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Are behavioural changes in parasitised aphids a protection against hyperparasitism?

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Aphididae, Aphidiidae, Megaspilidae, Pteromalidae, aphids, parasitoids, hyperparasitoids, modified host behaviour, coevolution

Abstract. Parasitised aphids often leave the aphid colony before mummification. It has been suggested that this behaviour is an example of host manipulation by the primary aphidiid parasitoid to reduce the risk of hyperparasitism after mummy formation. Mummification site and hyperparasitism risk are surveyed in 16 species of aphid. Mummification away from the colony was not associated with reduced hyperparasitism. In ant-attended species, and in species with well developed parasitoid defence behaviour (such as kicking), mummies formed within the colony tended to suffer less hyperparasitism. In laboratory experiments, two hymenopteran ectohyperparasitoids, *Dendrocerus carpenteri* (Curtis) (Megaspilidae) and *Asaphes vulgaris* (Walker) (Pteromalidae), were more successful attacking parasitised aphids [*Uroleucon jaceae* (L.) (Aphididae)] when the mummies were outside the colony, not surrounded by living aphids.

INTRODUCTION

After attack by a parasitoid, the behaviour of a host may change for one of several reasons (reviewed by Godfray, 1994). First, the trauma of parasitism may interfere with the host's normal behavioural repertoire. Second, there will be direct selection on the host to kill the parasitoid or, more controversially, to commit suicide or adopt other behaviours that lower the risk that its relatives are attacked (Smith-Trail, 1980; McAllister & Roitberg, 1987; McAllister et al., 1990). Third, the behaviour of the host may be manipulated by the parasitoid to its own advantage (Stamp, 1981; Fritz, 1982; Sato et al., 1983; Brodeur & McNeil, 1989, 1990, 1992; Schmid-Hempel & Müller, 1991; Müller, 1994). In many cases, the interests of both host and parasitoid are identical and distinguishing between selection acting on each will be very difficult. For example, host and parasitoid experience similar selection pressures due to predation and are likely to show similar adaptations to avoid this mortality (Jones, 1987). However, many parasitoids are attacked by obligate hyperparasitoids that only attack parasitised hosts, sometimes after the hosts have already died. The primary parasitoid will be strongly selected to manipulate host behaviour so as to lessen the risk of hyperparasitism. In contrast, there will be no selection on the host to avoid hyperparasitism. Thus novel behavioural features by parasitised hosts that reduces the probability of hyperparasitism are good candidate examples of host manipulation.

Host manipulation by parasitoids has been studied in aphids. Aphids are attacked by two main groups of hymenopteran primary parasitoids Aphidiinae (Braconidae) and

Aphelinidae (Chalcidoidea). Members of both groups of parasitoids are koinobionts, that is the host is not killed by the act of parasitisation but continues to feed and grow, the developing parasitoid remaining as an early instar larva in a state of suspended development until the aphid reaches a certain size, when the parasitoid develops rapidly and the aphid dies. The dried body of the aphid (the mummy) is attached to the plant and protects the parasitoid pupa. Primary parasitoids are subject to hyperparasitism from two guilds of insects (Sullivan, 1988; Mackauer & Völkl, 1993). Alloxystine wasps (Cynipoidea: Charipidae) attack the primary parasitoid larvae before the aphid dies, i.e. before mummification. Alloxystines are koinobionts, their larvae delaying development until the primary parasitoid has reached a certain size. These wasps are called endohyperparasitoids. The second guild of hyperparasitoids consist largely of Pteromalidae (Chalcidoidea) and Megaspilidae (Ceraphronoidea). They attack the mummy and are idiobionts, the act of parasitism killing the developing prepupa or pupa of the primary parasitoid. They feed inside the mummy but eat the primary parasitoid from the outside and hence are called ectohyperparasitoids.

Parasitised aphids often leave their colony and are mummified on the surrounding vegetation (e.g. Scheurer, 1964; Behrendt, 1968; Starý, 1970; Liebscher, 1972; Powell, 1980; Völkl, 1990; Höller, 1991). It has been suggested that this movement is an example of the manipulation of host behaviour by a parasitoid to reduce the chance of hyperparasitism. Brodeur & McNeil (1989, 1990, 1992) demonstrated that *Aphidius nigripes* Ashmead (Aphidiinae), a specialised parasitoid of the polyphagous aphid *Macrosiphum euphorbiae* (Thomas), benefitted from its host leaving the feeding site shortly before mummification. Most *M. euphorbiae* feed in loose colonies on the underside of leaves; aphids containing non-diapausing parasitoids mummify on the upper surface of leaves while those containing diapausing larvae move to a concealed site for mummification. Non-diapausing mummies in positions outside the colony suffer relatively lower rates of hyperparasitism, and some reduction in predation (Brodeur & McNeil, 1992). Diapausing mummies in concealed sites have a higher survival probability due to more favourable microclimatic conditions. Brodeur and McNeil concluded that the parasitoid manipulated the behaviour of its host to its own advantage.

