Note

Effect of *Erynia neoaphidis* infection and coccinellid foraging on the spatial distribution of aphids on plants

Pathogens and parasites can dramatically modify the behavior of their hosts (Arthurs and Thomas, 2001; Chow and Mackauer, 1999; Karban and English-Loeb, 1997; Moller, 1993; Maitland, 1994; Roy et al., 1999; Watson et al., 1993). The behavioral changes induced by pathogen or parasite attack are extremely diverse (Carruthers et al., 1992; Moller, 1993). Many studies have examined the modification of microhabitat selection by parasitised insects (Brodeur and McNeil, 1989, 1992; Maitland, 1994). However the combined effects of parasites and predators on host behavior have largely been ignored. In this paper, we consider the effect of a foraging predator, *Coccinella septempunctata*, on the spatial distribution of aphids infected with *E. neoaphidis*.

Two species of aphid (Hemiptera: Aphididae) were used in these studies, *Acyrthosiphon pisum* Harris and *Sitobion avenae* F. *A. pisum* were cultured on three to four week old dwarf broad bean plants (*Vicia faba* cultivar The Sutton) and *S. avenae* were cultured on one to two week old wheat (*Triticum aestivum* cultivar Beaufort). Both aphid species were maintained under controlled conditions of 18 °C and a 16-h photoperiod. The aphids were transferred to new plants every 1–2 weeks. Aphids were regularly harvested to feed a *C. septempunctata* colony and for culturing *E. neoaphidis*. *C. septempunctata* larvae were derived from eggs laid by adults collected in the field.

An in vivo isolate (X4 from the Rothamsted Research collection, original host, *A. pisum*) and an in vitro isolate NW305 (Isolate KVL603 from the Royal Veterinary and Agricultural University collection, Copenhagen, Denmark, original, *S. avenae*) of *E. neoaphidis* was used to inoculate 1–3 day old adult *A. pisum* and *S. avenae*, respectively (Wilding, 1973; Wilding and Brobyn, 1980).

Individual bean or wheat plants (20 plants) were infested with either ten uninfected or ten infected (day zero post-inoculation) 1–3 day old adult *A. pisum* or *S. avenae*. The plants were covered with lamp glasses and polythene covers and placed at 18 °C (16 h photoperiod). The polythene covers were replaced with nylon mesh after 24 h. After 72 h (three days post-inoculation), the adult aphids were transferred to new plants to reduce interference from the aphid nymphs they had produced and were left to settle for one hour. After this period an

individual *C. septempunctata* adult, which had been fed to satiation to minimise aphid consumption, was added to half the plants (five bean or wheat infested with uninfected aphids, five bean or wheat infested with infected aphids and the remaining bean and wheat plants served as controls). The adult coccinellids were removed after four hours. After a further 24 h (day four post-inoculation) the position of the aphids within the plant and on the soil was assessed.

In order to quantify the position of *A. pisum,* the bean plant was divided into distinct regions: upper closed (9–12 cm above soil), upper open (6–9 cm above soil), middle (3–6 above soil) and lower leaves, and stem (0–3 cm above). The number of aphids in each position and on the soil was counted. Aphid mortality due to *E. neoaphidis* was also quantified. The positions of the aphids on the bean plant were interpreted as ordered categories of distance up the plant and were analysed using proportional odds regression via the generalised linear model facilities of Genstat 5 (Genstat 5 Committee, 1995).

The position of aphids on wheat was not quantified as described for the aphids on bean because of the different architectures of bean and wheat plants. Instead the height above the soil of the aphids on the wheat was measured to the nearest five millimetre. Aphid mortality due to *E. neoaphidis* was also quantified. The height (centimetres) of the aphids on the wheat plants was analysed using analysis of variance (ANOVA).

There was a significant difference in the distribution of uninfected and infected *A. pisum* on bean plants with a foraging adult coccinellid compared to plants without a coccinellid ($F_{1,73} = 7.45$; $p < 0.01$; Table 1). There was no significance difference between the distribution of uninfected and infected *A. pisum* ($F_{1,73} = 3.76$; $p > 0.05$) and there was no significant interaction between presence/absence of a coccinellid and uninfected/ infected *A. pisum* ($F_{1,73} = 1.63$; $p > 0.05$).

