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Status of Exotic and Previously Common Native Coccinellids (Coleoptera) in South Dakota Landscapes

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ABSTRACT: In the last two decades, three previously common coccinellids (*Adalia bipunctata* (L.), *Coccinella transversoguttata richardsoni* Brown, and *Coccinella novemnotata* Herbst) have declined in abundance in South Dakota, while two invasive species (*Coccinella septempunctata* (L.) and *Harmonia axyridis* (Pallas)) have become established there. The objectives of this study were to survey coccinellids in various habitats in South Dakota to better characterize the current coccinellid fauna, determine the extent of exploitation by invasive coccinellids, and possibly identify refuge habitats of previously common coccinellid species. Overall, 2827 coccinellids, comprising 23 species, were collected on yellow sticky traps in field and woody habitats and during timed visual searches in field crops. *Adalia bipunctata* was found during additional sampling in Butte County in western South Dakota. However, it was not present in samples from eastern and central parts of the state, which is consistent with previous findings that this species is absent from those areas. *Coccinella transversoguttata richardsoni* and *C. novemnotata* were absent at all sites sampled. *Scymnus kansanus* Casey was collected for the first time in South Dakota among arboreal habitats. *Harmonia axyridis* (Pallas) expanded its geographic range into central South Dakota by 2002 and western South Dakota by 2004. Invasiveness of *H. axyridis* and *C. septempunctata* was evident by their presence in a wide variety of habitats surveyed, dominance of larval coccinellid assemblages, and predation upon non-target species of aphids. *Harmonia axyridis* was the most abundant larval coccinellid in maize and *C. septempunctata* was the most abundant larval coccinellid in intercropped wheat-alfalfa. *Harmonia axyridis* preyed upon *Stegophylla quercicola* (Monell), *Aphis nerii* Boyer de Fonscolombe, and *Aphis asclepiadis* Fitch in the field. Both *H. axyridis* and *C. septempunctata* preyed upon *Hyalopterus pruni* (Geoffroy) in the field.

KEY WORDS: *Harmonia axyridis*, *Scymnus kansanus*, *Adalia bipunctata*, *Coccinella transversoguttata richardsoni*, *Coccinella novemnotata*, invasive species

The Coccinellidae (Coleoptera) is a relatively large family of beetles that consists mainly of arthropod predators, but also includes phytophagous and mycetophagous species (Gordon, 1985). Kirk and Balsbaugh (1975) listed 66 taxa (species or subspecies) of Coccinellidae for South Dakota. Since then, two exotic coccinellids have established in the state: *Coccinella septempunctata* L. in the late 1980's (Elliott *et al.*, 1996) and *Harmonia axyridis* (Pallas) in the late 1990's (Hesler *et al.*, 2001). Establishment of *C. septempunctata* was associated with the decline of two, previously common native coccinellids, *Adalia bipunctata* L. and *C. transversoguttata richardsoni* Brown, in crop fields in eastern South Dakota (Elliott *et al.*, 1996). A third native species, *C. novemnotata* Herbst, a generalist once common in agricultural fields, has declined in eastern North America (Wheeler and Hoebeke, 1995) and in South Dakota (Hesler *et al.*, 2004). *Harmonia axyridis* has also been associated with declines in abundance of coccinellids (Michaud, 2002; Brown, 2003), but any impact on native coccinellids specifically in South Dakota is yet unknown.

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The impacts of biological invasions are usually mitigated to some degree both spatially and temporally (Elton, 2000; Morrison, 2002; Strayer *et al.*, 2006). Spatially, native species may limit or avoid interaction with invasive species if the two species occupy mutually exclusive habitat(s) (Elton, 2000). In the presence of a dominant invasive species, populations of native species may be largely confined to refuge habitats where there are still sufficient prey to maintain a metapopulation within the landscape (Evans, 2000; New, 2004). As competition with invasive species is an important factor that structures coccinellid assemblages in field-crop habitats, it is important to survey other habitats as potential refuges for native coccinellids (Elliott *et al.*, 1996; Evans, 2000).

Many coccinellid species found in field-crop habitats in South Dakota also occur in other habitats, although information about the relative abundances of coccinellids in other habitats is generally limited (Obrycki *et al.*, 2000). *Coccinella septempunctata*, *C. novemnotata*, and *C. transversoguttata* have been characterized as habitat generalists that are abundant in field crops and orchards (Maredia *et al.*, 1992; LaMana and Miller, 1996; Colunga-Garcia *et al.*, 1997; Brown and Miller, 1998). *Coccinella septempunctata* is also found in old fields dominated by herbaceous vegetation, whereas *C. transversoguttata* is found in old fields regenerating with woody vegetation and along forest edges (Gagné and Martin, 1968; Maredia *et al.*, 1992; Colunga-Garcia *et al.*, 1997). *Coccinella novemnotata* is found in herbaceous and wooded habitats throughout North America (Wheeler and Hoebeke, 1995).

Adalia bipunctata and *H. axyridis* are principally arboreal species (Coderre *et al.*, 1995; Koch, 2003; Omkar and Pervez, 2005). However, *H. axyridis* is known to reproduce in field habitats (Koch, 2003; Nault and Kennedy, 2003; Hesler *et al.*, 2004), whereas *A. bipunctata* generally occurs as adults in field habitats in North America but reproduction is limited to arboreal habitats (Putman, 1964; Maredia *et al.*, 1992; Elliott *et al.*, 1996; Colunga-Garcia *et al.*, 1997).

Common ecological or evolutionary processes may be expected to modulate the effects of an invasive insect species over time (Elton, 2000; Morrison, 2002; Strayer *et al.*, 2006). Biological invasions generally have an acute phase in the few years immediately after a new species arrives, followed by a chronic phase after ecological and evolutionary processes have come into play (Strayer *et al.*, 2006). Over time, invading species often show a manifold decrease in abundance relative to that in the acute phase. Parallel to this trend with invasive species, native species may show acute declines in abundance followed by chronic outcomes ranging from recovery to extirpation (Howarth, 2001; Morrison, 2002; Strayer *et al.*, 2006).

