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## INTERACTIONS AMONG VETCHES BEARING EXTRAFLOREAL NECTARIES, THEIR BIOTIC PROTECTIVE AGENTS, AND HERBIVORES<sup>1</sup>

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**Abstract.** The stipular nectaries of the common vetch (*Vicia sativa* L.) are present on young plants from about the seventh node and continue to secrete nectar through flowering, until fruit are mature. The ant *Myrmica ruginodis* is the primary visitor to these nectaries in North Yorkshire, England. The ants are effective at removing or disturbing some of the externally feeding insect herbivores (mostly Lepidoptera, and some Coleoptera), but leaves nevertheless sustain some damage from hard-bodied beetles. More devastating are the pod-feeding larvae of *Cydia* spp., tortricid moths that oviposit on ovaries of flowers and whose larvae feed in the developing legumes, safe from ants. In areas where ant abundance is highest, the pod-feeding larvae are apparently well protected by ants from their natural enemies, ichneumonid parasitoid wasps (*Scambus planatus* and *Campoplex punctulatus*). Plants in such areas have greater numbers of seeds damaged and produce fewer viable seeds than plants in areas of low ant abundance. The vetches are more successful where ant abundance is low; larvae in the pods get parasitized, and fewer seeds are damaged. These data imply that pod feeders may have successfully short-circuited extrafloral nectary-mediated ant defense for their own benefit.

**Key words:** antiherbivore defense; ants; Coleoptera; England; extrafloral nectaries; geographic variation; herbivores; internal feeders; Lepidoptera; parasitoids; protection.

### INTRODUCTION

Ants visiting extrafloral nectaries (EFNs) often protect plants against herbivores (Bentley 1977, Buckley 1982, Jolivet 1986) although protection is not universal (e.g., O'Dowd and Catchpole 1983, Boecklen 1984, Heads and Lawton 1984). In a facultative mutualism between alien *Vicia sativa* and nonnative ants in California, ant visitation to EFNs reduced damage from folivores and increased seed set (Koptur 1979). In that system, however, overall herbivore pressure was low, and none attacked flowers and fruits. In its native habitat in Britain, more guilds of herbivores feed on *V. sativa*, including insects whose larvae feed inside developing pods.

*Vicia sativa* is an aggregate species, containing both *V. sativa* sensu stricto (alien) and *V. angustifolia* (native to Britain) (Lees 1888, Robinson 1902, Clapham et al. 1962, Hollings and Stace 1978). We studied plants from the *V. angustifolia* end of the spectrum in North Yorkshire. The plants are annual, an ideal situation to investigate effects of ant visitation on reproductive output. We asked (1) Do ants protect vetches in their native habitat? (2) Do vetches receive protection from other visitors to their extrafloral nectaries? (3) How do interactions between the various protective agents and herbivores affect fitness of vetches?

### MATERIALS AND METHODS

During the 1984 field season we worked at two main sites: Heslington village ( $\approx 3$  km outside York), and Skipwith Common,  $\approx 13$  km south and east of Heslington. Two groups of 30 plants each were marked at both sites. For each plant we recorded the details of its phenology, herbivore damage and abundance, ant attendance, and the presence of other visitors at the nectaries. In early August the plants were harvested, and the pods and seeds were counted.

The abundance of ants and other potential nectary visitors in the habitat was measured every two weeks at three subsites within each site by baiting with honey (20 baits on index cards  $3 \times 3$  cm in one transect placed at 1-m intervals and monitored for 1 h) throughout the growing season.

Externally feeding herbivores and nectary visitors were collected from other plants in the vicinity of marked plants at both main sites. Internally feeding pod herbivores were sampled in haphazard collections from many plants at each subsite on three occasions during fruiting; more quantitative information was obtained from 20 groups of 30 pods each. Larvae feeding on developing seeds were reared both for identification and estimates of parasitism. To avoid disturbance, pods were not examined on marked plants until the end of the season when most had dehisced. It was then possible only to estimate the number of viable seeds produced from evidence on the pod wall; the presence of larvae in pods and whether or not they were parasitized was not discernible.

