ABSTRACT Among the methods used to evaluate field diets of insect predators is frass analysis. The potential of this infrequently used method was explored for determining prey consumption by adult ladybird beetles (Coleoptera: Coccinellidae) in alfalfa, Medicago sativa L., fields. A laboratory experiment revealed that at 20°C, within 48 h after consumption of prey [either pea aphids, Acyrthosiphon pisum (Harris), or larvae of the alfalfa weevil, Hypera postica (Gyllenhal)], almost all prey fragments had been voided by adults of five ladybird beetle species commonly occurring in Utah alfalfa fields. Among the five ladybird beetle species, aphid and weevil fragments were detected in frass of 80–95 and 29–73% of adults, respectively. A second laboratory experiment with adults of the most common of these predators (the introduced Coccinella septempunctata L.) more fully identified and enumerated diagnostic fragments for specific types of prey (aphids, weevil larvae, and conspecific larvae) as they occurred in frass. Frass pellets from the consumption of alfalfa weevil and conspecific larvae most often contained diagnostic cuticle and setae, and less often mandibles and head capsules. Frass from the consumption of pea aphids most often contained antennae and legs, and less often mouthparts, eyes, and tarsal claws. These laboratory results provide a foundation for using and interpreting the results of frass analysis as a technique to assess field diets of aphidophagous ladybird beetles in alfalfa.

KEY WORDS alfalfa, Coccinella septempunctata, cannibalism, frass analysis, predation

Numerous methods have been used to decipher the diets of predatory insects in the field. These include laboratory and field observational studies, gut dissection, serological and electrophoretic tests, and polymerase chain reaction (PCR). The relative merits of each of these methods have been extensively reviewed, including their usefulness in providing qualitative and quantitative field data on predator–prey relations (Sunderland 1987, Powell et al. 1996, Symanzick and Evans 2010). Frass analysis is one such method of assessing predator diets, but it has been used infrequently. In one approach, the mass of fecal material produced served as an index of predation rate (Phillipson 1960, Honek 1986). A second approach, in which the types of prey consumed were identified from frass contents, has been used for a few invertebrate predators, including species of Odonata (Lawton 1970, Thompson 1978) and Coleoptera (ladybird beetles; Coccinellidae; Putman 1964). Despite its infrequent use, frass analysis offers several advantages. Study insects need not be sacrificed but instead can be returned to the field, or used for additional laboratory experiments. The technique is inexpensive and simple, requires little specialized equipment, provides results quickly, and can be used even after samples have been stored for long periods (Powell et al. 1996).

Building on Putman’s (1964) study of ladybird beetles foraging in Ontario peach orchards, Davidson and Evans (2010) used frass analysis to determine and compare adult diets of three species of ladybird beetles in alfalfa, Medicago sativa L., fields of northern Utah. In consuming a broad variety of foods in alfalfa, these three species (Coccinella septempunctata L., C. transversoguttata richardsoni Brown, and Hippodamia convergens Guérin) fed especially frequently on pea aphids, Acyrthosiphon pisum (Harris), and larvae of the alfalfa weevil, Hypera postica (Gyllenhal) (Davidson and Evans 2010).

In the current study, a laboratory experiment was conducted to determine the time course over which ladybird beetle adults cleared their guts, and the temporal patterns associated with the appearance of diagnostic prey fragments in their frass, after ingestion of these two major prey species. A second experiment was conducted to document the frequencies with which different kinds of prey fragments (e.g., legs and mouthparts) occurred in the frass pellets. Conspecific ladybird beetle larvae also were included as prey in the second experiment because ladybird beetles are known to engage in cannibalism (and intraguild predation), especially when aphid densities are low (Schelhorn and Andow 1999, Pell et al. 2008). These experiments were conducted to provide further foun-
dation for applying frass analysis to explore diet and prey choice of ladybird beetles foraging in alfalfa, a major agricultural habitat exploited by many species of this prominent group of predators throughout the world (Neuenschwander et al. 1975, Hodek and Honček 1996, Elliott et al. 2002, Grez et al. 2008).