Temporally, the recent invasions by exotic coccinellids in South Dakota may be in different phases. The invasion by *C. septempunctata* may have reached the chronic phase, with expected moderation in abundance of this coccinellid. In contrast, the *H. axyridis* invasion is likely in the acute phase, with *H. axyridis* expected to occur at relatively high abundance, at least in particular habitats.

The abundance of native coccinellids in South Dakota may also have changed with respect to temporal phases of exotic coccinellid invasions. By now, it is possible that native coccinellid species that declined upon invasion by *C. septempunctata* may have recovered in abundance. However, the recent invasion by *H. axyridis* may also affect coccinellid assemblages and might preempt recovery of native species (Brown, 2003; Alyohkin and Sewell, 2004).

Table 1. Habitats sampled for coccinellids in South Dakota, 2001–2006.

Habitats	Location	Year(s)	Sampling method
Field-crop plots	Brookings County	2002–2003	Timed visual searches
Field-crop and arboreal habitats	Brookings and Hyde Counties	2002–2003	Yellow sticky traps
Woods and maize fields	Brookings County	2001, 2003	Yellow sticky traps
Maize, woods, relict prairie	Brookings County	2003	Yellow sticky traps
Miscellaneous habitats	Brookings and Butte Counties	2002–2006	Hand collections and observations

Strayer *et al.* (2006) suggested long-term monitoring to determine the effects of biological invasions. Several authors have called for monitoring populations of North American coccinellids to assess the status of indigenous coccinellids and the invasiveness of exotic coccinellids (Wheeler and Hoebeke, 1995; Ellis *et al.*, 1999; Hesler *et al.*, 2001). The objectives of the current study were to survey for coccinellids in various habitats in eastern South Dakota to assess the coccinellid fauna, particularly for recovery of previously common native species; to survey for refuge habitats of previously common native species of coccinellids; and to determine the extent of exploitation by invasive coccinellids.

Study Sites and Methods

Two principal methods were used to sample coccinellids from assorted habitats in South Dakota from 2001 through 2006 (Table 1). First, timed visual searches were used to sample common field-crop habitats in eastern South Dakota. Second, yellow sticky traps were used to sample coccinellids in field and wooded habitats in eastern and central South Dakota. In addition, anecdotal observations and collections of coccinellids were made in habitats in eastern and western South Dakota. Voucher specimens of coccinellids and aphid prey are deposited at the North Central Agricultural Research Laboratory, Brookings, South Dakota.

Timed Visual Searches

Because many of the native and invasive coccinellids occur readily in field-crop habitats, it was an obvious goal to sample in such habitats. Coccinellids were sampled by visual searches within 30.5 × 30.5 m plots of field crops at the Eastern South Dakota Soil and Water Research Farm in 2002 and 2003. The crops were grown in a four-year rotational sequence consisting of maize, soybeans, intercropped wheat-alfalfa, and alfalfa. Each crop was present each year, and they were randomly distributed among three replicate blocks. Sampling times were based on crop development and the likelihood of aphids occurring within particular crops (Table 2). Early season sampling of the wheat-alfalfa intercrop and second-year alfalfa occurred on the same dates, and late season sampling of second-year alfalfa, maize, and soybean occurred on the same dates.

Coccinellids were sampled within a plot by counting all adults and larvae seen during 4 min on vegetation and on the ground within three, 1-m^2 areas each in soybean, intercropped wheat-alfalfa, and alfalfa. A search area was approached from the north to avoid casting shadows and delineated by gently placing a 1 × 1-m frame on the ground. Maize was sampled for coccinellids by carefully laying a 1-m

Table 2. Dates of coccinellid sampling within field-crop plots, Eastern South Dakota Soil and Water Research Farm, Brookings, SD, 2002–2003.

Crops	Sampling dates
2002	
Wheat–alfalfa intercrop, alfalfa	21 May, 28 May, 5 June, 11 June, 26 June, 3 July
Alfalfa, maize, soybean	9 July, 19 July, 25 July, 7 August, 14 August, 23 August, 28 August
2003	
Wheat–alfalfa intercrop, alfalfa	20 May, 27 May, 5 June, 12 June, 27 June
Alfalfa, maize, soybean	10 July, 17 July, 28 July, 6 August, 13 August

stick between two rows and then searching all plants adjacent to the stick. Plots were searched when coccinellids were most likely to be active, i.e., between 1000 and 1600 hrs on sunny to partially sunny days with temperatures 20°C or greater and wind speed less than 30 km (Hesler *et al.*, 2004). Adult coccinellids were identified and counted in the field. Larvae were counted on site or collected into alcohol jars and taken to the laboratory for identification before counting (Rees *et al.*, 1994; Rhoades, 1996). Similarity of coccinellid assemblages was determined among habitats by using Kendall's rank correlation coefficient,

$$\tau = \frac{2S}{N(N-1)},$$

in which S is the sum in the number of agreements in species rankings between two habitats and N is the number of species common to both habitats (Siegal and Castellan, 1988; Kieckhefer *et al.*, 1992; Colunga-Garcia *et al.*, 1997). Similarity indices were calculated only for paired habitats with equal numbers of trap days (Southwood, 1978). In calculating similarity indices, counts were summed across years, and species with <4 individuals per habitat pair were either not included or combined with congeneric species into a genus-level group (Bullock, 1971; Colunga-Garcia *et al.*, 1997).

A chi-square goodness of fit was calculated to determine whether counts of different coccinellid species were distributed evenly within and among crops for each year of a particular sampling method (Zar, 1998; SAS Institute, 2002). Data sets with <5 mean expected counts per species were not subjected to analysis, and species with zero counts were not included in an analysis (Zar, 1998; SAS Institute, 2002). When the null hypothesis of even species distribution was rejected, counts within data sets of three or more coccinellid species were converted to proportions and a Tukey-type, multiple comparison procedure was used to separate proportions among species or habitats (Zar, 1998).