In the present study, we explore whether the induction of behavioural changes in aphid hosts is a general strategy of aphidiine wasps to reduce ectohyperparasitism, and whether there may be alternative explanations for this striking behaviour. First, we compare the rates of ectohyperparasitism suffered by mummies formed inside and outside aphid colonies for sixteen aphid-parasitoid systems on herbaceous plants and trees. Second, we examine whether ant attendance influences the behaviour of parasitised aphids. Ants are known to have an important influence on ectohyperparasitism rates and are thus likely to influence the evolution of host manipulation (Völkl, 1992). We predict mummification away from the colony to be less common in ant-attended species. Third, we studied the influence of aphid defence behaviour on the success rate of two common ectohyperparasitoids. Aphid defence behaviour that reduces the oviposition success of aphid primary parasitoids (e.g. Gerling et al., 1990; Völkl, 1991) may also lower the oviposition success of aphid ectohyperparasitoids which have to move past living aphids to reach mummies within colonies (Völkl et al., 1995). We compare the oviposition success of two ectohyperparasitoids searching for parasitised aphids inside and outside a colony.

MATERIAL AND METHODS

Field studies

We studied sixteen species of aphids that were all heavily attacked by aphidiine parasitoids. For each species, we searched intensively for mummies within the host aphid colonies as well as on the entire plant or along the branches of trees in the vicinity of the aphid colonies. We recorded where mummies were formed and made collections from each mummification site which we reared in the laboratory to determine hyperparasitism rates. We distinguished between individuals that had mummified within the aphid colony and those that had mummified outside the colony. We also recorded whether the aphids were attended by ants. Nine aphid species fed on herbaceous plant and seven species fed on trees. As long as the aphid colonies persisted, samples were collected at weekly intervals in the summer of 1993 at Silwood Park, Berkshire, England, and at weekly intervals in the summers of 1993 and 1994 near Bayreuth, Bavaria, Germany. We found no seasonal change in mummification site and have thus pooled samples collected on different dates. Table 1 provides a summary of aphid species, host plants, feeding and mummification sites, and sample sizes.

The mummies collected for rearing were kept individually in gelatine capsules until the emergence of the primary parasitoid or hyperparasitoid. The identities and numbers of the different parasitoids reared are given in Table 2.

Laboratory experiment

INSECTS. We studied the influence of aphid behaviour on the success of two ectohyperparasitoids of *Uroleucon jaceae* (L.) (Hemiptera: Aphididae), an aphid that feeds on *Centaurea jacea* (L.) (Asteraceae). A laboratory culture of the primary parasitoid, *Aphidius funebris* (Mackauer) (Hymenoptera: Braconidae: Aphidiinae), was established from mummies collected near Bayreuth, Bavaria, Germany. The parasitoids were maintained on *U. jaceae* feeding on potted *C. jacea* in a plant-growth chamber at 21 ± 0.5°C, approx. 60% r.h. and 16L : 8D. Females of *Dendrocerus carpenteri* (Curtis) (Megaspilidae) and *Asaphes vulgaris* (Walker) (Pteromalidae), two common hymenopteran polyphagous ectohyperparasitoids of *U. jaceae* (Völkl & Starý, 1988), were obtained from field-collected mummies of *U. jaceae*, and also from similar-sized mummies of *Macrosiphum rosae* (L.), *Sitobion fragariae* (Walker), *Macrosiphoniella millefolii* (DeGeer) and *Macrosiphoniella absinthii* (L.) (all Aphididae) via various *Aphidius* spp. All hyperparasitoid females were of similar size, between three and six days old when used in the experiment, and had been given the opportunity of previous oviposition. The wasps were deprived of hosts for 24 h before the experiments and fed only with diluted honey.

