

SHORT COMMUNICATION

Ant-dependent oviposition in the membracid *Publilia concava*

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Introduction

Ants enhance the survivorship and development of tended homopterans by protecting them from predators and facilitating feeding. In return, ants harvest the sugary excretions (honeydew) of these homopterans (reviewed by Way, 1954; Buckley, 1987). Recently, ant–homopteran interactions have become a model system for studies that consider the underlying causes of variation in the outcome of mutualism (i.e. conditionality; Cushman & Addicott, 1991; Bronstein, 1994). An increasing number of studies is finding that conditionality in the degree to which homopterans benefit is partly the result of variation in the level of ant tending (Breton & Addicott, 1992; Flatt & Weisser, 2000; Morales, 2000a,b; Fischer *et al.*, 2001). Some of the factors that influence the level of ant tending include the quality and quantity of honeydew production (Völkl *et al.*, 1999; Fischer *et al.*, 2001), homopteran density (Breton & Addicott, 1992; Morales, 2000a,b), and the spatial distribution of homopterans (Cushman & Whitham, 1991; Morales, 2000b).

Given the demonstrated importance of ant-tending level to the success of myrmecophilous homopterans and lycaenids, coupled with the limited mobility of homopteran nymphs and lycaenid caterpillars, ant-dependent host choice should be expected for many of these species (Dyck *et al.*, 2000). Nevertheless, while ant-dependent oviposition has been demonstrated or suggested for a large number of ant–lycaenid butterfly mutualisms (Pierce & Elgar, 1985), few data are available for ant–homopteran interactions.

Studies that have examined the influence of ants on oviposition in homopterans have done so primarily within the context of maternal care. In particular, studies have shown that treehopper females are both more (Wood, 1977; Olmstead & Wood, 1990) and less (McEvoy, 1979; Bristow, 1983) likely to abandon broods in the presence of ants, and

that females abandoning broods may subsequently initiate new broods on different host plants (Bristow, 1983; Olmstead & Wood, 1990). No studies have examined the influence of ants on the probability that oviposition will occur on a given host plant. To address this, ant-dependent oviposition was considered for the interaction between the treehopper *Publilia concava* Say and ants in the genus *Formica* Linné by comparing the frequency of oviposition for plants with access to ants relative to plants with ants excluded.

The potential for ant-dependent oviposition to generate a distribution of *Publilia* spp. aggregations centred on the nests of *Formica* spp. ants (described by McEvoy, 1979; Cushman & Whitham, 1991) was also considered. Two hypotheses have been advanced to explain this pattern of spatial distribution (McEvoy, 1977); these are not mutually exclusive. (1) The spatial distribution of treehoppers is generated by ant-dependent survival of eggs to adults (McEvoy, 1979; Bristow, 1984; Cushman & Whitham, 1989; Morales, 2000a,b). (2) The spatial distribution of treehoppers is generated by ant-dependent oviposition. In both hypotheses, the density of ants, and therefore survivorship or oviposition, declines as distance from the ant nest increases.

Methods

Study system

The treehopper *Publilia concava* (Hemiptera: Membracidae) is a univoltine, sub-social homopteran that commonly feeds on the goldenrod *Solidago altissima* L. and is tended by ants in the genus *Formica* for populations located in central Connecticut, U.S.A. *Publilia concava* adults overwinter in the leaf litter and emerge in early spring to mate. Dispersal occurs at this time, and treehoppers form mating groups from late May to early June that are attractive to ants (M. A. Morales, pers. obs.). Males die soon after mating, and females oviposit on the midrib of leaf veins, either on the same host plant or after selecting a new host

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(M. A. Morales, pers. obs.). Females produce one or two broods within a variable time period but usually not exceeding 1 month between broods (M. A. Morales, pers. obs.). Two broods from a given female can be found on a single or separate host plants (Bristow, 1983).

Both nymphs and adults are tended by ants, and ant tending has been shown to have a strong, positive effect on the survival of nymphs to adults for treehoppers of this species (McEvoy, 1979; Morales, 2000a,b). Here, an aggregation is defined as all nymph and adult treehoppers on a given host plant, and a patch is defined as all aggregations tended by a given ant colony.

Experimental design

Experiments were conducted at the Dennis Hill Farm Preserve of the Nature Conservancy (Putnam, Connecticut) for a patch tended by *Formica integra* Nylander. In 1998, 66 host plants on which neither ants nor treehoppers were observed (i.e. prior to selection of host plants by females) and located within 20 m of the ant nest were selected haphazardly. Ants were prevented from accessing half of these plants by applying Tangle-Trap[®] (Tanglefoot, Grand Rapids, Michigan) over a masking tape sleeve, and clipping surrounding vegetation. Plants with access to ants were handled similarly except that Tangle-Trap[®] was not used. Treatments began on 23 May, and plants were censused for the presence of treehoppers and egg masses (no egg masses were found on plants where treehoppers were not observed) approximately twice weekly until 29 July, at which time the majority of eggs masses had hatched. The number and length of egg masses was noted at the final census. Length of egg masses in *P. concava* has been shown to be correlated strongly with the total number of eggs (McEvoy, 1977).