Aphid abundance was estimated by sampling individual plants in wheat and alfalfa, and it was rated by examining plants in maize and soybean. The number of aphids was counted on 14 wheat stems in each intercropped wheat-alfalfa plot and on 14 alfalfa stems in each alfalfa plot. Aphid abundance on maize and soybean was rated by inspecting 14 plants per plot. Aphid abundance in maize was rated on a 1-to-5 scale ('1' = very light, 0 to 50 aphids per plant, to '5' = very severe, upper leaves and tassel virtually covered by aphids; Foott and Timmons, 1973). Aphid abundance in soybean was rated by using a 0-to-4 scale ('0' = no aphids, '4' >1000 aphids; Multi-State Soybean Aphid Survey Protocol, 2003).

Yellow Sticky Traps

Three different sets of yellow sticky traps (nonbaited Pherocon AM traps, Trece, Inc., Salinas, CA) were deployed in eastern and central South Dakota to survey for adult coccinellids in common field-crop habitats and in wooded sites that potentially serve as refuge habitats. Traps were attached by binder clips at the top of 1.5-m high wooden laths in each habitat.

Set 1: herbaceous and wooded habitats near Brookings and Highmore: Coccinellids were sampled for several weeks each summer in 2002 and 2003 by placing yellow sticky traps within seven different habitats near the city of Brookings (22 May–3 September 2002, 21 May–4 September 2003) and two habitats near the town of Highmore, South Dakota (Hyde County, central part of state; 24 May–30 August 2002, 23 May–3 September 2003). Two sites were sampled near Brookings. Each of the two sites was located <2 km north of Brookings, and they were about 5 km from one another. The first site included a 0.5-ha field of winter wheat, a 1-ha alfalfa field, and an 80 × 300 m shelterbelt comprised mainly of white ash (*Fraxinus americana* L.) with smooth brome (*Bromus inermis* Leyss.) and thistle understory. Trapping was terminated in wheat on 8 July 2002 and 18 June 2003 due to harvest; trapping was suspended in alfalfa from 17 June–1 July 2002, and from 11–26 June and 16–31 July 2003 due to cutting and baling. The remaining four habitats near Brookings were located at the N. E. Hansen Horticultural Research Center, South Dakota State University. Habitats at the horticultural center included an untended, 1-ha apple orchard; roughly 1-ha pure stands each of honeylocust (*Gleditsia triacanthos* L.) and pine (*Pinus strobus* L. with moderately dense understory of thistles); and an open, grassy interspace between the apple and honeylocust stands that was intermittently populated with common dandelion (*Taraxacum officinale* G.H. Weber ex Wiggers). Traps near Highmore were placed in a 1.2-ha fallow, grassy pasture and in a 0.8-ha, mixed hardwood (oak, ash, elm, etc.) shelterbelt. Both habitats near Highmore were at the Central Crops Research Station, South Dakota State University. None of the habitats at Brookings or Highmore received pesticide application during the study. The grassy stand at the horticultural center was mowed about weekly, except for a circular area (2 m diam) around each sticky trap.

Five yellow sticky traps were placed about 15 m apart along a transect within each habitat (4 traps in wheat due to plot dimensions). Traps were replaced roughly weekly, and coccinellids were identified to species and tallied in the laboratory. The numbers of coccinellids were summed across sampling dates and years. Coccinellid assemblages in each habitat were characterized by determining species richness, Berger-Parker dominance ($d_{\max} = n_{\mathrm{dominant}}/n_{\mathrm{total}}$) and Shannon-Weiner diversity ($H' = -\sum_{i=1}^{S}\left(\frac{n_i}{n}\ln\frac{n_i}{n}\right)$) (Southwood, 1978; Colunga-Garcia *et al.*, 1997). Kendall's rank correlation coefficient was used to measure similarity in coccinellid assemblages among field crops sampled on coincident dates. Chi square tests were used to compare the distribution of beetle counts within and between crops for each year. Data sets with expected counts <5 per species were not analyzed, and species with zero counts were not included in analyses. When a hypothesis of even species distribution was rejected, counts within data sets of three or more coccinellid species were converted to proportions, and a Tukey-type, multiple comparison procedure was used to separate proportions among species or habitats (Zar, 1998).

Set 2: commercial maize fields and wooded habitats: A second set of sticky traps was deployed from 23 July–7 August 2001 and 23 July–7 August 2003 in northeastern Brookings County to survey for adult coccinellids in commercial maize fields and in wooded natural areas. A different maize field was sampled each year, but the fields were located within 2 km of each other and about 8 km NE of the city of Brookings. Two wooded habitats (designated 'South Slope' and 'North Ridge') were located at Oak Lake Field Station, South Dakota State University, about 35 km NE of Brookings. Each was composed primarily of deciduous trees (bur oak, *Quercus macrocarpa* Michx.; ash, *Fraxinus* spp.; hawthorn, *Crataegus* sp.; box elder, *Acer negundo* L.). The South Slope site was on a gentle, south-facing slope with a closed canopy and appreciable shading, whereas the North Ridge site was on roughly level ground with intermittent openings in the canopy. Ten sticky traps were deployed ≥30 m apart per habitat and replaced roughly weekly. No insecticides were used in any of the habitats during sampling. All coccinellids captured on the traps were identified by using keys and descriptions found in Gordon (1985); Chapin and Brou (1991), and Gordon and Vandenberg (1991). For each year, results are reported as the total number per species captured per habitat.

Set 3: maize field, relict prairie, and woods: A third set of sticky traps was deployed as part of an organized, intensive biological survey of the Oakwood Lakes habitat complex about 18 km northwest of Brookings from 3–12 July and 21–28 August 2003. Three habitats were surveyed in the habitat complex, which was managed by the South Dakota Department of Game, Fish and Parks. The three habitats were within 1 km of each other and consisted of 1) a roughly 100-ha field of maize located within the West Oakwood Game Production Area, 2) a relict prairie on the northern half of the Goodfellow Waterfowl Production Area, and 3) a wooded habitat (e.g., oak; ash; and buckthorn, *Rhamnus carthartica* L.) on Scout Peninsula within Oakwood Lakes State Park. Five sticky traps were deployed per habitat during each sampling period. Coccinellids captured during each sampling period were identified and tallied, and total numbers collected per species are reported.

