Journal of Insect Behavior, Vol. 9, No. 1, 1996

Behavioral Strategies of Aphid Hyperparasitoids to Escape Aggression by Honeydew-Collecting Ants

Gerhard Hübner[1] and Wolfgang Völkl[1]

Accepted March 29, 1995; revised April 28, 1995

*We analyzed the behavioral interactions between two species of honeydew-collecting ants (*Lasius niger, Myrmica laevinodis*) and foraging females of four species of aphid hyperparasitoids (*Aphidencyrtus aphidivorus, Dendrocerus carpenteri, Pachyneuron aphidis, Asaphes vulgaris*) using* Aphis fabae *ssp.* cirsiiacanthoidis *and* Lysiphlebus cardui *on thistles as aphid and primary parasitoid, respectively. The observed interaction patterns and foraging parameters varied within hyperparasitoid species and revealed different strategies based upon behavioral and morphological constraints.* D. carpenteri *generally tried to avoid ant encounters. This avoidance strategy was successful in interactions with* M. laevinodis *but failed when encountering the more aggressive* L. niger, *which caused about 26% adult mortality. In contrast,* A. aphidivorus, P. aphidis, *and* A. vulgaris *possess jumping ability and were hardly exposed to mortality risks. The escape reaction "jump off" was used as soon as ants made physical contact with foraging females. While the flight strategy of* P. aphidis *is connected with cryptic movement patterns without avoidance behavior,* A. aphidivorus *first avoided ants and jumped off only as a last resort. Similar patterns, but less expressive, are displayed by* A. vulgaris. *We suggest that these different strategies are responsible for different foraging success in ant-attended resources in field.*

KEY WORDS: aphid hyperparasitoids; ants; patterns of interactions; escape behavior; adult mortality; foraging success.

INTRODUCTION

The relationship between ants and honeydew-producing insects such as aphids, coccids, psyllids, and membracids—usually called mutualism—was a common

---

[1] Lehrstuhl für Tierökologie I, Universität Bayreuth, P.O. Box 10 1251, D-95440 Bayreuth, Germany. Fax: +49-921-552784.

topic of historic and recent studies (for reviews see Way, 1963; Buckley, 1987; Sudd, 1987). One main feature of this phenomenon is the protective effect by ants which defend their mutualistic partners against predators and parasitoids (Bartlett, 1961; Banks, 1962; Bradley, 1973; Pierce and Easteal, 1986; Bach, 1991; Jiggins *et al.*, 1993). For example, honeydew-collecting ants may attack and kill many parasitoids or disturb the parasitoids' foraging activities or oviposition attempts (Wellenstein, 1930; Pierce and Mead, 1981; Takada and Hashimoto, 1985; Vinson and Scarborough, 1991; Völkl and Mackauer, 1993; Novak, 1994). Recent studies, however, revealed that ant protection is sometimes incomplete and could vary with the attending ant (Takada and Hashimito, 1985; Bristow, 1984; Völkl, 1992; Cudjoe *et al.*, 1993). Völkl and Mackauer (1993) pointed out two main strategies of aphidiid wasps parasitizing trophobiotic aphids to escape ant aggression. Parasitoids may avoid ant interactions and therefore have little oviposition success in ant-attended aphid colonies. These species generally focus their foraging efforts on unattended resources. In contrast, some specialized aphidiids have evolved morphological and behavioral adaptations to circumvent the ants' guarding behavior. For example, *Lysiphlebus cardui* (Marshall), the dominant parasitoid of *Aphis fabae* spp. *cirsiiacanthoidis* Schrank on thistles, gains access to ant-attended aphid colonies by chemical camouflage and cryptic behavior, and causes heavy mortality amoung its host independent of the guarding ant species (Völkl, 1992; Völkl and Mackauer, 1993). *L. cardui* benefits significantly from ant attendance by reduced larval mortality through hyperparasitism (Völkl, 1992). Ants guard and defend the parasitoids' progeny developing in still live aphids or in mummies in the same way as unparasitized aphids and, thereby, transferred the protective effect to the next trophic level. The magnitude of this ant protection differed for particular hyperparasitoid species. For example, *Pachyneuron aphidis* (Bouche) (Hym., Pteromalidae) occurred at an approximately 50-fold lower density in ant-attended resources, while the frequency of *Dendrocerus carpenteri* (Curtis) (Hym., Megaspilidae) decreased only about 3-fold in the presence of ants. Furthermore, the two ant species *Lasius niger* L. and *Myrmica ruginodis* (Nylander) differed in their impact on the particular hyperparasitoid species. Recently, Völkl *et al.* (1944) demonstrated that *Alloxysta brevis* (Thomson) (Hym., Alloxystidae), the most common endohyperparasitoid of *L. cardui*, applied chemical defense secretions to escape ant aggression. By this means, *A. brevis* not only ensured its adult survivorship after being caught, but was also able to hyperparasitize successfully ant-attended aphids. Oviposition success was higher in the presence of the less aggressive *Myrmica laevinodis* (Nylander) compared to *L. niger* (Hübner, 1994), a result consistent with field results (Völkl, 1992).

In this study, we compared the behavioral interactions between two ant species, *L. niger* and *M. laevinodis*, and four hyperparasitoid species. The endohyperparasitoid *Aphidencyrtus aphidivorus* (Mayr) (Hym., Encyrtidae) oviposits in live parasitized aphids as well as in aphid mummies (Kanuck and Sullivan, 1992), while *D. carpenteri*, *P. aphidis*, and *Asaphes vulgaris* Walker (Hym., Pteromalidae) are ectohyperparasitoids which attack exclusively mummified aphids (Sullivan, 1987, 1988). We tested (1) whether differences in hyperparasitoid attack can be related to different intensities of ant aggression and to different escape strategies of the hyperparasitoid species and (2) whether the ant–hyperparasitoid interactions and the effectiveness of the hyperparasitoids' escape strategy differ for the two ant species.

