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Polyphagous predatory rove beetles (Coleoptera: Staphylinidae) induce winged morphs in the pea aphid *Acyrthosiphon pisum* (Hemiptera: Aphididae)

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Key words. Staphylinidae, *Drusilla canaliculata*, *Tachyporus hypnorum*, Aphididae, *Acyrthosiphon pisum*, aphid polyphenism, predator-prey interaction, rove beetles, maternal effects, induced defence

Abstract. A number of aphid species have been shown to produce winged dispersal morphs in the presence of natural enemies. Previous studies tested specialized aphid predators such as ladybirds or lacewing larvae. We confronted colonies of pea aphids with the polyphagous rove beetles, *Drusilla canaliculata* and *Tachyporus hypnorum*. For both predators we found that the percentage of winged morphs increased in predator-attacked pea aphid colonies compared to a control. The behaviour of the two rove beetles species was noticeably different. *D. canaliculata* mostly foraged on the ground and rarely on the plant, while *T. hypnorum* was almost exclusively observed on the plants, causing a higher number of aphids to drop to the ground, which resulted in a stronger increase in winged morph production. Our results clearly show that not only monophagous aphid predators but also more polyphagous insect predators, which include aphids in their diet, can induce aphids to produce winged morphs.

INTRODUCTION

Polyphenism is a general phenomenon in aphid species (Kawada, 1987; Dixon, 1998) and appears to be a case of phenotypic plasticity; environmental conditions are often perceived by the mother and result in maternal effects on the offspring (Dixon, 1998; Kunert & Weisser, 2003; Müller et al., 2001; Whitman & Agraval, 2009). Winged dispersal morphs (alate virginoparae) are reported to be produced in response to crowding and a declining host plant quality, in many aphid species (Kawada, 1987; Dixon, 1998). More recently, it has been shown that the presence of natural enemies also induces the production of winged offspring, e.g. in the pea aphid, *Acyrthosiphon pisum* (Harris) (Dixon & Agarwala, 1999; Weisser et al., 1999; Sloggett & Weisser, 2002; Kunert & Weisser, 2003) and the cotton-melon aphid, *Aphis gossypii* Glover (Mondor et al., 2005), but not in the black bean aphid, *Aphis fabae* (Scopoli) and the Vetch aphid, *Megoura viciae* Buckton (Kunert et al., 2008; Dixon & Agarwala, 1999). At least in the pea aphid, wing induction caused by natural enemies seems to be a general phenomenon since they react to important enemies such as ladybirds (adults and larvae), lacewing larvae, hoverfly larvae and hymenopterous parasitoids (Weisser et al., 1999; Sloggett & Weisser, 2002; Kunert & Weisser, 2003). All these predators, however, are specific aphid predators. In contrast, the effect of polyphagous predators that consume a range of prey (including aphids) on aphid wing polyphenism has not yet been investigated.

One group of polyphagous predators that is involved in aphid control, but has generally received little attention, are rove beetles (Coleoptera: Staphylinidae). Bryan & Wratten (1984) demonstrated that several species of rove beetles aggregate in patches of aphids and show a numerical response to increasing aphid densities. Under laboratory conditions, aphid predation accounted for more than 34% of rove beetle body weight (Bryan & Wratten, 1984). Many rove beetles are omnivorous and include both arthropods and other organisms, in particular fungi, in their diet. Sunderland et al. (1987) found aphids, 61 non-aphid arthropods, rust and non-rust fungi in the gut of *Tachyporus* spp. Other species of polyphagous rove beetles do not feed on fungi, e.g. *Drusilla canaliculata* and *Philonthus* spp., but on a wide range of arthropod prey, including aphids at an average rate of 20 /day (Good & Giller, 1991). Overall, rove beetles are significant predators of aphids and pose a mortality risk to aphid colonies.

