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Foraging behaviour and resource utilization of the aphid parasitoid, *Pauesia pini* (Hymenoptera: Aphidiidae) on spruce: Influence of host species and ant attendance

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***Picea abies*, aphids, parasitoids, Aphidiidae, foraging behaviour, *Formica polyctena*, host morph, host microhabitat**

Abstract. We examined the foraging behaviour of the aphid parasitoid *Pauesia pini* (Haliday) (Hymenoptera: Aphidiidae) when foraging for *Cinara piceicola* (Cholodkovsky) or *Cinara pilicornis* (Hartig) (Hemiptera: Aphididae) on spruce. The foraging success of *P. pini* females differed for the two host species but depended also on the hosts' morph as well as on the presence of honeydew-collecting workers of *Formica polyctena* (Hymenoptera: Formicidae). Females found most hosts and laid most eggs when searching for *C. piceicola*-V1 morphs feeding on the stem. There, they succeeded in laying more eggs into ant-attended hosts than into those unattended. *C. piceicola* sexuparae feeding on two-year-old shoots were less often discovered, and *P. pini* females did not oviposit into these small morphs, independent of the presence of ants. *C. pilicornis*, which is not attended by ants, was least often attacked but *P. pini* females occasionally parasitized this host species.

INTRODUCTION

In Central Europe, Norway spruce, *Picea abies* (L.) Karst, serves as host plant for five conifer lachnid species of the genus *Cinara* (Hemiptera: Aphididae). These five species differ interspecifically in size, feeding sites, phenology and mutualistic relationships with ants (Scheurer, 1964a,b; Pintera, 1966; Fossel, 1972; Carter & Maslen, 1982; Kunkel & Kloft, 1985) but show also intraspecific within-season variations in some characters. First, all species decrease in size during the season, with the fundatrices being the largest and the sexuparae being the smallest morphs (Pintera, 1966; Fossel, 1972; Kunkel & Kloft, 1985). Second, two species (*Cinara pruinosa* Hartig, *Cinara piceicola* Cholodkovsky) alter their feeding sites during the season: colonies feed on 4–7-year-old wood in spring and early summer but on 2–3-year-old wood (*C. piceicola*) or roots (*C. pruinosa*) during midsummer. Three other species (*Cinara piceae* Panzer, *Cinara pilicornis* Hartig, *Cinara costata* Zetterstedt) occupy the same feeding niche throughout the year (Wellenstein, 1930; Scheurer, 1964a; Carter & Maslen, 1982). Third, the intensity of ant-attendance in *C. piceicola*, *C. pruinosa* and *C. piceae* may vary throughout the year. These differences between and within aphid species may also influence the foraging success of their specialized hymenopterous parasitoids, which exclusively belong to the family Aphidiidae (Starý, 1960, 1966, 1970; Mackauer & Starý, 1967). Differences in occupied feeding sites are usually connected with differences in plant structure at the respective microhabitats. These differences may influence both searching behaviour and oviposition success of parasitoids (e.g. Andow & Prokrym, 1990; Maini et al., 1991; Stadler & Völkl, 1991). Additionally, aphid size may be a factor that will determine host acceptance and thus reproductive success of the foraging female (Liu, 1985; King, 1989; Hardy et al., 1992; Sequeira & Mackauer, 1994).