MATERIALS AND METHODS

Insect Rearing Procedures

Mummies of *L. cardui* and *Lysiphlebus hirticornis* Mackauer were obtained from field samples collected in the vicinity of Bayreuth, Bavaria, Germany, on *Cirsium arvense* (L.) Scop. and *Tanacetum vulgare* L., respectively. All mummies were kept in a climate chamber at 21°C, 50% RH, and 16:8 L:D. Emerged adult hyperparasitoids were kept at 5°C and regularly fed with a honey–water solution. All females had had previous contacts with hosts but not with ants before being used in the experiments. Each female was tested only once.

Field Studies

Potted creeping thistles (*C. arvense*) infested with *A. f. cirsiiacanthoidis* colonies (100–1600 aphids per plant) were placed near ant nests (*L. niger* or *M. laevinodis*). Subsequently, *L. cardui* females were released on those thistles. They parasitized ant-attended colonies heavily, providing mummies required for the study. Experiments were started when at least 5% of all aphids within a particular colony were mummified.

Interactions Between Foraging Hyperparasitoids and Ants. Single hyperparasitoid females were released onto a plant about 5 cm next to the aphid colony and to the closest ant worker. The foraging behavior of the hyperparasitoid and its interactions with ants were observed until the hyperparasitoid left the plant. We measured residence time/plant, residence time/aphid colony, and number of host contacts. Responses of ants toward hyperparasitoids were defined as follows:

aggressive (AGG)—ant workers attacked and/or tried to seize and kill the hyperparasitoid; and

nonaggressive (NON-AGG)—ant workers touched the hyperparasitoid with their antennae or their legs or passed the hyperparasitoid in close vicinity (at least in an ~2-mm distance) without making physical contact.

The following reactions of the hyperparasitoid in response to an ant approach or ant encounter were distinguished:

- *escape by takeoff or drop off* (EBT)—hyperparasitoid flew away or dropped;
- *escape by jump off* (EBJ)—hyperparasitoid jumped away;
- *avoidance* (AV)—hyperparasitoid changed foraging direction or ran away in order to avoid physical contact with ants; and
- *ignoring* (IG)—hyperparasitoid did not change its previous behavior (foraging, host handling, cleaning, feeding, or sitting).

The hyperparasitoid displayed regularly one of the first three reactions (EBT, EBJ, or AV) due to ant movements, but at a distance of more than 0.5 cm far away from the next ant worker. Since the wasp prevented a close contact with the ant by such an early response, these cases were regarded separately and called *encounter preventing behavior* (EPB) by the hyperparasitoid. After an interaction sequence, the hyperparasitoid either had left the plant and was not found again on the thistle during the following 60 s (=Plant Leave in Figs. 1–4) or continued its foraging activities (CF = *continue foraging* in Figs. 1–4). The numbers of observed females were distributed as follows: *A. aphidivorus*—36 individuals with *L. niger*, 39 individuals with *M. laevinodis*;

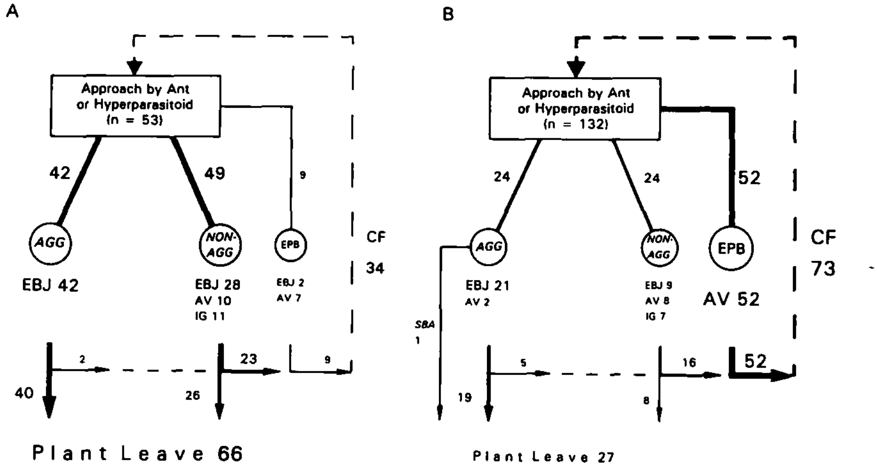

Fig. 1. Interaction patterns between *Aphidencyrtus aphidivorus* females and ants. (A) *Lasius niger*; (B) *Myrmica laevinodis*. n = number of observed ant–hyperparasitoid interactions. Further numbers are rounded percentage values of n. The data are pooled over all hyperparasitoid females. Italic letters, actions of ants; roman letters, reactions of hyperparasitoids. *AGG*, aggressive; *NON-AGG*, nonaggressive; EBT, escape by takeoff or drop off; EBJ, escape by jump off; EPB, encounter preventing behavior; AV, avoidance; IG, ignoring; *SBA*, seized by ant; CF, continue foraging; Plant Leave, hyperparasitoid left plant after an interaction sequence. For details, see Materials and Methods.

