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The exploitation of an ant-defended host plant by a shelter-building herbivore

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Abstract Larvae of a *Polyhymno* species (Lepidoptera: Gelechiidae) feed on the ant-defended acacia, *Acacia cornigera*, in the tropical lowlands of Veracruz, Mexico. *Polyhymno* larvae construct sealed shelters by silking together the pinna or pinnules of acacia leaves. Although larval density and larval survival are higher on acacias not occupied by ants, shelters serve as a partial refuge from the ant *Pseudomyrmex ferruginea* (Hymenoptera: Formicidae), which defends *A. cornigera* plants; thus, shelters provide *Polyhymno* larvae access to an ant-defended host plant. *P. ferruginea* ants act as the primary antiherbivore defense of *A. cornigera* plants, which lack the chemical and mechanical defenses of non-ant-defended acacias. Thus, defeating the ant defense of *A. cornigera* provides *Polyhymno* larvae access to an otherwise poorly defended host plant. Damage caused by *Polyhymno* larval feeding reaches levels which can kill *A. cornigera* plants.

Key words *Acacia Pseudomyrmex* · Gelechiidae · Herbivory · Mutualism

Introduction

One third of the plant species of the world employ ants in their arsenal of herbivore defenses (Huxley and Cutler

1991; Koptur 1992). Ant-defended plants are found on every continent except Antarctica, are representatives of all major plant growth forms, and comprise a diverse array of plant taxa (Beattie 1985; Schupp and Feener 1991; Koptur 1992). Ants usually feed on sugar-rich extrafloral nectar or food bodies containing lipids and amino acids produced by the plant (e.g., Müllerian bodies in *Cecropia* and Beltian bodies in *Acacia*) (Janzen 1967, 1969; Tilman 1978; Inouye and Taylor 1979; Schemske 1980, 1982; Boecklen 1984; Horvitz and Schemske 1984; Koptur 1984, 1985; Barton 1986; Koptur and Lawton 1988; Putz and Holbrook 1988; Fiala et al. 1991). Ants defend these food resources by attacking and removing eggs, larvae, and adults of insect herbivores or seed predators that attempt to feed on the plant (Janzen 1967, 1969, 1972; Tilman 1978; Schemske 1980; Messina 1981; Risch 1982; Stephenson 1982; Letourneau 1983; Horvitz and Schemske 1984; Koptur 1984; Barton 1986; Koptur and Lawton 1988). Ants routinely reduce from 50 to 100% the numbers and resulting damage of herbivores and seed predators (e.g., Janzen 1967; Schemske 1980; Stephenson 1982; Koptur 1984; Putz and Holbrook 1988). The consequences of ant defense are increased plant growth, survival, and reproduction (Janzen 1967; Inouye and Taylor 1979; Schemske 1980; Messina 1981; Horvitz and Schemske 1984).

No plant defense against insect herbivores is fool-proof (Denno and McClure 1983; Fritz and Simms 1992). Ant defense of plants is no exception to this general rule. Characteristics such as shelter construction (Janzen 1967; Koptur 1984, 1992; Barton 1986; Mackay and Whalen 1991), noxious or defensive chemicals (Jolivet 1991), sugar-rich excretions that encourage ant attendance (Horvitz and Schemske 1984), ant mimicry (Letourneau 1983, 1990; Jolivet 1991), symphyly (Jolivet 1991), hard exocuticles (Janzen 1967; Koptur and Lawton 1988), protected oviposition sites (Rashbrook et al. 1992), and escape behaviors (Janzen 1967; Messina 1981; Koptur 1992) are often associated with insects that feed on ant-defended plants. Many of the insects found

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on ant-defended plants are rare and inflict little damage (Janzen 1967). A few insects, however, are regularly found feeding on ant-defended plants and significantly reduce their growth, survival, and reproduction (Janzen 1967; Koptur 1984; Horvitz and Schemske 1984; Barton 1986; Koptur and Lawton 1988).