In the present study, we analysed the foraging behaviour of *Pauesia pini* (Haliday) (Hymenoptera: Aphidiidae), one of the major parasitoids of *Cinara* spp. on Norway spruce. *P. pini* is a solitary endoparasitoid whose host range includes a number of *Cinara* species feeding on spruce, pine and larch (Starý, 1960, 1966; Mackauer & Starý, 1967; Liebscher, 1972). On Norway spruce, two of its most abundant hosts are *C. pilicornis* and *C. piceicola* (= *C. piceicola* spp. *viridescens* Cholodkovsky = *Cinara cistata* var. *stroyani* Pašek) (see Danielsson, 1987). These species differ in a number of above mentioned characters: first, *C. pilicornis* is sucking on the respectively youngest parts of the tree throughout the season (previous year shoots in early spring, current year shoots later on in the season), while *C. piceicola* prefers older parts for feeding. *C. piceicola* fundatrices are found on 4–7-year-old wood, while summer morphs suck on 2–3-year-old shoots (Kunkel & Kloft, 1985). Second, *C. piceicola* is heavily attended by trophobiotic red wood ants (*Formica* spp.), while *C. pilicornis* is usually unattended (Scheurer, 1964a; Fossel, 1972). Third, colonies of *C. piceicola* grow, on average, larger than *C. pilicornis* colonies (Scheurer, 1964a). There are also striking differences between the various morphs within the two species: both species decrease gradually in size during the season (Fossel, 1970), with fundatrices having the ten-fold fresh weight compared to summer morphs (Völkl, unpubl. data). In the present study, we tested whether and, if so, in which way (1) the host aphid species, (2) its feeding site, (3) its morph and (4) the presence or absence of ant-attendance influence the searching behaviour and foraging success of *P. pini*.

MATERIAL AND METHODS

Insect rearings

Fundatrix colonies of *C. piceicola* and virginoparae (V1 generation) colonies of *C. pilicornis* were sampled in a spruce forest in the Fichtelgebirge, north of Bayreuth, Germany in May 1994 and 1995. Aphids were transferred to 7-year-old potted spruce plants. Colonies were subsequently kept in a growth chamber at 20° ± 1°C, ca. 65% r.h. and 16L : 8D. Each spruce was infested by only one aphid species that passed through several generations until autumn.

Pauesia pini-mummies originating from *C. piceicola* were sampled on spruce stems at the same site as *C. piceicola* in May and June, 1994 and 1995, respectively. Mummies were kept in gauze-covered plastic cages (diameter 5 cm, height 10 cm) at 20°C until adult emergence. Newly-emerged adults were fed with a water-honey solution and kept at 5°C for 4–5 days. 24 h before being used in experiments, females were transferred to the growth chamber (20°C) and supplied with males to have a chance for mating. Prior to the experiments, females had no contact with hosts or ants.

A small colony of *Formica polyctena* (approx. 500 workers) was established in a terrarium (70 × 35 × 35 cm) and kept at 20°C, 60% r.h., 3000 Lux and 16L : 8D in the same growth chamber as the aphid rearings. *F. polyctena* workers had access to the plants via sticks and tended the established *C. piceicola* colonies readily. Ant activity was assumed to resemble the situation out in nature. *C. pilicornis* exhibits no or only very weak mutualistic relationships with ants in the field (Scheurer, 1964a; Kunkel & Kloft, 1985; Völkl, unpubl.). Therefore, we excluded ants from the trees infested by this aphid species.

Experimental design

The foraging behaviour and resource utilization of *P. pini* females was studied using 7-year-old potted spruce plants consisting of the main stem and 4 whorls with 4 side shoots. Additional shoots were removed. We set up five experimental designs: (1) The 4–6-year-old sector of the main stem was infested by a colony of 35–45 virginoparae of *C. piceicola* (V1 generation), resembling the situation found in the field in spring. The aphid colony was attended by *F. polyctena* (n = 12 *P. pini* females; furthermore referred to as *C. piceicola*-V1/with ants). (2) Experiment 2 resembles experiment 1, except that the aphid colonies were not attended by *F. polyctena* (n = 10 *P. pini* females; *C. piceicola*-V1/without ants). (3) 5–6 two-year-old shoots were infested by *C. piceicola* colonies (size: 5–10 individuals of the sexuparae generation on each shoot), resembling the situation found in the field during mid-summer. The *C. piceicola* colonies were attended by *F. polyctena* (n = 22 *P. pini* females; *C. piceicola*-sexuparae/with ants). (4) 4 or 5 current-year shoots were infested by small *C. pilicornis* colonies (4–8 individuals of the V1 generation). These colonies were not attended by *F. polyctena* (n = 22 *P. pini* females). (5) Aphid-free spruces were used as a control (n = 15 *P. pini* females).