In the present study, we exposed pea aphid colonies to individuals of both the arthropod and fungus feeding *Tachyporous hypnorum* (F.) and arthropod-feeding *Drusilla canaliculata* (F.) to ask the following questions: (1) does exposure to these predators result in a significant reduction in the growth of aphid colonies?; (2) do aphids respond to the presence of the predator by increasing the number of winged morphs among their offspring?; and (3) are there differences among the rove beetles species in their effect on aphid population growth and wing formation?

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TABLE 1. The average percentage of adult aphids that survived and average numbers of offspring present at the end of the first and second-three day periods (Wilcoxon Signed Ranks Test).

<table>
<tr><td colspan="6">Percentage of adults surviving at the end of the first three-day period</td><td colspan="2">Percentage of adults surviving at the end of the second three-day period</td></tr>
<tr><td colspan="2">*D. canaliculata*</td><td colspan="2">Control</td><td colspan="2">*T. hypnorum*</td><td>*D. canaliculata*</td><td>Control</td></tr>
<tr><td colspan="2">56.4 ± 0.6%</td><td colspan="2">77.6 ± 0.7%</td><td colspan="2">58.6 ± 0.8%</td><td>54.6 ± 0.7%</td><td>74.3 ± 0.8%</td></tr>
<tr><td colspan="3">$Z = -1.93$
$p < 0.05$</td><td colspan="3">$Z = -0.98$
$p = 0.32$</td><td colspan="2">$Z = -0.72$
$p = 0.46$</td></tr>
<tr><td colspan="6">Number of offspring at the end of the first three-day period</td><td colspan="2">Number of offspring at the end of the second three-day period</td></tr>
<tr><td colspan="2">237.1 ± 10.82</td><td colspan="2">275.0 ± 12.35</td><td colspan="2">253.1 ± 18.71</td><td>124.4 ± 13.07</td><td>204.0 ± 12.29</td></tr>
<tr><td colspan="3">$Z = -1.95$
$p < 0.05$</td><td colspan="3">$Z = -0.29$
$p = 0.76$</td><td colspan="2">$Z = -2.37$
$p = 0.01$</td></tr>
</table>

MATERIAL AND METHODS

Experimental insects and plants

For the experiments, we used adults of two predatory species of rove beetles – *D. canaliculata* (F.) and *T. hypnorum,* and the red BP strain of the pea aphid *A. pisum* (Kunert et al., 2005). Rove beetles were collected in meadows in Jena, Germany, using dry pitfall traps, one week before the experiment started, and were kept in plastic tubes with sand in the bottom that was regularly watered to maintain high humidity, at 20°C. Beetles were fed ad libitum with mixed diets of *Aphis fabae*, *A. pisum*, fly larvae and fungus. Aphids were maintained on three week old plants of *Vicia faba* (variety "The Sutton", Nickerson-Zwaan, UK) in a walk-in climate chamber (Thermotec Germany) under long-day conditions (16L : 8D) at 20°C and about 75% relative humidity. Eighty five plants were covered with air-permeable cellophane bags. This transparent cover permitted the visual assessment of both the aphids and predators on the plants and ground without disturbing them.

Experimental design

To minimize maternal effects, a "split-brood-design" was used (Kunert et al., 2008). Thirty aphid lineages (n = 30) were established, each starting with a single adult asexual individual placed on a bean plant where it was allowed to reproduce for three days. The adult aphid was then removed. The offspring were reared until they reached the last (fourth) nymphal instar or the adult stage when they were transferred to new plants in groups of seven, where they reproduced for another three days and then removed from the plant. The second-generation offspring were reared until they reached the adult stage-after which they were used in the experiment. From each line, ten individuals were placed on each of three plants (ten adult aphids / plant with altogether 300 adult aphids on 30 plants). One of these plants served as a control (no predator), a second had a single adult of *D. canaliculata* placed on it and a third a single adult of *T. hypnorum*. By using individual aphids from one line in all the treatments, any confusion due to previous rearing conditions and treatment effects was avoided.