The costs of feeding on ant-defended plants for herbivorous insects are numerous and include reductions in survival or fecundity due to ant attack or harassment (Janzen 1967, 1969; Tilman 1978; Stephenson 1982; Horvitz and Schemske 1984). The benefits of feeding on ant-defended plants are less obvious, but are potentially just as dramatic, such as the removal of natural enemies or competitors (Atsatt 1981; Koptur and Lawton 1988). Furthermore, herbivores which avoid ant attack on ant-defended plants may gain access to host plants with reduced chemical and mechanical antiherbivore defenses (Janzen 1966, 1967; Rehr et al. 1973; Bentley 1977; Koptur 1985, 1992).

From the perspective of the plant, investment in ant defense (i.e., production of extrafloral nectar and food bodies) is costly (Koptur 1992). Plants may not have sufficient resources to invest in both ant defense and allelochemicals or morphological structures which deter herbivores. Thus, plant investment in ant defense may reflect an evolutionary trade-off which results in significant reductions in both chemical and mechanical defenses (Bentley 1977; Koptur 1992).

In spite of the extensive literature concerning plant-ant mutualisms, little is known about the herbivores which feed on ant-defended plants (Jolivet 1991). Most of the information concerning these herbivores has been produced from studies focusing on the relative costs and benefits to the plant and ant resulting from the mutualism (Huxley and Cutler 1991). The goal of this study is, instead, to focus on a herbivore and the behavior which allows it to feed on a well-known ant-defended plant. Larvae of a gelechiid moth construct shelters and feed on ant-defended *Acacia cornigera* plants in Veracruz, Mexico. Janzen's work (Janzen 1966, 1967) focused on the strength of the mutualism between *Pseudomyrmex ferruginea* and *A. cornigera* and the fate of the latter when experimentally denied ant protection. Our study focuses on a counter adaptation of a herbivore to ant attack, which allows it to feed on ant-defended acacias. In an attempt to quantify the costs and benefits to this herbivore of feeding on ant-defended plants, and the potential consequences to the plant of herbivory, we will test five hypotheses: (1) ants defending *A. cornigera* plants search leaves with larval shelters and attack larvae; (2) larval shelters provide protection from ant attacks; (3) ants are more abundant on *A. cornigera* plants with new foliage than on plants with old foliage; (4) shelter construction allows larvae to exploit not only *A. cornigera* plants with older foliage and unoccupied by ants, but also *A. cornigera* plants with young foliage and occupied by ants, and (5) larval feeding results in defoliation levels sufficient to cause serious injury or death to *A. cornigera* plants.

Study system. The ant, *P. ferruginea* (Hymenoptera: Formicidae) and the acacia, *A. cornigera* (Leguminosae: Mimosaceae) form an obligate mutualism throughout their neotropical range (Janzen 1966, 1967). *P. ferruginea* ant colonies inhabit the swollen thorns of acacia plants, almost exclusively *A. cornigera* plants (Janzen 1967). These ants rarely feed on insect prey and depend almost entirely on *A. cornigera* for their food. Workers feed primarily on extrafloral nectar produced by nectaries on the dorsal side of the petioles and/or rachis of acacia leaves. They also harvest modified acacia leaf segments called Beltian bodies (Janzen 1966, 1967). These tear-shaped structures are found on new foliage and are located on each pinnule, pinna, and leaf rachis of the bipinnate acacia leaves. Beltian bodies contain high concentrations of protein, and together with extrafloral nectar collected by the workers serve as the primary food of *P. ferruginea* larvae (Janzen 1967). Acacias previously unoccupied by ants are quickly colonized by *P. ferruginea* ants after they have produced new foliage with Beltian bodies, and *P. ferruginea* workers spend more time on branches with Beltian body-bearing foliage (Janzen 1966, 1967). Thus, ants are concentrated on acacias with young foliage, which is often preferred by herbivores and most susceptible to herbivory (Janzen 1967; Raupp and Denno 1983). Beltian bodies are removed by foraging workers within 5 to 15 days and, as a consequence, young foliage is easily identified by the presence of Beltian bodies (Janzen 1967).

P. ferruginea ants act as the primary herbivore defense of *A. cornigera* plants (Janzen 1966, 1967, Rehr et al. 1973). Workers aggressively defend their food resource by attacking and removing herbivorous insects (Janzen 1966, 1967). Most nonant acacias possess allelochemicals and tough leaves that deter or prevent herbivory by insects (Janzen 1967). *A. cornigera* plants do not possess allelochemicals and have relatively tender leaves (Janzen 1967; Rehr et al. 1973). As a result, acacias not occupied by ant colonies suffer repeated defoliation and loss of growing shoot tips and may die within 6 months (Janzen 1966, 1967).