P. pini females were released singly onto the twig of a 7-year-old spruce and observed continuously until they left the plant. Each female was used only once. To create a "quasi-natural" environment, we arranged four 6–8-year-old spruces and three 3–4-year-old pines (*Pinus sylvestris*) around the experimental tree and the *F. polyctena*-nest. The total experimental area consisted 1.2 m^2. We distinguished the following parasitoid behavioural patterns: (a) searching – the parasitoid searched the host plant but had no contact with hosts; searching was divided into "search on stem" (an area without needles) and "search on branches/twigs" (areas with needles); (b) feeding – the parasitoid fed on honeydew which had accumulated on the spruce; (c) resting – the parasitoid showed no obvious activity and sat motionless on the wood or on a needle; (d) cleaning – the parasitoid cleaned its legs, antennae or mouthparts; (e) host handling – the parasitoid had located a potential host, or it had made physical contact, or it showed a behaviour connnected with oviposition (e.g. waiting with bent abdomen, attacking a host or ovipositing); (f) interaction with ant workers – a foraging parasitoid encountered an ant worker; ants could be either aggressive or non-aggressive when coming into contact with *P. pini*, and *P. pini* females could either disregard the ant, retreat to a small dead shoot or leave the plant by dropping off or flying away.

When a *P. pini* female had located a host, host handling was divided in three responses: (a) contact – a female made either physical contact with the host or displayed other behavioural patterns showing clearly that it had recognized the potential host; (b) attack – the female bent its abdomen and tried to oviposit into the host; the ovipositor usually touched the host; (c) oviposition – a successful oviposition was characterized by an ovipositor insertion for 2–4 s and a strong and jerky withdrawal of the ovipositor. Stung aphids were removed after the trial and reared separately until the appeareance of mummies to confirm successful stings.

An aphid responded to an encounter by a foraging wasp either by defensive behaviour or by ignoring the attacking wasp. Defensive behaviour included physical defence reactions (kicking with hind legs, raising and shaking the body) or leaving the feeding site, but not the release of siphuncular secretion, as reported for other aphid species (e.g. Nault et al., 1976).

RESULTS

Foraging behaviour and time allocation of *P. pini*

All *P. pini* females foraging on trees infested by *C. piceicola*-V1 (experiments 1 and 2) found hosts, while only 12 out of 22 females foraging for *C. piceicola*-SP (experiment 3) and 12 out of 22 females foraging for *C. pilicornis* (experiment 4) encountered at least one host before leaving the tree.

Foraging was characterized by a high individual variability. Residence times on trees were longest on trees with *C. piceicola*-V1 and intermediate if females discovered *C. piceicola*-SP or *C. pilicornis*-colonies, or if they were foraging without success on trees infested by *C. piceicola*-SP (Fig. 1). By contrast, females remained significantly shorter on control trees or on trees searched without success for *C. pilicornis* (Fig. 1).

On plants with *C. piceicola*-V1, females spent equal proportions of their time for searching and for handling hosts (Tab. 1). By contrast, females spent less than 1% of their residence time with handling *C. piceicola*-SP or *C. pilicornis*. In these cases, and if no hosts were found or present, searching comprised between 70% and 85% of the total residence time. Cleaning, resting or feeding each comprised – with two exceptions – always

