

SHORT COMMUNICATION

Contrasting exotic *Solenopsis invicta* and native *Forelius pruinosus* ants as mutualists with *Catalpa bignonioides*, a native plant

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Abstract. 1. The suitability of the red imported fire ant *Solenopsis invicta* Buren and a native ant *Forelius pruinosus* (Roger) as participants in a food-for-protection mutualism with a native nectaried tree *Catalpa bignonioides* Walter was compared.

2. The mean mortality of folivore larvae of *Ceratomia catalpae* Boisduval was similar for *S. invicta* and *F. pruinosus* although *S. invicta* attacked fewer caterpillar aggregations and was a devastating pupal predator. *Solenopsis invicta* also differed from the native ant in that it attacked the parasitoid *Cotesia congregata* Say, another plant mutualist, and visited extrafloral nectaries less frequently.

3. Habitats invaded by *S. invicta* are characterised by a scarcity of both herbivores and of beneficial insects that visit extrafloral nectaries. The plants do not require protection, and extrafloral nectaries are visited rarely. Although plants are defended incidentally by *S. invicta*, the insect-plant mutualism therein is greatly simplified or defunct.

Key words. Exotic, extrafloral nectar, mutualism, parasitoids, pupa, tri-trophic interactions.

Introduction

It is well known that exotic ants can severely depress the diversity and abundance of native ants and other arthropods (Vinson, 1994; Hollway *et al.*, 2002), however less is known about the impact of ant invasions on interactions in which native arthropods participated previously, for instance mutualisms between ants and plants (but see Bond & Slingsby, 1984; Christian, 2001, regarding myrmecochory). The production of extrafloral nectar to attract insect bodyguards is a geographically and taxonomically widespread example of a food-for-protection mutualism typically involving ants and plants (Koptur, 1992). That the interaction functions as a *reciprocally* beneficial mutualism is contingent on at least three characteristics. (1) Visitors must defend vulnerable plants. This requires visitors capable of attacking herbivores successfully (Janzen, 1966), and herbivores in sufficient abundance to necessitate plant protection (Barton, 1986). (2) Plant protectors must utilise the food offered by the plant (Sagers *et al.*, 2000). (3) The interaction should not endanger other mutualisms

important to either participant (Willmer & Stone, 1997). Insofar as the displacement of native insect assemblages by exotic ants alters these *currencies* (plants' need for protection and procurement thereof, collection of food by bodyguards, and interactions with other mutualists), the food-for-protection mutualism may be disrupted.

The red imported fire ant *Solenopsis invicta* Buren and a widespread native ant *Forelius pruinosus* (Roger) were compared in terms of these three criteria, specifically as mutualists with a native tree *Catalpa bignonioides* Walter (Bignoniaceae). *Catalpa bignonioides* attracts ants and parasitic wasps to extrafloral nectaries, and these visitors can act as plant mutualists when the *C. bignonioides* requires protection against herbivores. Field observations and experiments illustrated that the two ants differed in their leaf patrolling rates, visitation at extrafloral nectaries, and predation of caterpillars. The ants also differed in their importance as pupal predators of both herbivores and other plant mutualists (parasitic wasps).

Study organisms and sites

Solenopsis invicta has displaced many native arthropods in the southern U.S.A. (Porter & Savignano, 1990; Gotelli &

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Arnett, 2000; but see Morrison, 2002). *Forelius pruinosus* is capable of co-existing at low *S. invicta* densities but is absent from heavily invaded sites (Camilo & Phillips, 1990). The sunlit, mesic, disturbed habitats readily dominated by *S. invicta* are frequently occupied by *C. bignonioides*, a native tree with five to 10 extrafloral nectaries per leaf. These nectaries typically attract a variety of visitors, including *F. pruinosus* and *Cotesia congregata* Say (Hymenoptera: Braconidae), that attack the gregarious caterpillar *Ceratonia catalpae* (Boisduval) (Stephenson, 1982; Ness, 2001). *Ceratonia catalpae* caterpillars are the only significant defoliator of *C. bignonioides* (Baerg, 1935); dry mass per fruit and per seed decreases with defoliation (Stephenson, 1980) and caterpillars feed on fruits of defoliated plants (J. H. Ness, pers. obs.). Folivory induces an increase in the sugar excretion rates of damaged leaves within 36 h, thereby attracting and retaining nectary visitors at leaves requiring protection (Ness, 2000). *Ceratonia catalpae* pupates in the litter layer beneath the host tree, and emerging adults commonly oviposit on these same trees (Baerg, 1935). Three generations are typically observed from June to October.