Aphids and predators were left on the plants for three days (first three-day period) after which the surviving adult aphids were counted and transferred to new plants. In the predator treatment, the beetles were also removed and new individuals placed on the new plants (one per plant). All aphid offspring remained on the plants where they were born until they reached the adult stage whereupon they were frozen for later counting and determination of the phenotype. The adult aphids and predators on the new plants remained for a further three days, representing the second three-day period. After this period, all adult aphids were removed from the plant and counted. Predators were also removed. The aphid offspring were again reared until adulthood and then frozen. Whilst there were 30 aphid lineages, only ten individuals of *T. hypnorum* were available initially. Thus, there were ten lines for all three treatments and another 20 lines for the control and *D. canaliculata* treatment. Because of the limited number of *T. hypnorum*, the experiment with this predator was only performed for one experimental period. Plants were inspected once every day during the experiment and the predators' position (on the plant or on the ground) and the number of aphids on the ground recorded. After the end of the experiment, the aphid offspring produced in both experimental periods were counted and examined for the presence of wings.

Statistical analysis

We compared the numbers of surviving adult aphids, numbers of offspring produced, the percentage of winged morphs among the offspring, and the percentage of aphids and predators on the ground in the predator treatments and control using a Wilcoxon Signed Ranks Test. This test takes into account the split-brood design. SPSS version 16.0 was used for this analysis. Predator activity on plant or ground was calculated by using the proportion of time they were observed on the ground (0, 0.33, 0.66, 1), and the means averaged over replicates. Because of the few replicates for *T. hypnorum*, the effects of this predator on aphids were analysed only after the first three-day period of assessment.

RESULTS

Aphid survival and reproduction

In the *D. canaliculata* treatment, the percentage of the initial number of adults transferred at the three-day period was lower than in the control. The average number of offspring produced during the first three-day period in the *D. canaliculata* treatment was significantly lower than in the control (Table 1). After six days, the percentage of adults remaining (from the initial number at the start of the experiment), did not differ between the *D. canaliculata* treatment and the control. The number of offspring produced in the second three-day period was lower in the *D. canaliculata* treatment than in the control (Table 1).

In the presence of *T. hypnorum,* adult aphid survival over the first three-day period was lower compared to the control but despite this trend, the apparent difference was not statistically significant. There was also no difference in the mean number of offspring counted after three days (Table 1).

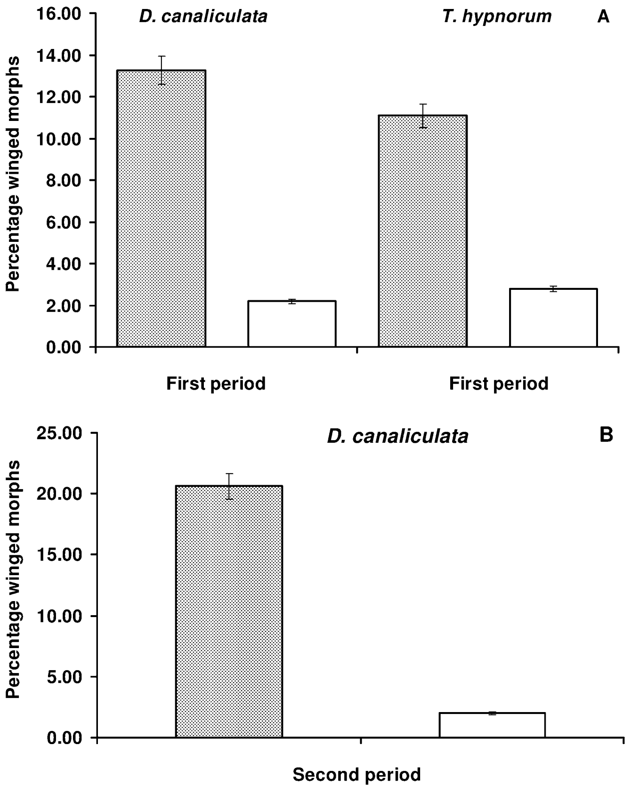

Fig 1. Percentage of winged morphs among offspring in the first (A) and second (B) three-day period in the experiment with the rove beetles *Drusilla canaliculata* (*n* = 30 lines) and *Tachyporus hypnorum* (*n* = 10 lines and first three-day period only). Full bars – predator treatment, open bars – control. Error bars refer to standard errors.