EXPERIMENTAL DESIGN. Each hyperparasitoid was allowed to search for mummies under two experimental treatments. In treatment one, three *U. jaceae* mummies (3–6 days old) were glued onto the central part of a cut *C. jacea* shoot. The gluing did not influence the hyperparasitoid's foraging behaviour or foraging success (Kranz, 1994; Völkl, unpub.). Subsequently, a large number of *U. jaceae* (L2, L3 and adults) were transferred to the shoot and allowed to settle. After 1 h, all aphids were removed from the stem except for 10 feeding around the mummies. In this treatment, the hyperparasitoids were unable to reach the mummies except by moving through the "colony" of aphids. In treatment 2, we glued three mummies onto cut *C. jacea* shoots and ensured that there were no aphids feeding in the vicinity of these mummies. However, ten aphids, feeding at least 3 cm distant from the mummies, were allowed to remain on the shoot.

Subsequently, either a *D. carpenteri* female (treatment 1: n = 21; treatment 2: n = 11) or a *A. vulgaris* female (treatment 1: n = 11; treatment 2: n = 5) was released onto the tip of the *C. jacea* shoot. All females were observed until they left the shoot. We recorded the total residence time of each female, the number of mummies she discovered, the number of oviposition attempts, and the nature of any interactions between aphids and hyperparasitoid females. All mummies attacked by the hyperparasitoids were removed after the experiment and dissected to assess oviposition success. All hyperparasitoid females were used only once and *C. jacea* shoots were replaced when they started wilting.

RESULTS

Field studies

In five aphid species [*Coloradoa tanacetina* (Walker), *Sipha agropyrella* Hille Ris Lambers, *Cryptomyzus korschelti* (Börner), *Metopeurum fuscoviride* Stroyan and *Cinara*

TABLE 1. Summary of all species of aphids, their host plants, the feeding site of the aphid colonies, the different plant structures from which mummies were collected, the number of collected mummies within (inside) and away from (outside) the aphid colonies and a remark on whether mummies were ant-attended or not.

Aphid species	Host plant	Feeding site	Mummification site	Inside colony	Outside colony	Ants	Sampling month
Microlophium carnosum (Buckton)	*Urtica dioica* (Stinging nettle)	Lower leaf-surface Flowers	Upper and lower leaf-surface Flowers Adjacent herbage	206	332	no	V-VI
Acyrthosiphon pisum (Harris)	*Cytisus scoparius* (Broom)	Pods Stem	Leaves Pods Stem	146	404	no	VI
Aulacorthum solani (Kaltenbach)	*Digitalis purpurea* (Foxglove)	Basal leaves	Basal leaves Main stem and stem-leaves Flowers and bracts	178	112	no	VI
Macrosiphoniella millefolii (De Geer)	*Achillea millefolium* (Yarrow)	Flowers Stem Leaves	Flowers Stem Leaves	192	110	no	VII-VIII
Uroleucon jaceae (L.)	*Centaurea jacea* (Brown knapweed)	Stem	Stem Leaves	88	118	no	VI-VIII
Coloradoa tanacetina (Walker)	*Tanacetum vulgare* (Tansy)	Leaf edges	Leaf edges	357	0	no	VI-VII
Metopeurum fuscoviride Stroyan	*Tanacetum vulgare* (Tansy)	Stem Flower-stem Stem Flower stem	Stem Flower-stem Stem Flower stem	1260 199	0 0	yes no	VI-VIII
Cryptomyzus korschelti Börner	*Ribes alpinum* (Mountain currant)	Leaves	Leaves	239	0	no	VI
Sipha agropyrella Hille Ris Lambers	*Arrhenatherum elatius* (False oat-grass)	Leaves	Leaves	257 148	0 0	yes no	VI-VII
Symydobius oblongus (von Heyden)	*Betula pendula* (Birch)	2 year old wood	Leaves	0 –	88	yes no	VII-IX
Periphyllus sp. van der Hoeven	*Acer campestre* (Field maple)	Buds Leaf-stem Inflorescence	Leaves Inflorescence	4 8	0 99	yes no	V-VI
Myzus cerasi (F.)	*Prunus avium* (Cherry)	Leaves	Leaves	48	22	yes	IV-V
Cinara pilicornis (Hartig)	*Picea abies* (Spruce)	Current year shoot	Current year shoot	29	66	no	V-VIII
Cinara piceicola (Cholodkovsky)	*Picea abies* (Spruce)	4–7 year old wood	4–7 year old wood	586	0	yes	V-VI
Cinara pinea (Mordvilko)	*Pinus sylvestris* (Scots pine)	Current year shoot	Needles	0 –	485	yes no	V-VIII
Cinara pini (L.)	*Pinus sylvestris* (Scots pine)	3-6 year old wood	3-6 year old wood Needles	236 –	198	yes no	V-VIII

piceicola (Cholodkovsky)] we found mummies only inside the aphid colony and there was no evidence of movement by parasitised aphids. In two species [*Cinara pinea* (Mordvilko) and *Symydobius oblongus* (von Heyden)], all mummies were found outside the colony where they were – in contrast to aphid colonies – not attended by ants. Mummies of the other species were found commonly both inside and outside colonies (data in Table 1).

