Habitat displacement of native natural enemies by an introduced ladybird: diet as the basis for invasion?

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Introduction

A long and colorful history surrounds the practice of classical biological control, wherein natural enemies of introduced pests are taken from the pest's native geographic range and released into new areas of the world where the pest has become established (e.g., Bellows and Fisher 1999). Dramatic successes over the years serve as continuing impetus and inspiration for this approach to pest control (e.g., Caltagirone and Doutt 1989). Concern has arisen in recent years, however, concerning the potential for adverse non-target effects of such practices (e.g., Simberloff and Stiling 1996). Introductions of natural enemies may lead to reduction in numbers of other species in addition to the target pest, thereby disrupting ecological communities (e.g., Mack et al. 2000). Such concern is especially worrisome for generalist predators released in new areas as biological control agents (e.g., van Lenteren et al. 2002).

The potential for adverse non-target effects of introduced ladybirds (Coleoptera: Coccinellidae) has been an issue of major concern over the past two decades in North America, as first *Coccinella septempunctata* L. and then *Harmonia axyridis* Pallas have become abundant and widespread following their initial establishment on the continent (e.g., Ruesink et al. 1995, Obrycki et al. 2000, Louda et al. 2003). The focus has been on adverse effects of these invasive species on native natural enemies, particularly North American ladybirds. There are now a number of published reports of reduced numbers and habitat displacements of native ladybirds following the arrival of these two species in different parts of North America (e.g., Michaud 2002, Alyokhin and Sewell 2004). As these reports have accumulated, researchers have attempted to determine the major mechanisms underlying competitive displacement. Much of this research has focused on the possibility of reduced survivorship of native ladybird larvae following the establishment of introduced species, either as the result of increased exploitative competition and/or intraguild predation (e.g., Snyder et al. 2004 and Yasuda et al. 2004 and references therein).

Here I will present some results of a continuing long-term case study of the impact of the establishment of *C. septempunctata* on native ladybirds in Utah alfalfa fields (Evans 1991, 2000, 2004). In so doing, I will consider potential mechanisms of species displacement that focus on attributes and interactions of adult ladybirds rather than larvae. Aided by USDA redistribution efforts following its establishment in eastern North America in the 1970s (Angalet et al. 1979), *C. septempunctata* rapidly dispersed westward and arrived under its own power in Utah in the early 1990s (Evans and England 1996). In the fifteen years since, it has become well-established in a variety of habitats in Utah, but is especially prominent and abundant in alfalfa fields.

Historically, alfalfa fields of Utah and, more generally, the intermountain west of North America, have harbored a rich fauna of more than a dozen native species of ladybirds (e.g., Evans and Swallow 1993). Upon its arrival, *C. septempunctata* rose rapidly in numbers in Utah alfalfa fields while numbers of these native ladybirds declined. Thus, in recent years, *C. septempunctata* has become consistently the most common ladybird occupying this habitat (Fig. 1).

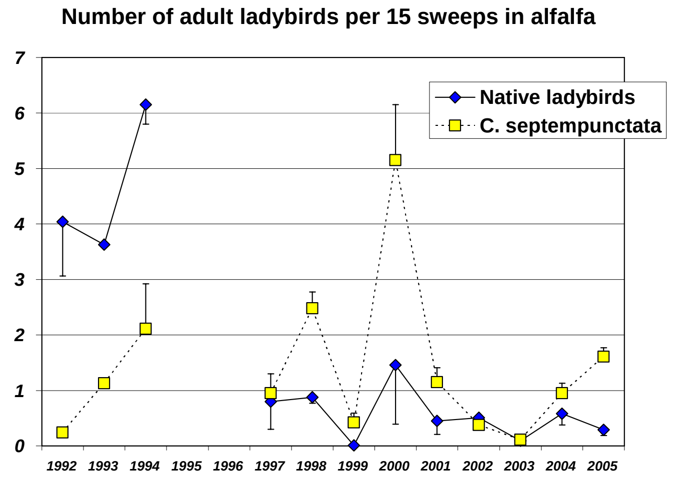

Figure 1. Numbers of adults of native ladybirds (all species combined) and the introduced species *C. septempunctata* collected per 15 sweeps of a net in mid-May in alfalfa fields of northern Utah, USA, in 1992-2005 (note: fields were not sampled in mid-May 1995-1996).

