

Behavioral and Morphological Adaptations of the Coccinellid, *Platynaspis luteorubra* for Exploiting Ant-Attended Resources (Coleoptera: Coccinellidae)

Wolfgang Völkl¹

*Larvae of the coccinellid *Platynaspis luteorubra* were found significantly more often in ant-attended aphid colonies than in unattended colonies. The larva of *P. luteorubra* are protected against detection by the ant *Lasius niger* by their unusual shape, by inconspicuous movements, and presumably by chemical camouflage. Pupae were attacked by *L. niger* but protected by their dense hair cover. Adults were also attacked and responded either by fleeing or by pressing their body tightly against the plant surface. Fourth-instar larvae foraging in ant-attended aphid colonies had a higher success rate in capturing large prey items and benefitted from this by higher adult weights. Larval parasitism was higher in individuals feeding in unattended than in ant-attended colonies.*

KEY WORDS: Coccinellidae; ants; ant-coccinellid interactions; foraging success; adult fitness; parasitism.

INTRODUCTION

Many ant species cover their necessary carbohydrate supply by collecting the secretions of extrafloral nectaries or of so-called 'honeydew-producing insects' (Carroll and Janzen, 1973; Hölldobler and Wilson, 1990). In return, these ants regularly protect their 'carbohydrate source' against predators and parasitoids (e.g., Way, 1954, 1963; Addicott, 1979; Pierce and Eastal, 1986; Buckley, 1987; Koptur, 1991). However, a number of recent studies showed that this protection is incomplete and that ants cannot always provide an enemy-free space for their mutualistic partners. A number of phytophages (Maschwitz *et al.*, 1984;

¹Department of Animal Ecology, University of Bayreuth, D-95440 Bayreuth, Germany.

Letourneau, 1990), predators (Eisner *et al.*, 1978; Pierce, 1987), and parasitoids (Stary, 1966; Takada and Hashimoto, 1985; Völkl and Mackauer, 1993) gain access to ant-protected resources by various morphological and behavioral adaptations or by chemical camouflage. Parasitoids that are able to develop within ant-attended colonies receive the same protection against natural enemies as the aphids. For example, the aphidiid wasps *Lysiphlebus cardui* (Marshall) and *Lysiphlebus hirticornis* Mackauer were significantly less attacked by hyperparasitoids when they developed in ant-attended aphid colonies (Völkl, 1992; Mackauer and Völkl, 1993).

Larvae and adults of many coccinellid species, which prey on honeydew-producing Homoptera, are attacked by ants and therefore concentrate their foraging widely on unattended host colonies (Banks, 1962; Way, 1963; Bradley, 1973; Kreiter and Iperti, 1986; Cudjoe *et al.*, 1993; Jiggins *et al.*, 1993). However, larvae of *Platynaspis luteorubra* Goeze (Coleoptera: Coccinellidae) were commonly found unmolested while feeding on aphids associated with the ant *Lasius niger* L. in ant-shelters (Zwölfer, 1958; Pontin, 1960) although there is no detailed information on the preference of the coccinellid for ant-attended aphid colonies. To achieve a sustained access to ant-attended resources, three requirements must be met by *P. luteorubra*: First, adults need to overcome ant aggression for oviposition; second, larvae must be able to feed and develop successfully in the presence of honeydew-collecting ants; third, pupae must be protected against predation by the foraging ants.

In this study, I investigated the larval distribution of *P. luteorubra* in relation to ant attendance and interactions between larvae, pupae, and adults of this ladybird species and the ant *L. niger*. First, I study the abundance of *P. luteorubra* in ant-attended and unattended aphid colonies to analyze the patterns of distribution in the field. Then, I show that the access to ant-attended aphid colonies is gained through different morphological and behavioral adaptations of these three developmental stages. In a next step, I analyze the larval foraging behavior and coccinellid-aphid interactions in *L. niger*-attended aphid colonies as well as the relationship between *P. luteorubra* and its specific parasitoid, *Homalotylus platynaspidis* Hoffer (Hymenoptera: Encyrtidae), on differently structured host plants. I show that *P. luteorubra* achieves increased fitness from its capability to exploit ant-attended resources by higher foraging success of the larvae, which results in higher adult weights, and by reduced larval parasitism in ant shelters.

METHODS

Field Samples

The field studies were carried out from late May to mid-August 1992 in urban ruderal areas in Bonn, Germany. Eggs and larvae of *P. luteorubra* were

sampled on *Cirsium arvense* L.(Scop.) infested by *Aphis fabae* ssp. *cirsiacanthoidis* (Schrank) (six sites), *Tanacetum vulgare* (L.) infested by *Metopeurum fuscoviride* Stroyan (four sites), *Lapsana communis* (L.) infested by *A. fabae* ssp. *fabae* Scop. (two sites), *Senecio vulgaris* L. infested by *Brachycaudus cardui* (L.) (one site), and *Pastinaca sativa* L. infested by *Anuraphis subterranea* (Walker) (one site). Aphid colonies on *C. arvense* were feeding on the stem; colonies on *T. vulgare* were feeding on inflorescences; colonies on *L. communis*, *S. vulgare*, and *P. sativa* were feeding either on the lower part of the stem near the soil surface or on the upper parts of the roots. Colonies on above-ground parts of the latter three plants were covered by earth galleries built by the ant *L. niger* (= "ant shelters").

The host plants could be ranked according to their structural complexity: The single plant stems protected by ant shelters represented the simplest structure since there were no additional plant structure at the aphids' feeding site. *C. arvense* was more complex, as thistle stems were usually branched and some leaves or leaflets met the aphid colony. On both plant types, aphid colonies have a more or less two-dimensional structure. *T. vulgare* inflorescences are heavily branched and aphids colonies have an almost three-dimensional structure. Thus, *T. vulgare* inflorescences represent the most complex aphid feeding site.

At each site, the number of plants with aphid colonies, aphid colony size, the number and developmental stage of *P. luteorubra* larvae (or eggs) present in a particular colony, and the presence/absence of honeydew-collecting ants were recorded. Recorded eggs or larvae were collected and reared in the lab until adult emergence. Some of these individuals were used in the experiments described below.