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TABLE 1. Ants vs. surface-feeding herbivores. Data are number of herbivores placed on plants initially (I) and the number remaining after 5 min (F).

Herbivore	With ants		Without ants		$\chi^2$ *	P
	I	F	I	F		
<i>Cnephasia interjectana</i> (Tortricidae)	10	10	10	2	16.9	.005
Undetermined Noctuidae	10	8	10	1	11.02	.005
<i>Apion</i> spp. (Apionidae)	10	8	10	3	5.3	.025
<i>Phyllobius pyri</i> (Curculionidae)	10	2	10	1	0.39	NS
<i>Phyllobius roboretanus</i>	10	3	10	0	0.69	NS
<i>Sitona lineatus</i> (Curculionidae)	10	3	10	2	0.27	NS

\*  $\chi^2$  values from analysis of deviance.

The protective ability of ants was measured by placing 10 individuals of each major species of defoliator on plants occupied by ants and 10 on control plants from which ants had been excluded with Tanglefoot. Each herbivore was monitored for 5 min.

## RESULTS

### *Vetch natural history*

Seeds that are released in the fall germinate the following spring. EFNs are not visible on the young plants until the sixth to eighth node and do not secrete nectar until the first flower buds are visible. EFNs are situated on stipules at the base of the leaves. Extrafloral nectar secretion continues throughout flowering, fruit initiation, and maturation. In 1984, flowering started in the 3rd wk of May. The plants flower indeterminately; a plant can have mature and developing fruit, flowers, and buds simultaneously. The first fruits matured in early July; flowering waned in early August, and nearly all fruits were mature by late August.

### *Herbivores*

The aphid *Megoura viciae* Buckton occurred sporadically on this and other legumes at the study sites. Adults of a number of beetles ate the foliage, principally weevils, *Sitona lineatus* (L.), *Phyllobius pyri* (L.), *P. maculicornis* Germar, *P. roboretanus* Gred., *P. vespertinus* (Fab.), *Apion gyllenhali* Kirby, *Ceutorhynchus assimilis* (Paykull), and a cantharid, *Cantharis livida* (L.). Lepidoptera included larvae of the tortricid moth *Cnephasia interjectana* (Haworth) and an unidentified noctuid (found several times, but not reared successfully).

Caterpillars of the tortricid moth *Cydia dorsana* (Fab.) = *C. lunulana* (D. & S.) were the most common pod occupants. *C. nigricana* (Fab.), an agricultural pest known as the pea moth, occurred in a small number of late-initiating pods. We also found a third species of *Cydia* in moderate numbers but failed to rear it for identification. Larvae are cannibalistic, and we normally encountered only one larva in a pod; on rare occasions, however, two larvae were found at opposite ends. Weevil larvae of the genus *Apion* are known to infest pods in other parts of England, but none were found in our Yorkshire study sites (and have never

been recorded this far north: D. Jones, *personal communication*).

### *Visitors to extrafloral nectaries*

Only one ant species, *Myrmica ruginodis* Nylander, visited the EFNs. This species has a long history in England (remains have been found in Viking York [Jorvik]; University of York, Environmental Archaeology Unit, *personal communication*), and workers frequently attend EFNs of any plant in the vicinity of their nest (e.g., Lawton and Heads 1984). Workers are  $\approx 4.5$  mm long.

The nectaries of *Vicia sativa* were also visited by the parasitic wasp *Scambus planatus* (Hartig) (Ichneumonidae: Pimplinae), a species that was reared from many larvae of the pod-feeding *Cydia* spp. *Campoplex punctulatus* (Szepligeti) (Ichneumonidae: Campopleginae) was also reared from *Cydia* larvae, but never observed at nectaries.