There were fewer *A. pisum* (uninfected or infected) on the upper closed leaves in the presence of a coccinellid than on plants without a coccinellid (Table 1). In the presence of a coccinellid the *A. pisum* were predominantly situated on the upper open and mid leaves of the plant. There were no uninfected *A. pisum* on the soil in

Table 1
Percentage of uninfected and infected *A. pisum* within a bean plant with or without a foraging coccinellid

Aphids (*A. pisum*)	Presence/absence of a coccinellid	Plant positions				
		Soil	Lower	Mid	Upper open	Upper closed
Uninfected	With coccinellid	3.2	3.2	22.6	61.3	9.7
	Without coccinellid	0	0	12.5	47.5	40
Infected	With coccinellid	2.7	8.1	27.0	48.6	13.5
	Without coccinellid	2.5	5	22.5	47.5	22.5

The positions (soil, lower leaves, mid leaves, upper open leaves, or upper closed leaves) are interpreted as ordered categories of distance from the soil to the upper closed leaves

the absence of a coccinellid. In contrast a few uninfected *A. pisum* were on the soil in the presence of a coccinellid. A small percentage of infected *A. pisum* were also situated on the soil.

There was no significant difference in the distribution of uninfected and infected *S. avenae* on plants with a foraging adult coccinellid compared to plants without a coccinellid ($F_{1,177} = 0.52$; $p > 0.05$). In the presence of a coccinellid uninfected and infected *S. avenae* were situated 9.2 cm (SE = 0.6) and 10.7 cm (SE = 0.8) above the ground, respectively. There was a significant difference in the distribution of uninfected and infected *S. avenae* ($F_{1,177} = 5.66$; $p < 0.05$) with infected aphids and uninfected aphids situated at 11.6 cm (SE = 0.8) and 9.6 cm (SE = 0.5) above the ground, respectively. There was no significant interaction between presence/absence of a coccinellid and uninfected/ infected *S. avenae* ($F_{1,177} = 0.10$; $p > 0.05$).

The behavior of different aphid species is highly variable (Dawson et al., 1982; Dawson et al., 1987), for example, individual *A. pisum* are highly responsive to alarm pheromone (Roy et al., 1999) and are more likely to move from a plant as a consequence of disturbance. In contrast *S. avenae* are not very responsive to alarm pheromone (Dawson et al., 1982) and are, therefore, more likely to remain stationary in the presence of a foraging predator. These behavioral differences are reflected in our results where it was apparent that after moving in response to the coccinellid neither uninfected or infected *A. pisum* re-colonised the upper closed leaves of the plant but commenced feeding in slightly lower plant positions (upper open leaves and mid leaves). In contrast the spatial distribution of infected and uninfected *S. avenae* on young wheat plants was not altered by the presence of a coccinellid.

From our study it was evident that *E. neoaphidis* infection did not alter the spatial distribution of *A. pisum* on bean plants. In contrast, Jensen et al. (2001) reported that *A. pisum* infected with *E. neoaphidis* were more likely to be found away from the original plant than uninfected aphids. The movement of aphids is affected by a number of abiotic and biotic factors including aphid density. High aphid densities result in increased local movement and dispersal of aphids and if these aphids were infected they would therefore be more likely to die off the plant (Bailey et al., 1995). The density of aphids on the plants used in our study was lower than that used by Jensen et al. (2001) and this could explain the difference in results.

Although we did not detect any differences in the distribution of infected compared to uninfected *A. pisum* within bean plants, it was apparent that infected *S. avenae* were located in higher positions on wheat plants than uninfected *S. avenae*. Migratory behavior to the tops of plants has been reported in lepidopteran, hymenopteran, and orthopteran insects infected with viral and fungal pathogens (Carruthers et al., 1992; Fuxa and Tanada, 1987). The elevated position is thought to favour the dissemination of pathogens.

The different responses exhibited by *A. pisum* and *S. avenae* to a fungal pathogen and a coccinellid demonstrate the complexities of the interactions between natural enemies and their prey. More research, both from an ecological and an evolutionary perspective, is required in order to gain a more thorough understanding of the dynamic relationships between predators, parasites, pathogens, and hosts. The successful manipulation of natural enemies for the control of insect pests is dependent on such an understanding.

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