Occurrence of winged morphs

During both experimental periods, the percentage of winged offspring was higher in the *D. canaliculata* treatment than in the control (first three-day period 13.5 ± 0.69%, $Z = -4.38$, $p = 0.001$, $n = 30$, second three-day period 20.61 ± 2.26%, $Z = -4.37$, $p = 0.001$, $n = 30$, Fig. 1A, B). For the *T. hypnorum* treatment, despite the low number of replicates, the percentage of winged individuals was also higher than in the control (11 ± 1.48%, $Z = -2.02$, $p = 0.01$, $n = 10$; Fig. 1A).

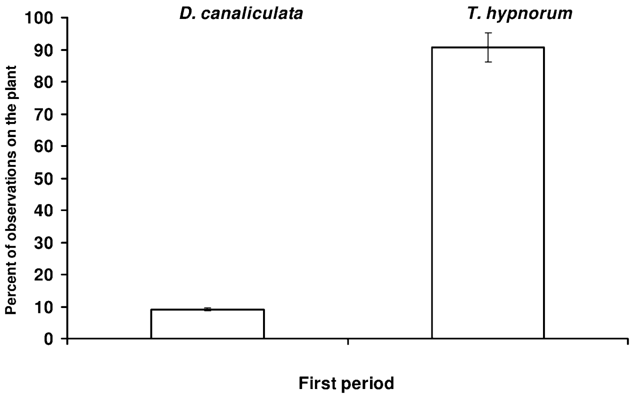

Fig 2. Percentage of *Drusilla canaliculata* and *Tachyporus hypnorum* on plants during the daily observations (average for three days). Error bars refer to standard errors.

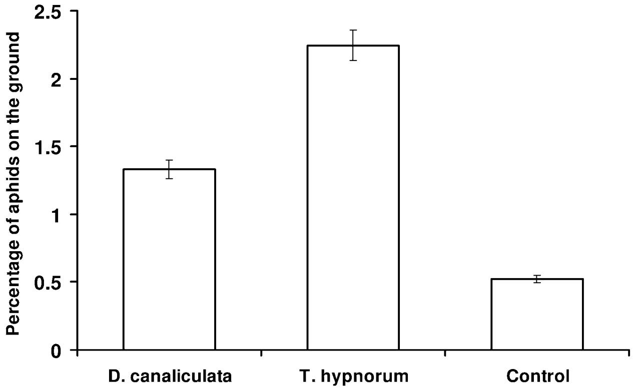

Fig 3. Percentage of aphids recorded on the ground (average for three days) in the *Drusilla canaliculata* and *Tachyporus hypnorum* treatments and the control. Error bar refers to standard errors.

Predator behaviour

The behaviour of the two predator species was noticeably different. In the three observations in the first three-day period, *D. canaliculata* spent less than 10% of the time on the plant (Fig. 2). Few aphids were observed on the ground during the daily checks (1.33 ± 0.31%). This, together with the short time spent on plants, shows that *D. canaliculata* mainly preys on aphids on the ground. In contrast, *T. hypnorum* was almost exclusively seen on the plants, either searching or feeding on aphids (Fig. 2), and the percentage of aphids that dropped from the plant on to the ground was higher (2.24 ± 0.53%) than in replicates with *D. canaliculata* (Fig. 3, $Z = -2.37$, $p = 0.01$, $n = 10$ lines with both predator treatments). The percentage of aphids on the ground in the control was very low (0.52 ± 0.09%) and much lower than in the predator treatments (comparison to *D. canaliculata* $Z = -1.97$, $p < 0.05$, $n = 30$, to *T. hypnorum* $Z = -2.19$, $p < 0.05$, $n = 10$, Fig. 3).