Pupae were kept singly in small petri dishes together with the leaves to which they were attached. After the pupal skin had burst, the fully developed adults were theoretically able to leave the pupal exuvia. However, preliminary observations showed that *P. luteorubra* seems to remain longer than other coccinellids within the pupal exuvia. Therefore, these adults were observed daily at 3-h intervals to determine the time for which an adult remains within the exuvia.

Interactions Between *Lasius niger* and *Platynaspis luteorubra*

L. niger was by far the most frequent ant species found in association with *P. luteorubra*. To get a detailed insight into the interactions between this ant and various developmental stages of *P. luteorubra*, four experiments were carried out.

1. *P. luteorubra* larvae are characterized by their unusual "flattened" coccid-like shape, a lateral circle of long setae, very short legs which are completely hidden under the thorax, and piercing-sucking mouthparts used for extraintes-

tudinal digestion (Korschefsky, 1937; Hodek, 1973; Ricci, 1979). Interactions between these larvae and *L. niger* were studied in *Aphis fabae* colonies on *Cirsium arvense* ($n = 10$ colonies, each with three or more larvae) and in *M. fuscoviride* colonies on *T. vulgare* ($n = 5$ colonies; each with three or more larvae). Each colony was observed for 15 min. During this period, the outcome of all direct interactions between *L. niger* workers and *P. luteorubra* larvae and the response, if any, of all ants passing larvae within a distance of 5 mm without direct contacts were noted.

2. Prepupae which were already fixed to the surface of a *C. arvense* leaf or leaf stem were exposed to *L. niger* on *Cirsium arvense* stems infested by *A. fabae*. The plant parts with the prepupae were fixed with a pin at the base of a side branch closely below the aphid colony in the direct neighborhood of the ants' trail, i.e., in an area where pupae of *P. luteorubra* were recorded in the field. All ant responses to the presence of the prepupae were observed for 15 min after presentation of the prepupae.

3. Unparasitized pupae were exposed to ants following the same procedure as the one used for prepupae. *P. luteorubra* pupae are characterized by a dense cover of long hairs on the whole pupal surface which appears after the molt from prepupa into pupa. The tips of these setae bear a fluid droplet consisting of an unknown substance which can persist for up to 6 months after adult emergence, even at high temperatures and low humidity (W. Völkl, unpublished data), but which is not renewed after being removed. The droplets can be washed off with water and thus might be regularly removed in the field, e.g., during heavy showers. To evaluate the potential role of hairs and fluid droplets in defense against ants, three different experiments were set up: (a) Normal pupae with setae and droplets ($n = 20$ trials); (b) pupae in which the droplets were completely removed by wet filter tissue ($n = 20$ trials) to simulate the potential situation after heavy rain, (c) pupae in which most setae were removed with microscissors ($n = 10$ trials). All ant responses to pupae in these three treatments were observed for 15 min after the pupa was presented.

4. To evaluate ant-adult *P. luteorubra* interactions, *C. arvense* stems with *L. niger*-attended *A. fabae* colonies (approx. 300 aphids) were cut and carefully transferred to the laboratory. Most ants continued to search for honeydew after this disturbance without showing any obvious behavioral differences. In total, between 6 and 11 ants were counted in colonies on cut twigs. Single adult *P. luteorubra* females (reared from current-year larvae and starved for 2 days before the experiments) were released close to the aphid colony and observed for 30 min or until they left the plant. Ant-coccinellid interactions were classified as follows:

Coccinellids responded to an encounter with an ant by (a) immediately flying away, (b) fleeing by running very quickly up the stem and trying to hide

within a flower head, or (c) sitting still, drawing the legs and antennae under the body and holding themselves tightly against the plant surface (= "cowering"). In the latter case, the coccinellids are like a "tank" and almost unsailable to ant attacks.

Ants (a) ignored *P. luteorubra* adults completely or tapped them only for a short time with the antennae, (b) treated "cowering" beetles in a very aggressive way (biting and trying to chew with the mandibles, applying formic acid), or (c) pursued fleeing beetles.

Experiment 4 was carried out (a) with newly emerged coccinellids whose elytrae had not yet hardened (= beetles which normally hide in the burst pupal exuvia; $n = 12$ replicates) and (b) with 10- to 15-day-old females with fully hardened elytra but no prior contact with ants ($n = 20$ replicates). These females were fed a surplus of *A. fabae* but starved for 2 days before the experiment.

Aphid-Coccinellid Interactions and Foraging Success of *P. luteorubra* Larvae in Relation to Ant Attendance

T. vulgare stems infested either by *L. niger*-attended *M. fuscoviride* colonies (size: between approx. 100 and 150 aphids) or by unattended colonies (size: between approx. 100 and 150 aphids) were cut and carefully transferred to the laboratory. Most ants continued to search for honeydew for about 1/2 day after this disturbance without showing any obvious behavioral differences compared to ants foraging in colonies. In total, between 5 and 13 ants were counted to visit colonies on cut twigs. *M. fuscoviride* on ant-attended and unattended colonies showed the same behavior as aphids in field colonies under these conditions.

Single first-instar larvae of *P. luteorubra* ($n = 10$ trials both in unattended and *L. niger*-attended colonies) of unknown feeding condition, or 1-day starved fourth-instar larvae ($n = 10$ trials both in unattended and *L. niger*-attended colonies), were released onto a *T. vulgare* stem close to the aphid colony and, after a time lag of 30 min, observed continuously for 60 min. During this time interval, the numbers and instars of aphids attacked, the aphids' response to coccinellid attack, the coccinellids' foraging success, and the response of neighboring aphids were noted.

To analyze the searching behavior of fourth-instar *P. luteorubra* larvae, I noted additionally position and distance of an encountered aphid in relation to the previous prey, and coccinellid larval movements in approx. 2-mm units (= approximately the size of an adult *M. fuscoviride*) after feeding had stopped or after an unsuccessful attack.

Potential fitness consequences of different larval foraging success, if any, in the presence/absence of ants were estimated by comparing the dry weight of

adult ladybirds. Ten males (white clypeus) and ten females (black clypeus) which had developed either in the presence or absence of ants in *M. fuscoviride* colonies were weighed with a microbalance (Microsartorius 4501).