Both *C. septempunctata* and native ladybirds feed primarily (as both adults and larvae) on the pea aphid (*Acyrthosiphon pisum* [Harris]) in Utah alfalfa fields, but they also consume other prey as well. Pea aphids occurred in high numbers in these fields at the time of *C. septempunctata*'s arrival in the early 1990s, but they have occurred only in low (economically insignificant) numbers since that time (Evans 2004). A frequent alternative prey of ladybirds is the larva of the alfalfa weevil (*Hypera postica* [Gyllenhal]), which is the most important and abundant pest insect of alfalfa in Utah, and which continues to occur in every year in very large numbers in most fields.

Native ladybirds in Utah first began exploiting pea aphids, alfalfa weevils, and other prey in alfalfa fields relatively recently (e.g., the alfalfa weevil first appeared in Utah in 1904; Hamlin et al. 1949). In contrast, the invasive *C. septempunctata* has a long history of interaction with these prey in alfalfa (lucerne) fields of the Old World (e.g., Honěk 1985). One hypothesis to account for the numerical dominace of *C. septempunctata* in Utah's alfalfa fields, therefore, is that this species acts as more of a generalist predator in alfalfa fields than do native ladybirds, and is more responsive to prey other than aphids, such as the alfalfa weevil. Thus, the decline in numbers of native ladybirds, and their displacement from alfalfa by *C. septempunctata*, may reflect that they have abandoned alfalfa fields in recent years as aphid numbers have dropped, whereas *C. septempunctata* has continued to persist in this habitat by exploiting alternative prey such as weevils in addition to the low numbers of aphids that are present.

This hypothesis was tested initially by experimentally creating localized outbreaks of aphids in alfalfa fields and testing whether native ladybirds would reappear in the habitat by aggregating in large numbers at these outbreaks (Evans 2004). As predicted, the native ladybirds did indeed reappear. They responded even more strongly than *C. septempunctata* to the aphid outbreaks, only to disappear again from the habitat once the aphid outbreaks collapsed. In contrast, *C. septempunctata* remained in larger numbers even in the absence of aphids, and appeared to respond positively to high weevil numbers when aphid numbers were low. Here I present further field and laboratory experiments to examine the responses of *C. septempunctata* and native ladybirds to alfalfa weevil larvae as alternative prey.

Materials and Methods

We conducted a field experiment during the first crop (May) in an alfalfa field near Logan, Utah. We manipulated local densities of pea aphids and alfalfa weevil larvae, and we measured the aggregative numerical responses of adults of *C. septempunctata* and native ladybirds (responses of individual species of native ladybirds were similar, so data for all native species are combined here). We laid out 2 m^2 plots in a grid with 15 m between adjacent plots. Using cages to temporarily protect prey from predators, we manipulated the numbers of weevil larvae or aphids in a 2 x 2 factorial, completely randomized design, such that there were eight plots each of the following four treatments: high numbers of both aphids and weevils (HaHw), high numbers of aphids and low numbers of weevils (HaLw), low numbers of aphids and high numbers of weevils (LaHw), and low numbers of both aphids and weevils (LaLw).

Upon removing the cages and exposing the prey to ladybirds, we censused the plots over the next eight days for weevils, aphids, and ladybird adults. We assessed prey (aphid and weevil) densities by taking stem samples from each plot at the start of the experiment and then again one week later. Throughout the experiment, we also censused daily for ladybirds by searching each plot visually in systematic fashion for two minutes. We identified to species and recorded all ladybird adults that we observed in our daily visual censuses, but otherwise we left these ladybirds and the plots undisturbed.