DISCUSSION

The results clearly demonstrate that the presence of rove beetles induces pea aphids to produce winged morphs. This is similar to other studies where predators have been found to increase wing induction in this aphid species (Kunert & Weisser, 2003). This trait modification increases the ability of aphids to disperse and to colonize new habitats, and hence has a bearing on the population dynamics of the prey, and one assumes, indirectly on the evolution of the aphids (Loxdale, 2010). Recent modelling has indeed suggested that such predator-induced dispersal can be adaptive if there is high mortality due to predation and a high correlation of the predation risk between two aphid generations (Poethke et al., 2010).

Despite the differences in feeding modes, both *D. canaliculata* and *T. hyphorum* significantly increased the number of winged morphs in the predator treatments; however, there was a difference in the percentages of winged morphs induced by the two predator species. *D.*

canaliculata is frequently found in agricultural fields and is considered to be a polyphagous predator with a preference for ant larvae (Andersen, 1991, 2000). All the predators survived and caused a significant decrease in the percentage survival of adult aphids in the first three-day period but not in the second, which indicates the predator mainly fed on offspring in this period. The number of offspring left on the plant at the end of the period was lower in the predator treatment in both three-day periods. This lower number of offspring is most likely the result of some predation of offspring by the beetle as well as the reduced fecundity of the aphids due to the production of winged morphs, as observed in several aphid species (Dixon, 1998). Nevertheless, even though the percentage of adult aphids surviving until the end of the experiment was the same in the predator treatment and the control, differences in offspring production and the percentages of winged offspring were highly significant.

The rove beetle *T. hypnorum* has also been reported as a potentially important aphid control agent in cereal fields (Kennedy et al., 1986). Apart from preying on insects, *T. hypnorum* is also a fungivore with a preference for mildew (Dennis et al., 1991). The females of *T. hypnorum* especially are unlikely to feed exclusively on aphids for long periods. Although field experiments have indicated that *T. hypnorum* may be attracted to aggregations of aphids, they may feed there on insects attracted to honeydew, on mildew growing on honeydew and on the aphids themselves (Monsrud & Toft, 1999). The absence of mildew or other fungi on our experimental plants may be the reason why only two *T. hypnorum* out of ten individuals survived until the end of the first three-day period. Of special interest is the fact that despite this high mortality and the low rate of predation, there was a clear difference in the percentage of offspring produced.

In our experiments, *T. hypnorum* spent most of the time on plants (90%), possibly also searching for fungi. As a result it caused a greater number of aphids to fall to the ground than *D. canaliculata*. This predator thus preferentially fed on the ground after brief visits to the plants. The lower percentage of aphids found below the plants in the *D. canaliculata* treatments is therefore most likely to be a result of (a) a lower rate of disturbance of aphids on the plant, resulting in fewer individuals falling from the plant; and (b), a higher rate of predation of aphids on the ground. In our experiment, there were significant numbers of aphids on the ground, showing the disturbance caused in the predator treatments compared to the control, even though adult aphid survival was not affected by the predators.

Importantly, the low rate of predation on adult aphids by both *T. hypnorum* and *D. canaliculata* give support to the hypothesis of "pseudo-crowding" put forward by Sloggett & Weisser (2002), whereby aphid wing induction through natural enemies is mediated by the disturbance caused by predators in the aphid colony, leading to an increasing number of contacts among aphid individuals. These contacts have been shown to be responsible for wing induction also at high aphid densities (Sutherland, 1969). In predators that cause significant mortality of aphids, such as the seven-spot ladybird, a high fraction of unwinged individuals escape from this predator by falling to the ground below the plant (Minoretti & Weisser, 2000). Importantly, however, not all the insects that walk on plants disturb aphid colonies sufficiently to induce wing induction (Sloggett & Weisser, 2002).

In conclusion, in the present study we have shown that polyphagous rove beetles can affect wing polymorphism in the pea aphid despite only causing a moderate level of aphid mortality. Both predators differed in their feeding mode and site of activity, but the disturbance they caused in aphid colonies was sufficient to induce the same response in the aphid as monophagous aphid predators.

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