Materials and Methods

Insects. Ladybird beetles used in the following laboratory experiments were collected as adults from the field (primarily in alfalfa fields) during spring and summer in Cache County, UT (41°39′59.2″ N 111°53′07.2″ W; Davidson 2005). Both before and during experiments, the ladybird beetles were maintained at 20°C and a photoperiod of 16:8 (L:D) h in an incubator. They were maintained as groups of a given sex and species in 14-cm-diameter petri dishes and fed an excess of pea aphids. Aphids were reared in a greenhouse on fava beans (Vicia faba L.) and collected the same day as used for food. Alfalfa weevil larvae used in the experiments were collected by sweep netting in alfalfa fields. Weevils were maintained in 2.8-liter plastic canisters with fresh alfalfa clippings in an incubator at 12°C and a photoperiod of 16:8 (L:D) h. Ladybird beetle larvae (provided as prey in experiments) were reared in the laboratory from eggs laid by field-collected adults. They were maintained under the same environmental conditions as described above for ladybird beetle adults.

Gut-Clearing Experiment. An experiment was conducted to determine patterns of frass pellet production and contents over time for ladybird beetle adult females feeding on pea aphids and alfalfa weevils (a preliminary experiment with C. septempunctata adults indicated little difference between females and males in these patterns; Davidson 2005). Females of the four most abundant ladybird beetle species that occurred in alfalfa fields of Cache County were studied: C. septempunctata, C. transversoguttata, H. convergens, and Hippodamia quinquesignata (Kirby). A fifth species, recently introduced and now increasing in its abundance in alfalfa, was studied as well: Harmonia axyridis (Fallas). Individual females of each species were provided with either pea aphids or alfalfa weevil larvae as prey, and the frass that they produced was dissected for prey remains.

For 48 h before the start of the experiment, females were held communally and without prey in 14-cm-diameter petri dishes with cotton-stoppered vials of sugar water (15% sucrose solution), to allow them to clear their guts and to stimulate their hunger. At the start of the experiment, females were transferred to individual, 5.5-cm-diameter petri dishes and were randomly assigned to receive aphids or weevils as prey. All females received a drop of sugar water each day in addition to the prey provided. Females fed aphids received an excess supply of mixed instars (without plant material). Females fed weevils (also in excess supply) received six weevil larvae (late second to late third instars). Some females laid eggs during the experiment, but in most cases these were removed before any had been cannibalized by the female and it was assumed therefore that egg consumption did not contribute substantially to frass production.

During the experiment, individuals were given fresh prey every day for 3 d (i.e., sufficient time to ensure consumption of considerable amounts of prey by most individuals). Although all individuals provided with aphids consumed the prey, some individuals did not consume weevil prey on any of the 3 d and therefore were excluded from the experiment (percentages of such individuals varied between 9 and 35% among the five species; Davidson 2008). Final sample sizes (Table 1) varied among species and diets (treatments) for this reason and because species were collected in different numbers due to their differing field abundances.

After 3 d of feeding on the supplied prey, the ladybird beetles were transferred to clean, 5.5-cm-diameter petri dishes with a drop of sugar water. At 24 and 48 h after this initial transfer, ladybird beetles were again transferred to new petri dishes (also without prey, and with only a drop of sugar water). The ladybird beetles were removed from the final petri dishes 72 h after removal from prey. The frass that was produced in the series of petri dishes enabled the extent of gut clearing to be quantified at 24, 48, and 72 h after removal from prey.

At each of these times, the number, color, and appearance of frass pellets produced by each female was noted. All frass pellets were dissected. Pellets were placed in the well of a depression slide and softened with a 20% solution of sodium hydroxide for ~5 min, until it was possible to break apart the peritrophic membrane with tweezers and dissecting needles. The slide was then inspected at 100× magnification by using a compound microscope to note the presence or absence of prey fragments. Identification of aphid and weevil fragments was aided by initial dissections of frass from additional (i.e., nonexperimental) ladybird beetles that had fed on these prey, and by illustrations from Trlitsch (1999) for aphids.

The number of pellets produced over time was analyzed with two-way repeated measures analysis of variance (ANOVA). Categorical data (e.g., proportion of individuals producing frass with diagnostic prey fragments) were analyzed with chi-square tests of independence. Analyses were conducted using SAS 9.1 (SAS Institute 2003).