TABLE 2. Parasitoids reared from mummies collected in our studies. The parasitoids are divided into primary parasitoid (all Braconidae: Aphidiinae), *Alloxysta/Phaenoglyphis* (Charipidae), hyperparasitoid attacking the primary parasitoid larva within the living aphid and ectohyperparasitoids attacking the parasitoid within the mummy (Pteromalidae and Megaspilidae). The rate of hyperparasitism refers to the percentage primary parasitoids and Charipidae that were destroyed by ectohyperparasitoids attacking the prepupa or pupa within the mummified aphid.

Host aphid species Primary parasitoids *Alloxysta/Phaenoglyphis* spp. Ectohyperparasitoids	Total	Rate of hyperparasitism
Microlophium carnosum	538	
Praon volucre	12	64.31%
Aphidius urticae	64	
Aphidius microlophii	104	
Alloxysta sp.	12	
Asaphes vulgaris	188	
Coruna clavata	54	
Dendrocerus carpenteri	104	
Acyrthosiphon pisum	550	
Praon volucre	3	50.18%
Aphidius ervi	21	
Aphidius eadyi	228	
Alloxysta/Phaenoglyphis spp.	22	
Asaphes vulgaris	67	
Coruna clavata	20	
Pachyneuron aphidis	10	
Dendrocerus carpenteri	179	
Aulacorthum solani	290	
Aphidius urticae	69	51.72%
Alloxysta/Phaenoglyphis spp.	71	
Asaphes vulgaris	100	
Coruna clavata	50	
Macrosiphoniella millefolii	302	
Aphidius absinthii	76	45.69%
Ephedrus campestris	1	
Alloxysta/Phaenoglyphis spp.	87	
Asaphes vulgaris	47	
Asaphes suspensus	2	
Coruna clavata	22	
Dendrocerus carpenteri	67	
Uroleucon jaceae	206	
Aphidius funebris	51	52.43%
Praon dorsale	12	
Alloxysta/Phaenoglyphis spp.	35	
Asaphes vulgaris	38	
Asaphes suspensus	14	
Coruna clavata	8	
Dendrocerus carpenteri	48	

TABLE 2 (continued).

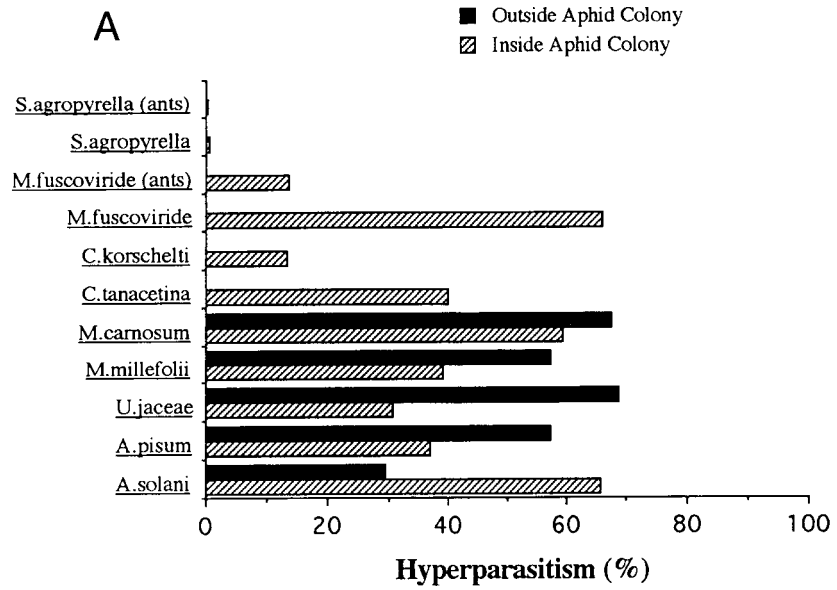
Host aphid species Primary parasitoids *Alloxysta/Phaenoglyphis* spp. Ectohyperparasitoids	Total	Rate of hyperparasitism
Coloradoa tanacetina	357	
Lysaphidus arvensis	193	40.06%
Alloxysta sp.	21	
Pachyneuron aphidis	66	
Syrphophagus aphidivorus	35	
Asaphes vulgaris	18	
Dendrocerus carpenteri	24	
Metopeurum fuscoviride	1459	
Lysiphlebus hirticornis	1119	20.70%
Alloxysta sp.	38	
Pachyneuron aphidis	106	
Syrphophagus aphidivorus	148	
Asaphes vulgaris	6	
Coruna clavata	1	
Dendrocerus carpenteri	41	
Cryptomyzus korschelti	239	
Aphidius ribis	133	13.39%
Alloxysta sp.	74	
Pachyneuron aphidis	5	
Asaphes vulgaris	2	
Asaphes suspensus	4	
Dendrocerus carpenteri	21	
Sipha agropyrella	405	
Adialytus arvicola	396	2.72%
Pachyneuron aphidis	9	
Dendrocerus carpenteri	2	
Symydobius oblongus	88	
Trioxys betulae	28	63.64%
Phaenoglyphis sp.	4	
Syrphophagus mamitus	31	
Asaphes suspensus	8	
Coruna clavata	11	
Dendrocerus carpenteri	6	
Periphyllus sp.	111	
Trioxys falcatus	32	71.17%
Asaphes vulgaris	12	
Asaphes suspensus	41	
Coruna clavata	16	
Dendrocerus carpenteri	10	
Myzus cerasi	70	
Ephedrus persicae	9	80%
Alloxysta sp.	5	
Asaphes vulgaris	8	
Asaphes suspensus	3	
Pachyneuron gibbiscuta	17	
Dendrocerus carpenteri	28	