Parasitization Rates by *Homalotylus platynaspidis*

The parasitization rates of *P. luteorubra* on particular host plants/host plant types were calculated from pooled data of fourth-instar larvae collected on a plant type. The restriction to the fourth instar was made because the only known parasitoid of *P. luteorubra*, *Homalotylus platynaspidis* (Klausnitzer, 1969), oviposits exclusively into larvae but completes its development in the pupa, or occasionally in the prepupa, of *P. luteorubra* (W. Völkl, unpublished).

Interactions Between *Lasius niger* and *Homalotylus platynaspidis*

To assess the potential impact of ant attendance on the foraging behavior of this parasitoid, single *H. platynaspidis* females ($n = 14$; all females reared from current-year samples) were released into small circular plastic cages (diameter 10 cm, height 8 cm) and observed for 20 min. The cages contained a cut piece of a *C. arvense* stem with *A. fabae*, two third-instar larvae of *P. luteorubra*, and 8–10 ants. Ant–parasitoid interactions were classified as follows:

Ants either ignored *H. platynaspidis* completely, tapped them shortly with the antennae (< 1 s), or responded with long antennal tapping and mouth–mouth contact.

Parasitoids responded to an approach of an ant by (a) immediately jumping away, (b) changing the walking direction to avoid a direct contact, or (c) antennal tapping and the attempt to establish a mouth–mouth contact with the ant (which resembled a mouth–mouth contact between two *L. niger* workers).

RESULTS

Larval Distribution in Relation to Ant Attendance and Aphid Colony Size

P. luteorubra larvae were found significantly more often in ant-attended aphid colonies than in unattended ones, both on *C. arvense* ($\chi^2 = 12.674$; $df = 1$, $p < 0.001$) and *T. vulgare* ($\chi^2 = 5.399$; $df = 1$, $p = 0.020$), and occurred commonly in ant shelters around root-collar feeding aphid species (Table I). *Lasius niger* was by far the most abundant aphid-attending ant species in the study area and accounted for 92% of all visits in ant-attended colonies (total $n = 158$), while *Myrmica rugulosa*, *Myrmica ruginodis*, and *Formica pratensis* played only a subordinate role. Consequently, the majority of *P. luteo-*

Table I. Distribution of *P. luteorubra* Larvae (in %) in Ant-Attended and Unattended Aphid Colonies on *C. arvensis* and *T. vulgare* and in Ant Shelters^a

	Ant-attended			Unattended		
	With larvae	Without larvae	<i>n</i>	With larvae	Without larvae	<i>n</i>
<i>C. arvensis</i>	60.3	39.7	68	13.6	86.4	22
<i>T. vulgare</i>	46.3	53.7	67	11.8	88.2	17
Ant shelters (all plants pooled)	60.1	39.1	23	—	—	—

^aData are pooled for all sites and sampling dates, *n*, Number of samples.

rubra larvae were found in association with *L. niger*, but larvae were also recorded within the two *A. fabae* colonies attended by *M. rugulosa*.

Different larval stages from first to fourth instar within the same aphid colony were found in 59.3% of the *P. luteorubra*-infested aphid colonies. However, since no ovipositing females were observed, it is not clear whether these larvae were progeny from the same or different mothers. The total numbers of larvae were correlated with aphid colony size both on *C. arvensis* ($r = 0.699$, $df = 39$, $p < 0.001$; Fig. 1a) and *T. vulgare* ($r = 0.520$, $df = 29$, $p = 0.003$; Fig. 1b) and in ant shelters ($r = 0.611$, $df = 12$, $p = 0.020$; Fig. 1c). The number of first-instar larvae was also correlated with aphid colony size ($r = 0.487$, $df = 43$, $p < 0.001$; all data pooled due to small sample sizes).

Behavior of Emerging Adults

Emerging adults of *P. luteorubra* remained within the burst pupal exuvia until all sclerotized parts of the body, especially the elytra, were fully hardened. This period lasted on average 2.9 ± 0.6 days ($n = 58$) and did not differ between males (2.9 ± 0.7 d; $n = 28$) and females (3.0 ± 0.6 d) ($U = 396.5$, $df = 56$, $p = 0.673$).

Interactions Between *Lasius niger* and *Platynaspis luteorubra*

P. luteorubra larvae were completely ignored by *L. niger* at all encounters (both with legs and with antennae), independent of the coccinellid larval instar. The ants "cleaned" the tended aphid colony of empty skins of aphids sucked during predation by *P. luteorubra* in the same way as they remove aphid exuviae. Prepupae were also completely ignored ($n = 36$ contacts). Both coccinellid larvae and prepupae did not secrete body fluid from the large pores in the abdominal segments when touched by an ant's antenna or leg.