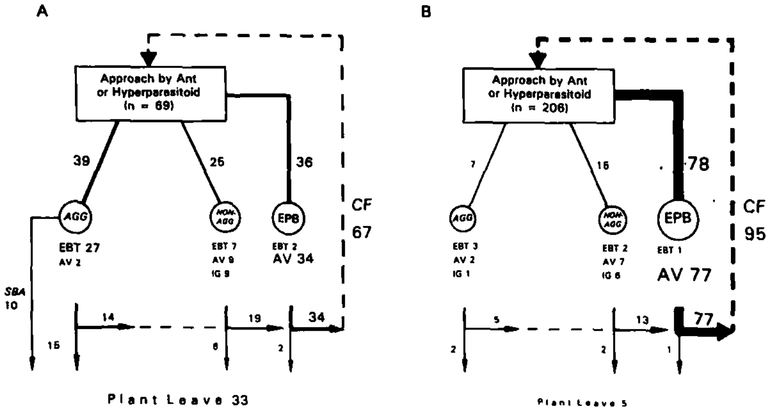

Fig. 2. Interaction patterns between foraging *Dendrocerus carpenteri* females and ants. (A) *Lasius niger*; (B) *Myrmica laevinodis*. *n* = number of observed ant-hyperparasitoid interactions. Further numbers are rounded percentage values of *n*. The data are pooled over all hyperparasitoid females. Italic letters, actions of ants; roman letters, reactions of hyperparasitoids. *AGG*, aggressive; *NON-AGG*, nonaggressive; EBT, escape by takeoff or drop off; EBJ, escape by jump off; EPB, encounter preventing behavior; AV, avoidance; IG, ignoring; *SBA*, seized by ant; CF, continue foraging; Plant Leave, hyperparasitoid left plant after an interaction sequence. For details, see Materials and Methods.

D. carpenteri—26 individuals with each ant species; *P. aphidis*—34 females with *L. niger*, 29 females with *M. laevinodis*; and *A. vulgaris*—29 females with *L. niger*, 31 females with *M. laevinodis*.

Behavioural patterns between hyperparasitoids species, or between ant species, were compared by chi-square tests using the total numbers of observations, which are given at the top of Figs. 1-4.

Ant Response Toward Dead Hyperparasitoids. Females of each hyperparasitoid species were killed by freezing them at −30°C. All females were stored at that temperature. Within 15 min after being thawed a dead hyperparasitoid was carefully placed in close vicinity to an aphid colony into a leaf axil which was frequently passed by ant workers. Subsequently, we observed the first 10 contacts between ants and the test individuals. We distinguished two broadly different patterns of ant behavior:

disregarding—ants did not seize the dead hyperparasitoid even if they tapped them frequently with antennae; and

removal—the ant seized the hyperparasitoid with its mandibles and removed it from the plant.

As a control we tested the response of ants to freshly killed *A. f. cirsiiacanthoidis*. Each trial was made for *L. niger* and *M. laevinodis* separately.

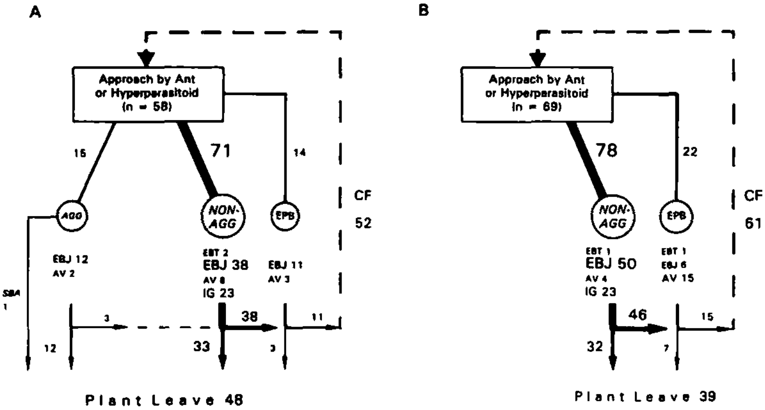

Fig. 3. Interaction patterns between *Pachyneuron aphidis* females and ants. (A) *Lasius niger*; (B) *Myrmica laevinodis*. *n* = number of observed ant–hyperparasitoid interactions. Further numbers are rounded percentage values of *n*. The data are pooled over all hyperparasitoid females. Italic letters, actions of ants; roman letters, reactions of hyperparasitoids. *AGG*, aggressive; *NON-AGG*, nonaggressive; EBT, escape by takeoff or drop off; EBJ, escape by jump off; EPB, encounter preventing behavior; AV, avoidance; IG, ignoring; *SBA*, seized by ant; CF, continue foraging; Plant Leave, hyperparasitoid left plant after an interaction sequence. For details, see Materials and Methods.

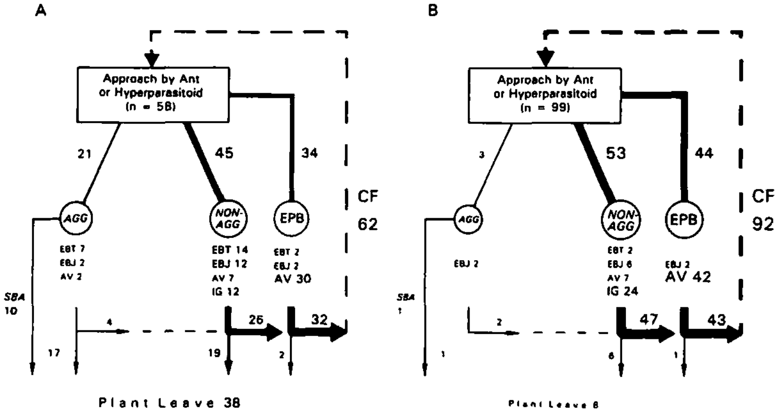

Fig. 4. Interaction patterns between *Asaphes vulgaris* females and ants. (A) *Lasius niger*; (B) *Myrmica laevinodis*. *n* = number of observed ant–hyperparasitoid interactions. Further numbers are rounded percentage values of *n*. The data are pooled over all hyperparasitoid females. Italic letters, actions of ants; roman letters, reactions of hyperparasitoids. *AGG*, aggressive; *NON-AGG*, nonaggressive; EBT, escape by takeoff or drop off; EBJ, escape by jump off; EPB, encounter preventing behavior; AV, avoidance; IG, ignoring; *SBA*, seized by ant; CF, continue foraging; Plant Leave, hyperparasitoid left plant after an interaction sequence. For details, see Materials and Methods.