### *Myrmica ruginodis as biotic protection agents*

*Myrmica* spent a considerable amount of time on the plants, primarily in the vicinity of the EFNs. The EFN-bearing stipules are on the leaf bases where leaves join the stem, and the flowers are sessile in the axils of the leaves. Ant activity was therefore concentrated around the bases of leaves, flowers, and developing fruits.

Ants were effective at removing three of the six experimentally placed insect species from the surface of leaves (Table 1), but not *Sitona* and *Phyllobius*. These weevils are larger than *Apion* (*Sitona* are 4.5 mm long, *Phyllobius roboretanus* 5 mm, and *Phyllobius vespertinus* 6 mm; *Apion* are 3.5 mm with snout, 2.5 mm without), and being relatively immune to ants, they accounted for the bulk of insect chewing damage on the leaves of vetches at our sites.

### *Natural levels of damage to plants*

Damage to foliage from externally feeding insects was <20% of total leaf area throughout the growing season in the marked populations at each site (Heslington: leaf damage areas [ $\bar{X} \pm SD$ ]  $12.0 \pm 6.6\%$  and  $19.25 \pm 6.57\%$ ; Skipwith:  $12.0 \pm 12.3\%$  and  $15.5 \pm 12.7\%$ ). Defoliation and fruit set were not significantly

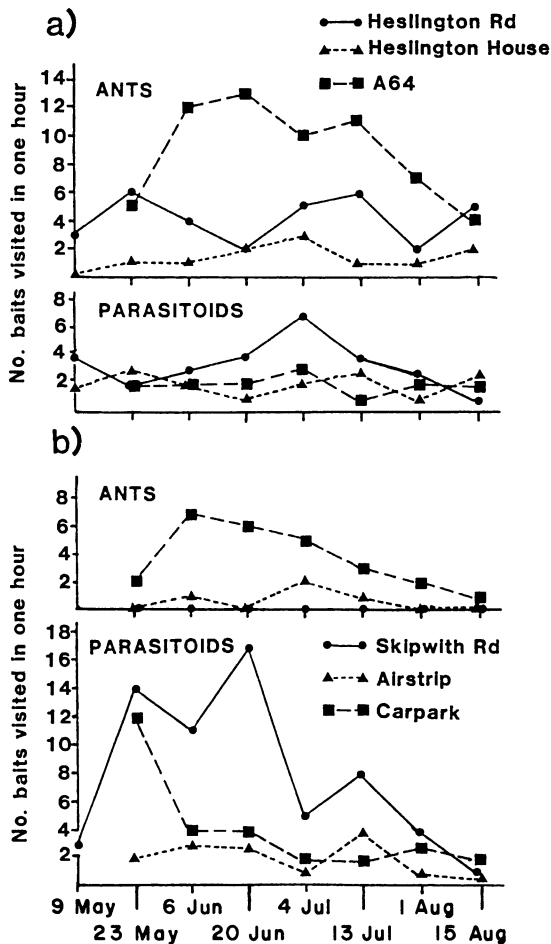


FIG. 1. Seasonal abundance of ants and parasitoids at (a) Heslington and (b) Skipwith sites, as measured by discovery of honey baits (20 baits in each transect each date). The mean numbers of baits discovered for each subsite over the season are recorded in Tables 2 and 3.

correlated. There were averages of  $36.0 \pm 13.72$  and  $26.3 \pm 11.7$  seed pods per plant at Heslington, and  $21.4 \pm 13.1$  and  $25.8 \pm 11.5$  pods per plant at Skipwith.