Anecdotal Observations and Collections

Anecdotal observations and collections of coccinellids were made from 2002 through 2006 in eastern and western South Dakota to document further the geographic distribution of *Adalia bipunctata* in South Dakota and the distribution and prey of *H. axyridis*. Aphids were identified by using keys in Blackman and Eastop (1994).

Results

Timed Visual Searches

Wheat-alfalfa intercrop and alfalfa plots: Totals of 160 adult and 46 larval coccinellids comprising six species were sampled from plots of intercropped wheat-alfalfa and alfalfa in 2002 and 2003 (Table 3). More adult coccinellids were collected in 2002 than 2003 in each crop. Abundance of adult coccinellids did not differ between crops in 2002, but adults were more abundant in wheat than in alfalfa in 2003. Abundance of adult coccinellids differed by species in 2002, with *Coleomegilla maculata* (DeGeer) as the dominant coccinellid in each crop. *Coccinella septempunctata* occurred at low levels in both crops. *Adalia bipunctata*, *Coccinella*

Table 3. Number of adult coccinellids sampled in wheat and early season alfalfa plots near Brookings, South Dakota.

Year	Species	Alfalfa	Wheat	Across–crop χ^2 (d.f. = 1)
2002	*Brachiacantha ursina*	1 b	0	–[1]
	Coccinella septempunctata	4 b	5 b	–
	Coleomegilla maculata	66 aA	39 aB	6.9*
	Hippodamia convergens	0	4 b	–
	Hippodamia parenthesis	1 bB	10 bA	7.4*
	Total count	72 A	58 A	1.5
	Within–crop χ^2 (d.f.)	171.0* (4)	56.3* (3)	
2003	*Coccinella septempunctata*	1	3 b	–
	Coleomegilla maculata	3	10 a	–
	Hippodamia convergens	3	7 a	–
	Hippodamia parenthesis	1	1 b	–
	Hippodamia tredecimpunctata	0	1 b	–
	Total count	8 B	22 A	6.5*
	Within–crop χ^2 (d.f.)	–	14.4* (4)	

*, $P < 0.05$. For each year within crops, nonzero counts within a column followed by the same lowercase letter do not differ statistically (chi square test with protected Tukey–type multiple comparison test for proportions). For each year across crops, nonzero counts within a row followed by the uppercase same letter do not differ statistically (chi square test).

[1] Dash indicates insufficient counts for analysis.

transversoguttata richardsoni, *C. novemnotata*, and *Harmonia axyridis* were absent from the plots.

All coccinellid larvae were found in intercropped wheat-alfalfa only on 27 June 2003. *Coccinella septempunctata* represented two-thirds of all larvae collected (Fig. 1, top graph) and was significantly more abundant than larvae of other coccinellids ($\chi^2{}_3 = 44.6$, d.f. = 3, $P < 0.001$). The occurrence of coccinellid larvae followed a peak in cereal aphid abundance ($\bar{x} = 3.5$ aphids per stem) in the plots on 12 June, whereas cereal aphids were present at low levels over the season ($\bar{x} = 0.78$ cereal aphids per stem per sampling date; no aphids on alfalfa). The absence of coccinellid larvae from the wheat-alfalfa intercrop in 2002 and from alfalfa in 2002 and 2003 was likely due, at least in part, to low numbers of aphids ($\bar{x} < 0.1$ per stem) in the plots. Species were not ranked similarly in abundance between crops ($\tau_{\text{alfalfa-wheat}} = 0.33$, d.f. = 7, $P > 0.05$).

Late-season alfalfa, maize, and soybean plots: A total of 188 adult and 204 larval coccinellids were collected from alfalfa, maize, and soybean plots in 2002 and 2003. The crops shared an assemblage of seven coccinellid species, but the species were not ranked similarly in abundance among crops ($\tau_{\text{alfalfa-maize}} = -0.28$, $\tau_{\text{alfalfa-soybean}} = -0.31$, $\tau_{\text{maize-soybean}} = 0.02$, $P > 0.05$ for each pair). *Adalia bipunctata*, *C. transversoguttata richardsoni*, and *C. novemnotata* were absent from the plots.

The abundance of coccinellids differed among habitats (Table 4). In 2002, counts of adult coccinellids were higher in maize and soybean than in alfalfa, whereas in 2003 counts were highest in soybean and higher in maize than alfalfa. Counts of some individual species also differed among habitats. For instance, adult *C. maculata* were more abundant in maize than soybean or alfalfa in 2002 and 2003. Counts of adult *Hippodamia convergens* Guerin-Meneville were higher in maize in 2003, but did not differ among crops in 2002.