TABLE 2 (continued).

Host aphid species Primary parasitoids *Alloxysta /Phaenoglyphis* spp. Ectohyperparasitoids	Total	Rate of hyperparasitism
Cinara pilicornis	95	
Pauesia pini	35	54.74%
Alloxysta /Phaenoglyphis spp.	8	
Euneura augarus	32	
Asaphes vulgaris	8	
Dendrocerus carpenteri	12	
Cinara piceicola	586	
Pauesia pini	581	0.85%
Euneura augarus	5	
Cinara pinea	485	
Pauesia picta	34	62.06%
Pauesia laricis	8	
Pauesia pini	26	
Pauesia silvestris	6	
Pauesia pinicollis	19	
Pauesia sp. males	76	
Alloxysta /Phaenoglyphis spp.	15	
Euneura augarus	207	
Asaphes vulgaris	12	
Asaphes suspensus	1	
Coruna clavata	25	
Dendrocerus carpenteri	36	
Dendrocerus ramicornis	11	
Dendrocerus liebscheri	9	
Cinara pini	434	
Pauesia picta	15	34.10%
Pauesia pini	37	
Pauesia silvestris	71	
Pauesia pinicollis	22	
Pauesia sp. males	128	
Alloxysta /Phaenoglyphis spp.	13	
Euneura augarus	77	
Asaphes vulgaris	23	
Asaphes suspensus	12	
Coruna clavata	9	
Dendrocerus carpenteri	19	
Dendrocerus ramicornis	8	

The percentage of mummies hyperparasitised is shown in Fig. 1. We distinguish between aphids attacking herbaceous plants and trees, between mummies formed inside and outside the aphid colony, and between colonies attended and not attended by ants. The overall average level of ectohyperparasitism across all species was 35.8% for aphids on herbaceous plants and 49.9% for aphid species on trees.

The rates of hyperparasitism of the five species that always mummified in the colony are very variable, ranging from 65.83% (*M. fuscoviride* not attended by ants) to 0.39% (*S. agropyrella* attended by ants). Ant attended mummies tended to have lower levels of hyperparasitism (13.39% for ant attended mummies, 49.9% for unattended mummies;



