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Role of larval tracks in reducing competition between aphid predators and the consequences for biological control

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Abstract. Predators of aphids exploit ephemeral but abundant resources. Aphid colonies are ephemeral because they hardly last longer than the time it takes the consumers to develop from egg to adult. Aphid colonies are also boom and bust resources that reach high numbers before collapsing. Many predators feed on these resources when they are abundant and as a consequence there is a high risk of cannibalism and intraguild predation. These circumstances favour the evolution of an optimal strategy for oviposition based on the assessment of aphid colonies in terms of visual or chemical information, depending on the predator species. As an adaptation to the ephemeral nature of their prey colonies, female predators should only lay eggs early in the development of these colonies. They should also refrain from ovipositing in colonies where they detect information signalling the presence of competitors. This behaviour has consequences for their use in the biological control of aphids.

Key words. Ladybird beetles, hoverflies, chrysopids, egg window, larval tracks, hydrocarbons, oviposition inhibition.

INTRODUCTION

Historians report that our ancestors already knew that ladybirds congregate in crops infested with aphids. These conspicuous and apparently voracious insects were seen as messengers of deities, sent to alleviate humans from famine due to crop failure as a result of infestation by aphids (Exell 1989). Modern research tends to confirm that ladybirds are among the natural enemies that have the greatest effect on aphid abundance (Diehl et al. 2013, Northfield et al. 2014). It is therefore understandable that attempts have been made to unravel the factors that influence the presence and abundance of ladybirds in fields. Early in his career Alois Honěk published several beautifully designed and analyzed supressed and moved at the place of studies of this problem (Honěk 1979, 1981, 1982a, b, Honěk & Rejmanek 1982). This field of investigation is still flourishing in terms of determining how landscape should be designed to favour biodiversity and crop protection (Chaplin-Kramer & Kremen 2012, Landis et al. 2000). However, even if ladybirds are able to positively respond to increased landscape complexity and contribute to the reduction in aphid abundance they are unable to always regulate their abundance or keep it below economic damage thresholds. In defence of ladybirds the economic damage thresholds are usually set at very low values (e.g. Morales et al. 2013). Field surveys of populations of several species of ladybirds indicate that eggs are laid before aphid populations peak in abundance (Hemptinne et al. 1992). In addition, ladybirds respond to increase in prey abundance by increasing oviposition up to a certain point. In the case of *Adalia bipunctata* (Linnaeus, 1758), oviposition becomes independent of prey abundance above 5 aphids/150 cm^2 (Mills 1982). As a consequence, aphid abundance is only slightly reduced by predators as shown, for example, by field surveys (Hironori & Katsuhiro 1997).

To understand the origin of the gap between expectations born from historical observations coupled with the common wisdom that so many predators must kill a tremendous number of aphids and so control them, and the results of modern research there is a need to decipher the life strategies of these predators. More precisely, one needs to go beyond a simplistic laboratory relationship that links killing potential, fecundity and prey density and ask what has shaped the optimal foraging strategies of adults. The populations of ladybirds we observe today are probably assemblages of individuals that are well adapted to their environment. That is, those that exploited prey optimally and passed this ability to their offspring. One key element in optimal exploitation is adaptation to the ecology of the prey. Being highly abundant over short periods of time, aphids attract many consumers. The risk of cannibalism and intraguild predation is therefore high (Lucas et al. 1998, Mills 1982). An additional constraint is that aphid colonies are ephemeral hardly lasting longer than the time it takes the consumers to develop from egg to adult (Hemptinne et al. 1992). Based on these constraints, a simple graphical model indicates that only a few eggs should be laid early in the development of aphid colonies, in a rather short time interval that has been named “the egg window” (Fig. 1) (Dixon 2000). The opening of the window possibly occurs when there is enough aphids for the survival of the first instar larvae of ladybirds (Dixon 2000). The closing mechanism will be discussed in the following paragraphs. The laying of eggs during the egg window is optimal in that it minimizes the risk of laying eggs in colonies already being exploited, where eggs and young larvae are likely to suffer from cannibalism or predation.