Laboratory Studies

We tested the influence of the jumping ability of *P. aphidis* to prevent mortality caused by ants. *P. aphidis* females ($n = 15$) were anesthetized with CO_2, had their hind legs and wings amputated, and were kept 1 h for recovering. *Cornus sanguinea* L. twigs were cut and put in a box (20 × 20 × 10 cm). The *Cornus* leaves were infested with small *Anoecia* sp. colonies (20–50 individuals) and attended by *L. niger* workers, which continued their activities for about 30 min after removal. Single *P. aphidis* individuals were released onto a leaf about 3 cm far away from an ant-attended colony. The interactions between ants and hyperparasitoids were recorded as described above until the hyperparasitoid left the twig or was killed by the ants. We used only well-recovered females that were still able to walk readily and showed no conspicuous changes in behavior compared to healthy individuals.

RESULTS

Interaction Patterns Between Foraging Hyperparasitoid Females and Honeydew-Collecting Ants

(1) The movements of *A. aphidivorus* females along thistles shoots and leaves were very quick compared to those of other aphid hyperparasitoid species. If a foraging female met a *L. niger* worker, the ant often showed aggressive behavior toward *A. aphidivorus*, but the hyperparasitoid could always jump away in time to prevent being captured by the ant (Fig. 1A). If *L. niger* was not aggressive, *A. aphidivorus* responded mainly by jumping away—mostly after being touched by the ant—running away or simply ignoring *L. niger* workers, which then in return disregarded the hyperparasitoid. Jumping usually led to plant leave. Encounter preventing behavior was hardly observed.

The general behavioral repertoire of *A. aphidivorus* did not change during interactions with *M. laevinodis* workers (Fig. 1B). However, females avoided significantly more often contacts with workers of this species ($\chi^2 = 25.641$, $df = 1$, $P < 0.000$). Therefore plants were significantly less often left after an interaction with *M. laevinodis* compared with *L. niger* ($\chi^2 = 25.839$, $df = 1$, $P < 0.000$).

(2) *D. carpenteri* was also a fast and striking forager. Being attacked by *L. niger*, *D. carpenteri* tried to take off or drop off, but *L. niger* workers succeeded in seizing the hyperparasitoid in about 10% of all interactions (Fig. 2A). Foraging females avoided direct contacts with *L. niger* more often than *A. aphidivorus* ($\chi^2 = 9.884$, $df = 1$, $P = 0.002$).

Direct contacts or even attacks by the rather slow-moving *M. laevinodis* could hardly be observed (Fig. 2B), since *D. carpenteri* displayed significantly stronger encounter preventing avoidance behavior toward this ant species in comparison to *L. niger* ($\chi^2 = 38.45$, df = 1, $P < 0.000$). Even after encounters *D. carpenteri* rarely left the plant but, instead, ran away or ignored the *M. laevinodis* workers. Plant leave due to ant interactions was significantly reduced in the presence of *M. laevinodis* compared with *L. niger* ($\chi^2 = 30.033$, df = 1, $P < 0.000$).

(3) In contrast to the preceding hyperparasitoid species, *P. aphidis* showed cryptic and inconspicuous movement patterns by walking slowly along plant parts. Foraging was often interrupted by pauses *P. aphidis* hardly avoided *L. niger* but instead jumped away when being attacked, touched, or simply approached by ant workers (Fig. 3A). Aggression by *L. niger* was observed to a lower extent in comparison to *D. carpenteri* ($\chi^2 = 7.527$, df = 1, $P = 0.006$) or *A. aphidivorus* ($\chi^2 = 8.444$, df = 1, $P = 0.004$).

Although *M. laevinodis* did not exhibit any aggressiveness toward foraging *P. aphidis*, the reaction patterns of the hyperparasitoid did not change (Fig. 3B). Females mostly jumped off in response to any touch by ant workers and remained in close proximity to ants only when no physical contact was made. As in *A. aphidivorus*, jumping by *P. aphidis* resulted mainly in plant leave. No significant differences were found between ant species in the extent of encounter preventing behavior ($\chi^2 = 0.859$, df = 1, $P = 0.354$) or plant leave caused by ant workers ($\chi^2 = 0.733$, df = 1, $P = 0.392$).

(4) *A. vulgaris* was a more agile forager than *P. aphidis*, but its movement speed was not as fast as in *D. carpenteri* or *A. aphidivorus*. Attacks or contacts by *L. niger* were answered with escape reactions, and *A. vulgaris* almost equally jumped off, took off, or dropped off in those situations (Fig. 4A). In contrast, *M. laevinodis* workers hardly attacked *A. vulgaris* females (Fig. 4B). Most encounters with this ant species resulted in nonaggressive interactions, during which both sides mainly ignored each other. Therefore plant leave because of ant interactions was significantly lower on plants with *M. laevinodis* present than with *L. niger* ($\chi^2 = 19.196$, df = 1, $P < 0.000$). Encounter preventing behavior by *A. vulgaris* was observed to a high degree for both ant species.