A similar experiment was conducted during summer 1999 except that host plants were selected on which treehoppers were already present (i.e. subsequent to discovery of potential host plants by females but prior to oviposition). Eighteen plants were selected, and ants were excluded from half of these as in the 1998 experiment (initially, ants were found tending treehoppers on 15 out of 18 host plants). Treatments began on 2 June (about the time that treehoppers began colonising host plants in 1998) and lasted for 3 weeks. Treehopper censuses were conducted daily for the first week, every other day for the second week, and twice during the last week. The number of egg masses was recorded at the final census.

Finally, the spatial distribution of treehoppers for a patch tended by *Formica pergandei* Emery was assessed at the same site during summer 1997 by mapping all aggregations located within 35 m of this nest.

Results and discussion

Host-choice hypothesis

Logistic regression was used to analyse the probability of oviposition, measured as the frequency of host plants with

clutches at the end of the census period for host plants on which at least one treehopper was observed. There was no effect of year on the frequency of oviposition (year, ant \times year | ant: $\chi^2_{d.f.=2} = 2.353$, $P = \text{NS}$) so data were pooled. Combining years, the frequency of oviposition was significantly higher on host plants with access to ants than on host plants with ants excluded ($\chi^2_{d.f.=1} = 8.033$, $P < 0.01$; Table 1).

Because treatments in 1999 were established on host plants where adults were present prior to manipulations, the net change in adult treehopper density between treatments was also examined for data collected from this year. Significantly more treehoppers disappeared from host plants with ants excluded than from host plants with access to ants (\bar{x} change \pm SE: -1.44 ± 0.65 vs. 1.22 ± 0.68 , where change = number of treehoppers at the final census – number of treehoppers at the first census; $t_{16} = -2.833$, $P < 0.05$).

The number of egg masses per ovipositing female did not vary between years or ant-exclusion treatments ($\bar{x} \pm$ SE: 1.23 ± 0.07 , $F_{3,23} = 0.263$, $P = \text{NS}$). Similarly, there was no significant difference between ant-exclusion treatments in mean egg mass length (data collected from 1998 only, $n = 13$, $\bar{x} \pm$ SE: 6.08 ± 0.56 mm vs. 6.17 ± 1.03 mm; Mann–Whitney $U = 17.0$, adj. $Z = 0.15$, $P = \text{NS}$).

Finally, there was no difference in the number of host plants on which at least one treehopper was observed for plants with access to ants relative to plants with ants excluded for data collected from 1998 [nine out of 33 for both treatments (all host plants began with treehoppers present in 1999)], suggesting that excluding ants did not influence the ability of treehopper adults to access these host plants.

Spatial distribution

Data collected from the *F. pergandei* patch showed that treehoppers were distributed centrally with respect to the location of their ant partner (Fig. 1). In particular, the number of treehoppers per m² decreased significantly as distance from the nest increased (adj. $R^2 = 0.77$, $F_{1,10} = 37.26$, $P < 0.001$; Fig. 1). In contrast, the number of treehoppers per aggregation did not vary with distance from the nest ($R^2 = 0.003$, $F_{1,49} = 0.14$, $P = \text{NS}$).

Discussion

Results presented here demonstrate that oviposition is 1.7 times more likely on host plants with access to ants than on host plants with ants excluded. Similarly, the change in adult treehopper density during the period of oviposition was positive for host plants with access to ants but negative for host plants with ants excluded (1999 data). There was no evidence that ants influence the total number of eggs deposited by a treehopper.

Two possible hypotheses to explain the observed pattern of ant-dependent oviposition are female host choice and

Table 1. Frequency of oviposition on plants with access to ants and on plants with ants excluded.

Oviposition	1998			1999			Combined		
	Yes	No	Per cent	Yes	No	Per cent	Yes	No	Per cent
Ant accessible	9	0	100	8	1	89	17	1	94
Ants excluded	4	5	44	6	3	67	10	8	56

predator protection. The predator-protection hypothesis predicts that oviposition is more likely on host plants with ants because treehoppers on these plants will be protected from predators. Support for this hypothesis comes from previous studies showing that ant tending increases the survivorship of nymphs to adults for *P. concava* in part due to protection from predators (Morales, 2000a,b). On the other hand, studies of the closely related species *P. modesta* have demonstrated benefits from ant-tending for nymphs but not for adults, possibly because the primary predator of that treehopper (salticid spiders) is inefficient at feeding on adults (Cushman & Whitham, 1989). For *P. concava*, predation by salticid spiders on first-summer but not second-summer adults is common at field sites in Connecticut, possibly because second-summer females will readily abandon host plants until oviposition, whereas first-summer adults and nymphs show high host-plant fidelity (M. A. Morales, pers. obs.). Thus, it is possible that predator harassment rather than predation *per se* decreases the likelihood of oviposition on host plant without ants.

