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Wax covers in larvae of two *Scymnus* species: do they enhance coccinellid larval survival?

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Abstract We tested the protective function of larval wax covers in the two ladybird beetle species, *Scymnus nigrinus* and *S. interruptus,* against cannibalism, predation and ant aggression, and its importance for the distribution of both species in the field. Cannibalism was generally very low and not influenced by the presence or absence of the wax cover, or by larval size. Fourth-instar larvae of three ladybird species, *Adalia bipunctata*, *Exochomus quadripustulatus* and *Harmonia quadripunctata,* consumed *Scymnus* larvae – which are much smaller – regularly, independent of the presence or absence of waxes. By contrast, first-instar larvae of the three species had generally little success when attacking *Scymnus* spp. larvae. Wax-covered *S. interruptus* larvae survived significantly more attacks by the predacious carabid beetle *Platynus dorsalis* than larvae without wax cover. Wax-covered *S. interruptus* larvae and *S. nigrinus* larvae survived attacks by workers of the ant species *Lasius niger* and *Formica polyctena*, respectively, significantly more often than larvae without wax covers. We show that, in the field, *Scymnus* larvae have higher densities in ant-attended resources than in unattended ones and conclude that both *Scymnus* species benefit from the ability to feed in ant-attended aphid colonies by a reduced predation risk.

Key words Coccinellidae · Field distribution · Protective waxes · Cannibalism · Ant predation

Introduction

Body coverings of waxes are frequently found among insect taxa. These waxes may have various functions, e.g. reflection of UV radiation (Pope and Hinton 1977), prevention of water transpiration or protection against natural enemies (Eisner 1970). The scale insect *Ceroplastes ceriferus* Anderson, for example, is protected by its thick wax layer against attacks by the parasitoid *Anicetus ceroplastis* Ishii (Takabayashi and Takahashi 1993), and larvae of the sawfly species *Eriocampa ovata* are protected by their cuticular waxes against ant attacks (Eisner 1994). The larvae of some chrysopid species cover themselves with waxes obtained from their homopterous prey to escape ant aggression (Eisner et al. 1978; Mason et al. 1991; Milbrath et al. 1993). The larvae of many coccinellid beetle species are also characterized by the presence of thick wax layers produced by dorsal epidermal cells (Pope 1979). These waxes have also been supposed to protect larvae against natural enemies (Bartlett 1961; Bradley 1973; Pope 1979; Richards 1985) but there are currently no detailed studies on the protective function of coccinellid waxes.

In the present study, we examined the protective function of waxes for larvae of *Scymnus nigrinus* Kugelann and *S. interruptus* (Goeze), two specialized univoltine ladybird species. We hypothesized that the potential protective effect of the wax layer might influence the species' distibution in the field: they might be able to exploit resources which otherwise would be difficult to expoit due to predation pressure. The larvae of the *Scymnus* species studied develop on conifers, especially Scots pine (*Pinus sylvestris* L.), and tansy (*Tanacetum vulgare* L.), respectively (Klausnitzer and Klausnitzer 1986; Majerus 1994), where they feed on a variety of aphid species. *Scymnus* larvae may face various mortality risks when foraging for prey on their host plant. First, larvae may be eaten by conspecifics. Cannibalism is widespread among coccinellids and may cause a considerable mortality – besides egg mortality – especially among younger larval stages (Mills 1982; Osawa 1989; Agarwala and Dixon 1992). Second, larvae are subject to interspecific predation by other ladybird larvae. Interspecific predation occurs among ladybirds as frequently as cannibalism (Evans 1991; Agarwala and Dixon 1992) if larvae of two species live in the same habitat. Both on pines and tansy, other ladybird species are frequently found