Ant behavior toward *P. luteorubra* changed after pupation. The ants attacked

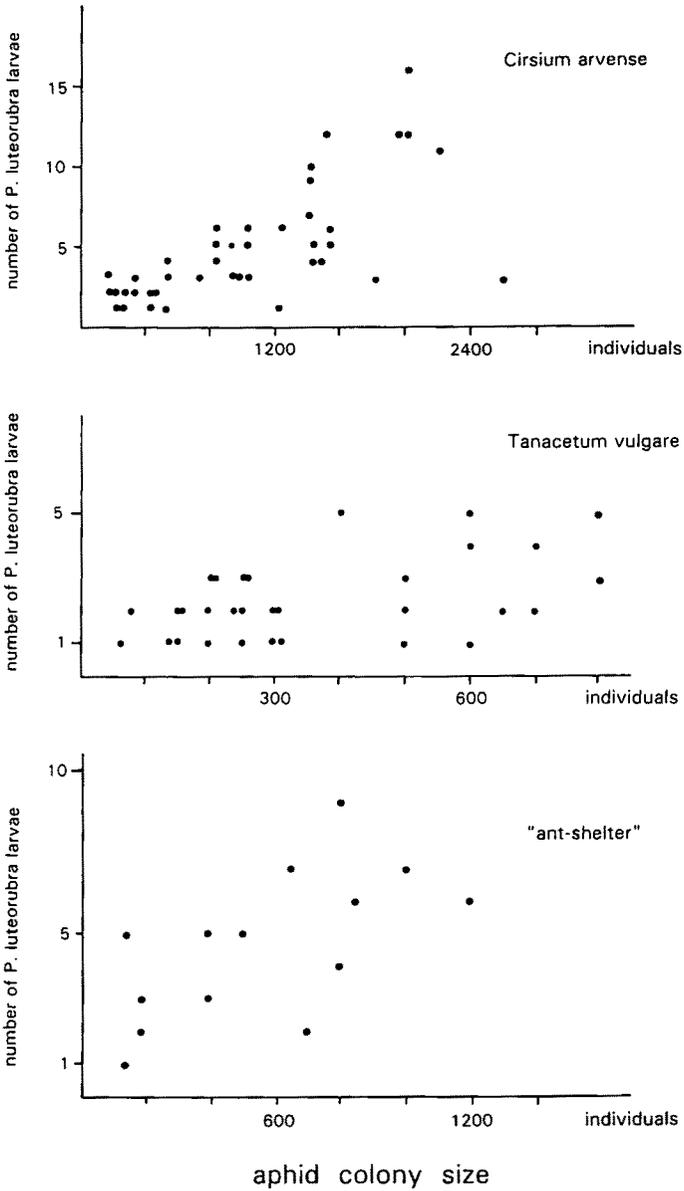


Fig. 1. Relationship between aphid colony size and the total number of *P. luteorubra* larvae in ant-attended aphid colonies on *C. arvense* and *T. vulgare* and in ant shelters.

Table II. The Outcome of *L. niger* Behavior (Values Given in %) Toward *P. luteorubra* Pupae in Three Different Designs

Design	<i>L. niger</i> aggressive		<i>L. niger</i> not aggressive
	Pupa removed within 15 min	Pupa not removed	
Pupa complete	5	90	5
Droplets removed	0	95	5
Setae + droplets removed	80	20	0

the pupae aggressively, and repeatedly, both in the presence and absence of fluid droplets on the pupal hairs (Table II). Ant workers tried to seize the pupa with their mandibles and presumably also squirted formic acid at them, since the ants' abdomens were bent forward during the attack. The dense setae of the pupae, whose length exceeded the mandible length of *L. niger* workers, prevented the pupa from being seized or injured, and all but one exposed pupa developed successfully into adult beetles. In contrast, all pupae with cut setae were seized by the ants. The majority of these pupae was removed from the plant surface and carried off by ants (Table II).

Ants also readily attacked adult beetles and tried to bite them with their mandibles. Both newly emerged adult *P. luteorubra* with soft elytra and fully developed adults either tried to escape ants by running away (newly emerged: $n = 3$ observations; fully developed; $n = 4$) or by cowering (newly emerged: $n = 9$; fully developed: $n = 14$). Two fully developed adults also left the plant by an immediate takeoff. Running coccinellids were pursued by ants, but in the majority of the observations ($>90\%$) the ants gave up after a few centimeters, since they could not catch up with the swift beetles. Cowering beetles were bitten and simultaneously squirted with formic acid for on average 47 ± 30 s (newly emerged: 50 ± 29 s, fully developed: 44 ± 32 s; Mann-Whitney $U = 53$, $n = 23$, $p = 0.528$). Adult coccinellids were not observed to "reflex bleed" when attacked by ants. If newly emerged cowering beetles were attacked, both elytra and hindwings were severely injured by the ants. Three attacked individuals died within 12 h; the surviving nine beetles had permanently damaged elytra and were unable to fly. Fully hardened beetles received no obvious injuries from the ant attacks and continued to forage on the plant after the attack. These individuals remained unmolested by ants at subsequent encounters during the next 20 min and were either totally ignored ($n = 38$ encounters with 12 females) or only tapped with the ants' antennae ($n = 19$ contacts with 9 females). These adults were also not attacked when feeding on tended aphids during this interval ($n = 13$). However, the same individuals ($n = 10$) were attacked by ants as described above when exposed to *L. niger* workers for 10 min 1 day later.

Aphid-Coccinellid Interactions and Foraging Success of *P. luteorubra* Larvae in Relation to Ant Attendance

The age structure of the aphids attacked by both first- and fourth-instar larvae did not differ significantly between unattended and *L. niger*-attended colonies (for first-instar larvae, $\chi^2 = 1.204$, $df = 4$, $p = 0.877$; for fourth-instar larvae, $\chi^2 = 0.963$, $df = 4$, $p = 0.915$; Fig. 2). In both treatments, however, first-instar larvae consumed only small *M. fuscoviride*. They were unable to bite into the femur of larger stages, probably due to a limited span of the mandibles.

By contrast, fourth-instar *P. luteorubra* consumed all *M. fuscoviride* stages. Their "success rate" (= % successfully attacked prey items; Fig. 2) was not influenced significantly by the presence of ants when small aphids (L_1 , L_2) were encountered ($\chi^2 = 0.091$, $df = 1$, $p = 0.764$).

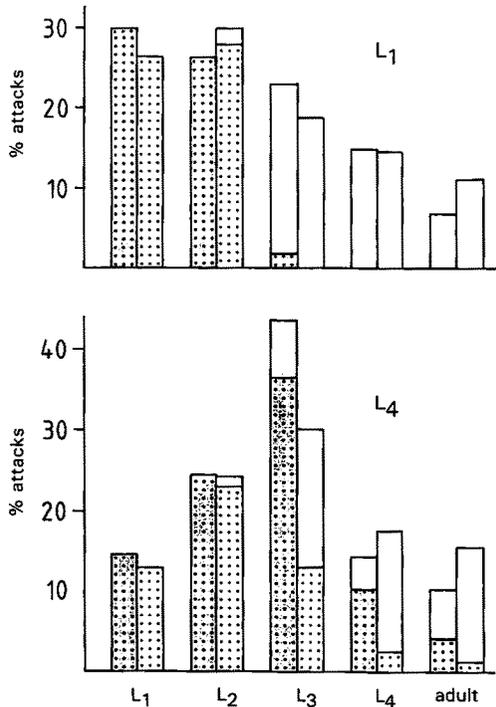


Fig. 2. Relationship between aphid stage and the proportion of attacks by first-instar larvae (L_1) and fourth-instar larvae (L_4) of *P. luteorubra* in the presence (shaded left bars) or absence (open right bars) of *L. niger*. Dotted areas indicate the proportion of eaten aphids (= successful attacks).

