

# INTERACTIVE-WEB OF FACTORS GOVERNING EFFECTIVE NATURAL ENEMY FORAGING BEHAVIOR: OVERVIEW OF FOOD RESOURCES AS A CRITICAL COMPONENT

D. M. OLSON<sup>1</sup>, W. J. LEWIS<sup>1</sup>, and K. TAKASU<sup>2</sup>

<sup>1</sup>USDA, ARS, Crop Protection and Management Research Unit  
P. O. Box 748  
Tifton, GA 31793, U.S.A.  
dolson@tifton.usda.gov, wjl@tifton.usda.gov

<sup>2</sup>Faculty of Agriculture, Kyushu University  
Fukuoka 812-8581, Japan  
takasu@brs.kyushu-u.ac.jp

## ABSTRACT

Effective biological control of pests is determined by the abundance, retention and searching efficacy of natural enemies. To assure their reproductive fitness, natural enemies such as predators and parasitoids must effectively balance competing resource needs such as an adequate frequency of encounter with prey and hosts for reproduction, requirements of food other than prey and hosts, and other needs such as shelter and mates. The other food requirements consist primarily of short-term nutritional needs and are often separate from the target pest, such as plant nectar in the case of parasitoids. The appropriate quality, adequate availability, and detectability of these non-mutually exclusive requirements in the target area, strongly affect the natural enemy's retention and pest foraging efficacy. We present a conceptual model of factors determining eventual foraging behavior of parasitoids that would guide empirical studies of the resource needs of parasitoids and other insects. An increased understanding of the interplay of the resource web with the habitat would allow us to leverage this information to design habitat management practices that allow the use of natural enemy species for biological control in a consistent and reliable manner.

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## THE IMPORTANCE OF ADULT FOOD FOR PARASITOIDS

The importance of adult food for natural enemy species such as predators and parasitoids has been recognized for decades. Parasitoid species (species that lay their eggs on or in other insect species, eventually killing them) are often used as models of natural enemy foraging behavior because of the relatively direct link between their foraging behavior and reproductive fitness when compared with predator species. Numerous laboratory studies have shown that suitable food sources can substantially increase longevity and fecundity of adult hymenopteran and dipteran parasitoids (reviews in Heimpel *et al.* 1997; Lewis *et al.* 1998). It is now appreciated that the consumption of non-host food can influence many other aspects of parasitoid biology such as egg viability, diapause in progeny, foraging decisions, searching

efficiency, the onset and rate of egg resorption, primary sex ratio of progeny, flight initiation, and timing of flight. As a consequence non-host food can affect parasitoid and host dynamics, competitive interactions and niche partitioning among parasitoid species, productivity in laboratory cultures, and the probability of parasitoid establishment in classical biological control (Jervis 1998).

Parasitoids can be separated into four broad categories in terms of adult feeding requirements: (1) Pro-ovigenic species where adult feeding is needed for maintenance but not for egg production (e.g., Jervis and Kidd 1996). Very few examples exist of truly pro-ovigenic species (Jervis *et al.* 2001). (2) Synovigenic species that do not host-feed but feed on non-host food for maintenance and egg production (e.g., *Microplitis croceipes* Cresson, Hymenoptera: Braconidae) (Takasu and Lewis 1993). (3) Synovigenic species whereby females host-feed for egg production and both males and females non-host feed for maintenance (e.g. *Ooencyrtus nezarae* Ishii [Hymenoptera: Encyrtidae]) (Takasu and Hirose 1991), (4) Synovigenic species whereby females host-feed for both maintenance and egg production (e.g., *Bracon hebetor* Say, Hymenoptera: Braconidae) (Jervis *et al.* 1994; Takasu unpublished). Thus, the basic drive for adult food sources will vary with the particular parasitoid species, which is determined by their genetic traits. The mouthparts and the size of the parasitoid as determined by their genetics are also important in their ability to access both host and non-host food sources. For host-feeding species, the host materials are mainly obtained directly from the opening of the puncture wound caused by ovipositor insertion, or for some species, through production of so-called feeding tubes that allow them to host-feed on less accessible hosts (e.g. Heimpel *et al.* 1997). Host materials mainly provide parasitoids with protein, vitamin and salt resources for reproduction, whereas plant nectars and honeydew provide energy resources mainly from the sugars present, although amino acids are also present (Harborne 1993). Several taxa have specialized mouthparts, referred to as a 'concealed nectar extraction apparatus' (CNEA), for reaching floral nectar (Jervis 1998; Quicke 1997). The CNEA's of parasitoids vary in length and are primarily utilized to extract nectar contained in long or deep tubular flower corollas that are not accessible to larger sized parasitoids or those lacking a CNEA. Those species lacking a CNEA appear capable of everting their labiomaxillary complex far enough to exploit nectar contained in very short, narrow, tubular flower corollas or for host feeding from the ovipositor puncture wound (Jervis 1998). Therefore, the morphology of parasitoid mouthparts and parasitoid size will influence the accessibility of both host and non-host food sources for parasitoid species.

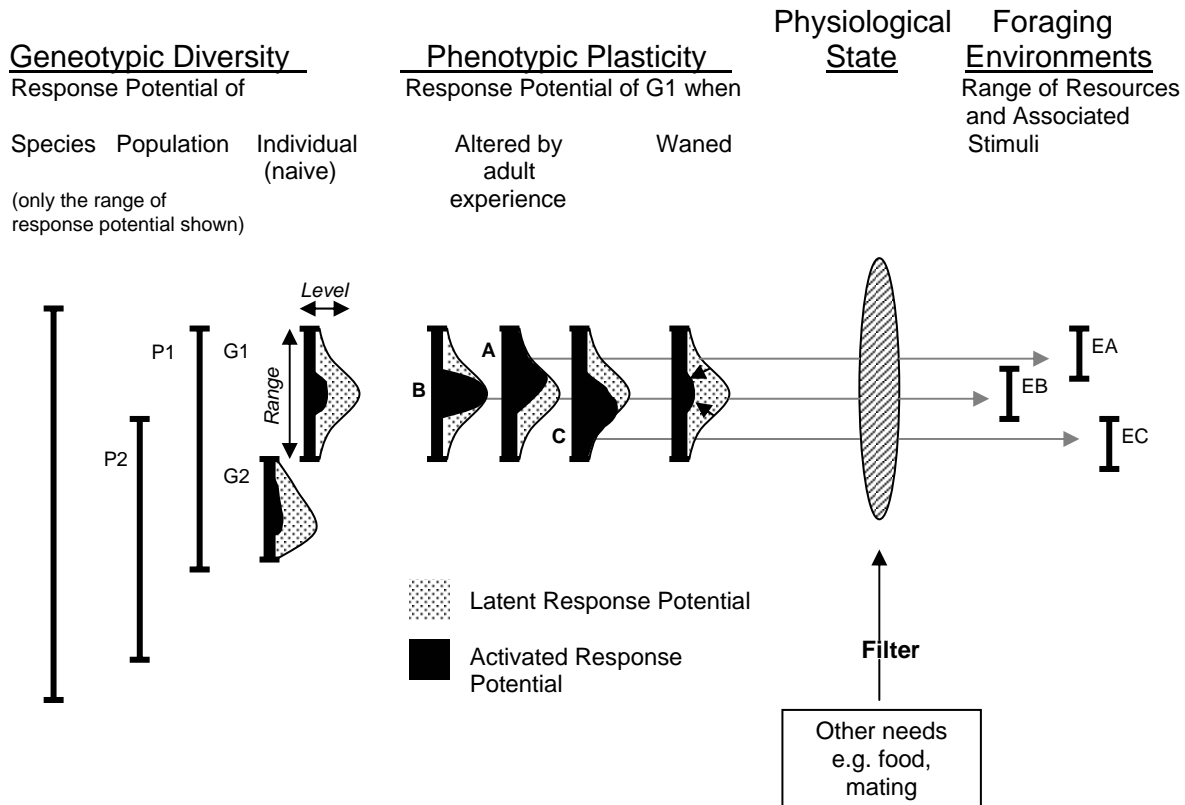
## RANGE OF RESOURCE NEEDS

In addition to adult food, parasitoids also need hosts, shelter and mates throughout their life cycle, and they must balance these needs by effectively responding to stimuli associated with each of these resources. The need for each of these resources may be more important at different times and/or seasons which would depend on the life cycle, and informational and physiological state of the parasitoid. Although little is known about the distribution of parasitoids with respect to their resource needs, several studies have shown innate and directed search by a range of species in response to food-related signals (Patt *et al.* 1997; Stapel *et al.* 1997; Wäckers and Swaans 1993). These responses can be similar to those towards host-related signals shown

by some parasitoids (e.g., Lewis *et al.* 1990), but may also be specific to the task of food foraging (Olson *et al.* 2003; Wäckers *et al.* 2002). Learning also plays a significant role in the search for food as well as hosts, and parasitoids are able to use different visual and olfactory cues in accordance with their physiological state and previous experience (Iizuka and Takasu; Lewis and Takasu 1990; Takasu and Lewis 1996; 1999; Tertuliano *et al.* 2004; Sato and Takasu 2000; Wäckers and Lewis 1994). Learning can be very useful as the quantity and quality of food resources often varies across plants or within the plant. This variation may be caused by factors such as the presence of other nectar-feeding species, the spatial and temporal secretion of nectar, and the nutritional value, repellency, or toxicity of different nectars (Jervis *et al.* 1993). Tertuliano *et al.* (2004) found that females that had learned to associate a particular odor with food rewards will continue to elicit food-searching behaviors after several unrewarding experiences with the odor when they are very hungry, whereas females that were less hungry ceased to respond to the learned odor after only two unrewarding experiences. Interestingly, food-searching responses of the less hungry females were recovered after a single exposure to the odor with a food reward (Tertuliano *et al.* 2004). Adult parasitoids are, therefore, predicted to respond to resource stimuli that are more strongly associated with their current needs and in accordance with prior experience.

The sources of variation discussed above are not mutually exclusive; rather they overlap extensively, even within a single individual. Therefore, it is important that we have a means of clearly delineating the sources, roles, and interacting effects of the variations. The conceptual model of Lewis *et al.* (1990) for collectively describing the various foregoing factors and their sum effect on foraging behavior of parasitoids are presented in Fig. 1. The three major sources of intrinsic variability in the behavior of foraging female parasitoids are represented: (1) genetic diversity among individuals, (2) phenotypic plasticity within individuals because of experience, and (3) the parasitoids's physiological state relative to other needs. The behavior manifested is also dependent on the foraging environment, so the final foraging effectiveness of a parasitoid is determined by how well the parasitoid's net intrinsic condition as a result of these three components is matched with the foraging environment in which it operates.

In Fig. 1, suppose there is a hypothetical parasitoid species and three foraging environments: EA, EB and EC. Under genotypic diversity the response of two representative individual genotypes,  $G_1$  and  $G_2$  are shown. This response potential consists of the genetically fixed maximum range of usable foraging stimuli and ultimate level with which the parasitoid could respond to the stimuli (the total darkened area plus shaded area). This maximum level of response to the array of stimuli is shown as a curve, which indicates that the maximum response level varies with different stimuli in its range. As reflected by the different range and curve configurations for  $G_1$  and  $G_2$ , the response potential may vary substantially among individuals within a population (Hoy 1988; Olson and Andow 2002; Prévost and Lewis 1990). The activated response potential of  $G_1$  and  $G_2$  (darkened area) that could be realized at any given time is somewhat less than their overall potential and depends on the experience of the individual. The balance of the response potential that is not currently activated due to the experience of the individual is the latent response potential (shaded area). In the case of naive individuals, the active response potential is that portion that is inherently activated and this does not require experience before it can be manifested. The stimuli of the three representative foraging environments, EA, EB and EC are all within the range of population P1; fur-



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**Figure 1.** Factors determining eventual foraging behavior of a parasitoid. From Lewis *et al.* 1990.