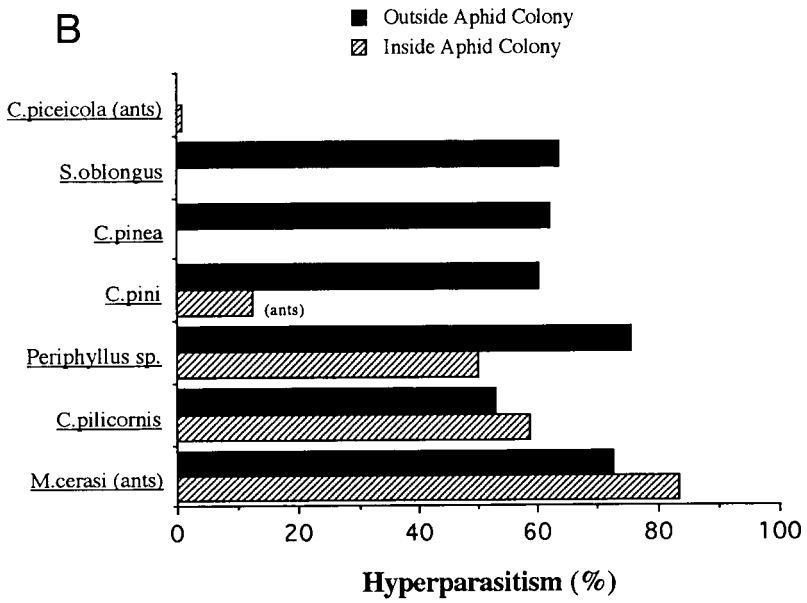


Fig. 1. Percentage ectohyperparasitism on (A) herbaceous plants and (B) trees dependent on mummification site. (ants) means ant attendance of the mummies. Note that for *C. tanacetina*, *C. korschelti*, *M. fuscoviride*, *S. agropyrella* and *C. piceicola* no mummies could be found outside the aphid colony; for *C. pinea* and *S. oblongus* no mummies could be found inside the aphid colonies (see Tab. 3 for statistical values).

t = 3.56, df = 20, p = 0.002). We found both ant attended and non-ant attended colonies of *M. fuscoviride*, *Periphyllus* sp. and *S. agropyrella*. In *M. fuscoviride*, mummies within ant-attended colonies experienced significantly lower levels of hyperparasitism (χ^2 = 285.9; df = 1; p = 0.0001). In *Periphyllus* sp., mummies were very rare in ant attended colonies (4 mummies in total) and these were never hyperparasitised. For *S. agropyrella*, hyperparasitism rates were extremely low for both types of colony.

The two species, *S. oblongus* and *C. pinea*, that always mummified outside the colony both showed relatively high levels of hyperparasitism (63.64% and 62.06%); we found no mummies in ant attended colonies of these two species (Table 1).

Of the nine species in which mummies were found both inside and outside the colony, no consistent pattern emerged as to which site was the safer for the primary parasitoid. In *Acyrthosiphon pisum* (Harris), *Uroleucon jaceae*, *Macrosiphoniella millefolium*, and *Cinara pini* (L.), mummies outside the colony suffered significantly higher rates of hyperparasitism than those within (Table 3). *C. pini* is a special case, because mummies inside the colonies are always ant-attended while in unattended colonies all the mummies always wander off. A fifth species, *Microlophium carnosum* (Buckton), showed a strong and nearly significant trend towards lower rates of hyperparasitism within aphid colonies. In three species [*Myzus cerasi* (F.), *Periphyllus* sp. and *Cinara pilicornis* (Hartig)] there was no significant difference in rates of hyperparasitism in the two sites. In a final species, *Aulacorthum solani* (Kaltenbach), mummies within the colony suffered significantly higher rates of hyperparasitism (Table 3). *M. cerasi* was the only one of the eight ant attended species which suffered comparatively high rates of hyperparasitism (83.3%) within aphid colonies.

TABLE 3. Statistical values of G-tests for Fig. 1a and b. In *A. pisum*, *U. jaceae* and *C. pini* we found significantly increased hyperparasitoid attacks on mummies outside the aphid colony. There was a trend in the same direction for *M. carnosum*, while *A. solani* and *M. millefolium* showed significantly increased hyperparasitoid attack on mummies inside the aphid colonies. For *M. cerasi*, *Periphyllus* sp. and *C. pilicornis* there was no statistically significant difference in hyperparasitoid attack between mummies inside and outside the aphid colonies.

Aphid species	G	n	p
M. carnosum	3.74	536	0.052
A. pisum	17.63	550	0.0001
U. jaceae	29.81	206	0.0001
M. millefolium	9.36	302	0.002
A. solani	37.04	290	0.0001
M. cerasi	1.02	70	0.30
Periphyllus sp.	2.25	107	0.12
C. pilicornis	0.25	95	1.61
C. pini	114.77	434	0.0001

Laboratory studies

Asaphes vulgaris females searched for significantly longer periods of time on *Centaurea jacea* stems when mummies were located outside an aphid colony in comparison to stems where the mummies were located inside a colony (Fig. 2a). The defense behaviour of the aphids had a significant influence on the foraging success of *A. vulgaris*. *Uroleucon*

