Say and *D. quinquenotatus*, and we assume the same mechanism of population regulation is occurring here.

It has been suggested that attendant ants help increase the survival of homopteran populations by

keeping populations smaller to regulate their supply of honeydew (Buckley 1987). By limiting *D. quinquenotatus* population size, ants indirectly ensure the survival of *T. dactyloides*, the *D. quinquenotatus* host plant. One way the ants kept *T. dactyloides* alive longer was by regulating leafhopper population size. This decreased feeding and oviposition damage by decreasing the number of leafhoppers living on each plant. These smaller populations of leafhoppers did not overwhelm and kill their host the way nontended populations did.

Another role ants played in keeping host plants alive and healthy involved the ants removing excess honeydew from the leaves. During this study, *T. dactyloides* in cages without tending ants had leaves covered with sticky honeydew and leafhopper exuvia. These accumulations of honeydew and exuvia were not observed on plants in cages with ants present. As excessive honeydew was produced, it collected on leaves of host plants and decreased host plant quality. Because *D. quinquenotatus* produces three to five times more honeydew than some of its congeners (Larsen et al. 1992a), it is beneficial for tending-ants to regulate honeydew production to maintain the health of the host plant so leafhoppers have a host to live on.

In this study, nabid predators played only a minor role in leafhopper colony population dynamics. While nabids alone did not ensure continued leafhopper colony existence over time, ants along with the predators maintained leafhopper survival throughout experiment 2, albeit at slightly lower levels (Fig. 3). Ants also effectively implemented some sort of control over the nabids to keep the leafhopper populations alive. When directly observing ant-predator interactions, we saw ants ward off intruding nabids that threatened tended-leafhoppers. Fritz (1982) showed significantly fewer predators of the treehopper *Vanduzeeia arquata* Say were found on branches with tending-ants than on branches where ants were absent. Without ants present, the sap-sucking eurytelid bug *Ipoidea melaleuca* Evans experiences a mortality rate 2.5 times higher than when ants are present, because of a lack of protection against nocturnal spider predation (Buckley 1990). Ants tending aphids have been shown to attack or carry off aphid predators such as syrphid larvae and the coccinellid beetle *Adalia bipunctata* (L.) (El-Ziady and Kennedy 1956). When redwood ants *Formica yessensis* Forel were removed from colonies of the aphid *Tuberculatus quercicola* (Matsumura), aphid colonies were extirpated by predators (Yao et al. 2000). In the field, the leafhopper *D. quinquenotatus* has been observed being protected from spiders and the dryinid parasitoid *Anteon ciudadadi* Olmi by tending-ants (Moya-Raygoza and Nault 2000).

Other studies have shown benefits to plants hosting ant/homopteran mutualisms. Ants tending the membracid *Publilia concava* (Say) were shown to attack adult herbivorous *Trirhabda* beetles on goldenrod (*Solidago altissima* L.) stems when encounters were staged, with significantly fewer beetles found on stems with tending ants than on stems without ants (Messina 1981). As a result, *S. altissima* stems inhabited by

membracids were up to 50 cm taller when membracids were tended by ants than were plants not tended (Messina 1981). The ant *Petalomyrmex phylax* Snelling has been shown to provide highly effective protection of young leaves of *Leonardoxa africana* (Baill.) Aubrév. against predators (Gaume and McKey 1999). When unprotected, the plant showed much more damage compared with ant-patrolled plants. It has been suggested that ants provide indirect protection of plant tissue by driving off more harmful herbivores while protecting the leafhopper *D. quinquenotatus* (Larsen et al. 1991).

This article reports that *D. quinquenotatus* develops more slowly from egg to adult in the presence than in the absence of tending ants. Previous studies have shown mixed effects of ant attendance on myrmecophilous homopteran development rates. For example, the aphids *Symydobius oblongus* (von Heyden) (Stadler and Dixon 1999) and *Aphis fabae* Scopoli (El-Ziady and Kennedy 1956) and treehopper *Publilia reticulata* Van Duzee (Bristow 1984) all developed faster when tended by ants. In contrast, Stadler and Dixon (1999) showed *A. fabae* developed slower with ant attendance. We believe the increased levels of honeydew production by *D. quinquenotatus* tended by ants may divert metabolic resources needed for the development of this leafhopper. However, one other possibility suggested by Kleinjan and Mittler (1975) that occurs in the aphid *A. fabae* is that mandibular secretions may be applied by tending ants while stroking the leafhopper bodies with their antennae. These ant-applied secretions may then affect homopteran developmental rates.

One question is whether *D. quinquenotatus* leafhoppers "benefit" in an evolutionary sense from control of their populations by tending ants. It would appear that in the field *D. quinquenotatus* colonies could benefit by producing larger populations that could easily disperse to neighboring hosts if their hosts died. However, *D. quinquenotatus* is extremely sedentary (Larsen et al. 1992a) and unlikely to fly even when disturbed (Heady and Nault 1985). In addition, the perennial *Tripsacum* grasses are rarely found in populations covering areas >0.25 ha, and are typically isolated from other populations by at least 3 km (Moya-Raygoza and Larsen in press). The availability of *Tripsacum* hosts at these relatively isolated sites is highly seasonal, becoming extremely limited during the dry season from October to May (Larsen et al. 1992b, Moya-Raygoza 1995). This decrease in available hosts results in a dramatic decline in abundance of *D. quinquenotatus* during the dry season (Larsen et al. 1992b). Therefore, the control of leafhopper population size by tending ants is crucial to the survival of these myrmecophilous leafhoppers.

In conclusion, this mutualism between *F. fusca* and the myrmecophile *D. quinquenotatus* is advantageous for both species as shown in this controlled study. The myrmecophile *D. quinquenotatus* receives protection from predation and host plant maintenance by *F. fusca* which ensures colony survival. The ants regulate the population size of *D. quinquenotatus* colonies, even when leafhopper predators were present, and thus

maintain a constant supply of food in the form of honeydew and potentially even individuals from the leafhopper colony.

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