We observed larvae of a *Polyhymno* species (Lepidoptera: Gelechiidae) feeding on *A. cornigera* plants at Los Tuxtlas, Veracruz, Mexico. *Polyhymno* moth larvae are small (last instar 7 mm in length) and inhabit shelters constructed by webbing together acacia pinnae or pinnules. Small larvae were seen to usually inhabit shelters constructed of two or more pinnae while larger larvae often inhabited shelters constructed of two or more pinnules. Shelters were sealed shut with virtually no openings, and pinnae or pinnules had to be peeled apart with forceps to expose the larvae. The pattern of feeding damage on acacias indicated that larvae fed primarily on the mesophyll of individual pinnules from inside the shelters. We never observed larvae outside their shelters either during the day or at night. Larvae pupated inside shelters. Most acacias at the study site experienced some feeding by the larvae of *Polyhymno* and some acacias

were severely defoliated. We also observed grasshoppers and an unidentified chrysomelid beetle feeding on acacias, but *Polyhymno* larvae were by far the most abundant herbivores, as was their characteristic feeding damage.

Materials and methods

Study site

The study site was a forest edge-pasture located 1 km northeast of the Universidad Nacional Autónoma de México Los Tuxtlas field station, Veracruz, Mexico. The study area was approximately 5 ha and contained roughly 100 *A. cornigera* plants. The Los Tuxtlas region comprises the northernmost limit of the tropical evergreen rain forest in the New World (Gomez-Pompa 1973). This study was conducted in January 1996, during the dry season.

Ants defending *A. cornigera* plants search leaves with larval shelters and attack larvae

We observed ant behavior to determine if ants searched acacia leaves with larval shelters and attempted to remove discovered shelters. First, we observed the foraging behavior of *P. ferruginea* ants to test the hypothesis that workers search leaf pinnules with larval shelters for longer periods than leaf pinnules without larval shelters. Second, we observed the recruitment behavior of ants to test the hypothesis that other workers join the search of acacia pinnules with shelters. We recorded the time focal workers searched individual pinnules of acacia leaves with and without larval shelters. We also recorded the number of workers which joined searches already in progress. We used a *t*-test to compare the mean time (seconds) ants searched acacia pinnules with and without shelters and a Kolmogorov-Smirnov two-sample test to compare the frequency distributions of the number of ants which searched acacia pinnules with and without larval shelters (Sokal and Rohlf 1981).

Larval shelters provide protection from ant attacks

To explicitly test the hypothesis that shelters provide larvae with defense against ant attack, we placed a sheltered and unsheltered larva on different leaves of ant-infested acacia branches and observed them for 30 min. During this period, we recorded the number of ant passes and ant attacks. A pass occurred when a worker searched the acacia pinnule on which a larva was placed but did not attack. An attack occurred when a worker bit or stung the larva. We replicated the experiment 11 times on 11 different trees. We performed a *G*-test to determine if there were significant differences in the number of ant passes and attacks on sheltered and unsheltered larvae.

Ants are more abundant on *A. cornigera* plants with new foliage than on those with old foliage

To determine if the presence or absence of ants on acacias was associated with foliage age, we sampled 83 *A. cornigera* trees at the study site. For each tree we noted the presence or absence of ants and the age of foliage as indicated by the presence or absence of Beltian bodies. We tested the hypothesis that acacias with young foliage were more likely to be occupied by ants by calculating a 2×2 contingency table (*G*-test) (Sokal and Rohlf 1981).

Shelter construction allows larvae to exploit not only *A. cornigera* plants with older foliage and unoccupied by ants, but also ant-occupied *A. cornigera* plants with new foliage

To test this hypothesis, we first quantified the abundance of *Polyhymno* larvae on acacias in relation to the presence or absence of ants and foliage age. Second, we conducted a field experiment to determine the survival of *Polyhymno* larvae placed on acacias occupied or not by ants and with old or young foliage. For 83 acacias we counted the number of leaves per tree, the number of moth larvae per tree, noted the presence or absence of ants, and determined foliage age. We then used analysis of variance to determine if the presence or absence of ants and foliage age explained variation in larval densities.