To explore the relative tendency and ability of *C. septempunctata* versus native ladybirds to feed on alfalfa weevil larvae versus pea aphids, we extended an initial laboratory feeding study of *C. septempunctata* (Evans et al. 2004) by comparing prey consumption of *C. septempunctata* with that of a native North American congener, *C. transversoguttata richardsoni* Brown. *Coccinella* transversoguttata is one of the ladybird species most heavily displaced by *C. septempunctata* in alfalfa and other habitats across North America (e.g., Elliott et al. 1996, Evans 2004). We collected overwintered adults of *C. septempunctata* and *C. transversoguttata* from alfalfa fields in the spring (first crop) and maintained them at first in the laboratory (at 20 ^{o}C,16L:8D) on a mixed diet of pea aphids and alfalfa weevils, whereupon they became very active reproductively and consumed prey in large quantities. We then provided individual females with excess numbers of aphids or weevils for twenty-four hours, and measured their rate of consumption (mg dry weight of prey consumed).

Results

In our field experiment in which local population sizes of both aphids and weevils were manipulated, initially (i.e, upon removal of cages and exposure of prey populations) all ladybirds (both natives and *C. septempunctata*) focused very heavily on plots with high aphid numbers, apparently independently of the number of weevil larvae present. One week later, however, when aphid numbers had dwindled in the plots, an interesting difference emerged in the aggregative response of *C. septempunctata* versus native ladybirds. Plots that had been manipulated to have high aphid densities still harbored about twice as many aphids as did control plots (with low background aphid densities), but the difference in aphid density between the two kinds of plots had diminished dramatically (Fig. 2). Native ladybirds still aggregated in plots with high density. *C. septempunctata* was also still most abundant in plots with relatively high aphid density, but the introduced predator had also become abundant in plots with low aphid density but also high weevil density (Fig. 2). Thus, the native species appeared to be especially responsive to local aphid density, whereas *C. septempunctata* was also responsive to weevil density in the absence of a dense population of aphids throughout the plots.

Our laboratory experiment was designed to compare consumption rates of weevils versus aphids by females of *C. septempunctata* and the native *C. transversoguttata*. Females of *C. septempunctata* were overall slightly more voracious than females of *C. transversoguttata*, but females of both species consumed more aphid biomass than weevil biomass (Fig. 3). Furthermore, and contrary to expectation, females of the two species did not differ in their relative rates of consumption of the two prey types.

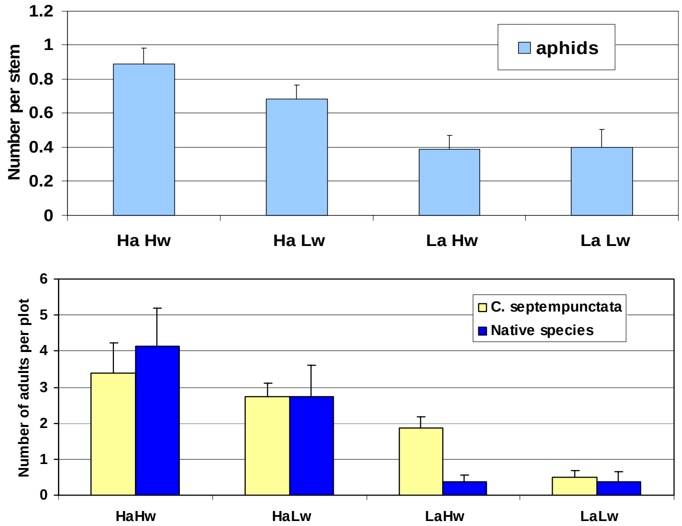

Figure 2. Numbers of pea aphids per stem (top) and numbers of adults of *C. septempunctata* or native ladybirds (bottom) at the conclusion of a field experiment in plots that had been manipulated at the outset to have high numbers of both aphids and weevils (HaHw), high numbers of weevils and low numbers of weevils (HaLw), low numbers of aphids and high numbers of weevils (LaHw), or low numbers of both aphids and weevils (LaLw).