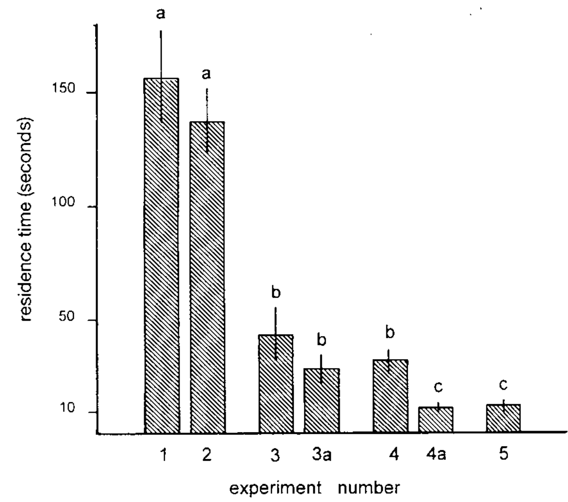

Fig. 1. Average residence times (in seconds; mean ± S.E.) of foraging *Pauesia pini* on spruces in relation to host species/host morph, presence/absence of host and presence/absence of ants. Exp. 1 – *C. piceicola*-V1 with ants; 2 – *C. piceicola*-V1 without ants; 3 – *C. piceicola*-SP with ants; 3a – *C. piceicola*-SP with ants, no hosts found; 4 – *C. pilicornis*; 4a – *C. pilicornis*, no hosts found; 5 – control without aphids. For details, see Material and methods. Means sharing the same letter do not differ at p < 0.05 (Tukey's test).

less than 10% of the residence time in all experiments (Tab. 1).

The time spent searching on stem and shoots differed considerably. *P. pini* females spent most of their time on the stem when *C. piceicola*-V1 were present (Fig. 2). By contrast, females searched much more time on shoots if no aphids were feeding on the stem (exp. 3–5). In those experiments, the relation between time spent on shoots (97.2 ± 1.1%) and time spent on stem (2.8 ± 0.6%) (Fig. 2) corresponded with the ratio between the total shoot length of the experimental trees (3,781 ± 843 cm) and the total stem lengths (95 ± 10 cm) (ratio shoot/stem = 97.5 : 1).

Resource utilization

Females had most host contacts (34.9 ± 2.6), and laid most eggs (9.1 ± 1.0), when foraging for ant-attended *C. piceicola*-V1. By contrast, they had significantly less contacts (17.4 ± 2.4), and laid significantly less eggs (4.2 ± 0.6), when foraging for unattended *C. piceicola*-V1, although the proportion of attacked aphids (attacks/contacts) was similar (with ants: 57.3 ± 3.7%; without ants: 59.7 ± 2.6%). Correspondingly, the rate of contacts and ovipositions per h was significantly higher on trees with ant-attended *C. piceicola*-V1 compared to trees with unattended *C. piceicola*-V1 (Fig. 3). In both cases, however, the number of ovipositions was significantly correlated with residence time (*C. piceicola* with ants: r = 0.85, n = 12, p < 0.001; *C. piceicola* without ants: r = 0.77, n = 10, p = 0.009).

TABLE 1. Relative time allocation (mean ± S.E.; given are percent of the total residence time) of *Pauesia pini* on spruce. Exp. 1 – *C. piceicola*-V1 with ants; 2 – *C. piceicola*-V1 without ants; 3 – *C. piceicola*-SP with ants; 3a – *C. piceicola*-SP with ants, no hosts found; 4 – *C. pilicornis*; 4a – *C. pilicornis*, no hosts found; 5 – control without aphids. Within a given behaviour, means sharing the same letter do not differ at p < 0.05 (Tukey's test).

Behaviour	Experiment No.						
	1	2	3	3a	4	4a	5
searching	43.8 ± 3.8^{a}	47.2 ± 2.2^{a}	84.3 ± 4.8^{b}	78.0 ± 5.6^{b}	67.4 ± 4.7^{b}	70.8 ± 5.0^{b}	85.9 ± 2.3^{b}
host handling	36.6 ± 4.2^{a}	35.4 ± 2.5^{a}	0.4 ± 0.1^{b}	—	0.2 ± 0.1^{b}	—	—
cleaning	10.9 ± 1.1^{a}	6.8 ± 0.7^{a}	7.5 ± 3.2^{a}	17.8 ± 3.2^{a}	10.4 ± 1.9^{a}	26.6 ± 5.1^{b}	11.6 ± 1.8^{a}
resting	5.1 ± 1.6^{a}	$7.2 \pm 1.0^{a,b}$			1.0 ± 0.6^{c}	0.3 ± 0.1^{c}	2.5 ± 1.5^{b}
feeding	3.7 ± 0.6^{a}	3.4 ± 0.8^{a}	7.8 ± 2.1^{a}	4.2 ± 2.0^{a}	20.9 ± 4.2^{b}	2.4 ± 1.9^{a}	—