To determine if larval survival is greater on acacias not occupied by ants and on acacias with new foliage, we conducted a 2×2 factorial experiment with presence or absence of ants and foliage age as treatments. We used the presence of Beltian bodies on leaves as an indicator of young foliage. One replicate of each treatment combination consisted of three larvae placed individually on randomly selected terminal leaves of a treatment acacia. Larvae which did not construct a shelter within 30 min were removed and replaced until larvae had constructed shelters. We carefully recorded the exact location of each larva (branch position, leaf position, pinnule position). Acacias were assigned to one of the four treatment combinations based on the presence or absence of naturally occurring ants and Beltian bodies. Each treatment combination was replicated seven times. We used analysis of variance to determine if presence or absence of ants, Beltian bodies, or their interaction explained variation in the angular-transformed proportion of larvae surviving after 6 days on treatment acacias.

Larval feeding results in defoliation levels sufficient to cause serious injury or death to *A. cornigera* plants

To test this hypothesis, we surveyed 64 acacias and quantified defoliation resulting from *Polyhymno* larval feeding. For each acacia surveyed, we recorded the number of *Polyhymno* larvae, number of leaves, the average number of pinnules per leaf, and the number of pinnules damaged by larval feeding. From these data, we calculated the proportion of acacia pinnules damaged by larval feeding at the field site. To determine if larval density and the angular-transformed proportion of pinnules damaged by larval feeding on acacia plants were correlated, we calculated the product-moment correlation coefficient. We used analysis of variance to determine if presence or absence of ants, foliage age, or their interaction explained variation in the angular-transformed proportion of acacia pinnules damaged by larval feeding. Although we did not directly determine the effect of *Polyhymno* herbivory on the survival or reproduction of *A. cornigera* plants, we compared the defoliation rates we measured with those recorded by Janzen during his long-term study of *A. cornigera* in Veracruz, Mexico, during which, field experiments were used to correlate feeding damage with the growth and survival of *A. cornigera* plants (Janzen 1966, 1967).

Results

Ants defending *A. cornigera* plants search leaves with larval shelters and attack larvae

Workers searched acacia pinnules with sheltered larvae significantly longer than acacia pinnules without sheltered larvae (121.3 ± 7.4 s versus 7.4 ± 4.6 s $F_{1, 38} = 171.69$, $P < 0.0001$). Significantly more workers joined searches in progress on acacia pinnules with

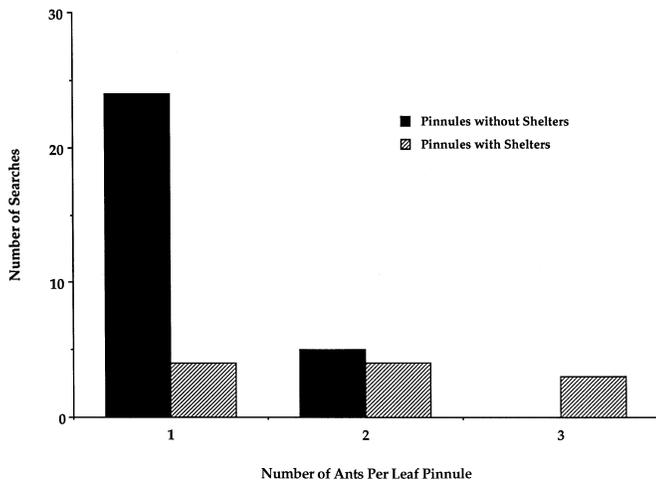


Fig. 1 Frequency distributions of the number of ants searching acacia leaf pinnules with and without larval shelters. Data include only those pinnules on which a focal ant was foraging. Significantly more ants joined focal ants in searching acacia pinnules with sheltered larvae than searches on acacia pinnules without sheltered larvae ($D_{n_{11}n_{29}} = 148.02, P < 0.01$)