However, the proportion of attacks of larger aphids (L_3 , L_4 , adults) that resulted in capture was significantly higher in the presence of ants ($\chi^2 = 15.133$, $df = 2$, $p < 0.001$; Fig. 2).

The only obvious aphid defense behavior in response to a contact with a *P. luteorubra* larva was to lift the encountered leg. This defense was highly efficient, prevented a successful bite by the larva in 95% of all observations and accounted for all unsuccessful attacks. Leg-lifting increased significantly with aphid instar and in the absence of ants (Fig. 2, shaded areas). A high proportion of the coccinellid attacks against large aphids failed, especially in unattended colonies, whereas first- and second-instar *M. fuscoviride* rarely responded to a tactile contact and were almost always captured and consumed in both treatments. Neighboring aphids were never observed to respond to a coccinellid attack regardless of the presence or absence of ants, not even in the few cases when the captured aphid released siphuncular secretion.

Fourth-instar larvae rarely moved more than 10 mm between two encounters (Fig. 3) and, when hungry, usually attacked the aphid feeding next to the last aphid encountered both in *L. niger*-attended and unattended colonies ($\chi^2 = 4.578$, $df = 5$, $p = 0.469$). However, the average distance covered within 1 h was significantly lower in ant-attended (24.4 ± 7.7 mm) than unattended colonies (40.2 ± 4.4 mm) (Mann-Whitney $U = 3$, $df = 18$, $p < 0.001$). This higher searching effort of the coccinellid larva corresponded to the increased aphid defense success in unattended colonies (Fig. 2). Nonfeeding larvae usually

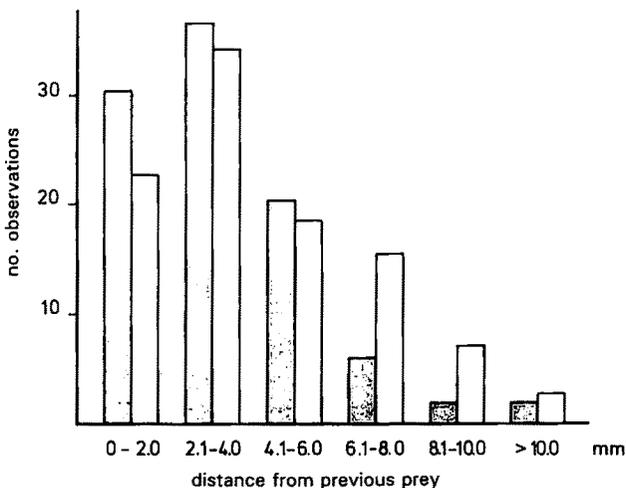


Fig. 3. Distance distribution of *M. fuscoviride* attacked by *P. luteorubra* larvae in relation to the previously attacked prey in the presence (shaded bars) or absence (open bars) of *L. niger*.

remained within the aphid colony where the last aphid was consumed. They were never observed on the plant outside an aphid colony.

Both male and female adults which developed on ant-attended colonies had on average a significantly higher body dry weight [males, *L. niger*-attended 0.918 ± 0.108 mg ($n = 10$); unattended 0.708 ± 0.125 mg ($n = 10$), $U = 10$, $p = 0.003$; females, *L. niger*-attended 0.994 ± 0.096 mg ($n = 10$), unattended 0.894 ± 0.099 mg ($n = 10$), $U = 22.5$, $p = 0.038$].

Parasitization Rates by *Homalotylus platynaspidis*

The highest percentage of *H. platynaspidis*-parasitized *P. luteorubra* larvae was found in unattended colonies and in ant-attended *M. fuscoviride* colonies on the inflorescences of *T. vulgare*, while parasitism was significantly lower in samples collected from ant-attended *A. fabae* colonies on *C. arvense* stems and from ant shelters (Fig. 4). The decrease in parasitization by *H. platynaspidis* in ant-attended aphid colonies was correlated with a decrease in this structural complexity of the aphids' feeding site (ant shelters < *C. arvense* < *T. vulgare*).

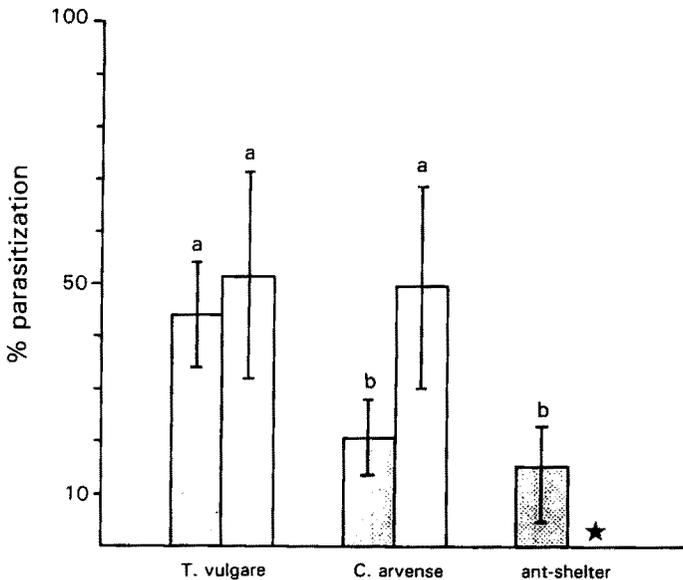


Fig. 4. Parasitization rates (means \pm 95% C.I.) of *P. luteorubra* by *H. platynaspidis* in ant-attended aphid colonies (shaded bars) and in unattended colonies (open bars) on *C. arvense* and *T. vulgare* and in ant shelters on different plant species. Means sharing the same letter do not differ at $p < 0.05$ (Z-test). *, No unattended colonies were found.

Interactions Between *L. niger* and *H. platynaspidis*

Ants did not attack searching *H. platynaspidis* females. Parasitoid females usually avoided contacts with approaching *L. niger* workers if ants were perceived early enough, for example if ant-parasitoid distance exceeded twice the ants' body lengths. In most cases, parasitoids changed the walking direction ($n = 48$ observations; all females pooled), but jumping away was also a common response ($n = 11$ observations; all females pooled). Quick ant approaches toward the parasitoids' front side prevented the parasitoid from changing direction. The resulting encounters led to mutual antennal tapping followed by contact between the mouthparts of the ant and the parasitoid ($n = 13$ observations). However, it could not be confirmed whether *H. platynaspidis* received regurgitation or not. In contrast, if an ant approached from behind (i.e., abdomen side of *H. platynaspidis*), the encountered parasitoid always jumped away ($n = 14$ observations).