Research was conducted using mature *C. bignonioides* trees 4–6 m tall at the Sandy Creek Nature Center and the University of Georgia Horticulture Farm, Athens, U.S.A. (33°52'N, 83°15'W), from May to November 1999–2000. Trees were adjacent to a stream and pond respectively. The Sandy Creek Nature Center site includes a grove of 75 *C. bignonioides* trees extending beneath an electrical powerline to mixed pine and hardwood forest on either side. The powerline cut contains a high density of *S. invicta* colony mounds; colonies were not found in the forest interior (J. H. Ness, pers. obs.). The Horticulture Farm includes six adult *C. bignonioides* trees and 50 2–4-year-old seedlings surrounded by mixed agricultural plots dominated by *S. invicta*. To facilitate the growth of native ant populations on and around the trees, fire ant mounds were excluded from a 325-m² rectangular plot around the trees with targeted pesticide bait applications (Amdro[®]) and manual destruction of mounds with shovels and water in 1999 and 2000. *Forelius pruinosus* (and rarely *Formica schaufussi*) foraged on the trees and ground at low levels prior to the exclusion of fire ants and were more abundant thereafter.

Methods

To correlate the phenology of extrafloral nectar production with leaf visitation by ants, sugar excretion was measured over the lifetime of leaves selected randomly at Sandy Creek in May 1999. Twenty leaves on four trees were encircled with Tanglefoot[®] (Tanglefoot Company, Cedar Rapids, Michigan) that excluded ants (the most common visitors), and each leaf was rinsed with water 24 h prior to nectar collection to avoid nectar accumulation. Nectar was collected from the largest nectary on each leaf using a microcapillary pipette, and sugar production (μg sucrose equivalents produced per nectary in 24 h) was estimated on site using a pocket refractometer. *Catalpa bignonioides*

produces new leaves with active nectaries from May to August (Ness, 2001), although nectar collection was limited to these spring-flushing leaves.

To contrast the two ants' visitation of extrafloral nectaries and/or leaf patrolling, the number of ants per leaf was surveyed at the two sites from June to November 2000. Six trees with large, active fire ant mounds at their bases were surveyed at Sandy Creek, and seven at the Horticulture Farm *S. invicta*-exclusion plot. During each survey, all the ants were counted on 15 mature leaves selected randomly from the north, south, east, and west sides of each tree. Surveys were made between 16.00 and 19.00 hours on sunny days to avoid morning dew and peak midday temperatures. *Forelius pruinosus* is a diurnal forager, and *S. invicta* is active at this time (Porter & Tschinkel, 1987).

To test the effect of ants on caterpillar survival rates and contrast this effect between the two ant species, workers were excluded from caterpillar aggregations at both sites. In July 1999, 56 isolated leaves were chosen randomly on trees at each site, and Tanglefoot[®] was applied to the petiole of half of these leaves to exclude ants. Six second-instar *C. catalpae* were added to each leaf. The 112 leaves (28 for each treatment \times ant combination) were surveyed for caterpillars and ants 2 days later. To compare ant recruitment at damaged and undamaged leaves, 58 randomly selected undamaged leaves within the same trees were also surveyed for ants at that time. This experiment was repeated in July–August 2000 with larger caterpillar aggregations (10 second instar), a greater duration of exposure (3 days), and branches rather than leaves ($n=20$ per treatment \times ant combination). In both experiments, isolated leaves and branches were chosen to decrease the likelihood of ants recolonising experimental leaves through contact with neighbouring foliage, and to limit the destinations available to dispersing caterpillars (although these instars are largely sedentary). Neighbouring leaves were surveyed to include locally dispersed caterpillars, and retention rates were assumed to approximate survival rate. General linear models were used to examine the effect of treatment, ant identity, and ant \times treatment interactions on caterpillar survival rates.