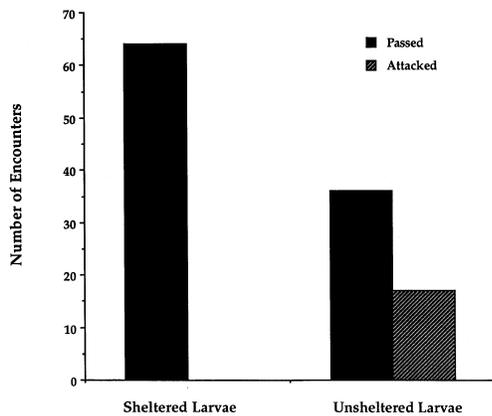


Fig. 2 The frequency of ant visits to sheltered and unsheltered larvae that were passes or attacks. Sheltered larvae were attacked significantly fewer times and were passed significantly more times than unsheltered larvae ($G = 30.48, P < 0.001$)

sheltered larvae than searches in progress on acacia pinnules without sheltered larvae (Kolmogorov-Smirnov two-sample test, $D_{n_{11}n_{29}} = 148.02, P < 0.01$; Fig. 1). Workers attempted to pull apart shelters with their mandibles and to insert their heads into any openings or cracks in the shelters. If the worker successfully inserted its head into an opening, it opened and closed its mandibles repeatedly in what appeared to be an attempt to bite the larva inside. We did not observe workers successfully pull or tear apart shelters and expose larvae. However, on four occasions, we opened larval shelters into which ants had inserted their heads: one of the four larvae was wounded, the cuticle of its last two or three abdominal segments being torn. Thus, workers spent considerable time searching acacia pinnules with sheltered larvae and investigated shelters when found. In

addition, other ants were more likely to join searches in progress on acacia pinnules with larvae than on acacia pinnules without larvae.

Larval shelters provide protection from ant attacks

Sheltered larvae were never attacked by workers during this experiment and ants passed sheltered larvae significantly more often than unsheltered larvae ($G = 30.48, P < 0.001, df = 1$ Fig. 2). Thus, shelters protect larvae from ant attack.

Ants are more abundant on *A. cornigera* plants with new foliage than on *A. cornigera* plants with old foliage

Of 83 acacias surveyed, 25 (30%) were occupied by ants. The presence or absence of ants on acacias was significantly associated with foliage age ($G = 53.68, P < 0.001, df = 1$). While 42% of ant-occupied acacias had young foliage, only 22% of acacias not occupied by ants had young foliage.

Shelter construction allows larvae to exploit not only *A. cornigera* plants with older foliage and unoccupied by ants, but also ant-occupied *A. cornigera* plants with new foliage

Of the 83 acacias surveyed, 52 (63%) were occupied by moth larvae. The average number of larvae per acacia was 2.31. The average larval density (number of larvae per acacia leaf) on the 83 acacias surveyed was 0.18, i.e., approximately one in every six acacia leaves was occupied by a *Polyhymno* larva. Larval densities (larvae/leaf) were significantly higher on acacias unoccupied by ants than on acacias occupied by ants (0.25 ± 0.04 versus $0.07 \pm 0.05, F_{1, 79} = 7.35, P = 0.0082$). Larval densities (larvae/leaf) were not significantly affected by foliage age (0.18 ± 0.05 and 0.15 ± 0.04 for old and new foliage, respectively; $F_{1, 79} = 0.29, P = 0.5947$). The pattern of increased larval densities on unattended plants was not influenced by foliage age, as shown by the nonsignificant interaction term ($F_{1, 79} = 2.97, P = 0.0887$).

Larval survival was greater on unoccupied than on ant-occupied acacias ($F_{1, 20} = 5.00, P = 0.0369$; Fig. 3). Larval survival was not affected by foliage age (0.17 ± 0.06 and 0.22 ± 0.06 for old and young foliage, respectively; $F_{1, 20} = 0.56, P = 0.4648$). The effect of ants on larval survival was not affected by foliage age ($F_{1, 20} = 0.18, P = 0.6772, \text{ant} \times \text{foliage age interaction}$).