#### Abundance of ants and parasitoids

Each subsite had a characteristic level of ant activity at baits (Fig. 1); differences in ant activity also occurred in our observations of nectaries, but baits were used as a more standard measure of ant activity. Analysis of deviance (Nelder and Wedderburn 1972, McCullagh and Nelder 1983) on ant activity at baits shows that, for Heslington, sampling date was not significant ( $\chi^2_6 = 6.9$ ), but subsite was ( $\chi^2_2 = 53.11$ ,  $P < .005$ ). Overall ant activity was lower at Skipwith than at Heslington. At Skipwith there was also a significant contribution to deviance from subsite ( $\chi^2_2 = 45.4$ ,  $P < .005$ ) but not from date ( $\chi^2_6 = 12.1$ ). We analyzed for effects of ant abundance within sites and then combined the

two sites to give six subsites with markedly different levels of ant activity based on mean numbers of baits (out of 20) discovered by ants at one subsite over the season (Table 2). We recognize that this latter procedure ignores differences between sites that we did not measure, and that may produce effects on the herbivores of *Vicia* unrelated to ant abundances. This caveat must be borne in mind when interpreting the analyses.

The number of parasitoids recorded at baits was not correlated with ant activity (Fig. 2a). However, parasitoid visitation to baits was higher overall at Skipwith, where ants were fewer. Analysis of deviance showed that none of the Heslington subsites differed significantly from each other in parasitoid numbers (subsite:  $\chi^2_2 = 4.2$ , NS; date:  $\chi^2_6 = 4.2$ , NS). Skipwith subsites differed significantly, with both subsite ( $\chi^2_2 = 40.8$ ,  $P < .005$ ) and date ( $\chi^2_6 = 44.4$ ,  $P < .005$ ) making a significant contribution to deviance.

#### Ant abundance and parasitization of pod-feeding larvae

The best indication of parasitoid activity is actual parasitization of hosts (Table 3). At Heslington there was a significant heterogeneity (analysis of deviance) in the proportion of larvae parasitized by both *Scambus* and *Campoplex* among subsites, with ant activity and percent parasitism inversely related. The subsite with the lowest ant activity (Heslington House; Table 2) had the greatest percentage of larvae parasitized (Table 3), while the subsite with the highest ant activity (A64) had the lowest. Skipwith subsites, however, showed no significant differences in levels of parasitism, although trends resemble those at Heslington. When subsites at both areas are combined (Fig. 2b), and each site ranked for ant abundance and percent parasitism, the Spearman Rank  $r_s = -0.83$  is very nearly significant ( $z = 1.85$ ,  $P = .06$ ). Overall, therefore, ant abundance appears to be more or less inversely correlated with parasitism of *Cydia* larvae.

Plotting percent parasitism against *Cydia* density (mean number of pods damaged) shows no sign of density-dependent (or inverse density-dependent) parasitism. Nor is there a correlation between parasitoid abundance at baits and percent parasitism. Variation in percent parasitism is better explained by ant density than by *Cydia* or parasitoid density.

#### Ant abundance and damage to pods

Damage to pods and seeds by *Cydia* larvae differed significantly among subsites (Table 2). In Heslington, the subsite with the highest ant activity (A64) also had the greatest damage to pods. Seed damage trends were the same as pod damage trends, and so more seeds were damaged in the area where ants were most attentive to nectaries than in areas where their activity was lower (Heslington Road site); where ant activity was lowest (Heslington House site) more than half the pods

TABLE 2. Damage to pods and seeds sampled from different sites (20 samples of 30 pods each from each subsite). Data are means  $\pm$  1 SD.

Sites Subsites	Ant activity (mean no. baits/20 discovered over season)	No. pods per plant damaged by <i>Cydia</i>	No. seeds per plant damaged by <i>Cydia</i>
Heslington			
Hes. House	1.6 $\pm$ 0.8	18.75 $\pm$ 2.69	106.6 $\pm$ 21.0
Hes. Rd.	4.3 $\pm$ 1.7	4.40 $\pm$ 1.70	22.0 $\pm$ 12.9
A64	8.9 $\pm$ 3.5	20.90 $\pm$ 2.94	110.5 $\pm$ 20.9
Kruskal-Wallis <i>H</i> (corrected for ties)		42.29§	39.54§
Skipwith			
Skipwith Rd.	0	3.10 $\pm$ 1.65	11.5 $\pm$ 6.4
Airstrip	0.6 $\pm$ 0.8	2.25 $\pm$ 1.41	6.6 $\pm$ 4.5
Carpark	3.7 $\pm$ 2.3	1.35 $\pm$ 1.09	5.8 $\pm$ 4.8
Kruskal-Wallis <i>H</i> (corrected for ties)		12.76§	9.46**

\*\*  $P < .01$ ; §  $P < .005$ .

were also damaged, but not quite as many as at the A64 site.