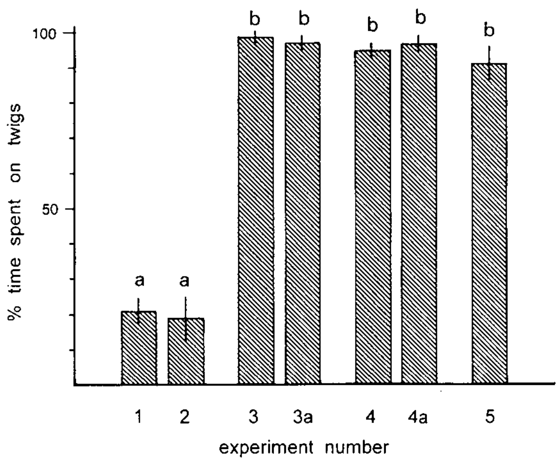

Fig. 2. Proportion of time spent searching on spruce shoots by *Pauesia pini* females in relation to host species/host morph, presence/absence of host and presence/absence of ants. Exp. 1 – *C. piceicola*-V1 with ants; 2 – *C. piceicola*-V1 without ants; 3 – *C. piceicola*-SP with ants, hosts found; 3a – *C. piceicola*-SP with ants, no hosts found; 4 – *C. pilicornis*, hosts found; 4a – *C. pilicornis*, no hosts found; 5 – control without aphids. For details, see Material and methods. Means sharing the same letter do not differ at $p < 0.05$ (Tukey's test).

Contacts with *C. piceicola*-SP never resulted in an assumed oviposition, although a similar proportion of aphids (43.1 ± 14.4%) was attacked as in the experiments with *C. piceicola*-V1.

P. pini females laid few eggs after encounters with *C. pilicornis* (0.4 ± 0.2), but the proportion of attacks after an contact was significantly lower (12.9 ± 3.8%) than after contacts with *C. piceicola*-SP or *C. piceicola*-V1. The comparably high oviposition rate per h on trees with *C. pilicornis* despite of the low number of laid eggs (Fig. 3) resulted from the low residence times in this experiment (see Fig. 1).

Influence of ants on foraging behaviour and oviposition success

P. pini females had significantly more contacts with ants when foraging for *C. piceicola*-V1 (9.3 ± 3.2 contacts/h) compared to *C.*

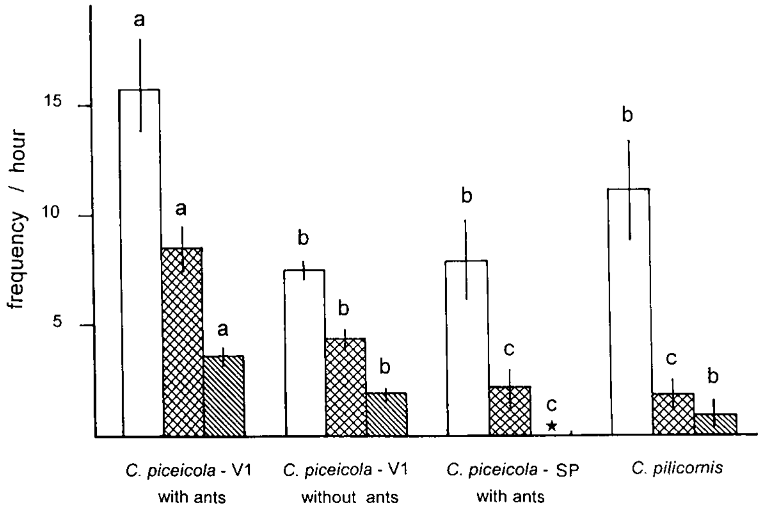

Fig. 3. Number of host contacts per h (open bars), attacks per h (cross-hatched bars) and ovipositions per h (hatched bars) (mean ± S.E.) of *Pauesia pini* females when foraging for different host species or host morphs feeding on spruce. For each kind of activity, means sharing the same letter do not differ at $p < 0.05$ (Tukey's test). * – no oviposition.