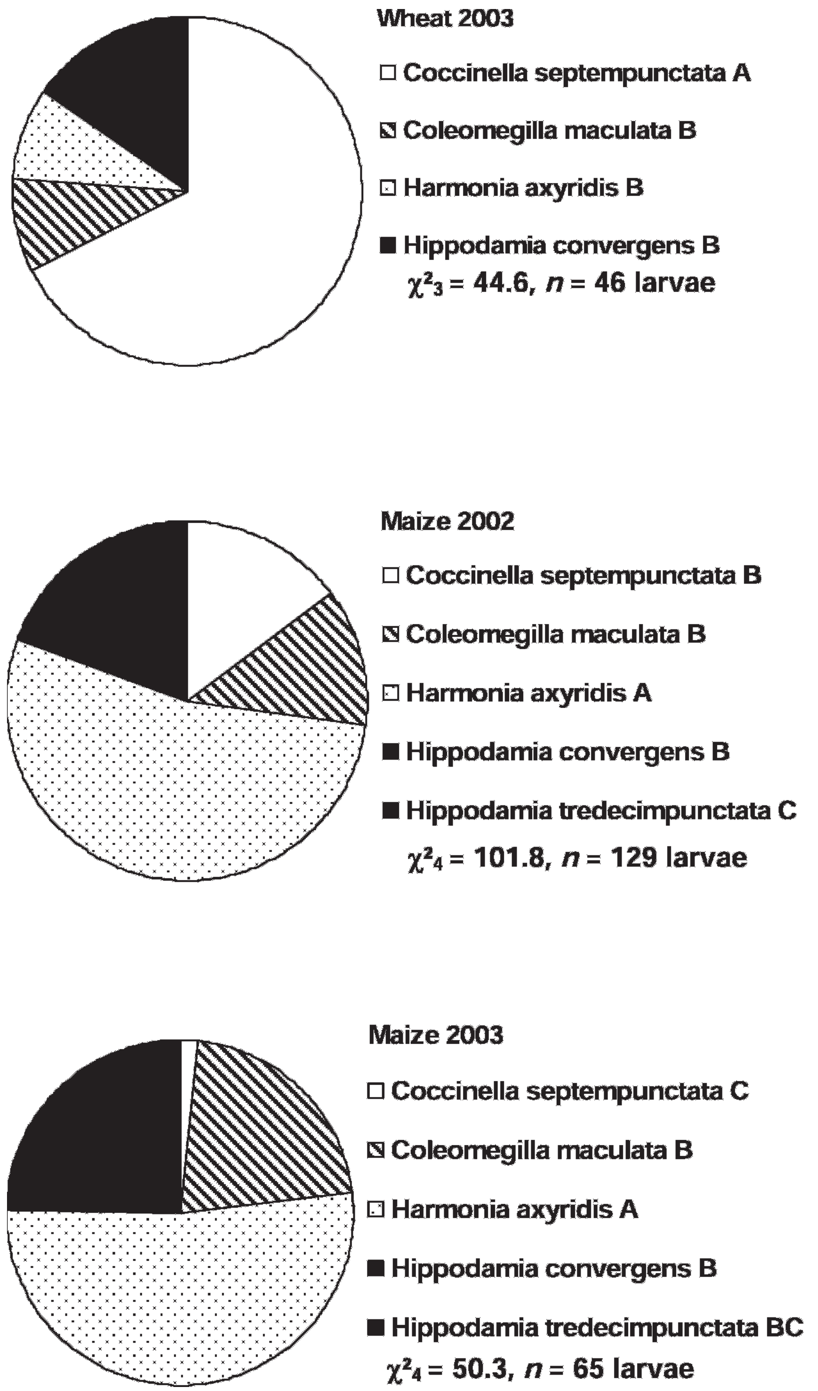

Fig. 1. Relative abundance of larval coccinellids in field-crop plots, Brookings County, South Dakota. For each chart, species followed by the same letter are not significantly different in relative abundance (chi square test followed by protected Tukey-type multiple comparison test for proportions).

Table 4. Number of adult coccinellids sampled in late season alfalfa, maize and soybean plots, Brookings County, South Dakota.

Year	Species	Alfalfa	Maize	Soybean	Across–crop χ^2 (d.f.)
2002	*Coccinella septempunctata*	4 aA	5 bA	11 aA	4.3 (2)
	Coleomegilla maculata	4 aB	33 aA	2 bB	24.6* (2)
	Cycloneda munda	0	0	1 b	–[1]
	Harmonia axyridis	0	20 aA	18 aA	0.1 (2)
	Hippodamia convergens	0	7 bB	22 aA	7.8* (1)
	Hippodamia parenthesis	3 a	0	1 b	–
	Hippodamia tredecimpunctata	0	2 b	0	–
	Total count	11 B	67 A	55 A	39.2* (2)
	Within–crop χ^2 (d.f.)	0.2 (2)	49.9* (4)	47.0* (6)	
2003	*Coccinella septempunctata*	3 B	0	17 aA	9.8* (1)
	Coleomegilla maculata	0	10 aA	1 cB	7.4* (1)
	Harmonia axyridis	0	3	6 b	–
	Hippodamia convergens	0	3 aA	9 bA	3.0 (1)
	Hippodamia parenthesis	0	0	0	–
	Hippodamia tredecimpunctata	0	3	0	–
	Total count	3 C	19 B	33 A	24.6* (2)
	Within–crop χ^2 (d.f.)	–	7.7 (3)	16.3* (3)	

*, $P < 0.05$. For each year within crops, nonzero counts within a column followed by the same lowercase letter do not differ statistically (chi square test with protected Tukey–type multiple comparison test for proportions). For each year across crops, nonzero counts within a row followed by the uppercase same letter do not differ statistically (chi square test plus Tukey–type multiple comparison test for proportions).

[1] Dash indicates insufficient counts for analysis.

Abundance of adult coccinellids sometimes differed within crops (Table 4). In 2002, *C. maculata* and *H. axyridis* were more abundant in maize than other coccinellids. In soybean, *C. septempunctata*, *H. axyridis*, and *H. convergens* were more abundant than other coccinellids in 2002, and *C. septempunctata* was more abundant than other coccinellids in 2003.

Invasive species represented the majority of larval coccinellids. Each year in maize, larvae of *H. axyridis* were >2 times more abundant than larvae of other coccinellid species (Fig. 1, middle and bottom graphs). Populations of larval coccinellids in maize peaked 1–2 wks after those of corn leaf aphid (*Rhopalosiphum maidis* (Fitch)), which were light to moderate in 2002 and light in 2003 (Fig. 2). Only 1 larval coccinellid (*C. septempunctata*, 2002) was collected from alfalfa, and aphid prey were virtually absent from alfalfa both years (1 aphid collected in 2002, none in 2003). In soybean, 8 larval coccinellids (3 *C. septempunctata*, 3 *H. axyridis*, and 2 *H. convergens*) were found in 2002 and 2 larval coccinellids (1 *C. septempunctata* and 1 *H. axyridis*) in 2003. Population levels of soybean aphid (*Aphis glycines* Matsumura) were low (<<100 aphids per plant) in both years of the study.