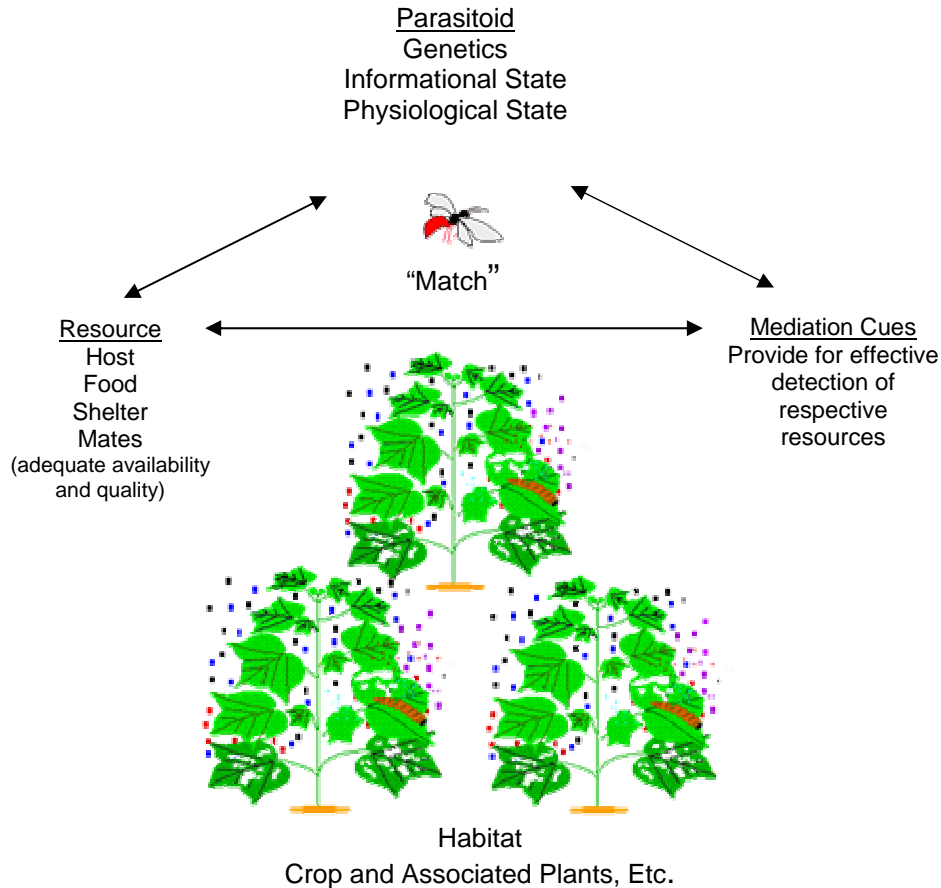
thermore, the response ranges of individuals with representative genotype  $G_1$  are best aligned with these environments, but the inherent preference of the genotype  $G_1$ , as indicated, is for environment EB.

As stated previously, a parasitoid's physiological state relative to other needs such as food, mating and hosts can strongly influence their foraging behavior. Thus, as shown in Fig. 1, the physiological state of the parasitoid relative to other needs can be considered as a gateway that filters the detection and responses to foraging stimuli based on priority of the needs.

### MATCHING PARASITOIDS WITH THEIR RESOURCE NEEDS

The range of needed resources of parasitoids that often differ in time and space suggests that habitats managed year-round to foster efficiency in the appropriate interplay of resource acquisition would ensure that the basic requirements are met. The resources must have quality and be adequately available (Fig. 2). Mediating cues of the resource are also needed to ensure detectability (Fig. 2). Plants may help parasitoids to increase availability, accessibility and detectability of resources needed by parasitoids. Many plants have traits that help to guide parasitoids to their hosts through chemical signaling in response to herbivory, and parasitoids have been shown to use the plant chemical signaling together with host derived chemicals and visual cues to orient to these plants (Turlings and Wäckers 2004; Wäckers 1994; Wäckers and Lewis 1994) at time in a very host-specific manner (DeMoraes *et al.* 1998). Cot-

ton (*Gossypium herbaceum* L.) and castor bean (*Ricinus communis* L.) plants not only emit volatiles to attract parasitoids but also increase their production of extrafloral nectar when attacked by herbivores (Wäckers *et al.* 2001).



**Figure 2.** Model of retention and effective performance of biological control agents.

These plants provide parasitoids with the chemical signaling needed to locate the plants and both the host and food resources that they need. Stapel *et al.* (1997) found that hungry parasitoids had higher retention times within a cotton patch when both food and hosts were present than when only hosts were present. Furthermore, parasitoids can improve their rate of food and host location through learning from prior experience (Olson *et al.* 2003; Takasu and Lewis 1993). At larger spatial scales (e.g., kilometers) little is known about how parasitoids locate needed resources (food, hosts, mates and shelter). However, it is likely that having resources available in relative close proximity would provide the most efficiency in their acquisition, especially for species that move only short distances. Thus, the designs of the individual plants supporting the various needed resources are important in foraging efficiency and retention as well as their spatial distribution in the landscape and the latter would depend on the movement behavior of particular species.

Although some crop plants supply more than one of the needed resources of parasitoid species, many requirements must be obtained elsewhere. These associated plants (Fig. 2) may be other crop plants, or vegetative patches within the landscape (e.g., woodlots, hedgerows, fencerows). In a recent study, Wäckers and Steppuln (2003) were able to demonstrate that parasitoids collected adjacent to a flowering field border had higher sugar levels as compared to individuals collected in control fields. Moreover, between 55% and 80% of the collected parasitoids contained honeydew-specific sugars, indicating the prevalent use of this sugar source. In another study of field borders, Olson and Wäckers (unpublished data) were able to show that the larval parasitoid, *Meteorus autographae* Muesebeck (Hymenoptera: Braconidae) captured in naturally regenerated field edge habitat constructed for Bob White Quail habitat along the edge of a cotton field had levels of sugar in their guts that were about equal to those found in non-fed (control) females, whereas those captured in a Cahaba White Vetch experimental plot at the same time of year had about four times the levels found in the Quail and control samples. These samples were taken early in the season prior to the cotton plant's secretion of nectar or when crop plant sugar sources were very limited. In addition, the crop plant at this stage is very small and the microclimate in the field often harsh for many insect species. The early growing stage of crops can include conditions of high heat and low relative humidity which precludes many insect species from early colonization (e.g., Dyer and Landis 1996). These results indicate that having appropriate associated plants available near the crop plant can be crucial to providing several of the parasitoid's needed resources.

## CONCLUSIONS

A conceptual model of factors determining eventual foraging behavior of parasitoids helps to guide empirical studies of the resource needs of parasitoids and other insects. Understanding the interplay of the resource web with the habitat allows us to leverage this information to design habitat management practices that allow the use of natural enemy species for biological control in a consistent and reliable manner. Year-round provisioning of resources is needed to account for the range of resource needs of species throughout their lifetime. Understanding the mechanisms involved in the various resource needs of parasitoids and other insect species and their effective acquisition would enable practitioners of biological control to ensure that species-specific resource needs are met.

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## IMPACTS OF SUGAR FEEDING ON PARASITOID BEHAVIOR IN THE FIELD

Jana C. LEE<sup>1</sup> and George E. HEIMPEL<sup>2</sup>

<sup>1</sup>Department of Entomology, University of California–Davis  
Davis, CA 95616  
jctlee@ucdavis.edu

<sup>2</sup>Department of Entomology, University of Minnesota  
St. Paul, MN 55108  
heimp001@umn.edu

### ABSTRACT

Diversifying agroecosystems with floral habitats has the potential to conserve natural enemies and enhance pest control. In the laboratory, many adult parasitoids readily utilize nectar sources that have substantially increased their longevity and parasitism rates. However, in the field, does the floral habitat retain parasitoids locally so they exert greater control on pests? We studied the post-feeding and aggregation behavior of *Diadegma insulare* (Cresson) (Hymenoptera: Ichneumonidae), an abundant parasitoid of the diamondback moth, *Plutella xylostella* (L.) (Lepidoptera: Plutellidae). First, sugar-fed and hungry *D. insulare* were compared for retention inside cabbage plots (12 x 20 m in 2003; 9 x 15 m in 2004). Sugar-fed and hungry wasps were marked, released inside the plot and recaptured outside the border over 1-3 days. Sugar feeding did not appear to affect dispersal behavior of *D. insulare* in the field. Second, we determined whether sugar sources attracted/retained parasitoids in the crop field by monitoring the abundance of *D. insulare* inside cabbage plots (12 m x 20 m) bordered by 3 m wide buckwheat strips and cabbage plots devoid of floral habitat. For three summers, *D. insulare* were monitored within plots using sticky traps, and the number of adults captured in plots with and without floral borders did not differ. Neither experiment showed evidence that buckwheat flowers increased retention of *D. insulare*.

### INTRODUCTION

Establishing nectar-producing floral habitats within or near crop fields can provide adult parasitoids with sugar and reduce risks and energetic costs of commuting between food and host sources (Lewis *et al.* 1998). Parasitoids orient towards nectar odors (Patt *et al.* 1999; Wäckers 2004) and floral colors (Wäckers 1994). Thus, the presence of sugar sources in a host patch should retain parasitoids locally. Host patches of five cotton plants with extrafloral nectar and sucrose have retained *Microplitis croceipes* (Cresson) (Hymenoptera: Braconidae) for 31.5-34.5 minutes whereas host patches without sugar retained parasitoids for 14 minutes (Stapel *et al.* 1997). Not surprisingly, parasitoids have been found to aggregate more among crops with floral vegetation (Berndt *et al.* 2002; Irvin *et al.* 2000; Stephens *et al.* 1998) or sugar

sprays (Jacob and Evans 1998) than crops without such resources. Also, parasitoid abundance (Platt *et al.* 1999) and parasitism rates (Baggen and Gurr 1998; Tylianakis *et al.* 2004) have been observed to decline in the crop as distance from a floral border increased.

Contrary to expectations, an increase in parasitism rates does not always occur in the presence of floral nectar (Berndt *et al.* 2002; Irvin *et al.* 2000). The expectation that supplementary nectar improves biological control, may not apply if parasitoids have sufficient sugar sources without supplemental floral nectar, parasitoids do not feed from the nectar, or if parasitoid longevity and fecundity are not improved with nectar feeding (Heimpel and Jervis 2005). The parasitoid *Diadegma insulare* has been studied for some of these criteria; it attacks diamondback moth larvae *Plutella xylostella* on cruciferous plants. Presence of supplementary floral nectar sometimes increased feeding by *D. insulare* (Lee *et al.* in prep), increased longevity and the number of eggs laid per female per hour (Lee and Heimpel in prep), but had little impact on resulting parasitism rates (Lee and Heimpel in review). The lack of correlation between feeding and parasitism puts into question whether the behavior of *D. insulare* following sugar feeding may differ from expected.

While sugar-fed parasitoids may search for hosts immediately near the sugar source, parasitoids may eventually disperse to other host patches. Feeding provides ample carbohydrate reserves (Fadamiro and Heimpel 2001; Lee *et al.* 2004; Olson *et al.* 2000) that fuel flight and may induce dispersal and not retention. Some studies support increased flight activity with sugar feeding. In flight chambers, *Trichogramma minutum* Riley (Hymenoptera: Trichogrammatidae) given honey showed a small but significant 6% increase in the propensity to fly than starved females (Forsse *et al.* 1992). Whether this would reflect a tendency for dispersal flight is not known. In a field study, *Hyposoter* sp. (Hymenoptera: Ichneumonidae) wasps were marked with the trace element Rubidium if they fed on marked floral nectar sources; and fed wasps were captured more frequently at 75 m than at 6 m or less from marked plants (Freeman-Long *et al.* 1998).

Parasitoids may also disperse to increase their fitness. First, parasitoids that cannot discriminate between hosts that have been parasitized may leave a patch early than risk superparasitism and wasting eggs (Rosenheim and Mangel 1994). *D. insulare* appears to lay eggs randomly among hosts in the field without avoidance of superparasitism (Lee and Heimpel 2004). Or, *D. insulare* may be dispersing to other patches to avoid inbreeding since this species can have severe inbreeding depression due to its single-locus complementary sex determination (CSD) (Butcher *et al.* 2000). Parasitoids may also disperse to avoid positively density-dependent hyperparasitism (Ayal and Green 1993). Or parasitoids may 'spread the risk' in case of widespread mortality occurring in a single host patch, but the conditions for using risk spreading over space are rather stringent (Hopper 1999).

While sugar feeding can benefit parasitoids including *D. insulare*, the impacts that floral sources have on longer-term parasitoid behavior are not known. Our objectives were to determine how sugar feeding influences *D. insulare*'s dispersal in and out of a host patch at a greater spatial and temporal scale: 12 x 20 m or 9 x 15 m cabbage plot for 8 hours or longer. Also, we compared the number of *D. insulare* in cabbage plots with/without floral borders for evidence of enhanced attraction/retention.

## MATERIALS AND METHODS

### FIELD PATCH STUDY

We conducted a mark-recapture experiment on sugar/nectar-fed and hungry *D. insulare* to study retention in a field plot. A 12 x 20 m cabbage plot with 12 cabbage rows was planted with seedling transplants on 5 June 2003 within a soybean field at the Rosemount Field Station. Three mark-recapture trials were started on 9, 15 and 23 September 2003. Experiments were conducted late in the season since natural populations of *D. insulare* had declined, and possible sugar sources such as honeydew from soybean aphids in the surrounding field were not available. Four large sticky traps were set up along each border of the plot, 16 traps total, during the 1<sup>st</sup> trial. Seven sticky traps were set up per side, 28 total, during the 2<sup>nd</sup> and 3<sup>rd</sup> trials (Fig. 1).