DISCUSSION

The foraging behavior of predacious insects has motivated a considerable number of theoretical and empirical studies (e.g., Hassell and May, 1974; Chesson, 1978; Sih, 1980; Carter and Dixon, 1982; Kareiva, 1984; Kareiva and Odell, 1987; Kareiva and Perry, 1989). Most studies have focused on the optimization of predation success and energy intake, but little attention has been paid to oviposition decisions (e.g., Hemptinne and Dixon, 1991). To optimize the long-term reproductive success, oviposition decisions should lead to an optimal survival and fitness of the progeny. Thus, females should select sites with low mortality risks and a predictable sufficient food supply for their descendants.

Aphidophagous coccinellids are confronted with the problem of an unstable and fluctuating food supply (Dixon, 1985), which should crucially influence the oviposition decisions. The survival of newborn larvae is dependent on the abundance of small aphids (Dixon, 1959; Ricci, 1979) (Fig. 3), and larvae foraging in too small colonies may be at risk of starvation. *P. luteorubra* meets this problem by a concentration of its progeny in ant-attended aphid colonies (Table I). Ant-attended colonies normally grow larger and persist longer than unattended ones (Addicott, 1979; Bristow, 1983; Völkl, 1990). They should therefore represent a much more stable and predictable resource in terms of coccinellid larval survival. *P. luteorubra* gains access to these ant-attended colonies by a number of morphological and behavioral adaptations. Several factors may account for the complete ignoring of larvae by foraging *L. niger* workers. The flat, "coccid-like" body shape, which is also highly adapted for moving and feeding in the narrow ant shelters and in underground ant runs, and the very slow, inconspicuous movements may help to prevent visual detection by ants.

Additionally, trophobiotic ants may also not respond directly to the presence of a predator but indirectly to a change in aphid behavior (Nault *et al.*, 1976). In contrast to other coccinellids (Klingauf, 1967; Stadler, 1991), feeding *P. luteorubra* larvae did not cause an evident aphid defense behavior which might elicit ant aggression. However, since larvae were not treated aggressively even by *L. niger* which tapped them with the antennae, chemical cues are probably also involved in the prevention of ant aggression. Such specific odor cues to avoid detection by ants were reported for several predators and parasitoids which live in close association with ants (Vandermeer and Wojcik, 1982; Vandermeer *et al.*, 1989; Howard *et al.*, 1990; Letourneau, 1990; Völkl and Mackauer, 1993) and were also assumed for the coccinellid species *Coccinella magnifica* (Redtenbacher) which is also not attacked by ants (Majerus, 1989). Ricci (1979) assumed that the release of a fluid from the large pores in the abdominal segments might deter ants. Such secretions were never observed in response to an ant encounter, but hardened residues of this fluid were regularly found on the body surface of parasitized larvae. Fluid secretion was common if larvae were heavily tweaked with a forceps (W. Völkl, unpublished). Some significance of this body fluid in the protection against ants cannot be excluded, though its role as a defense against *H. platynaspidis* or other enemies is more likely.

The potential chemical camouflage of the larvae disappeared after the molt from prepupa into pupa. Pupae were readily, and heavily, attacked by *L. niger*, but obviously protected against this aggression by their long, dense hair cover (Table III). These stiff hairs, which are built up during the prepupal period, are longer than the opening width of the mandibles of *L. niger* and represent a mechanical defense which prevents the pupae from being seized and injured, especially in ant shelters and on simply structured plants where pupae are usually fixed within the foraging range of honeydew-collecting ants. The fluid droplets at the tip of the hairs did not obviously repel *L. niger* workers. However, similar fluid droplets situated at the tip of hairs on the pupal body of the coccinellid *Epilachna varivestis* were reported to have a repellent effect on *Leptothorax longispinosus* workers (Attygalle *et al.*, 1993). Thus, further studies are necessary to clarify whether the fluid droplets of *P. luteorubra* protect pupae against natural enemies other than ants, or whether the fluid droplets may have a deterrent effect on ants in the absence of the mechanical defense.

Adult *P. luteorubra* were heavily attacked by *L. niger* when detected for the first time. Ant attacks were particularly detrimental to newly emerged individuals whose sclerotized body parts, especially the elytrae, were still soft and vulnerable. *P. luteorubra* avoided the threat of receiving severe injuries from surrounding ants by remaining in the burst pupal skin until all sclerotized body parts were fully hardened, a behavior which contrasts to other aphidophagous coccinellids species (Hodek, 1973). Fully developed beetles escaped *L. niger* attacks either by a quick "sprint" or by holding the body tightly against the

plant surface ("cowering"), in the same way as reported for the coccinellid *Hyperaspis congressis* in response to the attack of the wood ant *Formica obscuripes* (Bradley, 1973). Cowering adults were almost impregnable to ants and could feed on ant-attended aphids unmolested, at least for the next 20 min, after the ants had given up their attacks. This time interval should suffice for females to lay eggs close to ant-attended colonies. Attacked *P. luteorubra* adults did not display a "reflex bleeding" from femur joints to deter ants, as other adult coccinellids do (Tursch *et al.*, 1971; Pasteels *et al.*, 1973; Eisner *et al.*, 1986). This kind of defense might be widely useless since the legs are completely hidden below the body and held tightly to the substratum.

P. luteorubra larvae displayed an area-restricted search, as reported for many coccinellid species after an encounter with a prey (e.g., Carter and Dixon, 1982; Nakamuta, 1985; Kareiva and Odell, 1987). This behavior was not influenced by the presence or absence of ant attendance, although the distances covered within 1 h were higher when no ants were around. The reduced searching efforts corresponded with an increased success in capturing large prey items (Fig. 3). *P. luteorubra* benefitted from this better foraging success by higher adult weights of individuals which had developed in ant-attended colonies. In other coccinellid species, higher body weights were positively correlated with a higher reproductive biomass and a higher fecundity (Dixon and Stewart, 1991) and thus should account for an individual fitness gain. On the other hand, there seem to be no severe costs for *P. luteorubra* from the coexistence with *L. niger*, even if we assume an increased metabolic input for the buildup of the dense hair cover during the prepupal period. By contrast, such "costs" of ant attendance were shown for the lycaenid butterfly *Jalmenus evagoras*, in which ant-attended individuals had significantly smaller pupal weights than unattended ones (Pierce *et al.*, 1987).