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syntopically (Klausnitzer 1967, 1968). The larvae of most of these species – like *Exochomus quadripustulatus* L. and *Harmonia quadripunctata* (Pontopiddan) on pine and *Adalia bipunctata* L. on pine and tansy – are considerably larger than *Scymnus* larvae. Thus, *Scymnus* larvae may be an easy prey for them if aphid food is getting scarce. Another potential predator of *S. interruptus* may be the carabid beetle, *Platynus dorsalis* (Pontopiddan), a common polyphagous predator of aphids in cereal fields and field margins in Europe (e.g. Sunderland 1975; Edwards et al. 1979; Welling 1990). This species climbs on plants up to a height of 30 cm (Griffiths et al. 1985) and may thus occur syntopically with *S. interruptus* on tansy in field margins. Finally, both *Scymnus* species share their habitat with ant species which attend some of their aphid prey. On pines, *S. nigrinus* may frequently interact with red wood ants (*Formica* spp.) which attend and defend *Cinara* colonies (Scheurer 1971a; Fossel 1972). On tansy, *Lasius niger* L. frequently collects honeydew from *Metopeurum fuscoviride* Stroyan and *Brachycaudus cardui* L. (Klausnitzer 1968). This ant species is known to be aggressive towards aphidophagous insects (Banks 1962; Way 1963; Völkl 1990; Jiggins et al. 1993; Völkl and Mackauer 1993) and may also attack *S. interruptus* larvae.

We investigated whether the wax cover reduced (a) cannibalism, (b) predation by larvae of other three ladybird species or (c) predation by *P. dorsalis*, and whether it led (d) to an increased survival rate after ant aggression. Finally, we examined whether *S. nigrinus* larvae reached higher densities on ant-attended resources where they may be protected against predation by other ladybird larvae due to ant aggression towards these ladybirds (Jiggins et al. 1993).

Material and methods

Insect material

Larvae of *S. interruptus* were obtained from laboratory stock established from adults collected on tansy near the university campus in Bayreuth, Germany, in mid-May 1995. Additional larvae were collected in June 1995 on tansy infested with *Macrosiphoniella tanacetaria* at the university campus in Bayreuth. Larvae of *S. nigrinus* were obtained from laboratory stock established from adults collected on Scots pine in the vicinity of Bayreuth in April/May 1994 and in May 1995. Additional larvae were collected on Scots pines in the vicinity of Bayreuth in June 1994 and 1995. All larvae were kept singly in small gauze-covered plastic cages (diameter 5 cm, height 12 cm) at 20°± 1°C, 65–70% relative humidity and 16:8 L:D and supplied with first instar larvae of *M. tanacetaria* feeding on tansy leaves (*S. interruptus*) or with *Schizolachnus pineti* F. and *Pineus pini* L. feeding on parts of pine twigs (*S. nigrinus*). Additionally, larvae of both ladybird species were supplied with honeydew droplets.

To obtain larvae without waxes, we removed the wax layer by brushing the larva's abdomen with wet filter paper. This procedure did not injure the larva and created a situation with which the beetle larvae are frequently confronted in nature, e.g. after larval ecdysis or after a heavy rain. The wax layer usually recovered within 6 h. In the subsequent text, we will refer to larvae with complete wax layer as "waxy" and to larvae with the wax layer removed as "waxless".

The influence of the wax layer on cannibalism

The effect of the wax layer on cannibalism was determined for *S. nigrinus* with two sets of larvae. Larvae of the first set were waxy, while larvae of the second set were waxless. All larvae did not receive food for 24 h before used in an experiment to standardize their hunger level. Waxy larvae were individually caged in small plastic containers with either a waxless larva or a waxy larva, and any cannibalism was recorded at the end of 6 h. To account for size-specific patterns in cannibalism (Agarwala and Dixon 1992), we used two size classes, small (L1, L2) or large (L3, L4) larvae. The experiment was repeated 10 times for each treatment and size class. We did not account for differences between sibling cannibalism and non-sibling cannibalism (e.g. Osawa 1989) since it was not possible to obtain enough siblings of a particular size class for experiments.