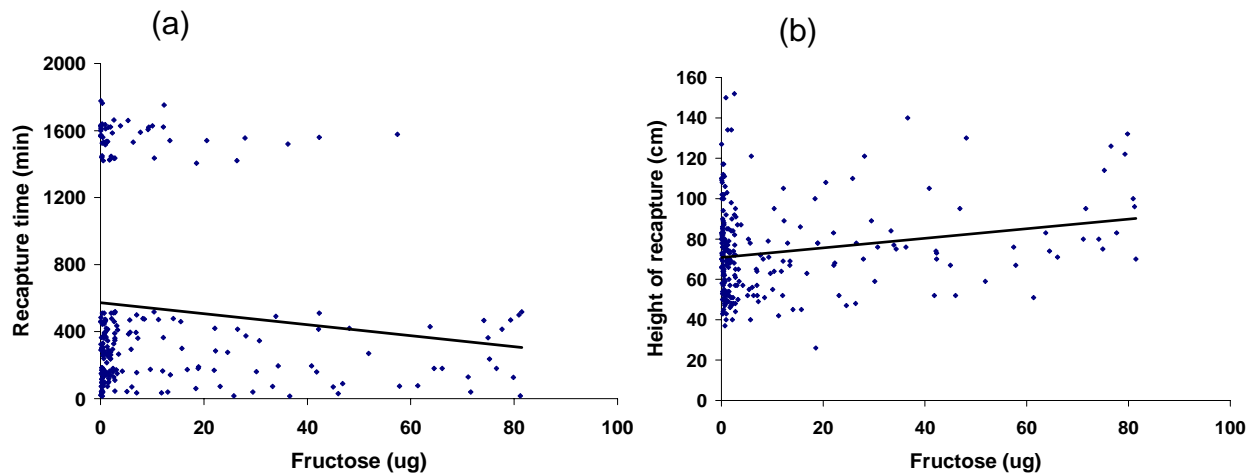


Figure 1. Field plot in experimental soybean field at the Rosemount Field Station.

Sticky traps were 1 x 0.91 m in size composed of grey window screening (mesh size 1 x 2 mm). Traps stood about 40-50 cm aboveground and ~2 m from the plot edge to increase the probability of catching dispersing wasps rather than wasps foraging low for hosts or seeking shelter. Screens were stapled to 4 x 4 x 183 cm wooden stakes pounded into the ground. At 8 am, an aerosol formula of Tangle-Trap<sup>®</sup> was sprayed onto the screening. Tangle-Trap<sup>®</sup> was reapplied at noon and at the end of the day.

In the following year (2004), a 9 x 15 m cabbage plot with 9 cabbage rows was handplanted with seedlings on 3 June 2004 in the St. Paul Agricultural Experimental Field. Field corn and soybeans were the predominant surrounding vegetation. Weeds were removed by hand and obvious floral nectar sources were not apparent. Mark-recapture trials were started on 18, 24 and 31 July 2004 before natural populations of *D. insulare* had built up. Seven sticky traps were set up along the length of the plot and six along the width, 26 traps total.

In 2003, we used *D. insulare* from our laboratory colony (1<sup>st</sup>-3<sup>rd</sup> generation) started in August 2003 from wild populations. In 2004, we used laboratory reared colonies from both Minnesota and Apopka, Florida. To recruit large numbers of wasps, all wasps emerging 1-5

days prior to the release date were randomly assigned to a 30.5 cm<sup>2</sup> mesh cage (Bug Dorm, BioQuip®) designated as the hungry or fed treatment. Fed wasps were given buckwheat flowers, 20% sucrose or 20% honey solutions *ad libitum*. Since *D. insulare* die in 1-2 days without food (Lee *et al.* 2004), hungry wasps were initially maintained on the same sugar foods until 20 h before release when only water was provided. *D. insulare* fed buckwheat nectar metabolize most of their gut sugars when starved for 12-36 h (Lee 2004). Wasps emerging within 20 h of release were also used, those placed in the hungry treatment did not have any opportunity to feed. Before release, wasps were sexed and aspirated in groups of 50 into 1 oz. plastic vials. To mark wasps, they were first chilled for 5 minutes at -10° C, transferred into a 1 oz. plastic cup with 6 mg of pink or yellow fluorescent powder (Day-Glo Color Corp.) and tumbled. This procedure moderately dusts *D. insulare* without affecting their longevity, and the powder remains visible in their thoracic crevices 13-16 days later despite the wasps grooming themselves (Lee 2004).

Wasps were released in the center of the cabbage plot at 9 am. Some overdusted wasps died or moved little. We counted dead/inactive wasps at the release site at 10 am and subtracted this number to estimate the number of wasps released. About 500 diamondback larvae were sprinkled onto cabbage plants to ensure hosts for females. Sticky screens were monitored every half hour after release of wasps, marked *D. insulare* were collected and frozen with the time, trap number, and height from ground recorded. For the 1<sup>st</sup> trial in 2003, *D. insulare* were monitored from 9:00-17:00 on day 1 only. For the 2<sup>nd</sup> trial, *D. insulare* were monitored from 9:00-18:00 on day 1, 10:30-15:00 on day 2, and 12:00-14:00 on day 3. During the 3<sup>rd</sup> trial, monitoring occurred from 9:00-18:00 on day 1, and 10:00-12:00 on day 2. In trial 1 of 2004, wasps were monitored from 9:00-18:00 on day 1, and 9:00-10:00 on day 2; in trial 2 from 9:20-18:00 on day 1, and 8:20-15:00 on day 2; in trial 3 from 9:00-19:00 on day 1, and 8:00-10:00 on day 2. Dead wasps collected during the morning of the second and third day had likely been captured the previous evening because *D. insulare* are not active at night or early morning (Idris and Grafius 1998). We therefore estimated that they had been caught by 8 pm of the previous day, which is the latest time that *D. insulare* have been reported active (Idris and Grafius 1998). Wind speeds exceeding 8.5 m/s prevented us from monitoring wasps for a longer duration during trials 1 and 3 in 2003. Collected wasps were frozen at -80° C until egg load determination and biochemical analyses could be done for lipid, glycogen, fructose and total sugar levels as described in Lee *et al.* (2004). Prior to biochemical analyses, the Tangle-Trap® was removed from wasps using the following protocol. Each wasp was vortexed for 30 s in a 1 oz. plastic cup with 0.5 ml of De-Solv-it® degreasing solvent and then vortexed in 2 ml of distilled water for 30 s and again with new water. Next, each wasp was transferred into a clean cup and vortexed with distilled water twice and blotted dry on a Kimwipe®.

The proportion of recaptured water-fed and sugar-fed wasps were analyzed by trial in a Chi-square analysis. The effect of treatment (water or sugar) on height and time of recapture were compared using an ANOVA. Effect of treatment on egg load, lipid, glycogen, fructose and sugar levels of wasps were tested in an ANCOVA with wing length as a covariate. Impact of feeding as measured by fructose levels (independent variable) on time and height of recapture and remaining egg load was tested with linear regressions. Analyses were conducted in JMP® (SAS Institute 1995).

## AGGREGATION NEAR BUCKWHEAT

We monitored the abundance of *D. insulare* in 12 x 20 m cabbage plots with and without 3 m wide borders of buckwheat *Fagopyrum esculentum* (Moench) as described in Lee and Heimpel (in review). In 2001, four buckwheat and four control plots were at least 67 m apart from each other and embedded in a soybean field. Another four buckwheat and control plots were spaced at least 800 m apart, embedded in separate soybean fields. These plots are referred to as nearby and isolated. In 2002 and 2003, eight cabbage plots were planted at least 800 m apart and in separate soybean fields. Cabbage plots were not treated with insecticide, and planted in new sites each year.

In 2001, four yellow sticky traps (Pherocon®AM) were set up randomly per plot. Traps were 30 cm aboveground and between two cabbage plants to collect *D. insulare* as they moved along a cabbage row. Traps were collected after one week in the field on 16, 23, 30 August 2001 from nearby plots and 14, 21, 28 August from isolated plots. In 2002-2003, six yellow sticky traps were set up per plot at random points and in the field for one week. Traps were collected on 22, 28 July, 5, 12, 19, 26 August and 2 September in 2002, and on 14, 21, 28 July and 4, 12, 18, 26 August in 2003. We tested the effects of treatment, year, and treatment x year interactions on the total number of *D. insulare* captured per trap using ANOVA on square-root transformed data. Since trap collections occurred at different times each year, only traps collected during the last three weeks of August were included in the three-year analysis. Male and female *D. insulare* were distinguished in 2002 and 2003. Average numbers of females captured per weekly trap over 7 weeks were tested in a similar ANOVA described earlier.

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## RESULTS AND DISCUSSION

### FIELD PATCH STUDY

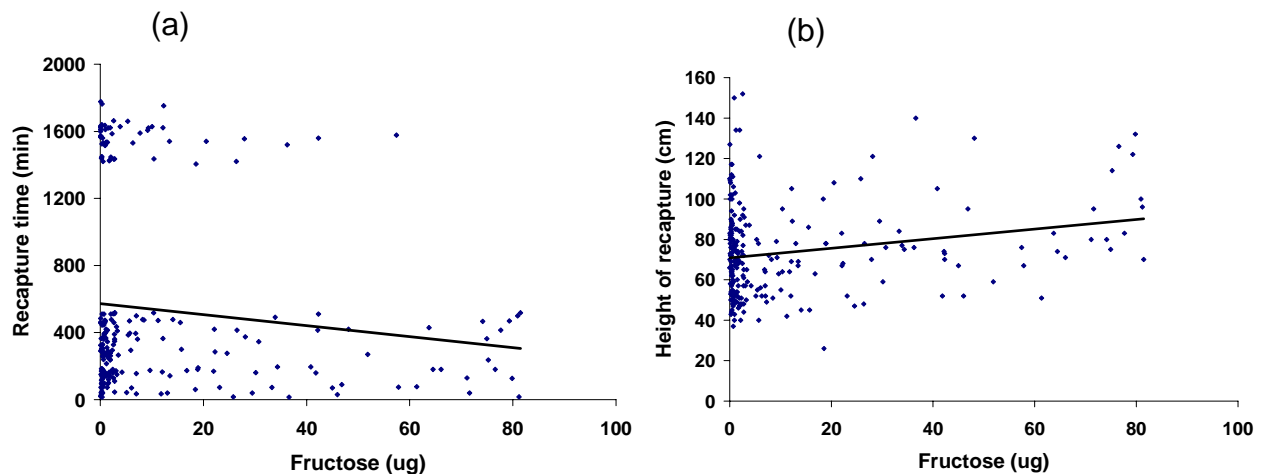
The field patch study did not support the prediction that feeding would lead to either greater retention or dispersal. Water- and sugar/nectar-fed wasps did not have different nutrient levels in the 1<sup>st</sup> and 2<sup>nd</sup> trial in 2003 and in 3<sup>rd</sup> trial in 2004 (Table 1) to adequately test treatment effects. In trial 2 of 2003, more water-fed than sugar-fed *D. insulare* were recaptured outside the plot but these wasps did not differ in their lipid, glycogen, total sugar and fructose levels. Since there was no physiological difference between water- and sugar-fed wasps, we cannot conclude that feeding enabled wasps to remain in the patch longer. When water and sugar-fed wasps differed physiologically in the 3<sup>rd</sup> trial of 2003, and 1<sup>st</sup> and 2<sup>nd</sup> trials of 2004 (Table 1), there were no significant differences in recapture rates, time and height of recapture, and number of eggs remaining in ovaries. Marginal differences were observed twice. Water-fed wasps had marginally greater egg loads than sugar-fed wasps ( $p=0.062$ ) in trial 1 of 2004. This may suggest that feeding enabled more ovipositional activity, but the analysis was based on only four females. Sugar-fed wasps were recaptured marginally later than water-fed wasps in 3<sup>rd</sup> trial of 2003 ( $p = 0.099$ ). This could indicate that being fed enables wasps to remain longer in a host patch (Stapel *et al.* 1997), but can also occur if sugar-fed wasps simply lived longer and were recaptured later.

**Table 1.** Proportion of recaptured sugar/nectar-fed versus water-fed *D. insulare*, average time of recapture, height of capture, number of eggs in ovaries, lipid, glycogen, total sugar and fructose levels of wasps.