A natural experiment compared survival rates of *C. catalpae* pupae in four habitats that differed in successional stage and ant composition: the powerline field and farm plots (both *S. invicta* invaded) and the *S. invicta*-exclusion plot and secondary forest (both including native ants). Laboratory-reared fifth-instar *C. catalpae* larvae were placed underneath 473 ml plastic cups anchored top-down in each habitat. This technique limits caterpillar dispersal, and the pupae can be collected readily while construction of a pupal chamber within the adjacent soil remains unimpeded (Lee *et al.*, 1990). Thirty-eight to 45 caterpillars were deposited in each habitat. The soil underneath and adjacent to the cups was excavated 18 days later, and sorted using a sieve to ascertain the fate of the pupae. Individuals were assigned to one of four categories: living pupae, ant prey, pupae removed by small mammals, and pupae killed by indistinguishable causes (e.g. parasitic nematodes, fungi).

Ant predation was distinguished by characteristically small entry holes in the pupae, only the head capsule remaining from the caterpillar, or the absence of remains beneath a securely anchored cup. Anchored cups lacking remains frequently contained entrances to ant foraging tunnels, and *S. invicta* generally transports prey fragments to the nest (Wilson & Oliver, 1969). Small mammal attack was indicated by overturned cups and excavated burial chambers.

To test whether the ants influenced survival rates of *C. congregata*, a potential plant mutualist, individual cocoons were placed on 112 leaves on five trees at each site and ants were excluded from half of those leaves using Tanglefoot®. *Cotesia congregata* pupate on their host's integument or, less frequently, adjoining vegetation (Kester & Jackson, 1996). Cocoons were stuck on these leaves using a single drop of Elmers® white glue. This glue dries quickly, and cocoons were handled using forceps to limit the deposition of additional semiochemicals. Three days later, each cocoon was identified as *eaten* (cocoons shredded or missing) or *surviving* (cocoons present and intact). The experiment was performed simultaneously at both sites between 22 July and 10 September 2000 when cocoons were available.

Results

The May cohort of *C. bignonioides* leaves produced extrafloral nectar at the greatest rate in mid-summer 1999 (Fig. 1). Leaf patrolling by *F. pruinosus* peaked in mid to late summer 2000, a pattern not observed for *S. invicta* (Fig. 1). The mean number of *F. pruinosus* ants per leaf in 2000 (mean \pm SE: 0.63 ± 0.13) was four-fold greater than the mean of *S. invicta* (0.16 ± 0.05).

Caterpillar survival rates were increased significantly on Tanglefoot®-encircled leaves in 1999 (approximately 1.5-fold; $F = 15.35$, $P < 0.001$) and 2000 (approximately four-fold; $F = 55.07$, $P < 0.001$), and fewer ants were found on these leaves (Mann-Whitney, $U = 4.24$, $P < 0.001$). Mean caterpillar survival rates were similar between the two ant assemblages in both years (ant identity main effect, 1999: $F = 0.53$; 2000: $F = 1.57$, both $P = \text{NS}$), and treatment \times ant interactions were not significant in either year (1999: $F = 0.0$; 2000: $F = 0.68$, both $P = \text{NS}$). The patterns of ant occupation and caterpillar survival within trees, however, differed between the ant species. *Forelius pruinosus* workers were more than twice as common on caterpillar-damaged leaves (mean \pm SE: 1.61 ± 0.46 ants per leaf) as on randomly selected undamaged leaves (0.67 ± 0.12) (Mann-Whitney, $U = 2.02$, $P < 0.05$), and killed $>60\%$ of the caterpillars in a majority of the aggregations. *Solenopsis invicta* numbers at damaged (0.72 ± 0.33) and undamaged (1.16 ± 0.57) leaves were indistinguishable ($U = 0.37$, $P = \text{NS}$). Predation by *S. invicta* was inconsistent among branches; all the caterpillars were killed in 42% of the aggregations, although the mortality rates in the remaining aggregations were indistinguishable from that on ant-excluded leaves (1999: $F = 0.83$; 2000: $F = 0.41$, both $P = \text{NS}$).