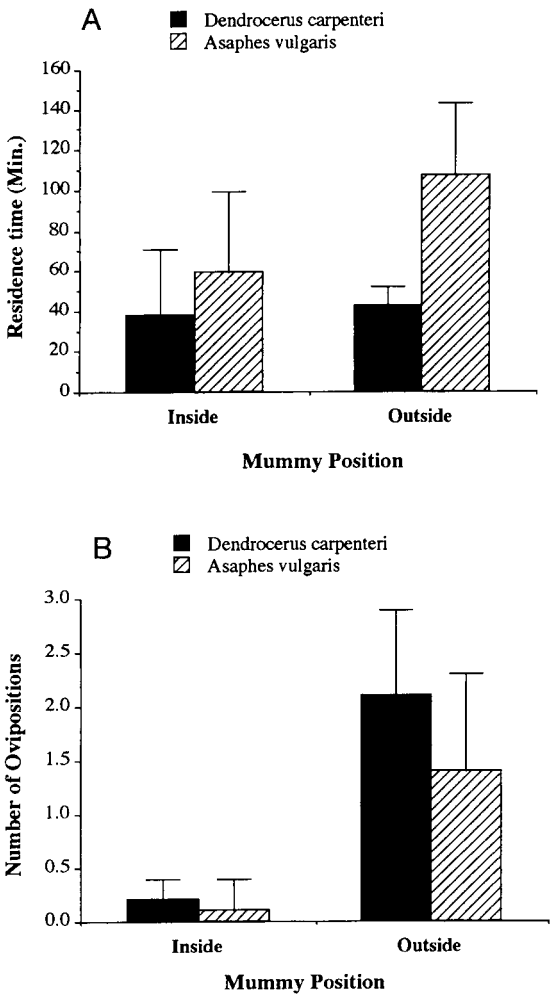


Fig. 2. Residence times (A) and oviposition attempts (B) of *Dendrocerus carpenteri* and *Asaphes vulgaris* when foraging on *C. jacea* stems with *U. jaceae* mummies. Mummies were located either inside or outside the aphid colony (mean ± S.D). For *A. vulgaris* females, residence time was significantly decreased inside aphid colonies (Mann-Whitney-U test: U = 10.0, n = 16, p = 0.047). The number of ovipositions was decreased within aphid colonies for both, *D. carpenteri* (Mann-Whitney-U test: U = 18.5, n = 32, p < 0.001) and *A. vulgaris* (Mann-Whitney-U test: U = 6.5, n = 16, p = 0.004).

jaceae females use their strong back legs to kick colony intruders, causing *A. vulgaris* females to retreat. In consequence, the hyperparasitoid achieved significantly more host contacts and significantly more successful ovipositions when attacking mummies that were not surrounded by living aphids (Fig. 2b).

In contrast, patch residence time of *Dendrocerus carpenteri* did not depend on the location of the mummies within or outside an aphid colony (Fig. 2a). But like *A. vulgaris*, they achieved significantly more host contacts and successful ovipositions (Fig. 2b) when mummies were situated outside the colony. As with *A. vulgaris*, *D. carpenteri* females retreated in the face of kicking by the live aphids surrounding the mummies.

DISCUSSION

Aphids differ in their readiness to move around the plant, particularly after disturbance by natural enemies (see also Nault et al., 1976). Movement away from the feeding site after parasitism tends to be found in more active, mobile aphids, while the mummies of less mobile species tend to be formed in the colony. The five species of aphids we studied, whose mummies always occurred in the colony, are all relatively immobile species, although they vary both in size and whether or not they are attended by ants.

In our study, the consequences of mummifying away from colony for rates of ectohyperparasitism were very variable and no single pattern emerged. One factor that greatly reduces ectohyperparasitism is ant attendance (Völkl, 1992; Mackauer & Völkl, 1993), and indeed most species examined in our study which