Table 1. Percentages of females (% individuals) of five ladybird beetle species provided with prey (either pea aphid or alfalfa weevil larvae) in the gut clearing exp that produced frass containing portions of prey fragments

| Species                  | with aphid fragments | with weevil fragments |
|--------------------------|----------------------|-----------------------|
| C. septempunctata         | 97.1 (34)            | 57.1 (35)             |
| C. transversoguttata      | 95.2 (21)            | 26.8 (35)             |
| H. convergens             | 80.7 (31)            | 36.4 (33)             |
| H. quinquesignata         | 57.5 (40)            | 65.4 (26)             |
| H. axyridis               | 90.9 (22)            | 73.3 (30)             |

Only those individuals that consumed the prey offered are included here.
Prey Indicator Experiment. A second experiment was conducted to examine further the quantity and nature of diagnostic fragments from different kinds of prey in ladybird beetle frass. In the laboratory, 80 males and 80 females of *C. septempunctata* were chosen at random from field-collected populations. Initially, each adult was held individually for 48 h in a 5.5-cm-diameter petri dish. During this time, food was withheld and water was offered in vials plugged with cotton.

Thereafter, 20 individuals of each sex were randomly assigned to each of four diets, provided daily: 1) six young alfalfa weevil larvae (second–early third instars), 2) four older alfalfa weevil larvae (late third instars), 3) four *C. septempunctata* larvae (second–early third instars), or 4) an excess number of pea aphids. Numbers of larvae (weevils and conspecifics) were chosen to ensure that adults were provided with an excess supply of prey (as was true also for aphids). Individuals were maintained on these diets for 5 d (i.e., 2 d more than in the first experiment, during which some individuals had failed to consume weevils during the 3-d feeding period). Individuals then were held for a sixth day with no food. As the objective of this experiment was to document the types of fragments produced in frass pellets from different types of prey, it was sufficient to hold individuals for only 24 h past their last feeding. If individuals did not consume any prey over the 5-d feeding period, they were removed from the experiment. All individuals provided with conspecific larvae or pea aphids consumed some of the prey offered. A small number of both males and females failed to feed on the weevil prey provided: three males and two females failed to consume young larvae (reducing sample sizes to 17 for each sex), and three males and two females failed to consume older larvae (reducing sample sizes to 17 and 18, respectively).

Frass was collected daily from each dish. A single pellet (the largest produced over the 6-d period) was examined microscopically for each individual as described above. Structures were categorized by type (e.g., mandible or leg), and sketches and photographs (Davidson 2008) were made of the most representative samples for subsequent comparison with frass produced by free-living individuals in the field. In addition, dissected pellets were scored (to address the amount of food consumed) as having few (≤20) or many (>20) pieces of prey fragments. Data concerning pellet contents were analyzed with chi-square tests of independence with SAS 9.1 (SAS Institute 2003).

Results

Gut-Clearing Experiment. Among female ladybird beetles of the five species (*C. septempunctata*, *C. transversoguttata*, *H. convergens*, *H. quinquesignata*, and *H. axyridis*) that fed on either aphids or weevils in the gut clearing experiment, individuals produced most frass pellets within the first 2 d after removal from prey, regardless of the prey type provided (Fig. 1). The number of frass pellets produced over the experiment differed among ladybird beetle species, prey species, and days (Fig. 1; two-way repeated measures ANOVA with Huynh–Feldt Epsilon correction for sphericity, interaction of time × ladybird beetle species × prey species: $F_{8,602} = 4.54; P = 0.0004$). Frass production declined over time similarly among ladybird beetle species, however (effect of time: $F_{2,602} = 279.01; P < 0.0001$). Overall, the ladybird beetles produced fewer frass pellets during each time period when fed weevils rather than aphids (effect of prey: $F_{1,301} = 19.56; P < 0.0001$). In addition, frass production of females fed weevils declined more rapidly with time than did frass production of females fed aphids (Fig. 1; interaction of prey species × time: $F_{2,602} = 12.41; P = 0.0001$).

Not all frass pellets contained fragments of the prey consumed. A much higher percentage of females produced frass pellets containing prey fragments among individuals that fed on aphids rather than weevils (Table 1; $\chi^2 = 46.48, df = 1, P < 0.0001$ for all species combined). Especially high percentages of females of the three largest beetle species (*C. septempunctata*, *C. transversoguttata*, and *H. axyridis*) produced frass with aphid fragments, but there was no significant difference in this regard among the five species (i.e., including the smaller *Hippodamia convergens* and *H. quinquesignata* as well; $\chi^2 = 5.76, df = 4, P = 0.22$). Greater differences occurred among species when individuals fed on weevils (Table 1; $\chi^2 = 15.16, df = 4, P = 0.0044$).