	Trial 1-2003	Trial 2-2003	Trial 3-2003	Trial 1-2004	Trial 2-2004	Trial 3-2004
Recapture—Chi-square test						
Water	1.4% 3/221	8.45% 41/485	9.3% 20/215	2.19% 8/365	8.13% 33/406	6.22% 25/402
Sugar	2.0% 4/201	4.56% 16/351	10% 35/350	1.91% 7/366	9.24% 28/303	6.60% 32/485
	X <sup>2</sup> =0.26 p=0.61	X <sup>2</sup> =5.08 p=0.02	X <sup>2</sup> =0.07 p=0.79	X <sup>2</sup> =0.07 p=0.79	X <sup>2</sup> =0.27 p=0.60	X <sup>2</sup> =0.05 p=0.82
Time of recapture (min)—ANOVA						
Water	121.3 ± 102.8	648.5 ± 109.0	451.5 ± 92.1	112.5 ± 45.5	689.3 ± 105.9	251.7 ± 55.2
Sugar	71.75 ± 42.4	1131.3 ± 174.4	645.5 ± 69.6	184.0 ± 48.7	686.5 ± 116.2	293.6 ± 41.8
	F <sub>1,5</sub> =0.25 p=0.64	F <sub>1,55</sub> =5.5 p=0.02	F <sub>1,53</sub> =2.8 p=0.099	F <sub>1,13</sub> =1.2 p=0.30	F <sub>1,59</sub> <0.01 p=0.99	F <sub>1,55</sub> =0.38 p=0.54
Height of recapture (cm)—ANOVA						
Water	105 ± 11.1	85.3 ± 5.1	85.3 ± 5.1	59.3 ± 3.7	64.2 ± 2.9	57.6 ± 2.5
Sugar	113.8 ± 9.0	91.3 ± 3.8	91.3 ± 3.8	60.4 ± 5.2	65.1 ± 3.1	59.5 ± 3.3
	F <sub>1,5</sub> =0.39 p=0.56	F <sub>1,55</sub> =0.13 p=0.72	F <sub>1,53</sub> =0.90 p=0.35	F <sub>1,13</sub> =0.04 p=0.85	F <sub>1,59</sub> =0.05 p=0.82	F <sub>1,55</sub> =0.18 p=0.67
Eggs in ovaries—ANOVA wing length as covariate						
Water	47, female n=1	17.4 ± 3.04, n=17	14.1 ± 3.9, n=7	31.5 ± 11.5, n=2	33.0 ± 5.7, n=9	25.0 ± 3.4, n=6
Sugar	17 + 3, n=2	17.5 ± 8.9, n=2	8.5 ± 3.1, n=11	28.0 ± 5.0, n=2	38.7 ± 9.7, n=7	28.4 ± 5.01, n=8
	*no analysis	F <sub>1,15</sub> =0.05 *p=0.82	F <sub>1,14</sub> =0.31 *p=0.59	F <sub>1,1</sub> =103 p=0.06	F <sub>1,12</sub> =0.61 *p=0.45	F <sub>1,11</sub> =0.25 p=0.63
Lipid (µg)—ANOVA wing length as covariate						
Water	43.4 ± 2.3	30.7 ± 1.8	30.4 ± 3.0	17.1 ± 2.1	20.5 ± 5.2	22.3 ± 1.5
Sugar	34.1 ± 4.5	27 ± 2.0	27.3 ± 1.8	16.9 ± 2.2	19.0 ± 1.5	23.4 ± 0.9
	F <sub>1,4</sub> =2.04 p=0.23	F <sub>1,49</sub> =0.12 *p=0.74	F <sub>1,46</sub> =4.1 *p=0.05	F <sub>1,12</sub> <0.01 p=0.93	F <sub>1,52</sub> =0.04 *p=0.84	F <sub>1,52</sub> =0.01 *p=0.92
Glycogen (µg) —ANOVA wing length as covariate						
Water	15.0 ± 8.4	8.3 ± 0.8	6.6 ± 1.0	5.4 ± 0.6	5.9 ± 0.84	6.4 ± 1.1
Sugar	17.1 ± 1.4	7.0 ± 1.0	14.3 ± 2.4	11.0 ± 3.8	7.3 ± 1.20	6.0 ± 0.7
	F <sub>1,4</sub> =1.53 p=0.28	F <sub>1,49</sub> =0.12 *p=0.74	F <sub>1,46</sub> =3.7 *p=0.06	F <sub>1,12</sub> =3.9 p=0.07	F <sub>1,52</sub> =2.4 *p=0.13	F <sub>1,52</sub> =0.36 *p=0.55
Total sugar (µg)—ANOVA wing length as covariate						
Water	39.1 ± 35.7	16.5 ± 4.8	16.6 ± 5.4	9.8 ± 3.8	18.7 ± 4.4	12.4 ± 3.1
Sugar	69.4 ± 9.2	10.1 ± 6.5	43.2 ± 7.8	28.0 ± 13.0	29.6 ± 7.1	15.0 ± 4.5
	F <sub>1,4</sub> =6.04 p=0.07	F <sub>1,49</sub> =0.61 *p=0.81	F <sub>1,46</sub> =4.0 *p=0.05	F <sub>1,12</sub> =2.5 p=0.14	F <sub>1,52</sub> =3.0 *p=0.09	F <sub>1,52</sub> =0.07 *p=0.79
Fructose (µg)—ANOVA wing length as covariate						
Water	27.9 ± 26.6	9.0 ± 2.8	7.9 ± 2.9	3.2 ± 1.5	5.8 ± 1.7	5.1 ± 1.5
Sugar	30.4 ± 5.1	5.4 ± 3.5	30.4 ± 5.8	17.6 ± 7.4	13.5 ± 4.1	8.1 ± 2.8
	F <sub>1,4</sub> =0.92 p=0.39	F <sub>1,49</sub> =0.06 *p=0.81	F <sub>1,46</sub> =5.9 *p=0.02	F <sub>1,12</sub> =7.1 p=0.02	F <sub>1,52</sub> =5.7 *p=0.02	F <sub>1,52</sub> =0.27 *p=0.61

\*Dead wasps and wasps without wing measurements were not included in the ANCOVA analysis of nutrients and eggs.

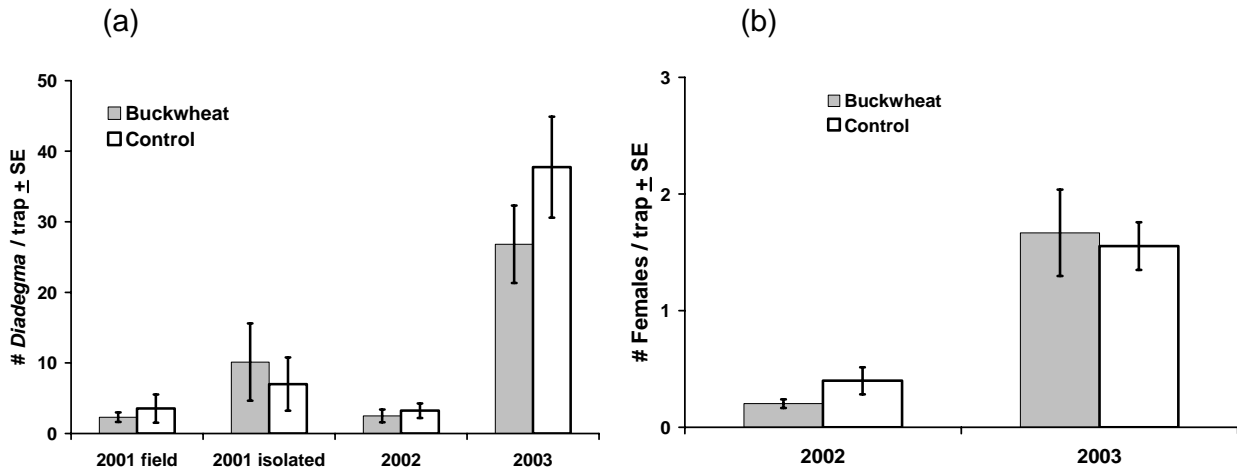
Linear regression of wasps from all trials revealed that fructose levels marginally impacted time of recapture ( $p = 0.06$ ) (Fig. 2a). A negative slope suggests that wasps with more fructose were caught earlier in the experiment, contrary to our previous finding that sugar-fed wasps were recaptured marginally later than water-fed wasps in trial 3 of 2003. This might reflect fructose levels having declined more in wasps caught at later times, particularly the next day. Next, *D. insulare* with higher fructose levels were recaptured higher on the traps (Fig. 2b) suggesting that feeding correlates with flying higher aboveground. If a higher flight level indicates dispersal behavior compared to foraging behavior, this study might support the hypothesis that feeding leads to more dispersal. However, the distinction between dispersal and foraging flight is not known. Lastly, there was no relationship between fructose levels and the number of eggs remaining in ovaries ( $F_{1,72} = 0.50$ ,  $p = 0.48$ ). Egg load is influenced by ovipositional activity and egg maturation rate. For *M. croceipes*, fed wasps oviposited more than did unfed wasps in host patches devoid of food (Takasu and Lewis 1995). Our results did not show *D. insulare* to be as amenable to sugar provisioning for improving biological control as other species. Yet, our experiment may have a limited scope since only wasps moving outside the plot were monitored. Wasps that remained within the host patch might have exhibited different behaviors based on their nutritional state but they were not monitored.



**Figure 2.** Linear regression of fructose levels of all *D. insulare* by (a) time of recapture,  $F_{1,239} = 3.56$ ,  $p = 0.06$ ,  $y = 572.4 - 3.28 \times \text{fructose}$ ,  $r^2 = 0.011$ ; and (b) height of recapture,  $F_{1,239} = 12.1$ ,  $p = 0.0006$ ,  $y = 70.8 + 0.24 \times \text{fructose}$ ,  $r^2 = 0.044$ .

### AGGREGATION NEAR BUCKWHEAT

From 2001 to 2003, captures of *D. insulare* per weekly trap during a 3-week period in August did not differ by treatment ( $F_{1,26} = 0.73$ ,  $p = 0.40$ ) nor by the treatment  $\times$  year interaction ( $F_{2,26} = 0.51$ ,  $p = 0.61$ ) (Fig. 3a). Captures varied significantly by year ( $F_{2,26} = 29.6$ ,  $p = 0.0001$ ) with the highest captures in 2003. In 2002-03, females were distinguished from males on traps and traps were placed in the field for a longer period of time. Females captured per trap per week over a 7-week period did not vary by treatment ( $F_{1,26} = 0.50$ ,  $p = 0.49$ ) nor by the treatment  $\times$  year interaction ( $F_{1,26} = 0.94$ ,  $p = 0.35$ ) but varied significantly by year ( $F_{1,26} = 52.4$ ,  $p = 0.0001$ ) (Fig. 3b).



**Figure 3.** Average number of (a) *D. insulare* wasps collected per week per trap during three weeks of peak activity, 14-30 August 2001, 12-26 August 2002, and 12-26 August 2003. (b) Average number of females collected per week per trap during seven weeks, 22 July - 2 September 2002, and 14 July - 26 August 2003.

Over three years, buckwheat borders did not enhance aggregation of *D. insulare* within cabbage plots. This differs from previous studies with buckwheat (Berndt *et al.* 2002; Irvin *et al.* 2000; Stephens *et al.* 1998), although English-Loeb *et al.* (2003) only found more parasitoids near the crop edge next to the buckwheat but not in the crop interior. *D. insulare* might not have responded to buckwheat borders since other sugar sources were present in vegetation surrounding cabbage plots, such as honeydew produced by soybean aphids, *Aphis glycines* Matsumura, that have recently invaded Minnesota soybean fields. However, floral nectar can have more attractive odors to parasitoids than aphid-infested leaves (Wäckers and Swaans 1992). Buckwheat flowers are white, a color that may elicit more responses by parasitoids (Begum *et al.* 2004). Also, female *D. insulare* live three-fold longer on buckwheat nectar than soybean aphid honeydew (Lee *et al.* 2004). Given the superiority of buckwheat flowers to other common foods in the field, we might still expect to find a numerical increase of *D. insulare* in buckwheat versus control plots. We did not observe such an increase suggesting that *D. insulare* was not attracted or retained by buckwheat flowers. Recent olfactometers studies confirm this, both fed and unfed *D. insulare* showed a little if any response to buckwheat floral odors compared to buckwheat foliage without flowers (Heimpel and Zimmermann, unpublished). An alternative interpretation is that buckwheat may increase local aggregation of *D. insulare* but feeding also reduces their activity levels such that no differences would be observed in the amount collected in the traps.