Larval feeding results in defoliation levels sufficient to cause serious injury or death to *A. cornigera* plants

Acacias at the field site incurred larval feeding damage on 33% of their leaf pinnules. Feeding damage was significantly correlated with larval density ($r = 0.684,$

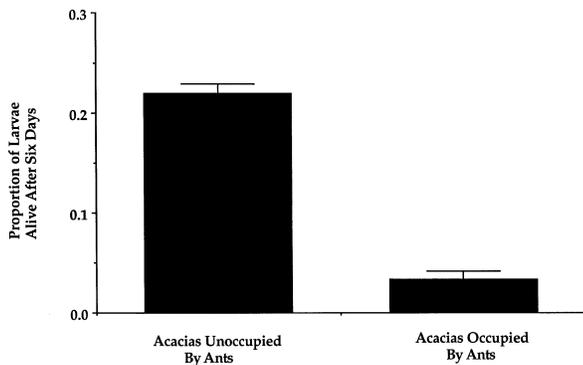


Fig. 3 Back-transformed mean and SE of the proportion of larvae alive after 6 days on acacias occupied and unoccupied by ants. The means are significantly different (LSD, $P < 0.05$)

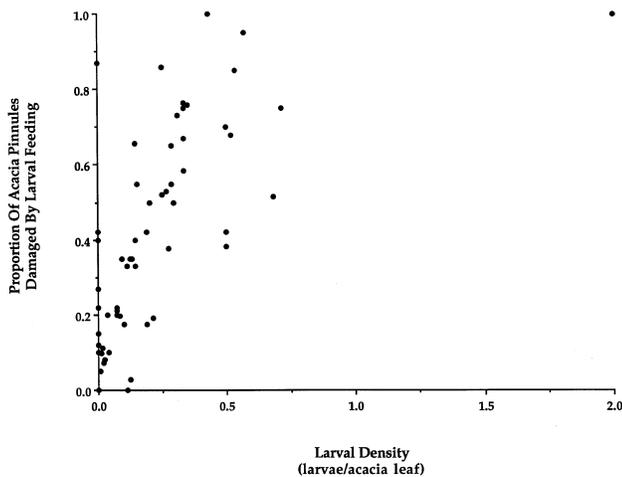


Fig. 4 Correlation of larval feeding damage and larval density. Increases in larval density are significantly correlated with increases in the proportion of pinnules damaged by larval feeding ($r = 0.684$, $P < 0.01$, $df = 73$)

$P < 0.01$, $df = 73$; Fig. 4). The proportion of pinnules with feeding damage was significantly higher on unoccupied than on ant-occupied acacias (0.41 ± 0.04 versus 0.17 ± 0.06 , $F_{1, 70} = 8.03$, $P = 0.0060$). Levels of feeding damage by *Polyhymno* larvae on acacias were not affected by foliage age (0.28 ± 0.05 and 0.29 ± 0.05 for old and young foliage, respectively, $F_{1, 70} = 0.11$, $P = 0.7411$). The pattern of increased feeding damage on acacias not occupied by ants was not affected by foliage age (nonsignificant interaction term, $F_{1, 70} = 0.03$, $P = 0.8603$).

Discussion

We have extended research in the acacia-ant system to include a herbivore with a counter adaptation to ant attack and studied the consequences of herbivory to ant-defended acacias. *Polyhymno* larvae construct sealed

shelters by silking together the pinna or pinnules of acacia leaves. Although larval density and survival are higher on acacias not occupied by ants, shelters serve as a partial refuge from the ant *P. ferruginea*. Shelters provide *Polyhymno* larvae access to an otherwise unattainable and poorly defended host plant.

During our short-term observations and experiments, workers did not attack sheltered larvae. Workers did attempt to pull apart shelters and joined searches in progress on pinnules with sheltered larvae. The presence of ants did, however, affect the long-term survival of larvae. We believe the persistent attempts by workers to open shelters and attack larvae ultimately resulted in many successful attacks and reduced larval survival on ant-occupied acacias. *Polyhymno* larval densities on ant-occupied *A. cornigera* plants were one-third those of unoccupied acacias. Defoliation as a result of *Polyhymno* larval feeding was 50% lower on ant-occupied acacias than on unattended acacias.

In spite of the vigilant efforts of patrolling *P. ferruginea* workers, however, a considerable number of *Polyhymno* larvae attacked ant-occupied acacias. Although shelter construction did not provide larvae complete protection against ant attack, shelters did dramatically reduce the frequency of ant attack. Eleven percent of sheltered *Polyhymno* larvae survived on ant-occupied acacias (as opposed to 28% survival on ant-free acacias). Nearly 10% of leaves were infested with larvae on ant-occupied acacias, and 17% of the foliage was consumed by *Polyhymno* larvae. Thus, shelter construction did provide some *Polyhymno* larvae access to ant-defended acacias.