A second benefit of ant attendance was the reduction of parasitism especially in ant shelters, although the specific parasitoid *H. platynaspidis* was not treated aggressively by *L. niger*. Direct ant-parasitoid contacts resulted in mutual antennal tapping and mouth-mouth contact, a behavior which is known for many symphiles (Hölldobler and Wilson, 1990). However, foraging *H. platynaspidis* females usually avoided encounters with *L. niger* by path changing or jumping off. Two explanations may hold for the decrease of parasitism on thistle stems and in ant shelters (Fig. 4). First, they are simply structured and provide only few retreat areas and path-changing possibilities for *H. platynaspidis*. Thus, *H. platynaspidis* may leave such areas earlier in response to permanent encounters with ants. Alternatively, the decrease of parasitism in ant shelters—and presumably also in underground ant runs on root aphids—may be the result of a reduced parasitoid-searching activity and host-finding rate in these concealed areas. Thus, the ability to forage and feed in concealed or underground resources provided a selective advantage for *P. luteorubra* through a reduced parasitoid attack.

To derive an optimal fitness gain from the exploitation of ant-attended aphid colonies, adult *P. luteorubra* females need to be positively influenced in their oviposition decision by foraging ants. Ant attendance can act as an attractant and oviposition stimulus for lycaenid butterflies (Pierce and Elgar, 1985) and aphidiid wasps (Völkl, 1992, 1994). Larvae of *P. luteorubra* were highly aggregated in ant-attended resources, and different age classes were usually found within the same colony, a fact which indicates multiple ovipositions in the presence of conspecific larvae. Thus, it may be that *P. luteorubra* females might also be attracted and stimulated to oviposit by ants, but a detailed analysis of female oviposition decisions in relation to ant attendance and of the proximate mechanisms involved is needed to fully evaluate this hypothesis.

ACKNOWLEDGMENTS

I thank H. Zwölfer, M. Majerus, M. Romstöck-Völkl, and G. Hübner for their critical comments on earlier drafts of the manuscript. The comments of two referees also helped to improve the manuscript. D. Hammer and B. Ohm kindly helped to carry out the experiments.

REFERENCES

- Addicott, J. H. (1979). A multispecies aphid-ant association: Density dependence and species-specific effects. *Can. J. Zool.* **57**: 558-569.
- 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.
- 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.
- Bradley, G. A. (1973). Effect of *Formica obsuripes* (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.
- Carroll, C. R., and Janzen, D. H. (1973). Ecology of foraging by ants. *Annu. Rev. Ecol. Syst.* **4**: 231-257.
- Carter, M. C., and Dixon, A. F. G. (1982). Habitat quality and the foraging behaviour of coccinellid larvae. *J. Anim. Ecol.* **51**: 865-878.
- Chesson, P. (1978). Predator-prey theory and variability. *Annu. Rev. Ecol. Syst.* **9**: 323-347.
- Cudjoe, A. R., 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.
- Dixon, A. F. G. (1959). An experimental study of the searching behaviour of the predatory coccinellid beetle *Adalia decempunctata* (L.). *J. Anim. Ecol.* **28**: 259-281.
- Dixon, A. F. G. (1985). *Aphid Ecology*, Blackie, Glasgow.

- Dixon, A. F. G., and Stewart, L. A. (1991). Size and foraging in ladybird beetles. In Polgár, L., Chambers, R. J., Dixon, A. F. G., and Hodek, I. (eds.), *Behaviour and Impact of Aphidophaga*, SPB Academic, The Hague, pp. 123–132.
- 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 (*Epilachni varivestis*). *Experientia* **42**: 204–207.
- Hassell, M. P., and May, R. (1974). Aggregation in predators and insect parasites and its effect on stability. *J. Anim. Ecol.* **43**: 567–594.
- Hemphill, J. L., and Dixon, A. F. G. (1991). Why ladybirds have generally been so ineffective in biological control? In Polgár, L., Chambers, R. J., Dixon, A. F. G., and I. Hodek (eds.), *Behaviour and Impact of Aphidophaga*, SPB Academic, The Hague, pp. 149–157.
- Hodek, I. (1973). *Biology of Coccinellidae*, Academia, Prague.
- Hölldobler, B., and Wilson, E. O. (1990). *The Ants*, Springer, Berlin.
- Howard, R. W., Akre, R. D., and Garnett, W. B. (1990). Chemical mimicry of an obligate predator of carpenter ants (Hymenoptera: Formicidae). *Ann. Entomol. Soc. Am.* **83**: 607–616.
- 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.
- Kareiva, P. (1984). Predator–prey dynamics in spatially structured populations: Manipulating dispersal in a coccinellid–aphid interaction. *Lect. Notes Biomath.* **54**: 368–389.
- Kareiva, P., and Odell, G. (1987). Swarms of predators exhibit "preytaxis" if individual predators use area-restricted search. *Am. Nat.* **130**: 233–270.
- Kareiva, P., and Perry, R. (1989). Leaf overlap and the ability of ladybird beetles to search among plants. *Ecol. Entomol.* **14**: 127–129.
- Klausnitzer, B. (1969). Zur Kenntnis der Entomoparasiten mitteleuropäischer Coccinellidae. *Abh. Ber. Naturkundl. Mus. Görlitz* **44**: 1–15.
- Klingauf, F. (1967). Abwehr- und Meidereaktionen von Blattläusen (Aphididae) bei Bedrohung durch Räuber und Parasiten. *Z. Angew. Entomol.* **59**: 277–317.
- Koptur, S. (1991). Extrafloral nectaries of herbs and trees: Modelling the interaction with ants and parasitoids. In Huxley, C. R., and Cutler, D. F. (eds.), *Ant-Plant Interactions*, Oxford Science Publications, Oxford, pp. 213–230.
- Korschefsky, R. (1934). *Platynaspis luteorubra* Goeze, ein neuer Larventypus der Coccinelliden. *Arb. Physiol. Angew. Entomol.* **1**: 278–279.
- Kreiter, S., and Ipert, G. (1986). Effectiveness of *Adalia bipunctata* against aphids in a peach orchard with special reference to ant–aphid relationships. In Hodek, I. (ed.), *Ecology of Aphidophaga II*, Academic, Prague, pp. 537–543.
- Letourneau, D. K. (1990). Code of ant–plant mutualism broken by parasite. *Science* **248**: 215–217.
- Mackauer, M., and Völkl, W. (1993). Regulation of aphid populations by aphidiid wasps: Does aphidiid foraging behaviour or hyperparasitism limit impact? *Oecologia* **94**: 339–350.
- Majerus, M. E. N. (1989). *Coccinella magnifica* (Redtenbacher): A myrmecophilous ladybird. *Br. J. Entomol. Nat. Hist.* **2**: 97–106.
- Maschwitz, U., Schroth, M., Manel, M., and Tho, Y. P. (1984). Lycaenids parasitizing symbiotic ant–plant partnerships. *Oecologia* **64**: 78–80.
- Nakamura, K. (1985). Mechanism of the switchover from extensive to area-contracted search behaviour of the ladybird beetle, *Coccinella septempunctata bruckii*. *J. Insect Physiol.* **31**: 849–856.
- Nault, L. R., Montgomery, M. E., and Bowers, W. S. (1976). Ant–aphid associations: Role of aphid alarm pheromone. *Science* **192**: 1349–1351.
- Pasteels, J. M., Deroe, C., Tursch, B., Braekman, J. C., Daloz, D., and Hootele, C. J. (1973). Distributions et activités des alcaloïdes défensifs des Coccinellidae. *J. Insect Physiol.* **19**: 1771–1784.
- Pierce, N. E. (1987). The evolution and biogeography between lycaenid butterflies and ants. In Harvey, P., and Patridge, L. (eds.), *Oxford Surveys in Evolutionary Biology*, Vol. 4, Oxford University Press, Oxford, pp. 89–116.

