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Rapid but limited aggregation of ladybird beetles (Coleoptera: Coccinellidae) in response to sugar availability in the field

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Abstract. Field studies of habitat use, settling behaviour and initiation of reproduction by aphidophagous ladybird beetles in alfalfa and other crops by Honěk (1978, 1980, 1982a, b) provided key insights for conceptualizing the intertwining of these predators' dispersal and reproduction among habitats. Recognition of such intertwining is fundamental both for understanding insect predator-prey interactions most generally, and for applying that understanding to strengthen insect pest management. Among the many applications upon which to build further from Honěk's studies is the use of sugar sprays (applied to foliage to serve as "artificial honeydew") as a means of aggregating ladybirds to suppress aphid populations. In the present study, sugar (sucrose) spray was applied repeatedly over the course of 5–10 days without rain in the spring to plots of alfalfa in two field experiments in 1996–1997 in northern Utah (USA). Densities of adult ladybirds (*Coccinella* and *Hippodamia* spp.) in the plots dramatically increased immediately following the first application of sugar but stabilized rapidly thereafter despite repeated application of sugar. Numbers of pea aphids, *Acyrthosiphon pisum* (Harris, 1776), in sprayed plots were reduced in 1997 when the aphids occurred in low numbers throughout the experimental field, but they were not reduced by ladybird colonization of sprayed plots when occurring at higher densities in 1996. In demonstrating a limit in the degree to which local densities of adult ladybirds could be increased by application of artificial honeydew, these experiments provide one example of building on the foundations laid by Honěk's field studies of ladybird use of alfalfa fields and their aphid populations.

Key words. Alfalfa, aphids, biological control, dispersal, habitat selection, honeydew, predation.

INTRODUCTION

In addressing predator-prey interactions, ecologists increasingly are focusing on the central issue of intertwined predator dispersal and reproduction among habitats across large, diverse landscapes. Such is of fundamental importance, for example, in influencing insect pest suppression by biological control from predatory insects and parasitoids (Schellhorn et al. 2014). Our ability to develop a sound conceptual framework to guide further inquiry has arisen in large part through key observations and inferences from field studies by perceptive ecologists. Alois Honěk's studies of aphidophagous ladybird beetles (Coleoptera: Coccinellidae) in fields of alfalfa and other crops (Honěk 1978, 1980, 1982a, b) are an outstanding example. Honěk engaged in these field studies to explore the settling behaviour of ladybirds (i.e., their tendency to remain and thereby increase in density in local habitats) and their commitment to reproduction in these local habitats. The results provided new insights regarding the central importance of prey (aphid) density in determining the ladybirds' behaviour. In essence, Honěk demonstrated clearly through these field studies that the relationship between populations of predator and prey (ladybirds and aphids) is highly dynamic over fine scales of both space and time. High capacity for dispersal leads the predators to distribute themselves continually across landscapes in response to constantly varying patterns of local prey density, and to initiate reproductive activity rapidly at local sites where prey numbers rise to sufficient levels. Hence, at any one time of the growing season, local populations of the predator differ markedly in key features even over small spatial scales (i.e., among sites only tens of meters to a km or two apart). The populations differ markedly in both their local density and degree of reproductive activity, reflecting local prey numbers.

Honěk's (1978, 1980, 1982a, b) studies reinforced inferences and conclusions of earlier studies that adults of aphidophagous ladybirds are highly responsive to local conditions and move extensively among many habitats (e.g., see discussions in Hemptinne et al. 1992, Ives et al. 1993, van der Werf et al. 2000). Honěk's studies also lent strong support for a basic model of adult ladybird searching and reproductive behaviour. In this model, adult females become less active and initiate egg production as they become satiated, and hence they typically lay their eggs near aphid colonies (Putman 1955, Banks 1956, Dixon 1959, as discussed in Evans 2003). Honěk's field observations lent support as well for the hypothesis that net flows of ladybirds to local areas with highest aphid densities within a crop field often prevent aphid outbreaks from arising more generally throughout the field (Frazer 1988), a hypothesis subsequently also supported experimentally both by restricting ladybird movement among aphid colonies (Kareiva 1987), and by creating localized outbreaks that were quickly extinguished by immigrating ladybirds (Evans 2004).