The influence of the wax layer on predation by ladybirds

Adults of the predacious ladybirds *H. quadripunctata*, *E. quadripustulatus* and *A. bipunctata* were collected on pines and kept in the laboratory until females had oviposited. Egg clusters were kept singly until emergence to obtain larvae of a defined age. Subsequently, larvae were kept singly in small plastic cages at 20°C, 60% relative humidity and 16:8 L:D and fed with a surplus of *Aphis fabae*. Waxy and waxless third- and fourth-instar larvae of *S. nigrinus* were tested with first- and fourth-instar larvae of *H. quadripunctata* (n = 10–11) and *E. quadripustulatus* (n = 12–14), while waxy and waxless third/fourth-instar larvae of *S. interruptus* were tested with first- and fourth-instar larvae of *A. bipunctata* (n = 15). First instar larvae of *H. quadripunctata*, *E. quadripustulatus* and *A. bipunctata* are somewhat smaller than their offered prey, while fourth instar larvae of either species are considerably larger.

Scymnus larvae were caged individually in a small plastic container together with a potential predator for 6 h. We recorded any interspecific predation. First-instar larvae were used in an experiment within 1 day after emergence and before having received any aphid food, while fourth-instar larvae were deprived of food for 24 h before used in an experiment to standardize their hunger level.

The influence of the wax layer on predation by a carabid beetle

Adults of the carabid beetle *Platynus dorsalis* were collected under stones in cereal fields and field margins in the vicinity of Bayreuth, Germany. Beetles (n = 16) were kept in small cages and fed with a surplus of *Aphis fabae* until used in an experiment. They were deprived of food for 24 h before used in an experiment to standardize their hunger level. Waxy (n = 16) and waxless (n = 16) *S. interruptus* larvae were released individually with a *P. dorsalis* in small plastic cages and observed until the *Scymnus* larva was attacked by *P. dorsalis*. Each *P. dorsalis* was used twice, once with waxy larva, and a second time with a waxless larva. To avoid any bias due to the sequence of presentation, we presented waxy larvae first for one beetle cohort (n = 8 beetles), while the second cohort was first tested with waxless larvae. The experiment was stopped after the carabid had either consumed the ladybird larva or the larva had escaped the first carabid attack.

The influence of the wax layer on ladybird-ant interactions

Single nests of *Formica polyctena* and *Lasius niger*, were established in small terrariums (lxbxh = 70×35×35 cm) and kept at 20°C, 60% relative humidity, 3000 lux and 16:8 L:D within a growth chamber. *F. polyctena* workers had access to *Cinara pinea* (Mordv.) and *Cinara pini* (L.) colonies on potted pines through an arrangement of sticks. *L. niger* had access to *Aphis fabae* colonies on creeping thistle and to *Brachycaudus cardui* (L.) colonies on tansy. Ant activity was assumed to resemble the situation in nature.

We analysed the interactions between foraging *Scymnus* larvae and honeydew-collecting ant workers at 20°C, 3000 lux and 60% relative humidity. A single *Scymnus* larva was released onto the main stem of a host plant (*S. interruptus*: tansy, *S. nigrinus*: pine), at a distance of about 1–3 cm from the aphid colony. To avoid provoking attacks by *F. polyctena* or *L. niger*, we took care that no ants were within about 5 cm of the point of release. We observed the following interactions, distinguishing between *non-aggressive* ant behaviour (i.e. the ant passed the larva within a distance of < 2 mm but did not make physical contact; or the ant made physical contact but did not respond otherwise) and *aggressive* (i.e. the ant attacked the larva and tried to seize it with its mandibles). Attacked larvae were either *injured* (larvae recovered within one day and completed larval development successfully) or *dead* (larvae died either immediately or within the next day, or they were transported into the nest by an ant worker). A trial was completed when the larva either left the plant (either by foot or by dropping off) or was carried off by an ant worker, or after 1 hour, whatever came first.