Ant Response Toward Dead Hyperparasitoids

L. niger workers responded more readily toward freshly killed hyperparasitoids than *M. laevinodis* and carried off dead females of either hyperparasitoid species significantly more often at first contact (Table I). The response of *L. niger* toward hyperparasitoids was also stronger than to control agents, dead *A. f. cirsiiacanthoidis*, while no such difference was found for *M. laevinodis*. However, both ant species did not differ significantly in their response toward particular hyperparasitoid species.

Table I. Ant Response (%) Toward Freshly Killed Hyperparasitoids and Aphids[a,*]

Species	Removed at first contact	
	Lasius niger	*Myrmica laevinodis*
A. aphidivorus	83.3^{a} (12)	25.0^{a} (16)
D. carpenteri	77.7^{a} (9)	7.1^{a} (14)
P. aphidis	61.1^{a} (18)	10.0^{a} (10)
A. vulgaris	76.5^{a} (17)	27.3^{a} (11)
A. fabae	20.0^{b} (19)	13.3^{a} (15)

[a] For details, see Materials and Methods. The number of tested individuals is in parentheses.

*All hyperparasitoid species differed significantly between *L. niger* and *M. laevinodis*. Within one ant species, values sharing the same superscript letter do not differ at $P < 0.05$ (Fisher's exact test).

Adult Hyperparasitoid Mortality

Although only 10% of *L. niger–D. carpenteri* interactions resulted in a successful attack (Fig. 2A), more than a quarter of *D. carpenteri* females were finally seized by workers of this ant species and killed (Table II). In contrast, the slowly moving *M. laevinodis* was not able to capture the quick *D. carpenteri* females, and thus the adult mortality dropped to zero. The same picture held for *A. vulgaris*: females were frequently caught by *L. niger* but hardly by *M. laevinodis*. However, *L. niger* did not kill—with one exception—*A. vulgaris* females, but released them without obvious injury. Foraging *A. aphidivorus* and *P. aphidis* could usually escape ant aggression in time by jumping off and were

Table II. Adult Mortality (%) of Four Aphid Hyperparasitoids Caused by *Lasius niger* or *Myrmica laevinodis*[a]

Species	*L. niger*	*M. laevinodis*
A. aphidivorus	0^{a}	2.6^{a}
D. carpenteri	26.9^{b}	0^{a}
P. aphidis	2.9^{a}	0^{a}
A. vulgaris	3.5^{a}	0^{a}

[a] For the number of tested hyperparasitoid females, see Materials and methods.

*Within columns, values sharing the same superscript letter do not differ significantly at $P < 0.05$. Within rows, only values for *D. carpenteri* differ significantly at $P < 0.05$ (Fisher's exact test).

hardly killed by either ant species. Thirty-three percent of *P. aphidis* females with amputated hind legs and wings were killed after an ant encounter. Mortality was significantly higher in comparison to nonhandicapped *P. aphidis*. (Fisher's exact test = 0.008). However, we observed that 33% of the individuals could still jump, only a few centimeters, but far enough to save their lives.

Foraging Parameters

We distinguished between residence times per whole plant and residence time per aphid colony, a smaller unit of foraging. Residence times per plant differed considerably between hyperparasitoid species: *D. carpenteri* and *A. vulgaris* remained on average longer on a plant than *A. aphidivorus* or *P. aphidis* (Table III). Furthermore, *D. carpenteri* stayed significantly longer on *M. laevinodis*-guarded plants than on *L. niger* ones (Mann–Whitney *U* test: $U = 206.5$, $n = 52$, $P = 0.016$). Within an aphid colony, however, *P. aphidis* females remained significantly longer than *D. carpenteri* or *A. vulgaris* in the presence of both *L. niger* and *M. laevinodis*.

The mean number of host contacts was significantly higher for *A. aphidivorus* than for any other hyperparasitoid species on plants guarded by *L. niger* (Table III). In the presence of *M. laevinodis*, however, *D. carpenteri* and *A. vulgaris* achieved significantly more host contacts, while no difference was found between *L. niger*- and *M. laevinodis*-attended plants for *A. aphidivorus* and *P. aphidis*.

Table III. Influence of Attendence by *L. niger* and *M. laevinodis* on Foraging Parameters of Four Aphid Hyperparasitoids Searching for Hosts on Thistles Infested with *Aphis fabae* ssp. *cirsiiacanthoidis*[a],*

Species	*A. aphidivorus*	*D. carpenteri*	*P. aphidis*	*A. vulgaris*
Lasius niger				
Residence time/plant (s)	178 ± 55^{b}	393 ± 111^{a}	237 ± 55^{ab}	391 ± 104^{a}
Residence time/aphid colony (s)	42 ± 10^{b}	35 ± 6^{b}	81 ± 15^{a}	34 ± 10^{b}
No. host contacts · female^{-1}	2.2 ± 0.5^{a}	1.2 ± 0.6^{b}	1.0 ± 0.3^{b}	0.7 ± 0.3^{b}
Myrmica laevinodis				
Residence time/plant (s)	207 ± 59^{c}	872 ± 152^{a}	371 ± 93^{b}	563 ± 105^{ab}
Residence time/aphid colony (s)	49 ± 8^{ab}	77 ± 16^{b}	90 ± 19^{a}	44 ± 7^{b}
No. host contacts · female^{-1}	1.9 ± 0.5^{b}	4.8 ± 1.0^{a}	1.4 ± 0.4^{b}	2.0 ± 0.5^{b}

[a] All values are means ± SE. For the number of tested hyperparasitoid females, see Materials and Methods.