Honěk's field demonstration of the importance of aphid density for ladybird settling behaviour within a habitat, coupled with laboratory demonstration of the stimulatory role of aphid honeydew for larval ladybird searching (Carter & Dixon 1984), suggested that the ladybirds' settling behaviour could be influenced by encounter with aphid honeydew. It also suggested that application of "artificial honeydew" might serve as a useful experimental tool in further exploratory field studies. Strong aggregation of aphidophagous predators, including ladybird adults, in response to sugar (sucrose) solution sprayed as fine droplets onto foliage (a treatment intended to simulate deposition of aphid honeydew) had been demonstrated earlier by Chiang and colleagues (Ewert & Chiang 1966, Schiefelbein & Chang 1966, Carlson & Chiang 1973), Hagen and colleagues (Hagen et al. 1971, Hagen 1986), and others (as discussed in Evans & Swallow 1993). Later studies demonstrated that localized application of such sugar solution to alfalfa foliage led to rapid redistribution of adult ladybirds within two days throughout entire fields (up to 150 m away from local areas sprayed with sugar; Evans & Richards 1997).

Here I present additional field experiments with sugar spray to address a further intriguing aspect of Honěk's (1978, 1980, 1982a, b) observations. In particular, I examine the extent to which dispersing ladybirds will continue to increase in numbers locally in response to repeated application of sugar spray to alfalfa foliage. Honěk stressed the importance of prey density itself in determining ladybird settling behavior. Hence one might predict that in the absence of unusually large or increasing numbers of aphids themselves in a local area, the presence of abundant sugar (artificial honeydew) alone may have only limited influence in promoting the aggregation of large numbers of ladybirds at a site. This prediction is tested here.

METHODS

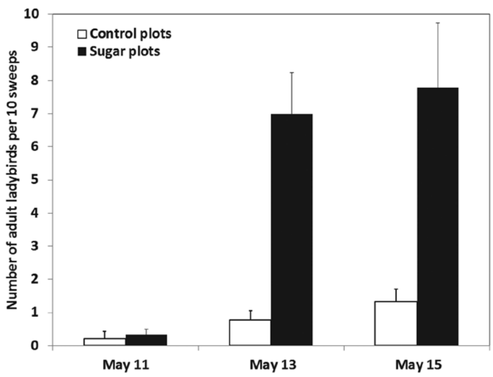
Early in the growing season in 1996 and again in 1997, nine control and nine sugar plots (each 16×24 m) were placed randomly in a grid in an alfalfa field near Logan, Utah. Adjacent plots were separated by 40 m along an east-west axis, and by 65 m along a north-south axis. Over a period of days in May in each year, the alfalfa in each plot was lightly sprayed repeatedly with sugar solution (150 g dissolved sucrose per liter of water; Evans & Richards 1997) or with water only (control plots), and was sampled by taking ten (in 1996) and five (in 1997) 180° sweeps with a net 38 cm in diameter. Plots were sprayed and sampled repeatedly on clear, calm days during spells without rain in both years, with the experiment terminated each year by rain.

In 1996, plots were first sprayed on May 11 (when the alfalfa stood 30–35 cm tall) after taking an initial set of sweep samples (ten sweeps per plot) from each plot before treatments were applied. The plots were sprayed again on May 13; sweep samples were taken from each plot immediately before spraying the plots. A final set of sweep samples was taken in the plots on May 15 (thereafter the plots were sprayed, but the treatments were nullified by rain the next day). In 1997, plots were sprayed with sugar solution or with water only on May 3, 6, 10, and 13, and in each case were sampled (five sweeps per plot) two days later (i.e., they were sampled on May 5, 8, 12, and 15). The alfalfa stood 15–20 cm tall on May 3, and 35–40 cm tall on May 15.

Adult ladybirds and aphids (pea aphids; *Acyrthosiphon pisum*) captured by sweep net sampling were counted in the laboratory after freezing the samples; ladybirds were identified to species. Results for numbers of ladybirds and aphids in plots over time, as influenced by experimental treatment and as determined from sweep sampling during the course of the experiment, were analyzed for each year individually by repeated measures analysis of variance (ANOVA) (SAS 2004).

RESULTS

In 1996, ladybird adults occurred in only small numbers on May 11 at the time that sugar solution was first applied to the experimental plots (Fig. 1). Thereafter, on May 13 and 15, ladybirds were significantly more abundant in sugar plots than in control plots, with no significant difference in their numbers in sugar plots (or in control plots) on the two dates (repeated measures ANOVA for ln [number of ladybirds+1] on May 13 and 15: treatment $F_{1,16}$=58.30, P<0.0001; date $F_{1,16}$=0.51,