An alternative (not mutually exclusive) hypothesis for ant-dependent oviposition is host choice by females. After landing on a potential host plant, a female treehopper must decide whether or not to initiate a clutch and, if so, determine the level of investment in that brood. For treehoppers with maternal care (e.g. *P. concava*), brood investment also includes the duration of maternal care. Interestingly, maternal care appears to confer no direct benefits in *Publilia modesta* – instead, it probably increases ant-tending

level early during the period of nymph development (Billick *et al.*, 2001). In some species, females are freed to initiate a second brood following discovery by ants. *Publilia reticulata* females are more likely to abandon broods and initiate a second clutch on a new host plant when tended by ants (Bristow, 1983). Similarly, the duration of maternal care is reduced when *P. concava* is tended by ants (McEvoy, 1979). These results indicate clearly that *Publilia* females are capable of assessing ant presence. It seems likely that *Publilia* females are similarly capable of assessing the presence of ants prior to initial oviposition.

Spatial distribution

Two possible hypotheses to explain the pattern of treehoppers centred on ant nests observed in this and other studies (McEvoy, 1979; Cushman & Whitham, 1991) are ant-density-dependent survivorship and ant-density-dependent oviposition. Both hypotheses posit that the density of ants, and therefore either survivorship of eggs to adults or the frequency of egg deposition, declines as distance from the ant nest increases. Cushman and Whitham (1991) argued that ant-density-dependent survival alone is unlikely to explain a clumped distribution in *P. modesta*, because emerging nymphs are rarely observed far from an ant nest. They suggested that the rarity of *P. modesta* far from ant nests is consistent with ant-dependent oviposition, particularly ant-dependent host choice by females.

Detailed observations on the movement of individual treehoppers as a function of treehopper and ant density will be needed to confirm experimentally the extent to which ant-dependent host choice contributes to a distribution of treehoppers centred on ant nests (for methodological details, see Turchin, 1998). Nevertheless, data from the present study suggest that ant-dependent oviposition may not contribute significantly to the observed spatial distribution of treehoppers for *P. concava*, at least for the patch observed in this study. In particular, of 18 plants with access to ants on which at least one treehopper was observed, egg masses were located on 17. Furthermore, the treehopper on the only ant-accessible host plant on which oviposition did not occur failed to attract any ants for a period of at least 3 days before its disappearance (1999 data; note that this plant was within 1.5 m of a heavily tended aggregation and was checked daily over this period; Table 1). The remaining 17 ant-accessible host plants on which oviposition did occur were distributed widely with respect to the ant nest (up to 20 m away). Thus, it does not appear that ant-dependent oviposition, regardless of mechanism (i.e. predator protection

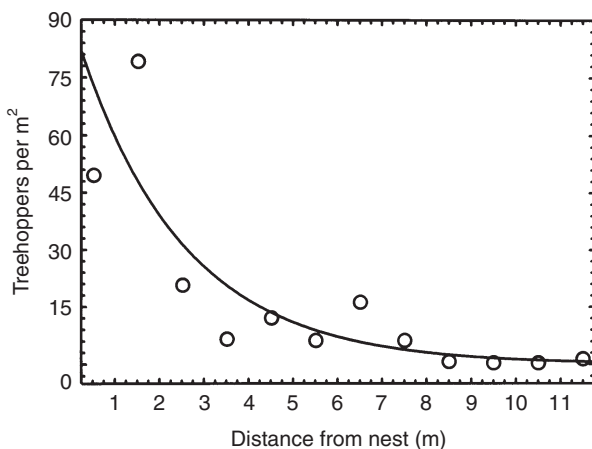


Fig. 1. Treehopper density as a function of distance from the nest. $\text{Log}(\text{number of treehoppers per m}^2) = 4.51 - 0.42 \text{ distance}$. Adj. $R^2 = 0.77$, $F_{1,10} = 37.26$, $P < 0.001$.

or female host choice), responds to fine-scale variation in the density of ants.

This conclusion is supported by the only experimental test of ant-density-dependent host choice in *P. concava*. McEvoy (1977) released marked *P. concava* females at increasing distances from a *Formica* mound but found no tendency for these treehoppers to redistribute themselves with respect to the ant nest. This finding is consistent with the results of the current study, suggesting that *Publilia* females do not appear to assess fine-scale variation in ant density. Alternatively, these results may be explained by the observation that *Formica* does not become dominant until late spring (M. A. Morales, pers. obs.). Consequently, the gradient in ant density during host-plant selection may not match the gradient in ant density during the period of nymphal development.

Finally, studies of ant-density-dependent survivorship of *Publilia* nymphs as a function of distance from the nest strongly support ant-density-dependent survivorship as contributing to the observed distribution of aggregations (Morales, 2000b). In particular, spatial variation in homopteran survivorship is determined by at least three factors (Morales, 2000b): the difference in homopteran survivorship as a function of ant-tending level, the functional form of ant-tending level relative to homopteran density at various spatial scales, and the relative importance of ant persistence vs. per-capita ant abundance to homopteran survivorship. Because the survivorship of *Publilia* nymphs is proportional to per-capita ant-tending levels, and because these levels decrease as distance from the nest increases, a gradient in treehopper density is in principle consistent with the ant-density-dependent survival hypothesis (Morales, 2000b).

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