DETECTING AND AVOIDING CONSPECIFICS COMPETITORS

From the point of view of individual females that lay eggs nearby aphids, competitors are indeed a major threat to their offspring. Conspecifics eat eggs, larvae and pupae so cannibalism is a constant threat throughout development. Other species of ladybirds, spiders and other preda-

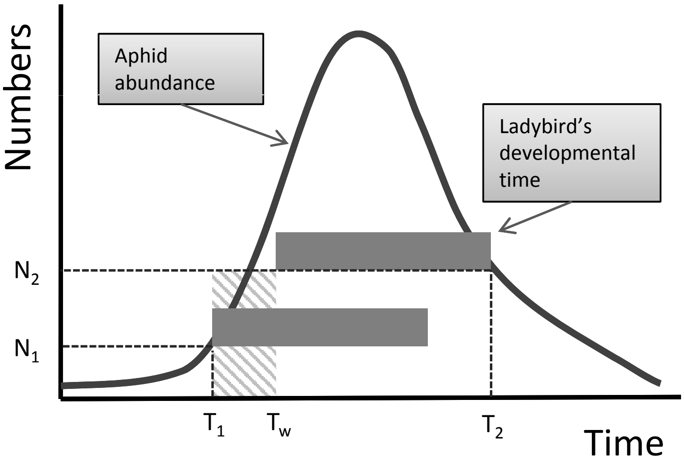

Fig. 1. Graphical model of the timing of oviposition and larval development of aphidophagous ladybirds relative to changes in the abundance of aphids in an aphid colony. Oviposition may begin at T_1 when there are sufficient aphids for the survival of first instar larvae (N_1). The minimum number of aphids to sustain fourth instar larvae (N_2) is reached at T_2. Based on the duration of ladybird development, optimal oviposition should occur from T_1 to T_w (the hatched area represents the oviposition window).

tors consume various developmental stages, which will be discussed later (Hironori & Katsuhiro 1997). Thus, females should select aphid patches where their offspring have the greatest chance of reaching adulthood. Back in 1989 we thought that ladybirds deciding where to lay eggs might use two sorts of information. First, as they tend to lay eggs early in the development of aphid colonies, it could be the age of those colonies, the phenology of the host-plant or a combination of these two. We later demonstrated that this was not the case (Hemptinne et al. 2000). Second, they may simply avoid laying eggs where there are competitors and do this by reacting to the presence of conspecifics, mainly larvae. In their presence, they refrain from laying eggs for some hours in laboratory conditions (Hemptinne & Dixon 1991, Hemptinne et al. 1992). In addition, upon perceiving the presence of conspecifics, females rapidly fly away (Frechette et al. 2003). They do this not by responding to the sight or smell but to chemicals in the tracks left by walking larvae (Doumbia et al. 1998). As explained later in this paper (p. 77) these chemicals are involved in the adhesion to plant surfaces. This makes sense because the probability of females encountering larval tracks when assessing an aphid colony is much greater than that of meeting larvae. Tracks left by larvae when walking (henceforth we will call them larval tracks) are a mixture of about 60 cuticular hydrocarbons the composition of which is species specific (Magro et al. 2010). Experiments with *Adalia bipunctata* indicate that the molecules that inhibit oviposition are produced by the anal disk at the end of the abdomen of larvae. This cocktail of molecules differs from that deposited by the tarsi (Laubertie et al. 2006). An analysis of crude extracts of 5,000 first instar larvae of *Cheilomenes sexmaculatus* (F.) led to the suggestion that Z-pentacos-12-ene is the active molecule inhibiting oviposition (Klewer et al. 2007). Larval tracks are therefore good candidates for studying the mechanism that closes the egg window.

The conclusion of Klewer et al. (2007) questions the complexity of the chemical nature of larval tracks: why 60 molecules or so if one is sufficient? The mathematical models of Martini et al. (2009) that explore the evolution of the intraspecific inhibition of oviposition by larval tracks offer an answer. According to these models, sibling cannibalism by larvae is favoured and has probably contributed to the success of families of siblings born from the same egg batches. However, females that can detect the presence of conspecifics, and so avoid cannibalism have a selective advantage. Any of the adhesive chemicals produced by larvae could trigger avoidance of occupied patches, leading to less cannibalism. However, models show that sibling egg cannibalism by larvae should always be selected for.