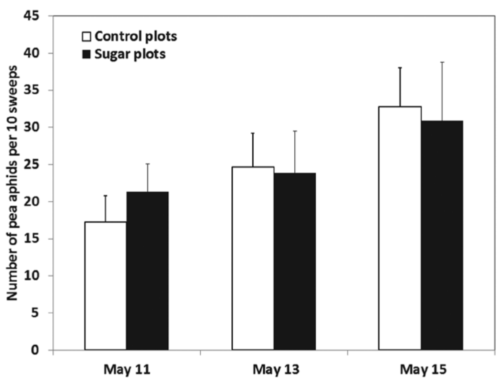


Fig. 1. The mean number (+ SE) of adult ladybirds (top) and pea aphids (bottom) per 10 sweeps in a set of plots of alfalfa, each of which was sprayed repeatedly with sucrose solution (sugar plots) or water only (control plots) in May 1996. Sweep samples were taken immediately before plots were sprayed initially on 11 May and again on 13 May, and a final (third) time on 15 May.

P=0.49; interaction treatment × date $F_{1,16}$=0.36, P=0.56). Most of the individuals present were of *Coccinella septempunctata* Linnaeus, 1758 (50% of individuals in all plots combined) or of *Hippodamia quinquesignata quinquesignata* (Kirby, 1837) (34%), with fewer individuals of *C. transversoguttata richardsoni* Brown, *H. convergens* Guerin, *H. sinuata crotchi* Casey, and *H. tredecempunctata tibialis* (Say) also present. An increase in pea aphid numbers in both sugar and

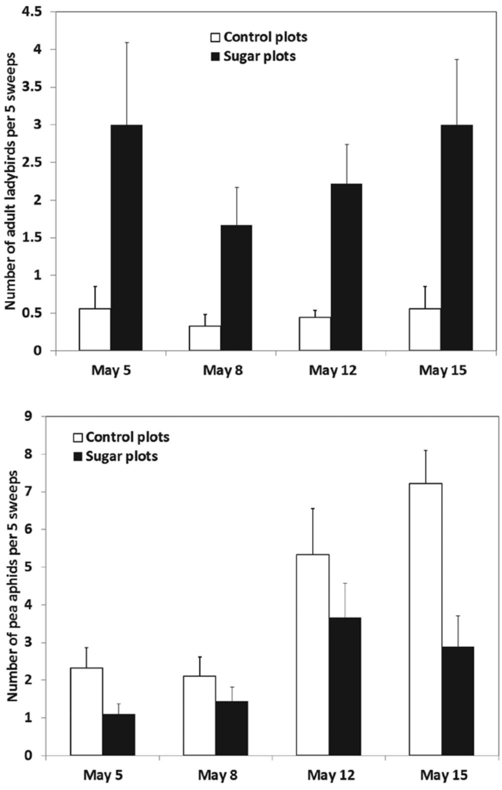


Fig. 2. The mean number (+ SE) of adult ladybirds (top) and pea aphids (bottom) per 5 sweeps in a set of plots of alfalfa, each of which was sprayed repeatedly with sucrose solution (sugar plots) or water only (control plots) in May 1997. For each of the four dates on which sweep samples were taken, sampling occurred two days after treatments were applied (e.g., sweep samples on May 5 followed application of treatments on May 3, the first date in 1997 on which treatments were applied to the plots).

control plots during the experimental period was marginally significant, but pea aphid numbers did not differ between the two sets of plots during the experiment (Fig. 1; repeated measures ANOVA for ln[number of aphids+1] on May 11–15: treatment $F_{1,16}$=0.04, P=0.85, date $F_{2,32}$=3.12, P=0.058; interaction treatment × date $F_{2,32}$=0.54, P=0.55).

In 1997, ladybirds were very abundant in sugar versus control plots when first sampled in experimental plots on May 5, two days after first applications of treatments to plots on May 3

(Fig. 2). The large numbers of ladybirds in sugar plots (and the low numbers in control plots) did not differ significantly among sample dates over the period May 5–15 as the plots were treated repeatedly every few days with either sugar solution or water only (Fig. 2; repeated measures ANOVA for ln [number of ladybirds+1] on May 5–15: treatment $F_{1,16}$=16.48, P=0.0009; date $F_{3,48}$=1.21, P=0.31; interaction treatment × date $F_{3,48}$=0.16, P=0.92). The species composition of ladybirds in the plots in May 1997 was similar to that in 1996: again most of the adults were of *C. septempunctata* (32% of individuals) or of *H. quinquesignata* (43%), while the other species present additionally included *Coccinella novemnotata* Herbst. Aphid populations again increased in plots over time, and were more abundant throughout in control plots than in the sugar plots (Fig. 2; repeated measures ANOVA for ln[number of aphids+1] on May 5–15: treatment $F_{1,16}$=9.39, P=0.0074; date $F_{3,48}$=9.48, P<0.0001; interaction treatment × date $F_{3,48}$=1.40, P=0.25). Overall, the numbers of ladybirds present in the plots in 1997 were similar to those present in 1996, while numbers of pea aphids were much lower in 1997 than they had been in 1996 (Figs. 1 and 2).