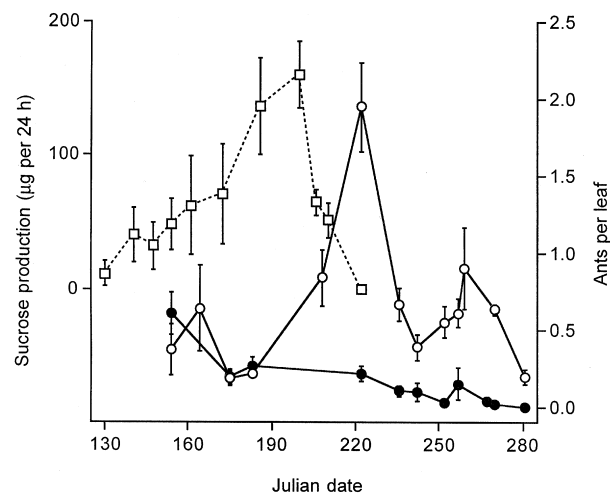


Fig. 1. Phenology of extrafloral sugar production and ant occupancy on *Catalpa bignonioides* leaves (mean and SE bars are shown). Sugar production per nectary (open squares) was estimated from 20 spring-flushing leaves at Sandy Creek Nature Center in 1999. Later leaves are not included. Visitation of leaves by *Forelius pruinosus* (open circles) and *Solenopsis invicta* (closed circles) was measured in 2000. Surveys included 60 leaves per tree on six *S. invicta*-dominated trees at the Sandy Creek Nature Center and seven *F. pruinosus*-dominated trees at the University of Georgia Horticulture Farm. Note: in order to distinguish lines better, y axes do not start at zero.

The proportion of *C. catalpae* pupae surviving differed among the four sites ($X^2 = 31.4$, $P < 0.001$). Moth emergence was decreased approximately eight-fold in *S. invicta*-invaded habitats relative to those controlled by native ants (Table 1). Most of this mortality was attributable to ant predation although mammals killed 27% of the pupae in an uninvaded forest.

The percentage of *C. congregata* pupae remaining intact after exposure to *S. invicta* (15%) was one-fifth of that in the presence of *F. pruinosus* (83%) or where either ant was excluded (86 and 93% respectively). That proportion differed among these four (ant \times Tanglefoot® treatment) groups ($X^2 = 102.25$, $P < 0.001$).

Discussion

This field study demonstrates that the exotic *S. invicta* and native *F. pruinosus* ants differ in their capacities to act as reciprocally benefitting mutualists with *C. bignonioides*, a native nectaried plant. In the following section, the two ants are contrasted with regard to on-plant nectar collection and caterpillar predation, effects on herbivore recruitment (an indirect measure of plant vulnerability), and their interactions with *C. congregata*, an additional plant mutualist.

Forelius pruinosus and *S. invicta* workers foraged on plants differently. *Forelius pruinosus* was more abundant on leaves, and killed caterpillars in most aggregations. *Forelius pruinosus* also appeared to be attuned better to reward

Table 1. Mortality rate of *Ceratonia catalpae* pupae at four sites varying in ant composition. Powerline field = Sandy Creek Nature Center powerline field, Forest = Sandy Creek Nature Center forest, Farm = University of Georgia Horticulture Farm, Exclusion plot = *S. invicta*-exclusion plot at the University of Georgia Horticulture Farm. Different letters indicate significant differences in the proportion of total pupae killed by ants (multiple comparisons by site, $P < 0.01$ in all cases).

Habitat	Ants	Per cent mortality of <i>Ceratonia catalpae</i> pupae		
		Total	By ants	By mammals
Powerline field	<i>S. invicta</i>	97.6	95.2 a	2.4
Forest	Native ants	58.5	31.7 b	26.8
Farm	<i>S. invicta</i>	92.3	87.2 a	5.1
Exclusion plot	Mostly <i>F. pruinosus</i>	55.3	50.0 b	2.6