piceicola-SP (1.6 ± 1.0 contacts) (M-W test: U = 11, n = 24, $p < 0.001$). In neither case, we observed aggressions of *Formica polyctena* workers towards a foraging *P. pini* female. The ants either disregarded the parasitoid or they approached quickly, obviously in order to repel it from the vicinity of the aphid colony. In return, *P. pini* females also either disregarded the ant worker (14.0%; total number of observations = 392), or made just "one step aside" to avoid physical contact (40.6%). If ants approached too quickly, *P. pini* females responded by a quick retreat backwards on stem or to a dead shoot (36.7%). In few cases, females let themselves drop off (8.7%). The time spent for interactions with ants averaged at 2.8 ± 0.3% of the total residence time on the stem and at 0.2 ± 0.01% of the total residence time on the branch.

However, *P. pini* achieved a significantly higher oviposition rate on the stem in the presence of ants than in the absence of ants (see above; M-W U-test: U = 1.0, n = 22, $p < 0.001$). This was the result of a considerably shorter amount of time necessary for handling a particular host before a successful oviposition in the presence of ants (170 ± 28 s per host) than in the absence of ants (309 ± 34 s) (M-W U-test: U = 157, n = 22, p = 0.004). The reduced handling times per host were mainly the consequence of a significantly reduced host defence behaviour in the presence of ants (Table 2).

TABLE 2. The response of *C. piceicola*-V1 to an attack of *P. pini*. n – total number of observations, given are values in percent. Ant-attended and unattended *C. piceicola* differed significantly ($\chi^2 = 60.89$, df = 2, $p < 0.0001$; analysis based on absolute values).

Response	With ants (n = 419)	Without ants (n = 172)
no defence	49.6	15.1
unsuccessful defence	15.3	24.4
successful defence	35.1	60.5

The rejection of all attacked *C. piceicola* feeding on branches was not a result of ant-attendance. 75% of these hosts were encountered when no ants were in the direct vicinity.

DISCUSSION

The searching behaviour and foraging success of *P. pini* was characterized by a high individual variability, as known for many aphid parasitoid species (e.g. Cloutier & Baudouin, 1990; Völkl 1994a; Weisser, 1995; Völkl & Kraus, 1996). Despite this high variability, we could identify some important factors that crucially influence parasitoid foraging. First, plant structure and the aphids' feeding site had a significant effect. Females had a higher foraging success when searching for hosts feeding on the stem than for host feeding on twigs. Females spent only a little time searching on the stem of host-free plants, but they passed all stem areas during this time. On spruce trees with hosts feeding on the stem, the colonies were therefore necessarily encountered. Consequently, all females foraging for *C. piceicola*-V1 – which fed on the stem – found hosts. If no hosts were found on the stem, females spent the vast proportion of their searching time on branches which comprised about 97% of the total tree area. Nevertheless, they were usually not able to search more than 50% of the branches, and about half of the females foraging for hosts feeding on twigs found no hosts at all. Furthermore, the parasitoids detected, in total, less hosts feeding between needles on a twig than hosts feeding on the stem although the number of contacts per unit time did not differ significantly. The reason for this difference was the considerably shorter residence time on trees infested by *C. piceicola*-SP and *C. pilicornis*. Similar plant structure-related differences in the foraging success were found for *Aphidius rhopalosiphi*, which discovered less hosts feeding on wheat ears than feeding on leaves (Gardner & Dixon, 1985), and for *Lysiphlebus testaceipes*, which did not attack colonies of the banana aphid feeding hidden under withered banana leaves (Stadler & Völkl, 1991). Second, aphid morph had a significant influence on the acceptance by *P. pini*. While aphids of the large V1-generation of *C. piceicola* were readily and heavily attacked, the small individuals of the sexuparae generation were completely rejected after the female had made ovipositor contact. Probably, females rejected hosts of minor quality which do not assure a complete development: if *P. pini* females were forced to oviposit into *C. piceicola*-SP, the major proportion of the resulting offspring died during pupal development (Völkl, unpubl.), similar as reported for some other parasitoid species (Starý, 1989). The few emerging parasitoids were extremely small males.