We tested in total 83 *S. nigrinus*/*F. polyctena* (46 waxy, 37 waxless individuals) and 82 *S. interruptus*/*L. niger* (40 waxy, 42 waxless individuals). Since preliminary experiments (K. Vohland and W.Völkl, unpublished work) had shown that larval size had no significant influence on the response of either ant species, we used second-, third- and fourth-instar larvae for our experiments. Data from all larvae were pooled for evaluation.

The distribution of ladybird larvae in relation to ant attendance

We analysed the distribution of *S. nigrinus*, *S. interuptus* and other ladybird beetles in relation to ant attendance. The studies were carried out at a south-exposed pine forest edge in the vicinity of Bayreuth (*S. nigrinus*) and at a ruderal area at the university campus in Bayreuth, Germany (*S. interruptus*). We counted all ladybird larvae on 20 aphid-infested pines (age: approx. 6–8 years) and on 20 aphid-infested tansy shoots every 2nd week between mid-May and end July 1995. All pines were infested by *Cinara pinea* (Mordv.) which fed mainly on current-year shoots, and by *Schizolachnus pineti* (F.), which sucks exclusively on pine needles. On one subsample consisting of ten trees, the colonies of *C. pinea* were heavily attended by workers of *F. polyctena*. On the other subsample, all aphid colonies were unattended. Tansy shoots were infested either by *Metopeurum fuscoviride* or by *Macrosiphoniella tanacetaria* (Kaltenb.). On one subsample of ten shoots, all aphid colonies (mainly *Metopeurum fuscoviride* colonies) were heavily attended by *L. niger*, while the subsample consisted of 10 unattended shoots (mainly infested by *Macrosiphoniella tanacetaria*).

Results

The influence of the wax layer on cannibalism

We observed only six successful cases of cannibalism (7.5%; n = 80). In two out of these six cases, a large "waxy" larva was consumed by another large "waxy" larva, while the four other "victims" were small larvae (three waxless, one waxy). Altogether, neither differences in beetle size nor the presence or absence of the wax layer seemed to influence the incidence of cannibalism.

The influence of the wax layer on predation by ladybirds

First-instar larvae of *A. bipunctata*, *E. quadripustulata* and *H. quadripunctata* showed only very low predation success, with less than 15% of *Scymnus* larvae eaten, while fourth-instar larvae consumed on average 90% of the *Scymnus* larvae (Fig. 1). Predation depended only on the age of the attacking potential predator (likelihood G^2 = 104.655, df = 1, P < 0.001) while predator species (likelihood G^2 = 0.026, df = 2, P = 0.987), the presence or absence of the wax layer (likelihood G^2 = 2.495, df = 1, P = 0.114) or any interaction between the three factors had no significant influence (likelihood G^2 = 7.829, df = 7, P = 0.348). Interestingly, we never observed a *Scymnus* larvae consuming a potential predator.

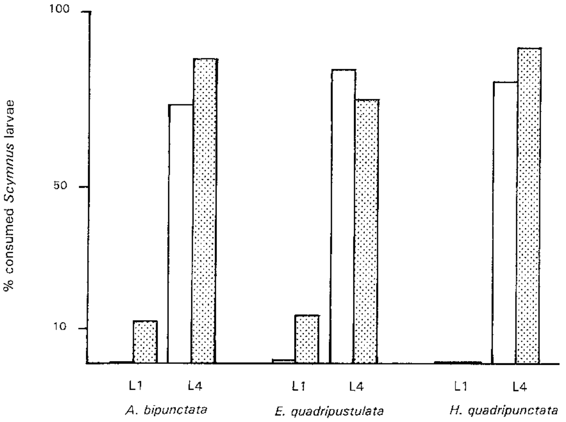

Fig. 1 Predation success of various predacious ladybird beetle larvae of different ages towards third- and fourth-instar larvae of *Scymnus nigrinus* and *S. interruptus* (*open bars* waxy larvae, *shaded bars* waxless larvae)

The influence of the wax layer on predation by *Platynus dorsalis*

Both waxy and waxless *S. interruptus* larvae were readily attacked by *P. dorsalis*: 88% of the waxy larvae escaped attack and survived. The beetles abandoned their attack after they had bitten into the wax cover and began to clean their mouthparts. By contrast, 75% of the waxless larvae were killed and subsequently consumed (χ^2 = 8.031, df = 1, P = 0.005).