production by *C. bignonioides*. Linking ant attendance with nectar production at the whole-plant scale is difficult, as the present study tracked extrafloral nectar production for a cohort of leaves rather than for entire trees. Estimates from spring leaves in 1999 give little indication of when plant-scale peaks in nectar production occur, although rates certainly increase from spring to summer (also see Stephenson, 1982). *Forelius pruinosus* attendance was greatest in mid to late summer 2000, and the ants recruited to herbivore-damaged leaves that can excrete more sugar (Ness, 2003). In contrast, the phenology of *S. invicta* leaf patrolling and extrafloral nectar production were not correlated, and attendance at damaged and undamaged leaves did not differ. These results are consistent with this ant's disinterest in carbohydrate-rich baits during warmer months (Stein *et al.*, 1990) and lack of a preference for nectars with higher sugar content (Lanza *et al.*, 1993). The disparity in the number of ants observed on the plants is particularly striking given Porter and Savignano's (1990) finding that *S. invicta* was 10–30 times more abundant than native ants in adjacent uninvaded habitats. Perhaps as a consequence of the poor match between *S. invicta* dietary preference and the rewards offered by *C. bignonioides*, most caterpillar aggregations showed no evidence of ant predation. The lower prey encounter rates of *S. invicta* appeared to be balanced by greater aggressiveness on locating caterpillar aggregations, as mean caterpillar mortality rates did not differ between trees dominated by the two ants. Differences among the ants nonetheless remain important. (1) If concentrated defoliation has a greater detrimental effect on plants than similar amounts of damage dispersed across the entire plant (e.g. Lowman, 1982; Edwards *et al.*, 1992; Marquis, 1992; Mauricio *et al.*, 1993), *F. pruinosus* may be a better plant bodyguard than *S. invicta*. (2) To the extent that *S. invicta* does not collect extrafloral nectar, it receives no reciprocal benefit from *C. bignonioides*. This ant–plant interaction may well be commensalistic but it is not mutualistic. (3) There was no evidence that *C. bignonioides* ceased to produce sugar at unvisited nectaries in invaded habitats, thereby avoiding the costs of the mutualism.

Solenopsis invicta was a devastating pupal predator in comparison with *F. pruinosus* and other predators. The

eight-fold decrease in *C. catalpae* moth emergence in *S. invicta*-invaded habitats benefits *C. bignonioides* indirectly, although two points should be noted. (1) Pupal predators that do not ingest plant rewards (e.g. small mammals and *S. invicta*) are plant commensalists rather than mutualists. (2) The plant's investment in bodyguard attractants is beneficial only when protection from herbivores is required. The absence of folivores obviates the need for (and benefits of) on-plant protection, and subsequent reward production probably incurs a net cost to the plant.

Solenopsis invicta also differed from *F. pruinosus* in attacking *C. congregata* pupae. This braconid parasitoid visits *Catalpa* extrafloral nectaries and attacks *C. catalpae* caterpillars (Stephenson, 1982; Ness, 2001). Because *C. congregata* can parasitise >50% of late instars on a tree (Ness, 2001) and these larvae are sufficiently large to avoid ant predation, attracting this wasp may benefit *C. bignonioides* even when other bodyguards are present. Whether the interaction between this plant and parasitoid constitutes a mutualism important to either population is uncertain. Other *Cotesia* species can increase host plant seed set by parasitising folivores (Hoballah & Turlings, 2001) and live longer when sugar nectar is available (Siekman *et al.*, 2001). Plants in invaded sites may require protection from herbivores less frequently than plants in uninvaded sites, although they also have fewer bodyguards available to attract.

An abundant and aggressive carnivore, *S. invicta* provides indirect protection to nectaried and unnectaried plants alike (Agnew *et al.*, 1982; Stiles & Jones, 2001). Nectar rewards are poorer attractants in these invaded sites as the dietary preferences and foraging strategies characteristic of species in the more diverse native arthropod communities are lost. The most familiar threats to food-for-service mutualisms between plants and insects are visitors that collect food but fail to provide reciprocal benefit to the plant (*nectar thieves*). By contrast, *S. invicta* disrupts the mutualism between *C. bignonioides* and native arthropods such as *F. pruinosus* by its indifference towards nectar, local extirpation of herbivores, and predation/exclusion of other plant bodyguards. Any resulting plant protection by *S. invicta* is incidental to, rather than a consequence of, the mutualism.

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