At Skipwith, the trend was more consistent with results expected if ant defense is operating: the site with no ant activity (Skipwith Road) had the greatest number of damaged pods, but this "high" level of damage was lower than that at the site with the lowest damage at Heslington. The site with an intermediate level of ant activity (Airstrip) had an intermediate number of pods damaged; and the site with the highest level of ant activity (Carpark) had the fewest pods damaged. Again, seed damage trends follow pod damage.

Combining the two areas, and ranking the six subsites in order of ant activity and pod damage, the Spearman Rank Correlation Coefficient,  $r_s = 0.49$ , is not significant ( $z = 1.09$ ,  $P = .28$ ).

DISCUSSION

In a study of this vetch species where it grows as an alien in northern California (Koptur 1979), levels of damage to foliage similar to those seen in Yorkshire were found. Ants (*Iridomyrmex humilis*, also nonnative) that visited the nectaries effectively reduced damage to foliage, and increased fruit and seed set, compared with plants that had ants experimentally excluded.

In Yorkshire, where *Vicia sativa* is native, the native ant *Myrmica ruginodis* had the same protective capacity against a variety of small or soft-bodied, foliage-feeding insects, but there were a number of tough surface-feeding weevils that made the protective ability of these ants less impressive. A potentially vulnerable native caterpillar, *Cnephasia*, may escape ant predation by silking itself between leaves, one of several escape methods described for herbivores against both this and other species of ants on *Pteridium aquilinum* in the same geographic region (Heads and Lawton 1985).

A major difference between Californian and Yorkshire *V. sativa* is the presence of a native pod-feeding guild (*Cydia* spp.) in Yorkshire. Contrary to the theory that ant visitors to EFNs protect plants against herbivores, *Cydia* were more devastating to the vetches

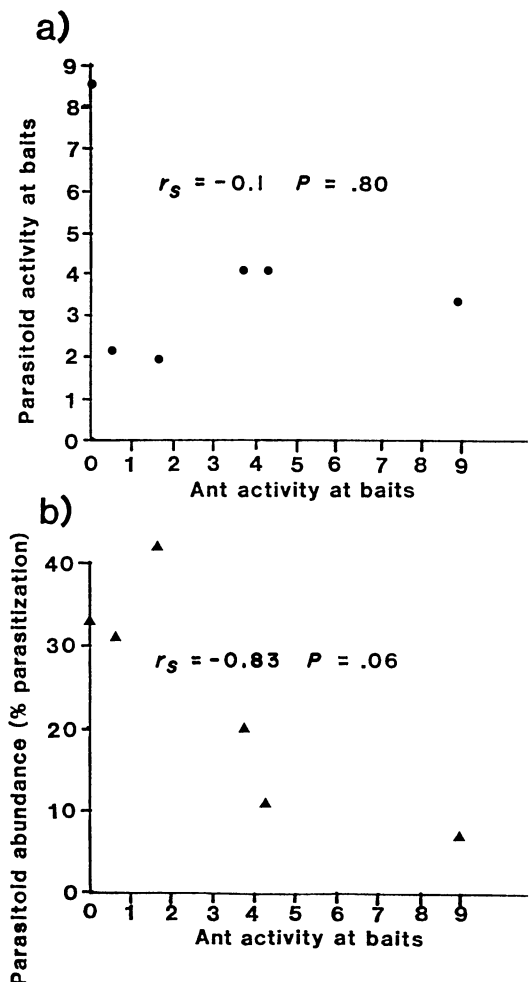


FIG. 2. Activity of ants vs. parasitoids at each subsite. Ant activity is the mean number of baits (out of 20) discovered by ants, averaged over all dates. Parasitoid activity is indicated in two ways: (a) the mean number of baits discovered by parasitoids (as for ant activity) and (b) the percent parasitization of *Cydia* herbivores within pods of *Vicia sativa*. The Spearman Rank Correlation Coefficient  $r_s$  is indicated for each, with its level of significance.