Frass pellets that contained prey fragments were generally larger and darker than frass pellets that did not. Also, frass pellets produced by individuals that fed on aphids tended to be larger than those produced by individuals that fed on weevils. Many weevil-fed individuals produced only a single pellet that contained weevil fragments during the entire experiment. In contrast, aphid-fed individuals produced multiple pellets that contained aphid fragments.

For each of the five species, the percentage of individuals producing at least one pellet containing prey fragments declined rapidly from day 1 to day 2, particularly for those individuals fed weevils (Fig. 1; pellet production in day 1 versus day 2 after removal from prey, for all five species combined: weevil diet $\chi^2 = 80.52, df = 1, P < 0.0001$, and aphid diet $\chi^2 = 144.16, df = 1, P < 0.0001$). Although females continued to produce small numbers of frass pellets on the third day, very few of these pellets contained prey fragments (Fig. 1). In particular, only a few females of *H. axyridis* and *C. septempunctata* that had fed on aphids produced pellets with prey fragments on the third day (Fig. 1).

Prey Indicator Experiment. Each type of food (weevil larvae, aphids, and conspecific larvae) yielded visually distinct (i.e., diagnostic) fragments within the largest frass pellet produced by a *C. septempunctata* adult that had fed on the prey during the experiment, and no frass pellet examined contained unusual fragments (e.g., pollen, fragments from other food types, or amorphous particles). Cuticular fragments from weevil larvae were very light colored and resembled shed snakeskin. Cuticular fragments from aphids were...
light tan with distinctive patterns of setae. Cuticular fragments from conspecific ladybird beetle larvae were dark, almost black in color, and marked distinctively with whorls of striations (photographs are presented in Davidson 2008).

The types of food differed significantly from one another in the percentage of frass pellets produced that contained many (i.e., at least 20) prey fragments, with lowest percentages recorded for weevil larvae (Fig. 2; $\chi^2 = 30.88, df = 3, P < 0.0001$, for the sexes combined). Frass pellets produced by females and males that fed on small or large alfalfa weevils were similar overall in the frequencies with which they contained fragments belonging to five main categories (Fig. 3). The frequencies with which fragments occurred in frass pellets differed among categories ($\chi^2 = 62.45, df = 4, P < 0.0001$). Cuticle alone or with setae attached occurred especially frequently (Fig. 3). Less of the carcass was left behind when ladybird beetles fed on young rather than older weevil larvae, and the frass contained more prey fragments, especially head capsules and mandibles. When older weevil larvae were fed upon, oftentimes a dried husk of the body was left behind in the petri dish.

On a diet of aphids, females and males produced frass pellets that were similar overall in the frequencies with which they contained prey fragments belonging to six main categories (Fig. 3). The frequencies with which fragments occurred in frass pellets differed among these categories ($\chi^2 = 39.76, df = 5, P < 0.0001$; pellets of both sexes combined), with antennae, legs, and cuticle occurring most commonly (Fig. 3). In general, the ladybird beetles seemed to consume an aphid in its entirety, especially when the aphid was small. With larger, winged aphids, the bee-
tle would often leave behind small bits of prey (although less than in the case of the weevils).

For the diet of conspecific ladybird beetle larvae, frass pellets produced by females and males were similar overall in the frequencies with which they contained fragments belonging to six main categories (Fig. 3). The frequencies with which fragments occurred in frass pellets (of both sexes combined) differed markedly among categories ($\chi^2 = 183.30, df = 5, P < 0.0001$). In general, the ladybird beetles tended to attack and begin consuming conspecific larvae mid-ventrally. This seemed to allow an adult to subdue and kill the larva before it could escape. *C. septempunctata* larvae have an array of bristle-like setae on their ventral side that are quite different in morphology from the simpler setae that occur on weevils. A large proportion of detached setae, or setae still attached to cuticular fragments, were ingested by adults preying on conspecific larvae (Fig. 3). Carcasses left behind almost always retained the head, reflecting the adult beetle's preference instead for body regions with softer tissues. In contrast to often simply taking a liquid meal of weevils, the ladybird beetles tended to consume considerable body tissue of conspecific larvae. With the exception of head capsules and mandibles, most categories of conspecific larval remains were found in almost all frass pellets with fragments (Fig. 3).

**Discussion**

As illustrated in this study, frass analysis can be useful in determining diets of ladybird beetles. Each type of prey examined in this study produced a variety of distinctive fragments in the frass voided by adult ladybird beetles; this can enable the diets of field-collected adults to be determined from inspection of their frass (Davidson and Evans 2010).