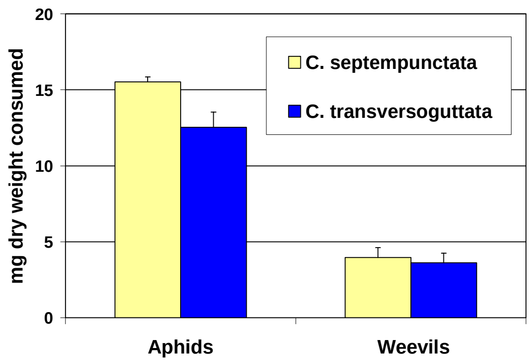

Figure 3. The biomass (mg dry weight) of pea aphids and alfalfa weevil larvae consumed in twenty-four hours by an adult female of *C. septempunctata* and *C. transersoguttata*, when females were provided with either aphids or weevils in excess.

Discussion

The responsiveness of field populations of *C. septempunctata* to weevil density when aphids are not abundant suggests that consumption of this prey may sustain this predator in alfalfa fields even when native ladybirds emigrate in response to low aphid density. This raises an additional question of whether this introduced species also feeds more readily and effectively on alternative prey such as the alfalfa weevil than do native ladybirds. In previous laboratory experiments on feeding behavior (Evans et al. 2004), we focused on the behavior of *C. septempunctata* adult females in attacking aphids and weevils (we examined such behavior when the predators had fed most recently on either aphids or weevils). In these early experiments, we found that *C. septempunctata* females attacked pea aphids more readily than alfalfa weevil larvae, regardless of whether the females had fed previously on aphids or weevil larvae. Nonetheless, *C. septempunctata* females attacked alfalfa weevil larvae with relatively little hesitation. Furthermore, upon overcoming the prey, *C. septempunctata* females fed for very similar amounts of time on individual weevils as they did on individual aphids.

In the laboratory feeding experiment presented here, *C. septempunctata* and *C. transversoguttata* females were very similar in their relative consumption rates of weevils versus aphids. Thus, these laboratory results suggest that *C. septempunctata*, in comparison to native ladybirds, is not unusually prone to attack weevils. It remains to be evaluated further, however, how well the results of these laboratory studies can be extrapolated to ladybird feeding behavior in alfalfa fields (as part of her graduate studies in our lab, L. N. Davidson is now investigating whether rates of weevil consumption differ between *C. septempunctata* and native ladybirds in the field).

In summary, an interesting picture is emerging from these and previous field and laboratory experiments. It appears that adult foraging and dispersal behavior may play a major role in the apparent habitat displacement of native ladybirds from Utah alfalfa fields by the introduced predator *C. septempunctata*. These native ladybirds appear to select their foraging sites largely on the basis of local aphid density. They return each spring to alfalfa fields in search especially of aphids, but it appears that they no longer linger in these fields now that *C. septempunctata* has become abundant and has had a significant effect in lowering aphid densities. *C. septempunctata* contrasts with native ladybirds in having a stronger habitat affinity for alfalfa. It remains in fields in relatively high numbers even in the absence of high aphid density. It may do so in part because of the availability of large numbers of alfalfa weevils. In comparison to native ladybirds, *C. septempunctata* is more responsive to variation in local density of these alternative prey (when aphids are low in number). Interestingly, however, the introduced *C. septempunctata* and its native congener *C. transversoguttata* consume weevils versus aphids in very similar proportions in laboratory feeding trials. Thus, native ladybirds such as *C. transversoguttata* may feed on weevils in alfalfa fields as readily as does *C. septempunctata*, but such consumption may have little influence on native ladybirds' tendencies to remain in or leave an alfalfa field. Consumption of alternative prey such as alfalfa weevils may be sufficient only to deter *C. septempunctata* (and not native ladybirds) from dispersing in the absence of preferred aphid prey. The distinctive behavior of *C. septempunctata* to remain in alfalfa even when aphid densities are too low to sustain the attentions of native ladybirds, combined with its impact on aphid numbers, leads to this introduced species' displacement of native ladybirds from Utah's alfalfa fields.

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