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## GUSTATORY ACCEPTANCE, LONGEVITY, AND UTILIZATION OF NECTAR AND HONEYDEW SUGARS BY *ANAPHES IOLE*, AN EGG PARASITOID OF *LYGUS* BUGS

Livy WILLIAMS III<sup>1</sup>, Timberley M. ROANE<sup>2</sup>, and J. Peirce BEACH<sup>1</sup>

<sup>1</sup>United States Department of Agriculture, Agricultural Research Service  
National Biological Control Laboratory, Southern Insect Management Research Unit  
Stoneville, MS 38776-0346, U.S.A.  
lwilliams@ars.usda.gov

<sup>2</sup>Department of Biology, University of Colorado  
Denver, CO, 80217-3364, U.S.A.  
Timberley.Roane@cudenver.edu

### ABSTRACT

Habitat management is a component of conservation biological control that aims to improve the availability of resources required by natural enemies. Access to non-host foods is a critical requirement for many natural enemies, and one that can be manipulated via habitat management. Food sources, usually in the form of nectar (floral or extrafloral), pollen, and honeydew supply natural enemies with energy for maintenance and reproduction. These food sources have different chemical compositions, and studies on parasitoid acceptance, survival, and longevity have helped identify the compounds most important to parasitoids, and therefore, habitat management. While pests may also exploit food sources intended for natural enemies, recent studies have shown that careful selection of food sources can reduce this possibility. Therefore, detailed knowledge of the biology of the pests and natural enemies present in the agroecosystem in question is crucial for selection of appropriate habitat management strategies.

The suitability of naturally occurring carbohydrates and a commercial food source was determined for *A. iole*. In a gustatory response study wasps responded to all 15 of the sugars at the highest concentration tested (2 M). At this concentration, sucrose, glucose, maltose, melezitose, fructose, trehalulose, and erlose all elicited >90% acceptance. Raffinose, trehalose, mannose, galactose, melibiose, rhamnose, stachyose, and lactose led to <50% gustatory response by the wasps at 2 M. Eliminate™ a commercial food supplement, was readily accepted (92%) by *A. iole*. With respect to gustatory response to nectar and honeydew sugars, *A. iole* differs markedly from other hymenopterans that have been studied in that this parasitoid accepted all the naturally occurring sugars with which it was tested. Moreover, for many of the sugars tested, this parasitoid had lower acceptance thresholds than other hymenopterans. Wasp survival varied depending on food source and temperature. Provision with sucrose led to the greatest increase in longevity over controls. Honeydew sugars were highly variable in their effect on survival. Results from sugar digestion trials were consistent with

those from gustatory discrimination and longevity trials, and suggested the presence of invertase in *A. iole* guts.

The broad and sensitive range of gustatory perception, coupled with enhanced longevity afforded by some sugars, might be helpful in the development of a food source for *A. iole* that is not exploited by *Lygus*.

## INTRODUCTION

Many adult parasitic wasps require food to satisfy energy needs (Quicke 1997). Nectar (floral and extrafloral) and honeydew excreted by homopteran insects are rich sources of carbohydrates that satisfy energy and maintenance requirements (Jacob and Evans 1998; Jervis *et al.* 1993; Longley and Jepson 1996; Rogers 1985). Provisioning parasitoids with carbohydrates generally increases longevity and subsequent rates of parasitism (Azzouz *et al.* 2004; Baggen and Gurr 1998; Fadamiro and Heimpel 2001; Stapel *et al.* 1997; Wäckers 2001). Therefore, provisioning parasitoids with an adequate food source is an important component of habitat management strategies aimed at enhancing the effectiveness of biological control agents (Berndt and Wratten 2005; Evans and Richards 1997; Landis *et al.* 2000; Wratten and Gurr 1999).

Successful foraging by parasitoids depends on the availability of a suitable food source at the time of foraging. Most parasitoids readily accept sucrose, fructose, and glucose (Jervis *et al.* 1993; Jervis *et al.* 1996), the most common components of most nectar and honeydew (Baker and Baker 1983a). However, other carbohydrates occur in nectar and honeydew as well (Baker and Baker 1983b; Davidson *et al.* 1994; Hendrix and Wei 1994; Koptur 1994). Spatial and temporal variability in the sugar composition, i.e. suitability, of nectar and honeydew can limit successful foraging by parasitoids. With the exception of the predominant carbohydrates, little is known about the suitability of most sugars present in nectar and honeydew for parasitic Hymenoptera. The gustatory response of *Cotesia glomerata* (L.) (Hymenoptera: Braconidae) wasps exposed to individual nectar and honeydew sugars varied greatly (Wäckers 1999), and was positively correlated with longevity (Wäckers 2001). Romeis and Wäckers (2000, 2002) demonstrated differences in sugar utilization patterns between *C. glomerata* and its host, *Pieris brassicae* L. (Lepidoptera: Pieridae). The parasitoid utilized several sugars to which the host did not respond. These findings have practical relevance for pest control, because they suggest that certain natural or artificial food sources might be used to benefit natural enemies to a greater extent than the pest.

In insects, ingested sugars are hydrolyzed into monosaccharide units, after which oxidation via glycolysis occurs. If not used immediately, carbohydrates in insects are sometimes stored as trehalose or glycogen. Boevé and Wäckers (2003) demonstrated that the rate of sugar digestion by *Myrmica rubra* (L.) (Hymenoptera: Formicidae) varied depending on the sugar ingested, and that metabolic suitability of sugars was correlated with gustatory acceptance.

*Lygus* bugs (Heteroptera: Miridae) are important pests of many crops in North America (Wheeler 2001). In cotton, *Gossypium hirsutum* L., annual losses due to *L. lineolaris* (Palisot de Beauvois) and *L. hesperus* Knight can exceed \$75 million (Williams 1999). Historically,

*Lygus* populations in cotton have been controlled largely by broad-spectrum insecticides aimed at several pests. However, the acceptance of transgenic cotton and the success of the boll weevil eradication program (Hardee *et al.* 2001) might lead to an overall reduction in insecticide use in the cotton belt of the United States. In turn, this may create a scenario in which biological control has greater potential for controlling *Lygus* in cotton (Ruberson and Williams 2000).

*Anaphes iole* Girault (Hymenoptera: Mymaridae) is an egg parasitoid that attacks *Lygus* and other mirids in North America (Huber and Rajakulendran 1988; Udayagiri *et al.* 2000). *Anaphes iole* is pro-ovigenic and adults do not require a food source in order to mature eggs (Jervis *et al.* 2001). Nevertheless, foraging by adult *A. iole* is important because increased longevity would allow the wasp more time to search for and parasitize hosts, thus leading to a possible increase in realized fecundity. An increase in longevity afforded by sugar foraging is especially important when host densities are low and parasitoids must spend considerable time searching. Adult *A. iole* does not host feed, and field observations of feeding by this tiny wasp are lacking. Under laboratory conditions, longevity of *A. iole* wasps is limited to <3 days in the absence of food, but can exceed 10 days when honey is provided (Jones and Jackson 1990). However, nothing is known about the suitability of individual sugars for *A. iole*. A better understanding of nutritional ecology of *A. iole* may facilitate the development of natural or artificial food sources that confer greater benefit to this parasitoid than to *L. lineolaris*.

Our objectives were to characterize and describe the effect of carbohydrate food sources on gustatory discrimination, longevity, and utilization by *A. iole*.

## METHODS AND MATERIALS

### INSECTS

*Anaphes iole* used in this study were obtained from a laboratory colony maintained on *L. hesperus* eggs at the USDA-ARS Biological Control and Mass Rearing Research Unit, Mississippi State, MS. Wasps were held in Plexiglass cages (26 x 26 x 20 cm) at 27±1°C, 65-85% RH, and 14:10 L:D photoperiod until experimentation.

### GUSTATORY RESPONSE AND ACCEPTANCE THRESHOLD

Acceptance thresholds for the following 15 sugars were determined for *A. iole*: sucrose, fructose, glucose, maltose, melezitose, erlose, trehalulose, raffinose, trehalose, mannose, galactose, melibiose, rhamnose, stachyose, and lactose. With the exception of lactose, all the sugars tested are known to be associated with plants (e.g., nectar) or insects (e.g., honeydew or bee honey). Lactose was included as a control sugar that *A. iole* is unlikely to encounter in nature. A 2 M concentration of each sugar was prepared with distilled water. This concentration approximates that found in nectar and honeydew (Baker and Baker 1983a). Serial dilutions were then made from the stock solution in a geometric progression (i.e., 1 M, ½ M, ¼ M, etc.) for each sugar.

Gustatory response by *A. iole* was also assessed for a commercial food supplement, Eliminate™ (Entopath, Easton, PA). Eliminate™ was developed as part of a conservation

biological control program to enhance the effectiveness of parasitoids of the southern pine beetle, *Dendroctonus frontalis* Zimmerman (Coleoptera: Scolytidae) (Hanano 1996; Mathews and Stephen 1999). For this study, Eliminate™ was prepared as recommended by the manufacturer.

Bioassays were setup in the following manner. Wasps used in the gustatory discrimination experiments were <3 day old females that were water-satiated (provided with distilled water *ad lib* via saturated absorbent matting and frequent misting), appeared healthy, and were assumed mated. Under the existing laboratory conditions, the longevity of food and water deprived *A. iole* is about 3 days (Williams, unpublished). All gustatory discrimination experiments were conducted between 0800-1700 h CST. Water-satiated wasps were placed individually into a 0.5 dram glass shell vial containing a 5 ml drop of the treatment (sugar solution or Eliminate™ in the bottom of the vial). Wasps were observed at 50x for 5 min. 'Acceptance' was recorded if the wasp fed for more than 5 seconds upon contact with the droplet, or if the total time spent feeding surpassed 5 seconds. Otherwise, the encounter was scored as 'rejection'. Each sugar-concentration combination was presented to 25 wasps in a completely randomized design, and sugar-concentration combinations were replicated 3-8 times. Fresh sugar solutions were prepared for each replicate. For the bioassays using Eliminate™ 50 wasps were included in each of two replicates. Laboratory conditions during the study were 24±3°C and 17-52% RH.

#### LONGEVITY

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Longevity of newly-emerged wasps was assessed after provision with a 1 M solution of the following sugars presented singly: sucrose, trehalulose, maltose, melezitose, trehalose, and rhamnose. Eliminate™ was included as an additional treatment. Two controls, distilled water only and no food or water, were also included. Bioassays were setup in a randomized complete block design with six replicates. Each experimental unit consisted of 15 parasitized host (*L. hesperus*) eggs placed into a 28 ml glass scintillation vial. These host eggs contained parasitoids ready to emerge within 12 h. Organdy was placed over the top the vial and two pipet tips (30 ml) were inserted into two small holes cut in the fabric. One pipet tip contained distilled water, and the other was filled with the treatment solution. Separate trials were run concurrently at 20 and 27°C, 65-85% RH, and 14:10 L:D photoperiod. Wasp survival was assessed daily with the aid of a dissecting scope, at which time pipet tips were replaced with fresh water and treatment solutions. Survivorship of wasps was analyzed as a function of time.

#### CARBOHYDRATE UTILIZATION

Wasps used in this study were 1 day old and were food and water deprived. About 300 wasps were placed in a 9.5 cm-diam glass Petri dish containing two discs of filter paper (Whatman no. 1, Whatman International Ltd., Maidstone, Kent, U.K.), one in the bottom of the dish and one on the top. Each piece of filter paper was saturated with a 1 M solution of sucrose, maltose, or melezitose. Controls were prepared using distilled water only. Petri dishes were then held at 25±1°C for one of three different time intervals; 15 min, 12 h, or 24 h. This time series allowed us to determine the digestion rate for the different sugars. At the appropriate

time, wasps were killed in 70% ethanol. Thirty individuals of each gender were placed in together in 1 ml microcentrifuge tubes with 70% ethanol and held at -20°C until analysis. Prior to analysis, wasps were rinsed in ca. 400 ml distilled water, and were macerated for 10 min in 300 ml distilled water with glass beads (0.4 ml, 400-600 mm diam) using a dental amalgamator.

High-performance anion-exchange chromatography analysis with pulsed amperometric detection (Beach *et al.* 2003; Byrne *et al.* 2003; Hendrix and Wei 1994; HPAEC) was used to identify and quantify the major carbohydrates present in *A. iole*. One hundred microliters of each sample was analyzed by HPAEC. Since detector response varies between individual sugars (Larew and Johnson 1988), peaks were identified and quantified by comparing the time of retention and peak areas of known sugar standards with unknown sugars. Based on daily calibration of the system, peak areas were determined using Dionex PeakNet software.

## RESULTS

### GUSTATORY RESPONSE AND ACCEPTANCE THRESHOLD

All 15 of the sugars tested elicited a response by *A. iole*, although marked differences were observed. At the 2 M concentration gustatory response partitioned into two groups. Sucrose, glucose, maltose, melezitose, fructose, trehalulose, and erlose evoked >90% acceptance at this concentration. These sugars were considered to be 'highly stimulatory'. The acceptance threshold for these sugars was 1/256 M, with the exceptions of glucose, maltose, and trehalulose, which was 1/16, 1/512, and 1/1024 M, respectively. Response curves of these sugars declined in a relatively linear manner.