Interpretation of results from frass analysis, as well as implementation of the technique, is enhanced with knowledge of how long diagnostic portions of prey remain in the digestive tracts of species being investigated. Such knowledge can assist, for example, in estimating how recently the predator is likely to have consumed its prey. Overall, individuals of each of the five ladybird beetle species considered here had largely cleared their guts of undigested prey fragments within 48 h at 20°C after ceasing to consume the prey.

Interpretation of results of frass analysis also must factor in the frequency with which individuals that have consumed foods fail to produce frass containing diagnostic fragments. In the current study, not all individuals that had fed on either aphids or weevils produced frass containing diagnostic prey fragments. In particular, a considerable percentage of adult ladybird beetles that fed on alfalfa weevil larvae in the first experiment did not incorporate weevil remains into their frass. As noted by Davidson and Evans (2010), such feeding behavior could lead to underestimates in the field of how often individuals use alfalfa weevil larvae as prey. It is interesting to note that in contrast to the first experiment, in the second experiment prey fragments were consistently detected in all dissected frass pellets of *C. septempunctata* adults that had fed on alfalfa weevil larvae. This difference in results between the two experiments may reflect that the predators were provided with weevils over a lon-
ger period in the second experiment (and only the largest pellet, produced when the predator was feeding most actively, was dissected in the second experiment). Additional experiments are needed to assess more fully the conditions under which frass may lack prey fragments after adult ladybird beetles have consumed alfalfa weevil larvae.

There has been much recent interest in the possibility that cannibalism and intraguild predation may occur frequently among insect predators such as ladybird beetles under field conditions (Rosenheim et al. 1995, Snyder and Evans 2006, Pell et al. 2008). The results of the current study indicate that at least for *C. septempunctata*, frass analysis can provide a reliable test for measuring the incidence of consumption of larvae by adults (in contrast, diagnostic fragments of cannibalized ladybird beetle eggs do not occur in the frass; Triltsch 1999).

A frequent goal in determining the diets of beneficial predators is to quantify how much they consume of the different dietary components. Although strict presence-absence data alone can suggest the importance of different types of prey in a predator’s diet, additional information on quantities consumed may be very useful in guiding the implementation of integrated pest management strategies (Harwood and Obrycki 2005). Distinguishing between frass pellets containing many or few prey remains (≥20 and <20 fragments, respectively) was used here to address amounts of prey consumed. As suggested from these fragment counts (and also from field results; Davidson and Evans 2010), adults of *C. septempunctata* seemed to consume pea aphids in greater quantity than alfalfa weevil larvae; the adults also more thoroughly consumed conspecific than weevil larvae. Unfortunately, however, simply counting the number of fragments in the frass may not adequately reflect the relative quantities of different prey types consumed. Counting fragments does not take into account the size of each individual prey fragment, for example, which could vary widely depending on the prey type, or on the section of the body from which the fragment came. Other approaches may yield more useful data. One method is to count particular types of fragments such as final tarsal claws or mouthparts to estimate numbers of individuals of given prey types consumed (Putman 1964, Triltsch 1999). Another possibility is to measure the total surface area of fragments for particular prey items in the frass.

An advantage of frass analysis in comparison to many other methods of determining the diet of ladybird beetles in the field (e.g., serological or molecular techniques) is that multiple prey types can readily be censused at the same time, or store for dissection at a later date. The current study illustrates the potential for using frass analysis to study ladybird beetle diet, and provides a foundation for using this approach to assess in particular these predators’ consumption of two major prey species, pea aphids and alfalfa weevil larvae, in alfalfa fields.

Acknowledgments

We thank M. Johnson, J. Bingham, D. Gunther, M. Anderson, S. Davidson, M. Venkataraman, and Y. Kajita for assistance with field and laboratory work; D. Knudsen for coordinating use of Utah Agricultural Experiment Station alfalfa fields; and D. Alston, R. Whitesides, and two anonymous reviewers for very helpful comments on earlier drafts of the manuscript. This research was supported by the Utah Agricultural Experiment Station, Utah State University, and is approved as journal paper 8253.

References Cited

Davidson, L. N. 2008. Diets of ladybird beetles (Coleoptera: Coccinellidae) in Utah alfalfa fields. M.S. thesis, Utah State University, Logan, UT.