The influence of the wax layer on ant-*Scymnus* interactions

L. niger responded significantly more often aggressively when encountering a *S. interruptus* larva than *F. polyctena* did after encountering *S. nigrinus* (Fig. 2: χ^2 = 12.898, df = 1, P < 0.001). Neither ant species differed in aggressiveness towards waxy and waxless larvae (*L. niger*: χ^2 = 0.017, df = 1, P = 0.897; *F. polyctena*: χ^2 = 0.407, df = 1, P = 0.523).

Waxy larvae survived an attack significantly more often than waxless larvae (Fig. 2: *L. niger*: χ^2 = 26.134, df = 1, P < 0.001; *F. polyctena*: χ^2 = 7.911, df = 1, P = 0.005). Both *L. niger* and *F. polyctena* usually aban-

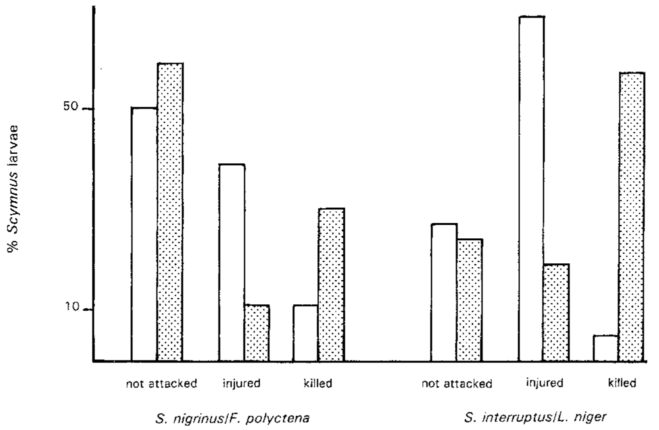

Fig. 2 The outcome of contacts between *S. nigrinus* and *Formica polyctena* ($n = 83$) and *S. interruptus* and *Lasius niger* ($n = 82$), respectively (*open bars* waxy larvae, *shaded bars* waxless larvae)

doned their attack after having bitten into the smeary adhesive wax and began to clean their mouthparts. During this time, *Scymnus* larvae were able to escape. There was also a slight but not significant tendency for *F. polyctena* to kill more waxy larvae than *L. niger* (Fig. 2: $\chi^2 = 2.426$, $df = 1$, $P = 0.119$). By contrast, most attacked waxless larvae were killed by both ant species and either transported to the bottom of the tree or, more often, into the ant nest.

Incidence of ladybird larvae in relation to ant-attendance

The frequency of *Scymnus* spp. larvae and of other ladybird larvae differed for ant-attended and unattended colonies (Fig. 3a,b). During peak infestations of *S. nigrinus*, we found significantly more larvae of this species on pines with ants than on trees without ants (Fig. 3a: Mann-Whitney *U*-test: 13 June: $U = 23.5$, $n = 20$, $P = 0.042$; 27 June: $U = 24.0$, $n = 20$, $P = 0.047$). By contrast, the density of other predacious ladybird larvae (mainly *E. quadripustulatus*, *H. quadripunctata*, *A. bipunctata*, *Coccinella septempunctata*) was significantly reduced at one date (Fig. 3a, 13 June, M-W *U*-test: $U = 13.0$, $n = 20$, $P = 0.004$). At a second date, there was a trend for reduced density of other predacious coccinellid larvae (Fig. 3a, 27 June, M-W *U*-test: $U = 30.0$, $n = 20$, $P = 0.119$).