*Within rows, means sharing the same superscript letter do not differ significantly at $P < 0.05$ (Mann–Whitney *U* test).

DISCUSSION

Many arthropods live in close association with ants and derive benefits from this relationship (for an overview, see Hölldobler and Wilson, 1990). To achieve this aim they have evolved different mechanisms to integrate into ant nests and to avoid ant aggression. Predators and parasitoids whose resources are ant-attended, like honeydew-producing aphids, need similar adaptations. In order either to exploit these resources or, at least, to escape ants without harm, they employ various strategies, based mainly upon different morphological, chemical, and/or behavioral adaptations. Some of them are of protective use and may help to defend themselves against ant attacks as in coccinellids. Adult coccinellids may hide their vulnerable legs under their well-armored body (Bradley, 1973) or deter ants by reflex bleeding (Tursch *et al.*, 1971; Eisner *et al.*, 1986), while pupae may be covered with protective long and stiff hairs that in some cases secrete repellent agents (Attygalle *et al.*, 1993; Völkl, 1995). Another helpful strategy is the use of camouflage (Eisner *et al.*, 1978) or chemical mimicry (Takada and Hashimoto, 1985; Vander Meer *et al.*, 1989; Völkl, 1992; Völkl and Mackauer, 1993; Liepert and Dettner, 1993; Dettner and Liepert, 1994). The preventive effect of camouflage is often supported by cryptic behavior. Chemical defense against ant aggression was recently reported for the aphid hyperparasitoid *A. brevis* (Völkl *et al.*, 1994). This species releases defense secretions when being attacked by ants to defend itself and to remain unmolested for several minutes, time enough to ovipost successfully. Finally, some strategies to escape ant aggression are based on behavior and are often combined with morphological adaptations such as jumping ability or a well-armored body (e.g., Wojcik, 1989; Hölldobler and Wilson, 1990; Larsen *et al.*, 1992; Novak, 1994). They serve to avoid ant encounters or to leave ant-attended resources immediately. The hyperparasitoids examined in this study belong to the latter group and represent either the avoidance type, whose representatives are expected to be good and flexible runners, the flight type, which requires a quick and effective escape response, or a combination of both.

The agile and quickly foraging *D. carpenteri* is a typical representative of the avoidance type. This species showed a striking high rate of avoidance behavior, which prevented direct ant contacts and kept up a security distance to the next ant worker. High running speed and corresponding flexibility in movements were also reported for some adult Diptera or Hymenoptera whose larvae parasitize or prey on ants (Ayre, 1962; Wojcik, 1989; Hölldobler and Wilson, 1990) and for the aphid primary parasitoid *Lysiphlebus testaceipes* Cresson (Vinson and Scarborough, 1991; Völkl and Mackauer, 1993). These species avoided direct ant contacts and ant aggression by quick movements. The avoidance strategy of *D. carpenteri* was especially successful when interacting with the slow and less aggressive *M. laevinodis*. In the presence of those ants, *D. carpenteri* achieved long residence times per plant and many host contacts and had low mortality risks. The effectiveness of this behavior, however, was reduced when meeting the aggressive and quicker *L. niger*. Adult mortality was high, since *D. carpenteri* is unable to jump and could only take off or drop off, two less effective escape reactions.

In contrast, *P. aphidis* females left the plant immediately when coming in contact with ants. Similar quick flights were reported for the closely related aphid hyperparasitoid *Euneura stomaphidis* Kamijo & Takada (Hym., Pteromalidae) when encountering *L. niger* workers (Kamijo and Takada, 1983). This sensitiveness toward any physical ant contact and following quick flight response, which is supported by an excellent jumping ability, ensured a high adult survival for *P. aphidis*. Tests with hind leg-amputated *P. aphidis* individuals proved that a reduced jumping ability increased adult mortality when aggressively responding ants were encountered. Additionally, *P. aphidis* moved slowly and almost cryptically on a plant. This unconspicious movement pattern suppressed immediate ant attacks. Thus, *P. aphidis* females were able to stay undetected for a comparatively long time interval in an aphid colony (Table III), the plant area where ants are usually concentrated, but their flight strategy resulted in short residence times per plant and low numbers of host contacts (Table III). The "cryptic" behavior seems not to be supported by chemical camouflage as in the aphidiid wasp *L. cardui*, which mimics the cuticular hydrocarbon profile of their host aphids (Völkl and Mackauer, 1993; Liepert and Dettner, 1993), since *L. niger* workers responded to dead *P. aphidis* more readily than toward control agents (dead *A. f. cirsiiacanthoidis*).

A. aphidivorus is an excellent jumper like *P. aphidis* and suffered also only low adult mortality from ant aggression, since foraging females could hardly be seized by attacking ants. However, *A. aphidivorus* females displayed characters of both previously described strategies: first, females avoided ant encounters with a high foraging speed and flexible movements. This strategy was more successful in the presence of the slow-moving *M. laevinodis* (Fig. 1), although this ant species acted more aggressively toward *A. aphidivorus* than toward other hyperparasitoid species, probably because of the disturbance caused in the aphid colony. Second, females left the plant by a quick jump off as a last resort if avoidance was not successful. Similar behavioral strategies were reported for other encyrtid species interacting with ants (Novak, 1994; Völkl, 1995).