Therefore, selection would favour quantitative or qualitative modifications of the composition of larval tracks, as long as their adhesive function is maintained. These modifications would in turn decrease recognition by females and increase egg cannibalism until females start recognizing modified tracks. Finally, once different mixtures evolve, selection favours those females able to recognize a mixture rather than a single molecule. Martini et al. (2009) predict that females should be able to detect and respond to mixtures of molecules and that there should be genetic variability in the types of chemical profiles recognized rather than in the ability to recognize a single compound. These conclusions indicate that Klewer's et al. (2007) suggestion regarding the biologically active component of larval tracks should be re-examined and the chemical composition of larval tracks investigated further.

All the predators that feed on aphids face the same constraints as ladybirds. It is therefore not unexpected that they have also evolved strategies to cope with the ephemeral nature of their prey and the risks posed by competitors. In a series of elegant studies Eiko Kan showed that several species of hoverflies prefer to lay eggs in young colonies of aphids, which differ from old colonies in the absence of winged aphids (Kan 1988a, b, 1989, Kan & Sasakawa 1986). Recently, it appeared that female hoverflies also react to volatile compounds in the tracks of conspecific larvae (Almohamad et al. 2010). This behaviour was confirmed by field observations that showed that the hoverfly *Epistrophe nitidicollis* (Meigen) lay some eggs well before aphids' peak in abundance and eggs are rarely deposited in the presence of conspecific third instar larvae (Hemptinne et al. 1993). Chrysopids too have been particularly well studied and they avoid laying eggs where conspecific larvae have walked (Ruzicka 1994). Moreover, Ruzicka (1994) noticed that female chrysopids do not need to physically encounter larvae to refrain from laying eggs. The deterring effect is a reaction to the perception of a secretion produced by the tip of the abdomen of the larvae, which they use to attach themselves to the substrate. The same behaviour was later observed in ladybird beetles, which also do not need to physically encounter larvae to avoid laying eggs (Doumbia et al. 1998).

DETECTING AND AVOIDING HETEROSPECIFIC COMPETITORS

In the field, several species of ladybirds and other predators frequently attack the same aphid colonies. Predators are rarely prey specific and so their habitats overlap and they breed in the colonies of a wide range of different species of aphids; this is rather well documented for ladybirds (Hodek & Evans 2012, Honěk 2012). Thus, an egg batch is not only at risk of being eaten by larvae and adults of the same species but also heterospecific predators. Therefore, it should also be advantageous for females to avoid colonies of aphids already exploited by any predators, not just conspecifics. This has been confirmed by several laboratory studies. Larval tracks do indeed induce heterospecific effects, with females reacting to tracks left by larvae of other species (Magro et al. 2007, Ruzicka 1996, 2001a, b, 2006). However, heterospecific inhibition is weaker than conspecific inhibition (Magro et al. 2010). It seems logical to think that there is a greater risk of predation by species with overlapping niches because they are more likely to meet regularly. One should therefore expect strong inhibition between species that coexist. Contrary to expectation, this is not supported by experimental results (Magro et al. 2007). These authors studied three sympatric species (*Adalia bipunctata*, *A. decempunctata* (L.) and *Coccinella septempunctata* L.), which co-occur in aphid colonies. They expected the strongest inhibition between *A. bipunctata* and *C. septempunctata* because their niches overlap. However, it was found that the intensity of oviposition inhibition was independent of niche overlap. Magro et al. (2007, 2010) discovered that the chemical composition of the larval tracks of the two *Adalia* species is very similar, only differing in the proportions of some molecules. They have also shown that the difference in the chemical composition of the tracks of two species increases with the phylogenetic distance between these species. This suggests a gradual evolution of the chemical composition of the tracks, a process during which species accumulate small changes in chemical components as they diverge. This results in phylogenetic conservation of the information (Magro et al. 2010, Roelofs & Brown 1982, Symonds & Elgar 2008). Gradual evolution is unlike saltational evolution in which substantial and sudden changes generate very different blends (Baker 2002, Symonds & Elgar 2008). Gradual evolution driven by genetic drift is expected when the information conveyed is not species-specific because its variation does not contribute to reproductive isolation (Symonds & Wertheim 2005). This gradual interspecific variation probably increases intraspecific variation, which is one of the conclusions of the models of Martini et al. (2009). Therefore, larvae and adults of ladybirds are exposed to a wide range of chemical information, which may account for their ability to recognize and respond to the presence of wide range of other species.