On tansy, we found no significant differences in the frequency of *S. interruptus* larvae on *L. niger*-attended and unattended shoots (Fig. 3b, M-W *U*-test, 16 June: $U = 42.5$, $n = 20$, $P = 0.505$; 1 July: $U = 38.5$, $n = 20$, $P = 0.282$). However, the density of other ladybird larvae (mainly *A. bipunctata* and C. septempunctata) was significantly reduced on *L. niger*-attended shoots not only during the peak of *S. interruptus* (Fig. 3b, M-W *U*-test, 16 June: $U = 16.5$, $n = 20$, $P = 0.009$; 1 July: $U = 17.5$, $n = 20$, $P = 0.010$) but throughout the whole season.

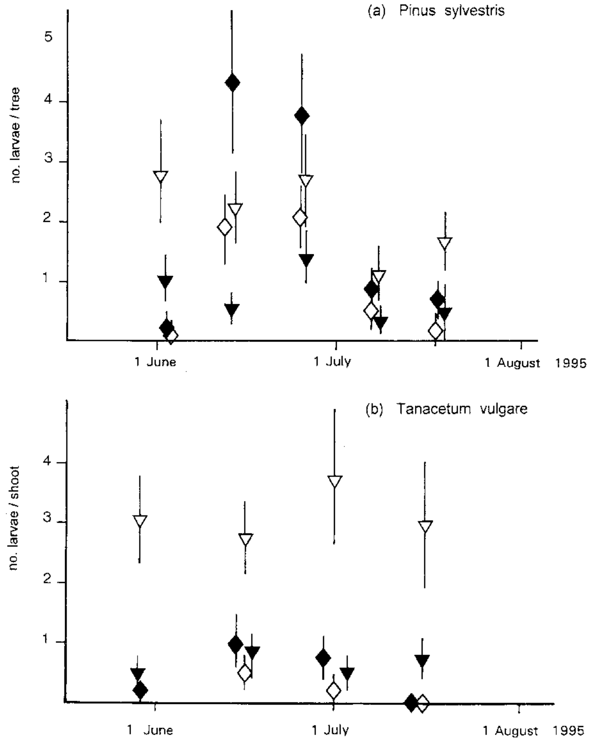

Fig. 3 Distribution and density of coccinellids **a** on *Pinus sylvestris* at a forest edge near Bayreuth, Germany and **b** on *Tanacetum vulgare* at the university campus at Bayreuth (*diamonds Scymnus* larvae, *triangles* larvae of other coccinelled species, *filled signs* plants with ant-attended *Cinara* colonies, *open signs* plants with unattended aphid colonies). All larval instars were combined. Values give means ± SE

Discussion

Coccinellids have developed various mechanisms to defend themselves against their enemies (Hodek 1973; Majerus 1994). Many species possess bitter-tasting alkaloids and volatile pyrazines and quinolines (Pasteels et al. 1973; Mueller et al. 1984; de Jong et al. 1991; Holloway et al. 1991) which are usually secreted by reflex bleeding. By this means, they may deter natural enemies such as ants (Völkl 1990; Jiggins et al. 1993; Majerus 1994), spiders (Majerus 1994) or carabid beetles (W. Völkl, unpublished work). *C. septempunctata* – which contains large amounts of the alkaloid coccinelline – is even toxic to nestling blue tits, *Parus caeruleus* L. (Marples et al. 1989). *Scymnus* species, however, do not possess alkaloids and thus lack this possibility of chemical defense (Pasteels et al. 1973). Instead, the larval body is covered by a thick layer of cuticular-borne waxes which are markedly sticky (Pope 1979). We hypothesized that these waxes might provide protection against cannibalism, against predation by other ladybirds or carabid beetles or against ant aggression.

Our experiments gave no evidence that cannnibalism – in contrast to other ladybird species (e.g. Mills 1982; Osawa 1989; Agarwala and Dixon 1992) – might be an important mortality factor for *S. nigrinus*. Most larvae ignored conspecifics although they had not been fed for 24 h, and cannibalism occurred only exceptionally. Although we did not check for differences between sibling and non-sibling cannibalism, it is unlikely that the wax cover serves as a protection against cannibalism, especially since *S. nigrinus* and *S. interruptus* lay their eggs singly and at low densities per host plant (W. Völkl and K. Vohland, unpublished work) compared to other coccinellid species.