Furthermore, *C. piceicola*-V1 were attacked to a much higher degree after an encounter than similar-sized *C. pilicornis*. In contrast to *C. piceicola*-SP, they were rejected after simple antennal contacts before the parasitoid bent its abdomen to attack the aphid. There may be several explanations for this behaviour. First, there may be an innate preference of *P. pini* for *C. piceicola* (Chow & Mackauer, 1991). Second, the egg-to-adult development lasts considerably longer in *C. pilicornis* (Völkl, unpubl.). Thus, *C. piceicola* may be a host of higher quality (Sequeira & Mackauer, 1992, 1994). Differences in aphid defence behaviour (mainly flight by leaving the feeding place in *C. pilicornis*, mainly hind leg kicking by *C. piceicola*-V1) had obviously no influence on host acceptance.

Ant-attendance had a considerable influence on the foraging behaviour of *P. pini*. The presence of honeydew-collecting *F. polyctena* on a spruce is usually connected with the presence of potential host aphids. Thus, encounters with *F. polyctena* workers provide obviously some information for the foraging *P. pini* female that leads to an increased searching effort and to longer residence times if compared to trees without ants (uninfested trees) or trees infested by *C. pilicornis*. A similar effect of ant-attendance on residence times in the absence of host contacts was found for a related species, *Pauesia silvestris* Starý on pine (Kroupa, 1995). Thus, we may expect that both physical encounters with ants and the presence of ant volatiles like trail pheromones may act as searching cues in the same way as aphid-borne cues (Bouchard & Cloutier, 1985; Grasswitz & Paine, 1992; Völkl, 1992; Battaglia et al., 1993). *P. pini* females achieved a higher parasitization success foraging in *Formica*-attended *C. piceicola*-V1 colonies compared to unattended *C. piceicola*-V1 although parasitoid females had to spend a considerable amount of time during interactions with ants. The higher foraging success was mainly the result of a considerably reduced host defence behaviour by kicking with hind legs (Tab. 1), as known for many aphids in the presence of ants (Nault et al., 1976) and of a considerably reduced handling time per individual host aphid. Therefore, *P. pini* females achieved a higher number of host contacts per unit searching time in the presence of ants which led to the higher number of ovipositions. Similar beneficial effects of ant-attendance on oviposition success were found for a number of other aphid parasitoid species like *Lysiphlebus cardui*, *Lysiphlebus hirticornis*, *Pauesia picta* and *Pauesia pinicollis* (Völkl, 1994b, 1997; Völkl & Mackauer, 1993). Like *P. pini*, these species are not attacked by ant workers. The mechanism for gaining access to ant-attended host colonies may be sought in behavioural adaptations and in a chemical mimicry of epicuticular hydrocarbon patterns of the aphid host (Völkl & Mackauer, 1993; Liepert & Dettner, 1996; Völkl, 1997).

The higher oviposition activity of *P. pini* in ant-attended colonies may be also interpreted in evolutionary terms as a result of the protective effects of ants for the parasitoid progeny (Völkl, 1992; Weisser et al., 1994). Most ant species heavily attack both foraging aphid hyperparasitoids and predators (who may consume parasitized aphids as well as unparasitized ones) (Way, 1963; Jiggins et al., 1993; Hübner & Völkl, 1996), while they do not prey selectively on parasitized aphids or aphid mummies (Völkl, 1997). Therefore, the aphidiid progeny developing in ant-attended host colonies benefit from a significantly reduced hyperparasitism and predation (Völkl, 1992; Völkl & Mackauer, 1993). This benefits can be also shown for *P. pini*: while ant-attended *C. piceicola*-V1-mummies were virtually not hyperparasitized (< 2% hyperparasitism by *Euneura augarus* Walker), unattended *Cinara*-mummies were highly hyperparasitized, mainly by *E. augarus* (Völkl, unpubl. data). *C. piceicola*-V1 are usually ant-attended in the field, while *C. pilicornis* is virtually unattended (Scheurer, 1964a; Kunkel & Kloft, 1985). Thus, the parasitoid's preference for *C. piceicola* may be also a choice for a higher offspring survival probability.

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