DISCUSSION

Ladybirds are major predators of aphids, and there is great interest in determining their potential for pest control in crops such as alfalfa (Dixon 2000, Hodek et al. 2012). Alfalfa fields in particular serve as major habitat for multiple species of ladybirds both in North America (e.g., Hagen et al. 1971, Evans & Swallow 1993) and in Europe (Honěk 1985a, Bianchi et al. 2007). As Honěk (1978, 1980, 1982a, b) demonstrated, the abundance of aphids in these alfalfa fields is a major factor in determining the use of this habitat by ladybirds.

As a substitute for aphid honeydew, the application of sugar solution to alfalfa foliage results in rapid aggregation of ladybirds in treated areas (e.g., see Evans & Richards 1997 and references therein). As shown by Hagen et al. (1971, 1976) and Nichols & Neel (1977), the presence of sugar serves to retain ladybirds after arriving at an area rather than to attract them to the area.

Two general results of the experiments presented here are particularly noteworthy. First, as has also been shown in as variety of settings previously (e.g., see discussions in Evans & Swallow 1993, and Evans & Richards 1997), ladybird populations rapidly increased immediately upon the application of sugar to alfalfa foliage. But secondly, equally rapidly thereafter the number of ladybird adults in a treated area stabilized even with repeated application of sugar. In essence, the local density of ladybirds was raised both very rapidly and substantially with repeated sugar application, but only so much.

This second result seemingly reflects that an equilibrial number of ladybirds was achieved rapidly in treated plots as the rate of emigration of ladybirds quickly rose to match the immigration rate (Cardinale et al. 2003, Křivan 2008). A rise in the emigration rate can be presumed to have arisen in part from a simple increase in the absolute number of ladybirds departing from treated plots per unit time as more ladybirds occurred in the plots. This background level of emigration (i.e., a given probability of an individual's departure from a treated plot) may well reflect departures prompted by low rates of encounter with aphid prey as suggested by Honěk's (1978, 1980, 1985b) studies. It may also reflect bet-hedging tendencies towards continual dispersal regardless of local conditions as suggested by Frazer (1988; see discussion in Evans 2003). In addition, the probability of an individual adult ladybird departing from a treated plot may well be density-dependent, for example rising with increasing ladybird density as individuals perceive local environments as decreasingly suitable sites for foraging and oviposition (Hemptinne et al. 1992, Dixon 1997). In any case, the results demonstrate that applied benefit from sugar application to foliage will quickly reach an upper limit in the effort to encourage the build-up of large numbers of ladybirds in particular habitats (e.g., to slow exponential growth of the prey population through heightened predation early in the season when aphid numbers are still low, or to draw ladybirds away from nearby crops scheduled for insecticide application; Evans & Richards 1997).

Considerable potential nonetheless remains to be explored further concerning field application of sugar in the spatial manipulation of natural enemies such as ladybirds for integrated pest management of agricultural insect pests (e.g., Carlson & Chiang 1973, Evans & Richards 1997, Evans et al. 2010, Seagraves et al. 2011). In this context, it is instructive to compare results from the two years in this study. In 1996, little benefit in pest control resulted from sugar application: the numbers of aphids were not significantly reduced (or slowed in their rate of increase) in sugar plots with high numbers of ladybirds. In 1997, however, when sugar was first applied early in the season at a time when aphid numbers were much lower than in 1996 across all plots, fewer aphids subsequently occurred in sugar plots as ladybird numbers swelled versus in control plots with low numbers of ladybirds.

In summary, in studying habitat selection and the settling behaviour of ladybirds leading to reproduction in fields of alfalfa and other crops, Honěk (1978, 1980, 1982a, b) highlighted a world of fascinating possibilities with significant implications both for understanding fundamental aspects of predator-prey interactions, and for applying that understanding to strengthen insect pest management. Honěk's studies provided key insights for understanding the dynamics of predator dispersal and reproduction among habitats across large, diverse landscapes, a topic of fundamental applied importance for insect pest suppression by biological control as provided by natural enemies such as ladybirds. Honěk's studies thus have served as a strong foundation from which to build further. The experiments presented here regarding the potential of sugar solutions as a pest management tool provide one such example of building upon the foundations laid by Honěk (1978, 1980, 1982a, b).

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