Davidson, L. N., and E. W. Evans. 2010. Frass analysis of diets of aphidophagous lady beetles (Coleoptera: Coccinellidae) in Utah alfalfa fields. Environ. Entomol. 39: 576–582.

Elliott, N. C., R. W. Kieckhefer, G. J. Michels, and K. L. Giles. 2002. Predator abundance in alfalfa fields in relation to aphids, within-field vegetation, and landscape matrix. Environ. Entomol. 31: 253–260.

Grez, A. A., T. Zaviezo, S. Díaz, B. Camousseight, and G. Cortes. 2005. Effects of habitat loss and fragmentation on the abundance and species richness of aphidophagous coccinellids and aphids in experimental alfalfa landscapes. Eur. J. Entomol. 105: 411–420.

Harwood, J. D., and J. J. Obrycki. 2005. Quantifying aphid predation rates of generalist predators in the field. Eur. J. Entomol. 102: 335–350.

Hodek, I., and A. Honček. 1996. Ecology of Coccinellidae. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Honček, A. 1986. Production of faeces in natural populations of aphidophagous coccinellids (Col.) and estimation of predation rates. J. Appl. Entomol. 102: 467–476.

Lawton, J. H. 1970. Feeding and food energy assimilation in larvae of the damselfly *Pyrrhosoma nymphula* (Sulz.) (Odonata Zygoptera). J. Anim. Ecol. 39: 669–689.

Neuenschwander, P., K. S. Hagen, and R. F. Smith. 1975. Predation on aphids in California’s alfalfa fields. Hilgardia 43: 53–78.

Pell, J. K., J. Baverstock, H. E. Roy, R. L. Ware, and M.E.N. Majerus. 2008. Intraguild predation involving *Harmonia axyridis*: a review of current knowledge and future perspectives. Biocontrol 53: 147–168.

Phillipson, J. 1960. The food consumption of different instars of *Mitopus morio* (F.) (Phalangida) under natural conditions. J. Anim. Ecol. 29: 299–307.

Powell, W., M. P. Walton, and M. A. Jervis. 1996. Populations and communities, pp. 223–282. In M. Jervis and N. Kidd (eds.). Insect natural enemies: practical approaches to their study and evaluation. Chapman & Hall, London, United Kingdom.

Putman, W. L. 1964. Occurrence and food of some coccinellids (Coleoptera) in Ontario peach orchards. Can. Entomol. 96: 1149–1155.
Rosenheim, J. A., H. K. Kaya, L. E. Ehler, J. J. Marois, and B. A. Jaffee. 1995. Intraguild predation among biological-control agents: theory and evidence. Biol. Control 5: 303–335.

SAS Institute. 2003. PROC user’s manual, version 9.1. SAS Institute, Cary, NC.

Schellhorn, N. A., and D. A. Andow. 1999. Cannibalism and interspecific predation: role of oviposition behavior. Ecol. Appl. 9: 418–428.

Snyder, W. E., G. M. Clevenger, and S. D. Eigenbrode. 2004. Intraguild predation and successful invasion by introduced ladybird beetles. Oecologia 140: 559–565.

Snyder, W. E., and E. W. Evans. 2006. Ecological effects of invasive arthropod generalist predators. Annu. Rev. Ecol. Evol. Syst. 37: 95–122.

Sunderland, K. D. 1987. A review of methods of quantifying invertebrate predation occurring in the field. Acta Phytopathol. Entomol. Hung. 22: 13–34.

Symondson, W. O. C. 2002. Molecular identification of prey in predator diets. Mol. Ecol. 11: 627–641.

Thompson, D. J. 1978. Prey size selection by larvae of the damselfly, Ischnura elegans (Odonata). J. Anim. Ecol. 47: 769–785.

Triltsch, H. 1999. Food remains in the guts of Coccinella septempunctata (Coleoptera: Coccinellidae) adults and larvae. Eur. J. Entomol. 96: 355–364.

Weber, D. C., and J. G. Lundgren. 2009. Assessing the trophic ecology of the Coccinellidae: their roles as predators and as prey. Biol. Control 51: 199–214.

Yasuda, H., E. W. Evans, Y. Kajita, K. Urakawa, and T. Takizawa. 2004. Asymmetric larval interactions between introduced and indigenous ladybirds in North America. Oecologia 141: 722–731.

Received 4 January 2011; accepted 31 March 2011.