TRACKS FROM A LARVA'S POINT OF VIEW

The study of the heterospecific effect of larval tracks revealed a potential conflict of interest between larvae and females with the former benefiting from cannibalism, but not the females. This forced us to consider larval tracks from a larval perspective. The primary reason for the evolution of these tracks is most likely that they aid locomotion on leaves. Plant tissues are protected from desiccation by the waxy cuticle on top of their epidermis (Juniper & Southwood 1986). Adhering to and moving on the cuticles of plants is challenging and to overcome this insects have evolved specific morphological adaptations of their tarsi, such as claws or bristles. The bristles are frequently wetted by an oily secretion (Dixon et al. 1990, Eisner & Aneshansley 2000). Similarly, the tarsal bristles of ladybird larvae secrete a liquid, which improves their adhesion to plants (Kosaki & Yamaoka 1996). This is advantageous for larvae in that it makes it easier for them to search for aphids but in doing so they leave tracks.

Most species of aphids cluster at the growing tips of plants although some species form smaller colonies on the underside of leaves or on twigs some distance from growing points where sap is probably richest (Dixon 1998). Larvae probably need to feed in several patches because each patch does not always contain enough aphids to sustain their full development. In addition, aphids react to larval attacks in various ways, depending on the species. They produce alarm pheromone, which induces colony dispersal (Dixon 1998). As a consequence, larvae have to move elsewhere to find prey. However, finding another colony on a plant may look like finding a small green needle in a green haystack. Larvae are guided by their negative geotropism, positive phototropism and the presence of honeydew droplets signalling the proximity of prey (Dixon 2000). However, these cues are not completely reliable so larvae may lose time by searching the same place several times. It has been shown that they are able to avoid searching previously explored places as *C. septempunctata* spends less and less time searching the same plant upon successive visits (Marks 1977). These observation were later confirmed by Meisner et al. (2011). They show that *C. septempunctata* larvae avoid searching areas marked with conspecific tracks as well as the tracks of *Harmonia axyridis* (Pallas) larvae and that this behaviour reduces the incidence of cannibalism and intraguild predation.

To conclude, larvae search much more efficiently and more survive when they avoid areas marked by other individuals. The direct benefits of this behaviour are so important that responding to tracks is likely to have a marked effect on their fitness (Meisner & Ives 2013). In addition, this behaviour sheds further light on the larva-female conflict discussed above (Martini et al. 2009). As a consequence, larval tracks might be more than a cue for females. In addition to their role as an adhesive it is possible larval tracks serve as indicators of the presence of competitors for both larvae and females. As females can discriminate between the tracks of their offspring and those of conspecifics (Martini et al. 2013) there is now a need to reconsider the evolution of larval tracks in aphidophagous predators.

It should also be noted that the tracks of larvae of ladybird beetles and chrysopids detected by females constitute a more complex system than the cues used in other cases of marking. In the present case, the markers (also the senders of information) are not those that are likely to later detect the marks (the receivers of information). This situation is a marked contrast to most of the other documented cases, in which the senders and receivers are the same. For example, female parasitoids mark hosts in which they lay an egg and so avoid laying several eggs in the same host, which would expose their offspring to cannibalism. Various phytophagous insects similarly chemically mark plants and so avoid wasting reproductive investment due to cannibalism by laying several eggs on the same parts of plants (Nufio & Papaj 2001).

LARVAL TRACKS AND APHID CENTERED FOOD WEBS

The level of activity and the distance covered by ladybird larvae searching plants for aphids is considerable and as a consequence a large proportion of the area of plants can be covered by larval tracks, which because of their chemical nature are persistent and a long-lasting source of information (Doumbia et al. 1998, Ruzicka 1997, 2002). It is likely these molecules are an important element in the functioning of aphid centered food webs.

That ladybirds and chrysopids can respond to one another's larval tracks is well documented. Of additional interest is the fact that females of several species of parasitoids can also detect and react to tracks deposited by the larvae of *C. septempunctata* and *A. bipunctata*. They avoid leaves marked by ladybird larvae, reacting specifically to three molecules, n-tricosane, n-pentacosane and n-heptacosane. As a result, percentage parasitism is significantly reduced because females do not lay eggs in areas where the risk of intraguild predation by ladybird larvae is high (Nakashima et al. 2004, 2006).