Although our study did not directly consider possible benefits gained by a herbivore attacking an ant-defended host plant, it does provide indirect evidence of potential benefits. We found no evidence that *Polyhymno* larvae experienced decreased pressure from natural enemies or competitors during our study. We observed no instances of predation or parasitization of *Polyhymno* larvae on either ant-occupied or unoccupied acacias and other herbivores were rare on acacias. However, by feeding on acacias, *Polyhymno* larvae gained access to a host plant with reduced chemical and mechanical defenses (Janzen 1966, 1967; Rehr et al. 1973; Bentley 1977; Koptur 1985, 1992). Larval survival was not affected by foliage age during our experiments. This result makes sense because acacia foliage does not toughen with age (Janzen 1966), unlike most other plant foliage (Raupp and Denno 1983). We believe this result is indicative of the benefits gained by herbivores which overcome the ant defense of acacias and feed on these mechanically and chemically undefended plants. This result and the relative abundance of acacias unoccupied by ants could suggest that *Polyhymno* larvae do not need to feed on young, ant-defended acacias. *Polyhymno* females could preferentially oviposit on ant-free acacias and larvae would avoid contact with ants altogether and survive well on acacias with older foliage. While we agree that *Polyhymno* larvae do not benefit from feeding on young foliage, this interpretation

of our results is flawed because the production of new foliage and ant attendance is variable in space and time (Janzen 1966). There is a substantial probability that an acacia will be occupied by workers at some point in the life history of a *Polyhymno* larvae. Thus, the ability of larvae to avoid ant attack is essential to the utilization of acacias by this herbivore.

The ability of *Polyhymno* larvae to circumvent the ant defense of acacias has profound consequences not only for the herbivores, but also for the plants. Acacias incurred high levels of damage (33% of leaf pinnules eaten) and many were severely defoliated by larvae. The level of feeding damage we observed on ant-occupied acacias due to *Polyhymno* larvae (17%) was very similar to the damage on ant-unoccupied acacias as a result of feeding by all herbivores (25%; other lepidopteran larvae, orthopterans, and coleopterans) during previous studies of *A. cornigera* (Janzen 1967). During previous studies, this level of defoliation resulted in severe reductions in plant growth and, when continued for periods of 5–6 months, resulted in plant death (Janzen 1966, 1967). Persistent feeding damage by *Polyhymno* larvae and other herbivores which defeat the ant defense of plants may provide selection pressure for increases in chemical and mechanical defenses and against production of expensive plant products such as nectar and food bodies employed to attract ants.

Shelter construction is a behavior of various lepidopteran species whose larvae attack ant-defended plants (Koptur 1992). The effectiveness of shelter construction as a defense against ant attack, however, varies among these lepidopteran species. Species whose larvae produce secure shelters by silking together leaves and feed inside these shelters are often successful at avoiding ant attacks (Koptur 1984; Barton 1986). Larvae of these species can exploit ant-defended host plants when plants are occupied by ants, whereas species whose larvae produce unsealed “webs” or “tents” and feed outside these shelters are less successful at avoiding ant attacks (Janzen 1967; Horvitz and Schemske 1984). Larvae of the latter species can only exploit ant-defended host plants when they are not occupied by ants.

We have demonstrated that *Polyhymno* larvae construct secure shelters which provide some protection against *P. ferruginea* ant attack. This behavior promotes the exploitation of the ant-defended acacia, *A. cornigera*, as a host plant. *A. cornigera* plants have poor chemical and mechanical defenses, and may be particularly vulnerable to herbivores which avoid ant defense. Thus, the ability of *Polyhymno* larvae to exploit *A. cornigera* plants may reduce the growth and survival of acacias. Our study is one of only a few detailed investigations of herbivores with counter adaptations to ant attack which feed on ant-defended host plants. Counter adaptations to ant attack such as shelter building are poorly documented, but are likely to be common in nature. Further detailed research on herbivores which feed on ant-defended plants may provide evidence of selection against ant defense.

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