The combined strategy of avoidance and flight can also be recognized—although less expressed—in the behavior of *A. vulgaris*. Foraging speed was obviously slower in comparison to *D. carpenteri* or *A. aphidivorus*. Nevertheless, *A. vulgaris* could often avoid ant encounters with both ant species. *A. vulgaris* females are also able to jump but this flight reaction was not as effective as in *P. aphidis* or *A. aphidivorus*. As a consequence, a high percentage of foraging females was captured by quick *L. niger* workers, while *M. laevinodis* was less aggressive (Fig. 4). However, most captured females were released without an obvious damage in a similar manner as for females of the endohyperparasitoid *Alloxysta brevis* (Völkl *et al.*, 1994), and adult mortality remained low.

These different behavioral strategies may have a different impact on foraging success in the field. Hyperparasitism of *P. aphidis* is heavily reduced in ant-attended resources (Völkl, 1992), obviously as a consequence of its very sensitive flight behavior, which leads to immediate plant leave. In contrast, *D. carpenteri*, which tried to avoid ant contacts, was less diminished in the presence of ants (Völkl, 1992). Females of this species could stay for a comparatively long time on ant-attended plants (Table III), and they may reach some opportunities for ovipositions, especially when the ants' guarding activities are reduced (e.g., due to bad weather conditions) or generally weak (e.g., in large aphid colonies with high mummification). However, the costs of this avoidance strategy are high mortality risks in the presence of the very aggressive *L. niger* (Table II). A compromise between the sensitive flight behavior and the avoidance tactic may be a combination of both, as applied by *A. vulgaris* and *A. aphidivorus*. Although the foraging activities of both species were considerably reduced by ants (Table III), they were found sometimes in high densities on individual ant-attended plants (Völkl, 1990; Völkl and Hübner, unpublished). There is some evidence that plant structure might considerably influence the foraging success. For example, *A. aphidivorus* was more successful on richly ramified thistles and within the richly ramified inflorescences of *Tanactum vulgare* (with *Lysiphlebus hirticornis* being the primary parasitoid; Mackauer and Völkl, 1993) than on poorly ramified thistles, while *D. carpenteri* was less abundant in *T. vulgare* inflorescences (Hübner and Völkl, unpublished). A detailed examination of ant–hyperparasitoid interactions on differently structured plants may give a better insight into the overall effectiveness of the escape strategies of the four studied hyperparasitoid species.

ACKNOWLEDGMENTS

We benefited much from critical discussions with H. Zwölfer, P. Kranz, M. Rauh, and W. Weisser. The comments of two referees helped to improve the manuscript.

REFERENCES

Attygalle, A. B., McCormick, K. D., Blankespoor, C. L., Eisner, T., and Meinwald, J. (1993). Azamacrolides: A family of alkaloids from the pupal defense secretion of a ladybird beetle (*Epilachna varivestis*). *Proc. Natl. Acad. Sci. USA* **90:** 5204–5208.

Ayre, G. L. (1962). *Pseudometagea schwarzii* (Ashm.) (Eucharitidae: Hymenoptera), a parasite of *Lasius neoniger* Emery (Formicidae: Hymenoptera). *Can. J. Zool.* **40:** 157-164.

Bach, C. E. (1991). Direct and indirect interactions between ants (*Pheidole megacephala*), scales (*Coccus viridis*) and plants (*Pluchea indica*). *Oecologia* **87:** 233-239.

Banks, C. J. (1962). Effect of the ant, *Lasius niger*, on insects preying on small populations of *Aphis fabae* Scop. on bean plants. *Ann. Appl. Biol.* **50:** 669-679.

Bartlett, B. R. (1961). The influence of ants upon parasites, predators and scale insects. *Ann. Entomol. Soc. Am.* **54:** 543-551.

Bradley, G. A. (1973). Effect of *Formica obscuripes* (Hymenoptera: Formicidae) on the predator-prey relationship between *Hyperaspis congressis* (Coleoptera: Coccinellidae) and *Toumeyella numismaticum* (Homoptera: Coccidae). *Can. Entomol.* **105:** 1113-1118.

Bristow, C. (1984). Differential benefits from ant-attendance to two species of Homoptera on New York ironweed. *J. Anim. Ecol.* **53:** 715-726.

Buckley, R. (1987). Interactions involving plants, homoptera, and ants. *Annu. Rev. Ecol. Syst.* **18:** 111-135.

Cudjoe, J. H., Neuenschwander, P., and Copland, M. J. W. (1993). Interference by ants in biological control of the cassava mealybug *Phenacoccus manihoti* (Hemiptera: Pseudococcidae) in Ghana. *Bull. Entomol. Res.* **83:** 15-22.

Dettner, K., and Liepert, C. (1994). Chemical mimicry and camouflage. *Annu. Rev. Entomol.* **39:** 129-154.

Eisner, T., Hicks, K., Eisner, M., and Robson, D. S. (1978). "Wolf-in-sheep's-clothing" strategy of a predaceous insect larva. *Science* **199:** 790-794.

Eisner, T., Goetz, M., Aneshansley, D., Fersting-Arnold, G., and Meinwald, J. (1986). Defensive alkaloid in blood of Mexican bean beetle (*Epilachna varivestis*). *Experientia* **42:** 204-207.

Hölldobler, B., and Wilson, E. O. (1990). *The Ants*, Springer Verlag, Berlin, Heidelberg, New York.

Hübner, G. (1994). *Interaktionen zwischen fouragierenden Blattlaushyperparasitoiden und honigtausammelnden Ameisen: Verhaltensstrategien in ameisenbelaufenen Ressourcen.* Diploma thesis, University of Bayreuth.