When aphids move on plants, whether to escape predators searching for prey or reach other parts of their host plant, they are likely to encounter tracks deposited by larvae. Surprisingly, pea aphids are sensitive to the presence of these tracks. They respond by producing a greater proportion of winged offspring, which avoid the impending risk of predation by dispersing and colonize other plants (Dixon & Agarwala 1999, Weisser et al. 1999). Interestingly, the black bean and vetch aphids, which are afforded some protection from attack by ladybirds because they are ant attended or unpalatable, do not respond in this way to the presence of larval tracks (Dixon & Agarwala 1999).

These results indicate that hydrocarbons deposited by ladybird larvae, and also probably those of other aphidophagous predators, influence the behaviour of all the members of aphid centred food webs. They are therefore likely to shape the dynamics of these food webs and the relationships among members of aphidophagous guilds. The implication of this for biological control still remains to be explored.

LARVAL TRACKS AND BIOLOGICAL CONTROL

As ladybirds lay eggs early in the development of an aphid colony and stop doing so as soon as they detect larval tracks their reproductive behaviour is not directly linked with the abundance of aphids (Hemptinne et al. 1992). Rather, it is shaped by the necessity to avoid initiating an early extinction of aphid colonies. Should this occur, most of their larvae would die due to starvation and cannibalism. Therefore, their numerical response to aphid abundance is restricted to a narrow range of prey densities, and rapidly reaches a plateau (Hemptinne et al. 1992). This reasoning can probably be extended to other aphidophagous predators (Hemptinne et al. 1993). By modelling the interactions between predators and aphids, taking into account the constraints imposed by the relative life span of predators and prey, it appears that these predators are unlikely to regulate the abundance of aphids (Kindlmann & Dixon 2001). At best, they reduce their abundance but probably not enough to protect crops. Biological control by ladybirds is further impaired by the reduction in percentage parasitism that results from parasitoids responding to the presence of ladybird larval tracks (Nakashima et al. 2004 and 2006). On the other hand, ladybirds increase the dispersion of aphids (Dixon & Agarwala 1999, Weisser et al. 1999). To our knowledge there is no proper assessment of the consequences of these opposite influences on the development of aphid populations and therefore damage to crops.

The foregoing does not mean that biological control is not feasible but rather that it is clearly more complicated than initially thought following the outstanding successes in controlling coccids by some species of ladybirds (Dixon 2000). A consensus has emerged among ecologists that herbivore abundance is regulated by a combination of top-down and bottom-up effects and the debate is now on their relative importance (Chase et al. 2000). Natural enemies only regulate herbivores when specific conditions are fulfilled (Schmitz 2008). Kindlmann and Dixon's model, which incorporates the effect of larval tracks on the efficiency of aphidophagous predators, predicts that the importance of top-down factors is likely to be weak (Kindlmann & Dixon 2001). Therefore, cropping systems need to minimize the potential for aphid growth either by using resistant varieties (e. g. Broekgaarden et al. 2011), carefully managing nutrients (e.g. Garratt et al. 2010, Sauge et al. 2010) or mixed cropping (e.g. Ndzana et al. 2014).

Research on biological control cannot afford to neglect individual behaviour (Kareiva 1996). The current interest in landscape management ignores what is important at the individual level and focuses on increasing natural enemy populations with the hope that this will decrease the abundance of pests. It is now widely accepted that natural enemies respond strongly and positively to management practices that increase landscape complexity.

However, very few studies assess how this positive response translates into crop protection (Bianchi et al. 2006, Chaplin-Kramer & Kremen 2012). There is now a need to determine how to assemble communities of natural enemies that complement each other so that their killing power adds up and complements bottom-up mechanisms of control. In order to achieve this objective, the species in these communities should be far less sensitive to interspecific than to intraspecific competition (Northfield et al. 2010). For the biological control of aphids, we suggest that a way forward would be to assemble species that react more strongly to their species' larval tracks (intraspecific inhibition of egg laying) than to other species' tracks (heterospecific inhibition). This raises the question, is it possible?

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