Sticky Trap Samples

Set 1: herbaceous and wooded habitats near Brookings and Highmore: A total of 1954 coccinellids, comprising 19 species, were captured during the two trapping seasons in field and woody habitats at Brookings and Highmore (Table 5). Species richness ranged from 16 species in honeylocust in 2002 to only 5 species in the Highmore pasture in 2003. Shannon-Weiner diversity indices ranged between 1.15

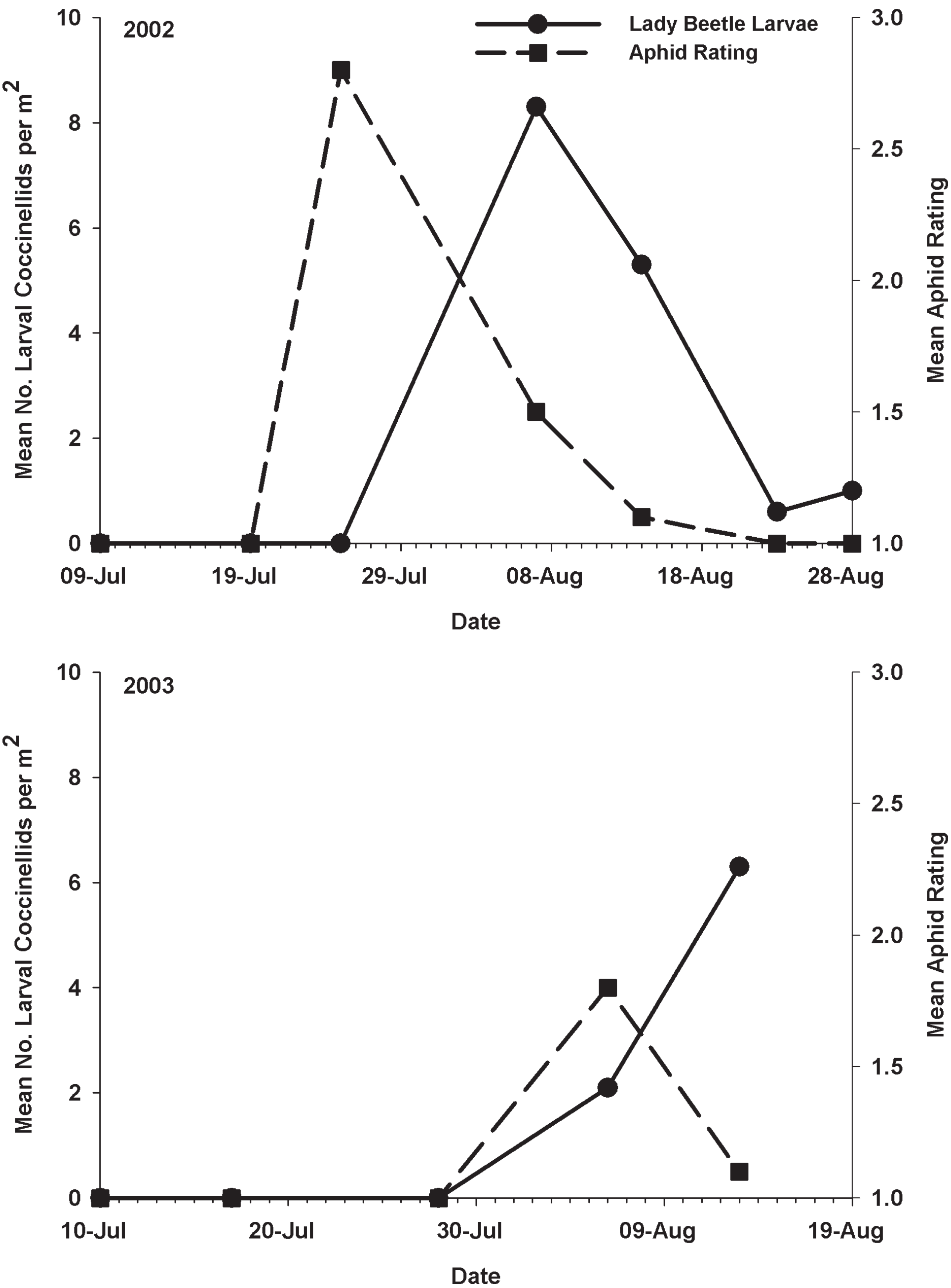

Fig. 2. Mean number of larval coccinellids per m^2 (n = 3 plots) and mean aphid-infestation ratings (n = 3 plots, 14 plants per plot) in maize plots, Brookings County, South Dakota, 2002 and 2003. Aphid abundance on maize plants was rated using a scale that ranged from 1 (very light infestation) to 5 (very severe infestation) (Foott and Timmons, 1973).

and 2.21, with the highest values in apple each year. At Brookings, 1137 and 618 coccinellids were captured in 2002 and 2003, respectively, and 87 and 112 coccinellids were captured in 2002 and 2003, respectively, at Highmore. Numbers of coccinellids captured per habitat each year ranged from 41 (apple, 2003) to 394 (honeylocust, 2002).

Different species of coccinellids were dominant among the various habitats and years. *Coleomegilla maculata* was often a dominant coccinellid. In 2002, it was dominant in the grassy interspace, alfalfa and winter wheat, and co-dominant in the Brookings shelterbelt and in honeylocust. In contrast, *C. maculata* was generally sparse in 2003, except for being the second-most abundant coccinellid in winter wheat.

Coccinella septempunctata was unevenly distributed among habitats. Counts of *C. septempunctata* differed among Brookings shelterbelt, apple, grass, honeylocust, and pine-thistle habitats (2002: $\chi^2 = 90.2$, d.f. = 3, $P < 0.001$; 2003: $\chi^2 = 74.9$, d.f. = 3, $P < 0.001$), with the highest counts in grass. Counts at Highmore were greater in pasture than in the shelterbelt (2002: $\chi^2 = 10.7$, d.f. = 1, $P < 0.001$; 2003: $\chi^2 = 13.7$, d.f. = 1, $P < 0.001$). Counts were relatively high in alfalfa, but not winter wheat.