- Pierce, N. E., and Eastaie, S. (1986). The selective advantage of attendant ants for the larvae of a lycaenid butterfly, *Glaucopteryx lydamus*. *J. Anim. Ecol.* **55**: 451–462.
- Pierce, N. E., and Elgar, M. A. (1985). The influence of ants on host plant selection by *Jalmenus evagoras*, a myrmecophilic lycaenid butterfly. *Behav. Ecol. Sociobiol.* **16**: 209–222.
- Pierce, N. E., Kitching, R. L., Buckley, R. C., Taylor, M. F. J., and Benbow, K. (1987). Costs and benefits of cooperation between the Australian lycaenid butterfly, *Jalmenus evagoras* and its attendant ants. *Behav. Ecol. Sociobiol.* **21**: 237–248.
- Pontin, A. J. (1960). Some records of predators and parasites adapted to attack aphids attended by ants. *Entomol. Monthly Mag. Lond.* **95**: 154–155.
- Ricci, C. (1979). L'apparato boccale pungente succhiante della larva di *Platynaspis luteorubra* Goeze (Col., Cocc.). *Boll. Lab. Ent. Agrar. Portici* **36**: 179–198.
- Sih, A. (1980). Optimal foraging: Partial consumption of prey. *Am. Nat.* **116**: 281–290.
- Sokal, R. R., and Rohlf, F. J. (1981). *Biometry*, 2nd ed., Freeman, San Francisco.
- Stadler, B. (1991). Predation success of *Coccinella septempunctata* when attacking different *Uroleucon* species. In Polgár, L., Chambers, R., Dixon, A. F. G., and Hodek, I. (eds.), *Behaviour and Impact of Aphidophaga*, SPB Academic, The Hague, pp. 265–271.
- Stary, P. (1966). Aphid parasites (Hymenoptera, Aphidiidae) and their relationship to aphid-attending ants, with respect to biological control. *Insect Soc.* **13**: 185–202.
- Takada, H., and Hashimoto, Y. (1985). Association of the root aphid parasitoids *Aclitus sappaphis* and *Paralipsis eikoe* (Hymenoptera, Aphidiidae) with the aphid-attending ants *Pheidole fervida* and *Lasius niger* (Hymenoptera, Formicidae). *Kontyu* **53**: 150–160.
- Tursch, B., Daloz, D., Dupont, M., Pasteels, J. M., and Tricot, M. C. (1971). A defensive alkaloid in a carnivorous beetle. *Experientia* **27**: 1380–1381.
- Vandermeer, R. K., and Wojcik, D. P. (1982). Chemical mimicry in a myrmecophilous beetle, *Myrmecaphodius excavaticollis*. *Science* **218**: 806–808.
- Vandermeer, 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.
- Völkl, W. (1990). Fortpflanzungsstrategien von Blattlausparasitoiden (Hymenoptera, Aphidiidae): Konsequenzen ihrer Interaktionen mit Wirten und Ameisen. Ph.D. thesis, Universität Bayreuth.
- Völkl, W. (1992). Aphids or their parasitoids: Who actually benefits from ant-attendance? *J. Anim. Ecol.* **61**: 273–281.
- Völkl, W. (1994). The effect of ant-attendance on the foraging tactic of the aphid parasitoid *Lysiphlebus cardui*. *Oikos* **70**: 149–155.
- Völkl, W., and Mackauer, M. (1993). Interactions between ants and parasitoid wasps foraging for *Aphis fabae* spp. *cirsiiacanthoidis* on thistles. *J. Insect Behav.* **6**: 301–312.
- Way, M. J. (1954). Studies on the association of the ant, *Oecophylla longinoda* (Latr.) (Formicidae) with the scale insect *Saissetia zanzibarensis* Williams (Coccidae). *Bull. Entomol. Res.* **45**: 113–154.
- Way, M. J. (1963). Mutualism between ants and honeydew-producing homoptera. *Annu. Rev. Entomol.* **8**: 307–344.
- Zwölfer, H. (1958). Zur Systematik, Biologie und Ökologie unterirdisch lebender Aphiden (Hom., Aphidoidea) (Anoeciinae, Tetraneurini, Pemphigini und Fordinae). *Z. Angew. Entomol.* **43**: 1–52.