The remaining sugars (raffinose, trehalose, mannose, galactose, melibiose, rhamnose, stachyose, and lactose) led to <50% gustatory response by the wasps. These sugars were categorized as 'moderately stimulatory sugars'. The acceptance threshold for these sugars did not exceed 1/4 M, except for raffinose, which was 1/256 M. Response curves for these sugars were also relatively linear, with the exception of raffinose, which displayed an irregular response and never exceeded 30% gustatory acceptance between 2 and 1/512 M. Eliminate™ a commercial food supplement, was readily accepted (92%) by *A. iole*.

### LONGEVITY

Wasp survival varied depending on food source and temperature. For the trial conducted at 27°C, average survivorship was lowest (ca. 3 days) when wasps were held without food or water, or were provisioned with only water, or with rhamnose. Provision with trehalose or melezitose increased survival only to a slight degree (ca. 4 days). However, wasps provided with sucrose, trehalulose, maltose, and Eliminate™ had the greatest longevity (maltose, ca. 8 days; sucrose, ca. 15 days). Temperature was also an important factor; longevity of wasps was significantly greater at 20°C than at 27°C. For example, average survival of wasps fed sucrose was nearly 2x at 20°C than at 27°C.

## CARBOHYDRATE UTILIZATION

Results of HPAEC analysis indicated that trace amounts of glucose and fructose were found in control wasps fed only distilled water. Sugars fed to wasps could be clearly detected within 15 min. However, the rate of digestion appeared to vary depending on the sugar that was ingested. For example, within 15 min of sucrose ingestion, glucose, fructose, trehalose, and sucrose were detected. These sugars were also present at 12 h, with the exception of sucrose. However, at 24 h sugar levels were comparable to controls. In contrast to sucrose, melezitose was still detected 24 h after ingestion. Trace amounts of other carbohydrates were also present in some samples.

## DISCUSSION

Female *A. iole* wasps responded to all the carbohydrates tested. The parasitoids were most sensitive to seven sugars present in nectar (sucrose, glucose, and fructose), honeydew (glucose, trehalulose, melezitose, erlose, and fructose), and bee honey (maltose and erlose). Of these sugars, *A. iole* was most sensitive to sucrose, and it is interesting that this parasitoid was significantly more sensitive to sucrose than to its components, glucose and fructose. These sugars are usually the primary components of nectar (Baker and Baker 1983a), an important food source for parasitoids (Jervis *et al.* 1993). Sucrose is the most widely found disaccharide in nature, and is the primary form in which fixed carbon and energy are translocated in plants. The acceptance thresholds for sucrose and other highly stimulatory sugars were much lower than the concentrations (10-50% w/v) at which they naturally occur (Baker and Baker 1983a). High sensitivity to these carbohydrates by *A. iole* would enable this wasp to exploit sources with low concentrations of these sugars. The remaining sugars were moderately stimulatory (<50% acceptance at 2 M). These sugars are found in bee honey (mannose, trehalose, raffinose, and melibiose), honeydew (trehalose, raffinose, and stachyose), plant seeds (raffinose, galactose, stachyose, and rhamnase), and phloem sap (raffinose, melibiose, and stachyose) (Baker and Baker 1983a,b; Donner 1991; Hendrix *et al.* 1992; Kuo *et al.* 1988; Nakajima *et al.* 1980; Wei *et al.* 1996). Our results suggest that *A. iole* can detect a wide range of potential food sources, some of them at very low concentrations. In particular, it appears that nectar and honeydew are natural sources of sugars that *A. iole* can perceive, even if the sources have been diluted by precipitation or dew.

Similar feeding studies conducted with other hymenopterans allow us to put our results with *A. iole* into perspective. For half of the sugars tested, *A. iole* exhibited lower acceptance thresholds than for any hymenopteran tested to date (see Beach *et al.* 2003). Moreover, *A. iole* was the only hymenopteran tested that accepted all the sugars. Differences in sensitivity and range of carbohydrates detected by parasitoids may be a function of the insect's reproductive physiology. Like many egg parasitoids, *A. iole* is pro-ovigenic and produces eggs that rely on the host egg's protein for nourishment (Quicke 1997). Conversely, the parasitoid studied by Wäckers (1999), *C. glomerata*, is synovigenic, meaning that female wasps emerge with a limited number of nutrient-rich eggs (Quicke 1997). When provided with a protein-

rich diet, synovigenic wasps can mature additional eggs. In the absence of food, these wasps sometimes resorb their eggs and utilize the resources for self-preservation. Therefore, protein may not be an important component in the diet of a pro-ovigenic wasp that emerges with a full complement of matured eggs. Carbohydrates, which provide a source of quick energy for locomotion, may play a more important role in the nutritional ecology of *A. iole* than proteins. Nevertheless, *A. iole* readily accepted Eliminate™ a protein-rich commercial food supplement developed for synovigenic parasitoids. Its acceptance by *A. iole* suggests that this wasp is capable of utilizing complex food sources that include proteins and other compounds that are not required for its survival. Reliance on carbohydrates may explain the high sensitivity and range of perception to sugars by *A. iole*. Future studies with other pro-ovigenic and synovigenic parasitoids are necessary to better understand the relationship between gustatory response and reproductive physiology in parasitoids.

Our studies demonstrate the importance of food source and temperature on the longevity of *A. iole*. Several food sources were not suitable for wasp survival (rhamnose, trehalose, and melezitose), while others were beneficial (Eliminate™, maltose, trehalulose, and sucrose). Sucrose is common in nectar, suggesting that plant resources are important for *A. iole* survival in the field. However, rhamnose, another component of nectar, was unsuitable for *A. iole*, and acted as a feeding deterrent to this wasp when mixed with maltose (Beach *et al.* 2003) and to *C. glomerata* when mixed with glucose (Wäckers 2001). These findings indicate the importance of understanding the chemical composition of nectar and its effects on beneficial insects when developing habitat management strategies for biological control. The three honeydew sugars tested (trehalose, melezitose, and trehalulose) had variable effects on survival of *A. iole*, suggesting that honeydews differ in their suitability to this wasp. Increased longevity at the lower temperature, 20°C, may be a function of reductions in behavioral activity and metabolism. Longevity of *A. iole* was relatively consistent with results from gustatory discrimination. The exception was melezitose, which was readily fed on (ca. 75% acceptance at 1 M concentration), but was a poor source of nutrition.

Results from the HPEAC analysis suggested that *A. iole* hydrolyzes some sugars more efficiently than others. This was clearly observed in the comparison between sucrose, which was readily metabolized, and melezitose, which was not. These results are consistent with those in the gustatory discrimination and longevity studies. Our results suggest the presence of invertase, which hydrolyzes sucrose, in the gut of *A. iole*. However, this does not preclude the presence of other enzymes, and further studies of sugar digestion by *A. iole* are underway.

The ability of *A. iole* to detect and utilize a broad range of food sources has practical implications for the development of a food supplement for this parasitoid. However, it must be remembered that *L. lineolaris* might also utilize a food supplement intended for *A. iole*. The presence of nectar can benefit pest herbivores (Adjei-Maafa and Wilson 1983; Belcher *et al.* 1984) as well as their natural enemies (Bugg *et al.* 1989). Therefore, knowledge of the nutritional ecology of *L. lineolaris* as well as *A. iole* is critical for the development of a selective food source. Use of foods that benefit the biological control agent to a greater extent than the pest herbivore may have broad potential in other biological control programs (Cortesero *et al.* 2000; Lewis *et al.* 1997).

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# THE VEGETARIAN SIDE OF CARNIVORES: USE OF NON-PREY FOOD BY PARASITIDS AND PREDATORS

Felix L. WÄCKERS<sup>1</sup> and Henry FADAMIRO<sup>2</sup>

<sup>1</sup> Netherlands Institute of Ecology (NIOO-KNAW), Centre for Terrestrial Ecology  
P.O. Box 40  
6666 ZG Heteren, The Netherlands  
f.waeckers@nioo.knaw.nl.

<sup>2</sup>Department of Entomology and Plant Pathology  
Auburn University  
Auburn, AL 36849, U.S.A.  
fadamhy@acesag.auburn.edu

## ABSTRACT

Predaceous and parasitic arthropods can play an important role in the regulation of herbivore populations. However, the majority of predators and parasitoids also use plant-derived foods as a source of nutrients. This vegetarian side of the menu may include various plant-provided substrates, such as nectar, pollen, fruits or foods indirectly derived from plants (e.g., honeydew or pycnial fluid of fungi). Predators and parasitoids may either use plant-derived food as a supplement, or they may strictly depend on these foods during part of their life.

Despite the obvious importance of non-prey food, little is known about the extent to which particular categories of plant-derived foods contribute to the diet of predators and parasitoids under field conditions. To the foraging insect the potential value of a given food source will depend on its availability, detectability, accessibility and nutritional composition. Plant-provided foods can have a dramatic impact on longevity, fecundity, and distribution of predators and parasitoids. As each of these parameters affects the local number of carnivores, the availability of suitable plant-derived food can have a major impact on mass-rearing programs, as well as on herbivore-carnivore dynamics in the field.

## OVERVIEW OF RESOURCE USE

### NON-PREY FEEDING BY CARNIVOROUS ARTHROPODS

Predators and parasitoids are usually identified by their carnivorous lifestyle. Due to this bias, we easily overlook the fact that the majority of these “carnivores” also require plant-derived foods as a source of nutrients.

The level in which predators or parasitoids depend on primary consumption varies. (Wäckers and van Rijn 2005) distinguish between the categories of ‘life-history omnivores’, ‘temporal omnivores’ or ‘permanent omnivores’. Life history omnivores include those natu-

ral enemies that are strictly dependent on plant-derived food during part of their life cycle, such as hoverflies and many parasitoids. Temporal omnivores supplement their carnivorous diet during part of their life (e.g., host-feeding parasitoids), whereas permanent omnivores retain an assorted diet throughout their lifecycle (e.g., predatory mites and ladybirds).

### **WHAT'S ON THE MENU? NON-PREY FOOD ITEMS USED BY PREDATORS AND PARASITOIDS**

Predators and parasitoids may feed on various substrates. Their fare may include carbohydrate-rich foods such as floral nectar, extrafloral nectar, fruits, plant sap, gall secretions, honeydew, Lycaenid dorsal gland secretions, and fungal fluids as well as lipid- or protein-rich sources such as pollen, food bodies, and elaiosomes (Wäckers 2005). In some cases predators may also feed on plant productive tissue, which would classify them as potential herbivores (Coll and Guershon 2002; Eubanks and Styrsky 2005). A few predators exploit a broad range of the above-mentioned food items. This applies especially to ants, which have been the driving force in the evolution of many food-mediated mutualisms (Beattie 1985). The majority of predators and parasitoids restrict their diet to one or a few alternative foods. Most parasitoid species are restricted to feeding on sugar-rich solutions such as nectar and honeydew. Many predators like hoverflies, lacewings, anthocorid bugs, ladybeetles, and predatory mites feed on pollen as well as nectar/honeydew (Wäckers and van Rijn 2005).

### **EFFECTS ON LONGEVITY AND FECUNDITY**

Plant-provided food can have a strong effect on life-history parameters of predators and parasitoids. Temporal or permanent omnivores can use foods like (extra-) floral nectar, pollen or honeydew as an alternative to prey. This diet extension therefore allows them to bridge periods of low prey availability (Limburg and Rosenheim 2001). When combined with predation, nectar and pollen feeding can increase predator fitness over prey feeding alone (Porter 1989; van Rijn and Sabelis 2005). Life-history omnivores, on the other hand, fully depend on non-prey food, usually during their adult stage. Their longevity and fecundity are often seriously compromised in the absence of these food sources. An example of the latter category is the large category of parasitoids that do not engage in host-feeding. At the time of adult emergence, their energy reserves often cover no more than 48 hours of the individual's energetic requirements. Sugar feeding can increase a parasitoid's lifespan considerably; up to 20-fold under laboratory conditions for several hymenopteran parasitoids (Fadamiro and Heimpel 2001; Jervis *et al.* 1996; Wäckers 2001), and 2-3-fold for the phorid fly, a dipteran parasitoid of imported fire ants (Chen *et al.* 2005; Fadamiro *et al.* 2005). In addition, sugar feeding can benefit a parasitoid's fecundity, not only through an increase in reproductive lifespan, but also through a positive effect on the rate of egg maturation (Jervis *et al.* 1996). This means that parasitoids that fail to replenish their energy reserves through sugar feeding will suffer severe fitness consequences.

### **DIFFERENCES IN SUITABILITY**

Not all potential food sources are suitable for a given predator or parasitoid. There is substantial variation between and among food categories with regard to their availability, apparency,

accessibility and chemical composition (Olson *et al.*, this issue; Wäckers 2005). Whereas food sources may vary widely, consumers may show an even broader variation in foraging behavior, mouthpart morphology and physiology. An effective exploitation of food sources requires that there is a good fit between consumer attributes and food source characteristics (Olson *et al.*, this issue). Identifying and quantifying mechanisms that allow or obstruct successful food source exploitation is not only essential if we want to understand the functioning of food supplements in plant-insect and insect-insect interactions, it also has direct implications for the use of food supplements in biological control programs.