Coccinella septempunctata was dominant in the grassy interspace and the Highmore pasture in 2003, and was also co-dominant in alfalfa in 2003. It was also the most numerous coccinellid in the Highmore pasture in 2002, although overall numbers of coccinellids were too low to compare relative abundances.

The greatest number of coccinellids was captured in pine-thistle habitat, due principally to dominance by the mycetophage *Psyllobora vigintimaculata* (Say) in 2002 and 2003, and secondarily to the abundance of *Cycloneda munda* (Say) in 2002. Counts of *P. vigintimaculata* were not evenly distributed among Brookings shelterbelt, apple, grass, honeylocust, and pine-thistle habitats (2002: $\chi^2 = 435.5$, d.f. = 3, $P < 0.001$; 2003: $\chi^2 = 299.2$, d.f. = 4, $P < 0.001$), and counts in pine-thistle habitat were roughly 10 times greater than in other habitats. Reasons for the abundance *P. vigintimaculata* and *C. munda* in pine-thistle in 2002 were not evident. We searched pine and thistle plants for *P. vigintimaculata* and *C. munda*, but only a few adult *C. munda* were found. A persistent infection of powdery mildew on thistle leaves may have been responsible for the abundance of *P. vigintimaculata*, although none was ever observed in association with the fungus.

Brachiacantha ursina (F.) was co-dominant with *C. maculata* in honeylocust in 2002 and dominant in honeylocust in 2003. It was also the most numerous coccinellid in apple in 2002 and 2003, but numbers of coccinellids were too low in this habitat for statistical analysis. Counts of *B. ursina* were not distributed equally among apple, honeylocust, pine, grass, and the Brookings shelterbelt (2002: $\chi^2 = 174.7$, d.f. = 4, $P < 0.001$; 2003: $\chi^2 = 132.5$, d.f. = 4, $P < 0.001$), with greater counts in honeylocust each year.

Hippodamia tredecimpunctata tibialis (Say) was the dominant coccinellid in winter wheat in 2003, and it was second-most abundant in 2002. *Hippodamia convergens* was the most numerous coccinellid in the Highmore shelterbelt, but numbers of coccinellids in this habitat were too low for comparisons of species abundance.

Harmonia axyridis was co-dominant in the Brookings shelterbelt in 2002, and the most numerous coccinellid there in 2003, although overall numbers of coccinellids were too low for comparisons among species. *Harmonia axyridis* was also co-dominant in alfalfa in 2003.

Table 5. Indices of coccinellid fauna from habitats near Brookings and Highmore, South Dakota, 2002–2003.

Year	Species	Brookings							Highmore	
		Shelterbelt	Apple	Grass	Honeylocust	Pine and thistle	Alfalfa	Winter wheat	Shelterbelt	Pasture
2002	*Brachiacantha albifrons*	0	0	1 d	2 bc	0	0	1 d	0	0
	Brachiacantha ursina	8 bc	12	6 cd	80 a	10 cd	0	3 d	0	0
	Chilocorus stigma	4 c	1	0	5 bc	0	1 d	0	0	0
	Coccinella septempunctata	0	1	36 b	2 bc	1 d	25 b	5 cd	4	20
	Coleomegilla maculata	29 a	7	76 a	57 a	4 d	49 a	62 a	1	1
	Cycloneda munda	7 bc	9	0	12 b	120 b	1 d	1 d	2	0
	Harmonia axyridis	18 ab	3	9 cd	11 bc	1 d	20 bc	5 cd	1	1
	Hippodamia convergens	5 bc	0	13 c	7 bc	24 c	8 cd	18 bc	19	11
	Hippodamia parenthesis	0	0	4 cd	2 bc	0	3 d	4 d	1	7
	Hippodamia tredecimpunctata	0	0	6 cd	2 bc	0	7 cd	23 b	0	1
	Hyperaspis binotata	2 c	0	0	1 c	0	0	0	0	0
	Hyperaspis undulata	3 c	0	4 cd	1 c	2 d	0	1 d	3	1
	Psyllobora vigintimaculata	2 c	4	0	13 b	173 a	0	0	1	0
	Scymnus compar	0	0	0	0	2 d	0	0	0	0
	S. kansanus	0	2	0	1 c	0	0	0	0	0
	S. lacustris	0	1	0	0	1 d	0	0	1	0
	S. postpictus	2 c	0	0	0	0	0	0	3	1
	S. iowensis	0	4	0	5 bc	24 c	0	0	5	1
	Scymnus spp. undet.	4	1	0	2	13	0	0	1	0
	Stethorus spp.	0	8	0	5 bc	19 c	0	0	1	0
Within-habitat χ^2 (d.f.)		87.5 (9)	–[1]	276.2 (8)	588.3 (15)	1066.9 (11)	135. 1 (7)	265.2 (9)	–	–
Total		88	53	155	210	394	114	123	43	44
Species richness, *s*		10	10	9	16	12	8	10	12	9
Dominance, *d*		0.345	0.226	0.490	0.381	0.439	0.430	0.504	0.442	0.455
Diversity, *H'*		1.87	2.11	1.53	1.86	1.47	1.54	1.52	1.89	1.51
Trap days		104	104	104	104	104	90	47	98	98

Table 5. Continued.