Predacious ladybird larvae were also not hindered by the wax from consuming *Scymnus* larvae. The predation success depended only on the predator's age – and thus size – but not on the presence or absence of waxes (Fig. 1). While first-instar larvae of *E. quadripustulatus*, *H. quadripunctata* and *A. bipunctata* generally failed to overwhelm *Scymnus* larvae, fourth-instar larvae of either species – which are much larger than *Scymnus* larvae – attacking waxy larvae were as successful as individuals attacking waxless prey. A similar effect of size was found by Evans (1991) who demonstrated this factor to be most important in determining the outcome of interspecific predation in ladybirds. Furthermore, it should be noted that the large ladybird species tested commonly feed on wax-covered aphid species, such as *Eriosoma lanigerum* (Hausmann), *Stagona xylostei* (De Geer) and *Schizolachnus pineti* (F.) (Klausnitzer and Klausnitzer 1986; Mols 1993; Majerus 1994; W. Völkl, personal observations). Although the aphid waxes may differ in their structure from *Scymnus* wax, the ability to consume wax-covered prey shows the lack of effectiveness of mechanical protection by wax against these ladybirds

By contrast, the waxes provide a considerable protection against attacks by the carabid beetle *P. dorsalis* or by ants. The predation success of *P. dorsalis* was significantly lower when attacking waxy *S. interruptus* larvae compared to waxless individuals. Similarly, significantly more waxy larvae of *S. interruptus* and *S. nigrinus* survived attacks by *L. niger* or *F. polyctena*, respectively (Fig. 2). Workers of both ant species usually attacked both waxy and waxless *Scymnus* larvae readily but abandoned attacks after their mouthparts were smeared with the adhesive wax. Thus, waxes probably mainly function as mechanical protection – similar to the stiff hairs on the surface of *Platynaspis luteorubra* (Goeze) pupae (Völkl 1995) – rather than in mimesis or camouflage (see Eisner et al. 1978; Mason et al. 1991). Similar protective effects were reported by Bartlett (1961) and Bradley (1973) for wax-covered larvae of *Scymnus* sordidus and *Hyperaspis congressus*, respectively. We found also size-related differences between the two ant species: *F. polyctena* is much larger than *L. niger*, and consequently the absolute opening width of mandibles is also much broader. This difference might explain why *F. polyctena* killed more waxy larvae than *L. niger* (Fig. 2) although *L. niger* was much more aggressive.

S. nigrinus achieved higher densities on *F. polyctena*-attended trees than on unattended trees, while we found no such difference in *S. interruptus* (Fig. 3). These differences might be explained by the higher aggressiveness of *L. niger* workers (Fig. 2), which may force more larvae to leave the shoot than *F. polyctena* workers. Alternatively, *L. niger* workers may be more successful in warding off adult beetles from oviposition than *F. polyctena* (Hübner and Völkl 1996). By contrast, the density of other predacious ladybird larvae was significantly reduced in the presence of ants on both host plants (Fig. 3; see also Majerus 1989; Völkl 1990). Larvae, and probably also adults, of these species may be important predators of *Scymnus* larvae (Fig. 1) especially in situations when aphids are getting scarce. Both *Scymnus* species may obtain additional benefits from their ability to survive in ant-attended resources. First, ant-attended colonies are more predictable resources for ladybird beetles since they grow larger and persist longer (Scheurer 1971b; Addicott 1979; Bristow 1984; Majerus 1989; Völkl 1990). Second, there may be less competition for prey by other ladybird larvae on ant-attended resources than in unattended ones. Thus, the energetic costs of producing the wax (Pope 1979) and the risk of being killed by an ant despite of the wax cover (Fig. 2) may be balanced by increased survival due to reduced interpecific predation and competition.

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