## CONSEQUENCES FOR BIOLOGICAL CONTROL

Biological control workers have regularly suspected that the scarcity of sugar- and/or pollen sources in agriculture could impose a serious constraint on the effectiveness of natural enemies in the field (Hocking 1966; Illingworth 1921). Hocking (1966) pointed out that lack of food availability could also hamper the establishing of natural enemies in classical biological control programs. We still have little data on the nutritional status of natural enemies under field conditions (Casas *et al.* 2003; Lee and Heimpel 2003), but recent studies indicate that natural enemies can indeed be food-deprived in the absence of (suitable) flowering vegetation (Olson and Wäckers unpublished data; Wäckers and Steppuhn 2003). Thus, adding suitable food sources to agro-ecosystems could be a simple and powerful tool to enhance the effectiveness of biological control programs. Three types of approaches have been proposed to alleviate the shortage of food in agricultural systems.

- 1. Diversification of agro-ecosystems.** Food sources can be provided by enhancing plant diversity in agro-ecosystems, either through the use of non-crops in undergrowth or field margins (Gurr *et al.* 2005; Landis *et al.* 2000; van Emden 1965), or by growing crops devoid of alternative food alongside crops featuring flowers or extrafloral nectaries. However, not all plant-provided food is suitable as a food source for parasitoids and predators. Flowers may not be perceived by (some) natural enemies, or can be unattractive or even repellent (Wäckers 2004). Other flowers may be attractive, but hide their pollination rewards within constricted floral structures that prevent those natural enemies with unspecialized mouthparts to exploit these food sources.
- 2. Artificial food supplements.** An alternative to the use of (flowering) plants is the use of artificial food supplements such as food sprays (Hagen 1986). Artificial food supplements typically consist of a carbohydrate solution in combination with a source of protein/amino acids. Insects that utilize honeydew as food source may be especially adapted to exploit this 'artificial honeydew'. Many studies have identified short term increases in numbers of natural enemies such as parasitoids, lady beetles, lacewings, and predatory bugs as a result of these food supplements. The impact of food supplements on pest insects has rarely been investigated (Rogers and Potter 2004).
- 3. Crop-provided food.** Some crops produce suitable food supplements themselves. Many crops flower during part of their growing period. In crops grown for their seeds or fruits (e.g., cereals, citrus, beans) this flowering period may coincide with the period that the plant is specifically vulnerable to pest attack. Some crops, such as peppers and tomatoes, even flower during a large part of the growing season, thereby maintaining populations of

predatory mites and anthocorid bugs, that can effectively suppress thrips pests (Van den Meiracker and Ramakers 1991). A number of crops also provide nectar outside the flowering period. These so-called 'extrafloral nectaries' may be found on leaves, stems or fruits. Examples of extrafloral nectar producing crops include *Prunus* spp. (e.g., cherry, plum, peach, and almond), cassava, faba bean, zucchini, pumpkin, cashew and cotton. Extrafloral nectaries are generally believed to have evolved as a mechanism for plants to attract sweet-toothed carnivores and to benefit from their protective services (Turlings and Wäckers 2004). The fact that extrafloral nectaries have evolved numerous times shows that food supplements are a successful method to enhance biological control under natural conditions. The extrafloral nectar trait is also found in a number of crops and can be a useful element in biological pest control. The crop-produced nectar may suffice as food sources for predators and parasitoids. In other cases, there may be room for plant breeding to improve the timing, quantity and quality of nectar production, to better match the nutritional needs of biological control agents.

Whereas the concept of enhancing biological control through the use of alternative food might seem self-evident, the anticipated effects are not necessarily realized under field conditions (Heimpel and Jervis 2005). In their contribution Lee and Heimpel (this issue) investigate whether food provision has an impact on parasitoid retention under actual field conditions. In a series of experiments they studied dispersal behavior of the parasitoid *Diadegma insulare* (Cresson) (Hymenoptera: Ichneumonidae), in response to nutritional state or the presence of nectar flowers. No evidence for the hypothesis that dispersal behavior is affected by sugar feeding was found. Using a modeling approach, Sabelis and van Rijn (this issue) review the conditions under which alternative food enhances pest suppression by biological control agents as well as the conditions where no effects are expected. Regarding the nutritional value and life stage affected by the alternative food, they show that alternative food can bring pest locally to extinction only when it is substitutable with prey, rather than complementary.

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#### **A FLY IN THE OINTMENT: WHEN HERBIVORES BENEFIT FROM FOOD SUPPLEMENTS**

Whereas the provision of food supplements is potentially an effective method to enhance biological pest control, the indiscriminate addition of nectar or pollen sources to agro-ecosystems may also backfire. Many arthropod pests are dedicated flower feeders as well (Romeis *et al.* 2005), and some are more effective in flower exploitation than their natural enemies. When herbivores, rather than their antagonists, gain profit from the available nectar or pollen sources, the net impact on pest control could be negative. This potential problem can be avoided by screening flowers with respect to their suitability for biological control agents (Patt *et al.* 1997; Wäckers *et al.* 1996) as well as herbivores (Baggen *et al.* 1999; Winkler *et al.* 2003).

#### **POSSIBILITIES FOR SELECTIVE USE OF FOOD SUPPLEMENTS**

We have seen that nectar and pollen sources vary substantially with regard to their suitability as food for particular arthropods. To optimize the impact of food provision in biological control, feeding requirements of both natural enemies and herbivorous pests should be con-

sidered when selecting food supplements. Differences in food ecology between both groups can be exploited in selecting flowers that cater for biological control agents, while being unsuitable for herbivores (Baggen *et al.* 1999; Baggen *et al.* 2000; Wäckers 1999; Winkler *et al.* 2003). The fact that nutritional requirements of natural enemies often differ considerably from those of pest insects can also be used to develop selective food sprays, i.e. food sprays that sustain biological control agents without providing a nutritional benefit to the pest insect (Romeis and Wäckers 2002; Wäckers 2001; Winkler *et al.* 2005).

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# WHEN DOES ALTERNATIVE FOOD PROMOTE BIOLOGICAL PEST CONTROL?

Maurice W. SABELIS<sup>1</sup> and Paul C. J. VAN RIJN<sup>2</sup>

<sup>1</sup>Section Population Biology, Institute for Biodiversity and Ecosystem Dynamics  
University of Amsterdam  
Amsterdam, The Netherlands  
sabelis@science.uva.nl

<sup>2</sup>Netherlands Institute of Ecology (NIOO-KNAW)  
Boterhoeksestraat 48  
6666 GA Heteren, The Netherlands  
p.vanrijn@nioo.knaw.nl

## ABSTRACT

That alternative food, whether or not provided by a plant or introduced artificially, promotes biological pest control via its effect on the predators, is not immediately obvious. On the one hand it enhances survival, reproduction and searching. On the other hand it may reduce the rate of predation, which is the case when alternative food and prey are substitutable – as opposed to complementary – food sources. Moreover, it is not immediately obvious how the impact of alternative food on the outcome of biological pest control differs depending on the type of dynamics (e.g., equilibrium vs. transient dynamics), the type of predator (e.g., stage-related consumption and life history effects of alternative food), the spatial structure of the environment (e.g., source-sink, metapopulation) and food web structure (presence of hyperpredators or intraguild predators). We review the conditions under which alternative food can lead to either prey/pest extermination, to a decline of the prey/pest towards a positive, asymptotic density or to no effect on prey/pest density at all.

## INTRODUCTION

Carnivorous arthropods such as predators and parasitoids supplement their diet with plant-provided food (PPF), such as nectar or pollen. Depending on the arthropod taxa under consideration, this type of omnivory may occur in all or only in specific feeding stages. It usually stimulates survival, development and/or reproduction, thereby promoting the numerical response of the carnivore to the density of prey or host. Whether this numerical effect on the carnivore also translates in reduced prey/host densities, is not immediately obvious because consumption of PPF may negatively affect consumption of prey, because prey consumption and PPF consumption vary with life history stage, because prey and PPF vary in spatial distribution and because prey and PPF may be eaten by other members of the food web. Assessing the conditions, under which PPF reduces density at the second trophic level via its impact

on the third, is of crucial importance to designing strategies for biological control of crop pests.

Here, we summarize the results of theoretical exercises with consumer-resource models presented elsewhere (Van Rijn and Sabelis 2005). First, we consider the lessons from simple consumer-resource models that ignore stage or spatial structure. Second, we discuss results from stage-structured consumer-resource models to investigate how the impact of PPF on herbivory may depend on the life history and feeding requirements of the carnivorous arthropods. We compare parasitoids and predators, as well as predators with different types of omnivory. Third, we consider spatial structure and ask how the distribution of PPF and prey relative to each other matters to reducing herbivory. Finally, we step beyond consumer-resource interactions and ask when food web complexities (omnivory, hyperpredation, intraguild predation, competition) alter the predictions from simple consumer-resource models. All this will be discussed with a keen eye for how the theory can be applied to reduce crop damage by herbivores.

## WELL-MIXED, UNSTRUCTURED CONSUMER-RESOURCE MODELS

To understand how PPF – through its effect on the carnivore – affects herbivore abundance, consider a system where a predator population directly controls a herbivore population, where individuals of each species are identical (e.g., no stage structure) and populations are well mixed (no spatial structure). These conditions apply to Lotka-Volterra or Rosenzweig-MacArthur models. The addition of PPF will initially result in an increase of the predator population, simply because there is more food available. This increase will come to a halt at equilibrium, i.e., when births exactly compensate for deaths. At this point, the herbivore population has decreased to an extent that compensates for the supply of PPF. Thus, adding food will lead to a decrease in the herbivore population via the consumers they share. This effect of a non-reproducing food source is very similar to the case where adding a second, reproducing prey species causes a decline of the first via the predator they share (Holt and Lawton 1994; Van Baalen *et al.* 2001; Van Rijn *et al.* 2002). The effect of one prey species on the other looks like competition, but in fact it is only apparent, because the mechanism is predator-mediated. This is why Holt (1977) termed it apparent competition, to create a contrast with resource and interference competition.

From the equilibrium equations of the one-predator-two-prey or predator-PPF-prey models, some counterintuitive conclusions emerge. If prey and PPF are substitutable food sources for the predator (Tilman 1982), addition of PPF will reduce equilibrium prey density, even when per capita consumption of PPF leads to a decrease in per capita consumption of prey. This insensitivity of the herbivore equilibrium to per capita prey consumption arises because equilibrium implies that the predators will increase to larger densities to achieve an overall prey mortality rate that compensates the overall prey birth rate. As long as the per capita predation rate exceeds zero, increasing the amount of PPF can even lead to extinction of the prey. At prey extinction, the predator population is maintained only by PPF. This prediction of prey extinction by adding PPF does not hold when food and prey are not substitutable, but complementary. Two food types are thought to complement each other when

they influence different components of the predator's life history. As an extreme example, consider the case where prey affects reproduction and PPF affects mortality. Then, increasing the amount of PPF also reduces herbivore density, but can never lead to extinction of the prey. This is because herbivore density declines asymptotically to a fixed level determined by background (= minimum) predator mortality.

As long as assimilation of PPF and prey will have a positive effect on predator reproduction and survival (which is why PPF should be eaten by the predator anyway!), PPF will reduce equilibrium prey densities irrespective of its effect on the prey consumption rate. Thus, it does not matter whether the predator switches to PPF at low prey densities or whether it becomes satiated for PPF at another level of ingested biomass than for prey (Van Baalen *et al.* 2001; Van Rijn, unpublished data). It even does not matter whether the herbivore consumes PPF and therefore survives, reproduces or develops faster (Van Rijn *et al.* 2002)! At equilibrium, the enhanced herbivore performance due to PPF will be compensated by predation from a larger predator population.

The equilibrium approach holds when environmental conditions, such as climate, availability of PPF to predators and plants to herbivores, remain unchanged over a sufficiently long period. How long the conditions need to be constant to approximate the equilibrium depends on the initial densities of the interacting populations, their generation times, and other traits of predator and prey that determine the dynamics around the equilibrium. For carnivorous mites and herbivorous thrips with generation times of about 3 weeks, populations were already within the 10% range of their equilibrium level after 12 weeks following their introduction in a cucumber crop (Van Rijn *et al.* 2002). After this period the impact of a regularly supplied food source on mite and thrips populations can adequately be predicted from equilibrium equations only. Arthropods larger than mites and thrips generally have longer generation times and their populations require more time to settle around the equilibrium (Sabelis 1992). For insects with only one or two generations per year and with food sources available only during part of the year, an equilibrium approach is unlikely to hold. In that case, one should rather focus on the dynamics displayed before the system approaches its equilibrium state (so-called 'transient' dynamics). Models of such systems require proper representation of developmental delays and age-dependent reproduction and this may make them mathematically less tractable. Although numerical techniques are available to simulate transient dynamics (Caswell 1989; De Roos and Persson 2001; Nisbet, 1997), obtaining transparent insight requires simplification.