Jiggins, C., Majerus, M. E. N., and Gough, U. (1993). Ant defence of colonies of *Aphis fabae* Scopoli (Hemiptera: Aphididae), against predation by ladybirds. *Br. J. Entomol. Nat. Hist.* **6:** 129-137.

Kamijo, K., and Takada, H. (1983). A new *Euneura* species hyperparasitic on *Stomaphis* aphids and a note on the genus *Gygaxia* Delucchi. *Akitu* **55:** 1-8.

Kanuck, M. J., and Sullivan, D. J. (1992). Ovipositional behavior and larval developement of *Aphidencyrtus aphidivorus* (Hymenoptera: Encyrtidae), an aphid hyperparasitoid. *J. N.Y. Entomol. Soc.* **100:** 527-532.

Larsen, K. J., Heady, S. E., and Nault, L. R. (1992). Influence of ants (Hymenoptera: Formicidae) on honeydew excretion and escape behaviors in a myrmecophile, *Dalbulus quinquenotatus* (Homoptera: Cicadellidae), and its congeners. *J. Insect Behav.* **5:** 109-122.

Liepert, C., and Dettner, K. (1993). Recognition of aphid parasitoids by honeydew-collecting ants: The role of cuticular lipids in a chemical mimicry system. *J. Chem. Ecol.* **19:** 2143-2153.

Mackauer, M., and Völkl, W. (1993): Regulation of aphid populations by aphidiid wasps: Does parasitoid foraging behaviour of hyperparasitism limit impact? *Oecologia* **94:** 339-350.

Novak, H. (1994). The influence of ant-attendance on larval parasitism in Hawthorn psyllids (Homoptera: Psyllidae). *Oecologia* **99:** 72-78.

Pierce, N. E., and Easteal, S. (1986). The selective advantage of attendant ants for the larvae of a lycaenid butterfly, *Glaucopsyche lygdamus*. *J. Anim. Ecol.* **55:** 451-462.

Pierce, N. E., and Mead, P. S. (1981). Parasitoids as selective agents in the symbiosis between lycaenid butterfly caterpillars and ants. *Science* **211:** 1185-1187.

Sudd, J. H. (1987). Ant aphid mutualism. In Minks, A. K., and Harrewijn, P. (eds.), *Aphids—Their Biology, Natural Enemies and Control. World Crop Pests, Vol. 2A*, Elsevier, Amsterdam, pp. 355-365.

Sullivan, D. J. (1987). Insect hyperparasitism. *Annu. Rev. Entomol.* **32:** 49-70.

Sullivan, D. J. (1988). Hyperparasites. In Minks, A. K., and Harrewijn, P. (eds.), *Aphids—Their*

Biology, Natural Enemies and Control. World Crop Pests, Vol. 2B, Elsevier, Amsterdam, pp. 189–203.

Takada, H., and Hashimoto, Y. (1985). Association of the root aphid parasitoids *Aclitus sappaphis* and *Paralipsis eikoae* (Hymenoptera, Aphidiidae) with the aphid-attending ants *Pheidole fervida* and *Lasius niger* (Hymenoptera, Formicidae). *Kontyu* **53:** 150–160.

Tursch, B., Daloze, D., Dupont, M., Pasteels, J. M., and Tricot, M. C. (1971). A defensive alkaloid in a carnivorous beetle. *Experientia* **27:** 1380–1381.

Vander Meer, R. K., Jouvenaz, D. P., and Wojcik, D. P. (1989). Chemical mimicry in a parasitoid (Hymenoptera: Eucharitidae) of fire ants (Hymenoptera: Formicidae). *J. Chem. Ecol.* **15:** 2247–2261.

Vinson, S. B., and Scarborough, T. A. (1991). Interactions between *Solenopsis invicta* (Hymenoptera: Formicidae), *Rhopalosiphum maidis* (Homoptera: Aphididae) and the parasitoid *Lysiphlebus testaceipes* Cresson (Hymenoptera: Aphidiidae). *Ann. Entomol. Soc. Am.* **84:** 158–164.

Völkl, W. (1990). *Fortpflanzungsstrategien bei Blattlausparasitoiden (Hymenoptera, Aphidiidae): Konsequenzen ihrer Interaktionen mit Wirten und Ameisen*, Ph.D. thesis, University of Bayreuth, Bayreuth.

Völkl, W. (1992). Aphids or their parasitoids: Who actually benefits from ant-attendance? *J. Anim. Ecol.* **61:** 273–281.

Völkl, W. (1995). Behavioral and morphological adaptations of the coccinellid *Platynaspis luteorubra* for exploiting ant-attended resources. *J. Insect Behav.* **8:** 653–670.

Völkl, W., and Mackauer, M. (1993). Interactions between ants attending *Aphis fabae* ssp. cirsiiacanthoidis on thistles and foraging parasitoid wasps. *J. Insect Behav.* **6:** 301–312.

Völkl, W., Hübner, G., and Dettner, K. (1994). Interactions between *Alloxysta brevis* (Hymenoptera, Cynipoidea, Alloxystidae) and honeydew collecting ants: How an aphid hyperparasitoid overcomes ant aggression by chemical defense. *J. Chem. Ecol.* **20:** 2621–2635.

Way, M. J. (1963). Mutualism between ants and honeydew-producing homptera. *Annu. Rev. Entomol.* **8:** 307–344.

Wellenstein, G. (1930). Beiträge zur Systematik und Biologie der Rindenläuse (Lachnidae CB.). *Z. Morph. Ökol. Tiere* **17:** 737–767.

Wojcik, D. P. (1989): Behavioral interactions between ants and their parasites. *Fla. Entomol.* **72:** 43–51.