mummified inside ant-attended colonies benefitted from significantly decreased ectohyperparasitism rates (Fig. 1a, b). However, some unattended species also suffered low levels of ectohyperparasitism and another ant attended species, *M. cerasi*, suffered very high levels of hyperparasitism. In the latter case, it is perhaps significant that the main ectohyperparasitoid attacking *M. cerasi* within aphid colonies is *Pachyneuron gibbiscuta*, a species that appears much less sensitive to ant encounters than other ectohyperparasitoids (Hübner & Völkl, 1996; W. Völkl, unpublished). Despite the obvious benefit of ant attendance, mummies of some obligatory (*S. oblongus*) or facultatively (*Periphyllus* sp., *C. pinea*, *C. pini*) ant attended aphid species were either generally or facultatively found outside the colony (Table 1), where they suffered from high ectohyperparasitism. The moving behaviour of the host might be adaptive for *Trioxys betulae* and *Trioxys falcatus*, parasitoids of *S. oblongus* and *Periphyllus* sp. respectively (Table 2), as these species are readily attacked and killed by ants if they emerge within attended aphid colonies (Völkl, 1996). Thus, the high incidence of hyperparasitism in mummies outside the colony may be balanced by the mortality of newly emerging *Trioxys* spp. caused by aphid attending ants in mummies inside the colony. However, *Pauesia* species – the parasitoids of *C. pini* and *C. pinea* – do not generally suffer from this ant-caused mortality (Völkl, 1996). For these species, alternative explanations for the moving behaviour of parasitized aphids are necessary.

For parasitoids attacking unattended aphid species, the consequences of mummification outside the colony were variable with a tendency for ectohyperparasitism to increase. Our experiments showed that both *A. vulgaris* and *D. carpenteri* – two of the most common aphid ectohyperparasitoids (Table 2) – laid fewer eggs (Fig. 2b) if mummies were located among living aphids, because of disturbance by the behaviour of *U. jaceae*. Thus, reduced hyperparasitoid foraging efficiency may explain the lower rate of hyperparasitised mummies of *M. carnosum*, *U. jaceae*, *A. pisum*, *M. millefolii* and *C. pini* within aphid colonies. All these species are relatively large, active and robust aphids that display strong defense behaviour against primary parasitoids (Gerling et al., 1990; Völkl et al., 1995; Weisser, 1995). It may be advantageous for the primary parasitoids of these species to mummify inside a colony where they are protected by the living aphids. In contrast, *D. carpenteri* seems to be less disturbed by small, relatively inactive aphid species such as *Aphis fabae* (Völkl et al., 1995), *M. cerasi*, or *C. tanacetina* (W. Völkl, unpubl. data), and indeed these species showed a high incidence of ectohyperparasitism inside colonies.

Could moving away from the colony reduce predation on mummies? Syrphid and coccinellid larvae, the major predators of aphids, usually consume living aphids and do not normally attack mummies. Predatory bugs do cause heavy mortality among mummies (Liebscher, 1972; Novak, 1994) but there is currently no evidence that these species are more successful inside colonies. Indeed, predatory bugs foraging inside aphid colonies are disturbed by ants (Novak, 1994) and by aphid defence behaviour (Dixon, 1985).

There are several alternative explanations for the moving behaviour of parasitised aphids, which are not mutually exclusive. First, movement may simply be an epiphenomenon, a consequence of the trauma of parasitism (Godfray, 1994). Many aphids react to disturbance by local dispersion, and parasitism may trigger this response. Those aphid species that leave the colony when parasitised tend also to disperse in the presence of predators. Alternatively, parasitism may change the hormonal state of the host (for

reviews, see Beckage, 1985; Lawrence, 1990; Strand & Pech, 1995) in a way that promotes dispersal. The final instar larva of an aphid parasitoid usually consumes all the neurosecretory cells of its host, and these aphids may therefore behave as if allatectomised. Allatectomisation may alter JH-III titres (e.g. Loher et al., 1992; Hoffmann & Sorge, 1996) and thus the ratio of JH-III and ecdysone, two hormones that play a role in aphid moulting (Hardie, 1987). There is some indication that mummification site correlates with moulting site in some aphid species which leave the colony for mummification. Thus, the parasitised aphids may simply behave like aphids shortly before moulting. Of course, disruption of the host endocrine system may be the proximate means by which the parasitoid manipulates host behaviour, but the alternative non-adaptive explanation must also be considered.

Another alternative explanation is that host manipulation is involved but that the selective advantage of moving is not avoidance of parasitism but the location of more suitable microclimate for mummification (Brodeur & McNeil, 1990). This hypothesis is supported by observations of the aphid parasitoid, *Aphidius rosae* (Haliday), attacking the aphid *Macrosiphum rosae* (L.) on *Rosa* sp. Mummies of this species are usually found on rose leaves outside the colony. In spring, when temperatures are low, most mummies are found on the upper side of the leaves. In summer, when temperatures and insolation are high, the majority of mummies occur on the lower side of the leaf (Fink, 1995).

To conclude, many but not all aphid species leave the colony after parasitism. Although this behaviour may have evolved through host manipulation by primary parasitoids to avoid hyperparasitism, the results presented here suggest that avoidance of hyperparasitism alone cannot explain the diversity of patterns found in different species.

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