TABLE 3. Parasitization of *Cydia* spp. larvae reared from pods collected at different sites.

Sites Subsites	Parasitoids at baits (mean no./20) discov- ered	Total no. larvae reared	% larvae para- sitized	Analysis of deviance
Heslington				
Hes. House	2.0	26	42	$\chi^2 = 20.48$ $P < .005$
Hes. Rd.	4.1	9	11	
A64	3.4	213	7	
Skipwith				
Skipwith Rd.	8.6	15	33	$\chi^2 = 0.3373$ $P > .1$
Airstrip	2.1	13	31	
Carpark	4.1	5	20	

at subsites in one area where ants were abundant (Heslington) than at subsites in an area where ants were rarer (Skipwith); and at Heslington, most damage was caused by *Cydia* at the subsite where ants were most abundant. At Skipwith, ant defense apparently functioned in a more expected way in the three subsites: more ant activity, less damage to plants (pods and seeds). Percent parasitism of *Cydia* larvae was apparently inversely correlated ( $P = .06$ ) with ant activity when all six subsites were combined.

Negative interactions between ants and parasitoids of herbivores have been demonstrated in various nectar-reward situations, e.g., ant-attended lycaenid caterpillars (Pierce and Mead 1981) and cynipid gall wasps on Californian oaks (Washburn 1984). Internally feeding herbivores on plants with EFNs, such as the pod-feeding *Cydia* in the present study, may benefit in a similar way from the presence of ants at the secretions, if the aggressive behavior of ants toward other plant visitors drives away parasitoids. For example, at sites where ants are not present in great numbers, EFNs of *Inga* are more attractive to parasitoids (Koptur 1985). However, because we never observed ants driving away parasitoids from *V. sativa* EFNs or pods, the proposal is speculative, albeit plausible.

Of all the herbivores found on *Vicia sativa* in Yorkshire, the internal feeders have the greatest impact on plant fitness. Other experiments in a controlled garden (S. Koptur and C. Smith, *personal observation*) showed that unlike the present field observations, increasing levels of defoliation led to decreased pod and seed production, but even at 100% defoliation (all leaflets removed from all leaves) the plants still grew, flowered, and set substantial amounts of seed. Larvae that feed inside the pods on developing seeds may completely devour all of the seeds, or damage parts of nearly all the seeds; some partly eaten seeds are dead (if the embryo is gone), but others can still germinate and grow (S. Koptur, *personal observation*). However, damaged seeds, if successfully dispersed from the plant, may not

be able to overwinter; our observations show that they usually germinate in the fall, and invariably die over the subsequent winter.

In native environments, specialist herbivores evolve that can short-circuit plant defenses, including ants at EFNs (Heads and Lawton 1985). In the *Vicia* system, *Cydia* moths may exploit ant protection: when in pods on plants with ants, they are apparently protected from their parasitoids. Where these herbivores are abundant, ant protection can be a problem: vetches in areas of high ant activity and high *Cydia* abundance get damaged heavily, and set much less viable seed than their counterparts in areas with either low ant activity and low *Cydia* abundance, or low ant and high *Cydia* abundance. Clearly, the benefits that plants derive from EFNs may vary from place to place, and depend crucially on the particular combination of ants, other protective agents, and herbivores, a point that has been made by a number of other recent studies (Inouye and Taylor 1979, Horvitz and Schemske 1984, Koptur 1984, Barton 1986, Kelly 1986, Smiley 1986, Sato and Higashi 1987).

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