We reduced complexity by focusing on the first generation after predator release (Van Rijn and Sabelis 2005). We assumed predators to be subject to a constant (i.e., herbivore-independent) per capita mortality rate, whereas the per capita prey mortality depends on predator density. Solving the integral over the first generation of the predators yields an expression relating prey density to background (= predator-independent) prey mortality, predation rate and predator mortality. If prey and PPF are complementary food sources, PPF may reduce predator mortality without affecting the predation rate. Then, reducing predator mortality by adding PPF translates into reduced prey density. If, however, PPF and prey are substitutable, then adding PPF may reduce predator mortality as well as predation rate. To make herbivore density go down requires that PPF reduces predator mortality more than it

reduces the predation rate. If PPF is not only utilized by predator, but also by prey, adding PPF as a complementary food to prey will only reduce herbivore density when its reducing effect on predator mortality is disproportionately larger than that on background prey mortality. This demand will be even more extreme when substitutability of foods is assumed and therefore consumption of PPF will likely go at the expense of that on prey. Thus, for prey density to go down in the first generation after predator release adding PPF is subject to stringent conditions. It is then critically important to know whether foods are substitutable or complementary and whether herbivores utilize PPF as well. These conclusions are quite complex, yet they are intuitively much more obvious, than the simple general conclusion drawn for the case of equilibrium conditions stating that: PPF always reduces herbivore density irrespective of its effect on predation and irrespective of its utilization by the herbivore.

### STAGE-STRUCTURED CONSUMER-RESOURCE MODELS

Real-world predator-prey and parasitoid-host interactions differ in the life stages that are affected by prey (or host) density and/or PPF. In general, three scenarios can be observed that differ in whether (A) adult performance (survival, attack, oviposition), (B) juvenile performance (survival, development) and (C) both adult and juvenile performance are affected by prey density. The different types of PPF (nectar, pollen) can also have three different effects as it may (1) promote survival, (2) provide fuel (when rich in sugars as in nectars) for searching and (3) enhance assimilation processes (when rich in amino acids as in pollen), and thereby development and oviposition. As defined above, PPF and prey can be substitutable or complementary food sources and they are called essential if their absence causes the carnivore population to decline even at the highest abundance of the other food source (i.e., reproduction does not compensate mortality or the basic reproduction ratio  $R_0 < 1$ ). Assuming the prey/host is always essential, PPF is never essential when substitutable, but when complementary it can be either essential or not.

Scenario A applies to parasitoids. Here, the larva is carnivorous. It feeds in or on a single host. So there is no need to search for hosts. The adult female searches for hosts and she makes decisions on whether to lay eggs in hosts. Usually the adult female feeds on PPF, but some species also feed on hosts. Thus, host density affects the oviposition rate of the adult parasitoid, but not the survival or development of the larvae. Scenario B comes close to hoverflies. Here, the purely carnivorous larvae actively search for prey, whereas the adult females feed on PPF and lay eggs near areas with prey. Thus, prey density will here most strongly affect juvenile performance. Scenario C is best illustrated by ladybeetles, predatory bugs, earwigs and predatory mites, where carnivory and search for prey occurs in all active stages. Here, prey density will affect the juvenile, as well as adult performance. Lacewings have always actively searching larvae, but some species are carnivorous as adults and other are not. Thus, they represent either scenario B or C. If the oviposition rate of hoverflies strongly depends on how much prey the area harbours, then they are more close to scenario C than to B. Scenario C also becomes more applicable to parasitoids when they kill and feed on hosts to obtain nutrients essential for egg maturation.

For each of the three scenarios on stage-related prey density dependence models were developed that incorporate the effect of substitutable or complementary PPF affecting (1) survival, (2) searching or (3) development and reproduction, plus any combination of 1, 2 and 3. Parameters ranges were based on literature data. From the equilibrium equations of those models we derived how equilibrium prey density changes with an increase in PPF. Such calculations are particularly meaningful when populations return to the equilibria after perturbation (i.e., equilibria are stable). This is likely when not all prey stages are vulnerable to predator attack (Murdoch *et al.* 1987), which holds for many arthropod predator-prey systems (Sabelis 1992; Sabelis and Van Rijn 1997). These calculations show that increasing PPF – whether substitutable or complementary, essential or not essential – causes equilibrium prey density always to decline under all scenarios, but the mode and quantitative details of the decline depend on the scenario under consideration. Extinction above a critical level of PPF availability can only be achieved when the predators eat PPF and prey as substitutable foods in all life stages (and are thus true omnivores) whereas both mortality and reproduction are affected by PPF. In all other cases increasing PPF can never drive the prey population to extinction. Instead, prey density will asymptotically approach some positive value set by the level of background (= minimum) predator mortality. Under each of the three scenarios (A, B and C) the strongest decline in prey density is achieved when PPF is substitutable (and hence non-essential) and when PPF promotes both survival and reproduction of the predator; effects of PPF on survival alone come second in prey suppression efficiency and effects of PPF on searching alone come third. When PPF is essential (and hence complementary), there is a minimum amount of PPF required for the predator population to persist and thereby to suppress the prey population.

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## SPATIALLY STRUCTURED CONSUMER-RESOURCE MODELS

The models discussed above are based on the assumption that predators, herbivores as their prey, and food plants of the herbivores are well mixed and therefore do not take the spatial component of predator-prey interactions into account. This assumption is valid as long as the grain size of the spatial heterogeneity is well below the average foraging range of the consumers. In many cases, however, this assumption does not hold. When herbivores as prey and their food plants co-occur only at spatial scales that are beyond the search range of individual predators, new mechanisms may come into play that are absent in fine-grained environments: predator aggregation, spatial subsidies, and metapopulation dynamics.

Suppose there are two types of sites, plants with herbivores as prey and plants providing alternative food (PPF). When the two plant types occur sufficiently close together, or even merged into one plant species harbouring sites with PPF and sites without, predators may disperse fast enough to achieve a distribution proportional to the amount of food (prey and PPF) on those sites (so called Ideal Free Distribution). Suppose Rosenzweig-MacArthur models govern predator-prey dynamics on each of the two sites and the predators distribute themselves ideal free over the two sites (Van Rijn *et al.* 2002). Then, for a constant PPF supply the predator distribution stabilizes at equilibrium. The more PPF, the stronger the predators

aggregate at the PPF site and the stronger the suppression of herbivores at this site, whereas the suppression in the PPF-free site is weak. Decreasing the area of the PPF site relative to the total area intensifies the impact on herbivore density in this area, but leaves the herbivore density in the non-target area unaffected (Van Rijn and Sabelis 2005). Thus, target sites or plants can be protected against herbivory by arresting predators with the aid of alternative food (PPF). The mode of decline in herbivore density (linear decline to extinction or asymptotic decline to constant level) will be much like those observed in the models of well mixed populations and thus depend on whether PPF and prey are substitutable or complementary, essential or non-essential foods. This local indirect effect of PPF on the herbivores via dispersal of the predator is comparable with 'apparent (predator-mediated) competition', but as it results from behavioral rather than life-history responses, it acts already on time scales shorter than a generation, and has therefore been termed 'short-term apparent competition' (Holt and Kotler 1987). Clearly, this short-term effect of PPF will work most effectively when large areas of (semi)-natural habitat surround agricultural fields and have low numbers of potential pest organisms and some redundancy in the carnivorous species feeding on the pest organisms.

When plants with PPF and those without are further apart, the plants with PPF may subsidize the predator population on PPF-free plants, and help to suppress herbivore numbers there. This represents a source-sink system at the landscape scale (Dunning *et al.* 1992; Polis *et al.* 1997; Pulliam 1988) and can be modelled by two Rosenzweig-MacArthur, predator-prey models, one for the source and one for the sink, that are coupled by dispersal. The impact of PPF via the predators on herbivores on the distant PPF-free plant will vary depending on whether PPF and prey are substitutable or complementary, essential or non-essential. If PPF in the source habitat is complementary and essential yet absent in the sink habitat, it may contribute to suppression of herbivores in the sink habitat (even though here – following the definition of a sink – predator reproduction does not cancel out mortality). When PPF is non-essential, the predator population can persist anyway and by definition the PPF-free habitat cannot be a sink. The habitat with PPF will harbour fewer herbivores and more predators, causing dispersal into the PPF-free habitat. Here, the impact on herbivore density is less pronounced, however, than if PPF is essential. When PPF and prey are substitutable, herbivore density is reduced in the habitat with PPF to a level that exactly compensates for the amount of PPF available. Hence, predator density in that habitat remains unaltered and there will be no net migration into the PPF-free habitat and, hence, no change in prey density. If, however, PPF availability is such that it just supports the predator population and drives prey extinct, any further increase in PPF availability will no longer be compensated by a decrease in prey density, but will translate directly into a larger carnivore population. Predators dispersing into the PPF-free habitat will now cause herbivore density to decrease.

For many real-world systems of arthropod predators and their prey, equilibria may not be feasible. Sources may turn into sinks and vice versa depending on the season or local predator-prey dynamics is intrinsically unstable. In some acarine predator-prey systems in orchards PPF (e.g., pollen) emerging early in the growing season plays a critical role in building up a predator population large enough to suppress the prey population later in the year. In other acarine predator-prey systems predators tend to overexploit their prey and then disperse aerially to find new prey patches (e.g., Pels and Sabelis 1999; Pels *et al.* 2002; Sabelis and

Van der Meer 1986). Here, PPF may either alter the outcome of transient dynamics in local predator-prey populations or it may provide indispensable fuel for dispersal. According to metapopulation models of the patch-occupancy type (Levins 1969) increased rates of dispersal due to PPF will result in a decrease of the number of prey patches. If, however, PPF promotes the within-patch per capita growth rate of the predators this is likely to result in earlier prey extermination and lower numbers of predators that disperse from a patch. This implies a lower dispersal predator dispersal rate and hence an increase of the number of prey patches in the metapopulation. Thus, to understand the metapopulation consequences of PPF it is critical to assess how it influences between-patch predator dispersal as opposed within-patch predator-prey dynamics.

## DISCUSSION: BEYOND CONSUMER-RESOURCE MODELS

In this article we provided a review of the conditions under which PPF gives rise to herbivore suppression via a shared consumer. In particular, we considered how the impact of PPF is modified by stage- and space-related interactions. With few exceptions, the overall pattern is that PPF somehow promotes herbivore/prey suppression. The underlying assumption was that the system consists of one species at the third trophic level, one species at the second trophic level and PPF, as an influence from the first trophic level. In reality, herbivore and carnivore are part of a much more complex food web of species interacting with each other, (Polis and Strong 1996). How will these interactions affect the conditions under which PPF leads to herbivore suppression?

Consider first the presence of a fourth trophic level. Carnivores may have their own suite of (hyper-)predators, (hyper-)parasitoids, and pathogens (Rosenheim 1998; Sullivan and Volkl 1999). Trophic cascade models predict that the top-carnivore will at equilibrium control the primary carnivore, so that the herbivore is released from top-down control (Oksanen *et al.* 1981). The equilibrium density of the primary carnivore would be determined by the traits of the top-carnivore, whereas the herbivore would grow to a density where it is limited from bottom up. This implies that at equilibrium, food provided to the primary carnivore would no longer affect the density of the primary carnivore, nor that of the herbivore! In some cases, PPF can (also) be used by the top-predator or hyperparasitoid (Chang *et al.* 1994). PPF will now likely reduce the density of the primary carnivore, and consequently have a negative rather than a positive impact on biological control of the herbivores. Thus, the presence of a fourth trophic level may dramatically alter the predictions for the impact of PPF on herbivore suppression.

At the third trophic level, competition for herbivores as prey and intraguild predation may alter the species composition and thereby the impact on herbivore suppression (Polis and Holt 1992; Polis *et al.* 1989; Rosenheim 1998). PPF may change the outcome of competition and intraguild predation by promoting one species more than others (e.g., Evans and England 1996). If PPF supports the species that in absence of PPF is a worse competitor but a good intraguild predator, PPF may reduce the density of the better competitor and promote herbivore density (Briggs and Collier 2001; Holt and Polis 1997; Hunter *et al.* 2002; Mylius *et al.* 2001; Rosenheim 2001; Rosenheim *et al.* 1995; Snyder and Ives 2001). However, beyond the PPF level that results in exclusion, PPF will have the same effects as predicted from simple

carnivore-herbivore models. Thus, rather restrictive conditions are required for competition and intraguild predation to alter the predictions for the impact of PPF on herbivore suppression obtained from simple predator-prey models.

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