Year	Species	Brookings							Highmore	
		Shelterbelt	Apple	Grass	Honeylocust	Pine and thistle	Alfalfa	Winter wheat	Shelterbelt	Pasture
2003	*Brachiacantha albifrons*	0	0	0	2 b	0	0	0	0	0
	Brachiacantha ursina	3	12	10 b	63 a	6 cd	0	0	0	0
	Chilocorus stigma	0	1	0	0	0	1 d	0	0	0
	Coccinella septempunctata	1	1	32 a	3 b	0	34 a	3 c	9	33 a
	Coleomegilla maculata	1	0	2 b	1 b	0	7 cd	18 b	2	2 c
	Cycloneda munda	6	3	0	1 b	27 b	0	1 c	2	18 b
	Harmonia axyridis	14	3	4 b	5 b	1 d	31 ab	4 c	1	2 c
	Hippodamia convergens	1	0	6 b	1 b	0	14 bc	15 b	23	0
	Hippodamia parenthesis	0	0	0	0	0	1 d	0	2	0
	Hippodamia tredecimpunctata	4	0	3 b	0	0	0	65 a	0	2 c
	Hyperaspis binotata	3	2	1 b	9 b	0	0	0	1	0
	Hyperaspis undulata	1	3	2 b	1 b	0	2 d	0	1	0
	Psyllobora vigintimaculata	10	5	1 b	3 b	98 a	0	0	0	0
	Scymnus compar	0	0	0	0	0	0	0	0	0
	S. iowensis	2	2	0	5 b	14 bc	0	0	3	0
	S. kansanus	1	1	0	1 b	0	0	0	0	0
	S. lacustris	0	4	0	6 b	7 cd	0	0	1	0
	S. postpictus	0	0	0	0	0	0	0	4	0
	Scymnus spp. undet.	1	0	0	0	0	0	0	1	0
	Stethorus spp.	3	4	0	0	14 bc	1 d	0	5	0
Within-habitat χ^2 (d.f.)		–[1]	–	115.3 (8)	434.8 (12)	286.2 (6)	117.3 (7)	165.7 (5)	–	68.0 (4)
Total		51	41	61	101	167	91	106	55	57
Species richness, *s*		13	12	9	13	7	8	6	12	5
Berg-Parker dominance, *d*		0.275	0.293	0.525	0.564	0.587	0.374	0.613	0.418	0.579
Shannon-Weiner diversity, *H'*		2.16	2.21	1.55	1.49	1.31	1.45	1.15	1.91	1.03
Trap days		106	106	106	106	106	76	76	103	103

* , $P < 0.05$. For each year within crops, nonzero counts within a column followed by the same lowercase letter do not differ statistically (protected Tukey-type multiple comparison test for proportions).

[1] Dash indicates insufficient counts for analysis.

Table 6. Rank correlation coefficients among coccinellid fauna on sticky traps in habitats near Brookings and Highmore, South Dakota, 2002–2003.

	Alfalfa	Shelterbelt	Apple	Grass	Honeylocust	Pine
Brookings						
Winter wheat[1]	0.33	−0.09	−0.39	0.33	−0.03	−0.49
Alfalfa[2]	–	−0.10	−0.44	0.64*	−0.12	−0.47
Shelterbelt[3]	–	–	0.11	0.05	0.62**	0.19
Apple[3]	–	–	–	−0.24	0.54*	0.32
Grass[3]	–	–	–	–	0.12	−0.22
Honeylocust[3]	–	–	–	–	–	0.41*
Highmore						
Pasture vs. shelterbelt[4]	0.00					

* , $P < 0.05$; **, $P < 0.01$.
[1] Coefficients calculated for 77 trap days.
[2] Coefficients calculated for 168 trap days.
[3] Coefficients calculated for 212 trap days.
[4] Coefficients calculated for 203 trap days.

The westward range expansion of *H. axyridis* into central South Dakota was documented by use of sticky traps. A single *H. axyridis* caught on a trap in the Highmore shelterbelt on 1 July 2002 was the first record of *H. axyridis* from central South Dakota. Another *H. axyridis* was captured in the Highmore pasture on 20 August 2002. In 2003, one additional *H. axyridis* was captured in the Highmore shelterbelt and two were captured in the Highmore pasture.

Scymnus spp. and *Stethorus* spp. were found almost exclusively in wooded habitats, generally in relatively low numbers. An exception was the relative abundance of *Scymnus iowensis* Casey and *Stethorus* spp. in pine-thistle habitat. *Scymnus kansanus* Casey, a species not recorded previously from South Dakota, was found in low numbers in several wooded habitats. Males of *S. kansanus* were captured in three habitats that included 3 specimens from apple (5 June and 8 July 2002, 24 June 2003), two from honeylocust (29 July 2002, 31 July 2003), and one from the Brookings shelterbelt (9 July 2003).

Other coccinellid taxa (i.e., *Brachiacantha albifrons* (Say) and *Hyperaspis* spp.) were captured only in low numbers in some habitats. *Adalia bipunctata*, *C. transversoguttata richardsoni*, and *C. novemnotata* were not captured in any habitat.

Community indices revealed trends in coccinellid faunal composition among habitats (Table 5). Habitats in which one species composed a majority of coccinellids, as indicated by the Berg-Parker dominance index, *d*, were winter wheat in 2002, and grass, honeylocust, pine-thistle, winter wheat and pasture in 2003. Different species were dominant, except for dominance by *C. septempunctata* in grass and pasture. The Shannon-Weiner diversity index, *H'*, ranged from a low of 1.15 in winter wheat 2003 to a high of 2.21in apple 2002, and low diversity generally corresponded with high dominance indices.

A relatively rich number of species was found among habitats, but habitats did not necessarily have comparable rankings in species abundance. As a result, coccinellid assemblages were similar in only 4 of the 22 possible habitats pairs (Table 6). Honeylocust shared similar coccinellid assemblages with three other arboreal habitats (apple, pine, and Brookings shelterbelt), and assemblages were also similar

Table 7. Total number of adult coccinellids captured on 10 yellow sticky traps each in a maize field and at two wooded sites, South Slope and North Ridge, Brookings County, South Dakota.

	23 July–7 August 2001			23 July–7 August 2003		
		Wooded			Wooded	
Species	Maize	South Slope	North Ridge	Maize	South Slope	North Ridge
Harmonia axyridis	1	0	0	0	1	0
Coccinella septempunctata	3	0	0	2	0	0
Coleomegilla maculata	27	0	0	54	0	0
Hippodamia convergens	3	0	0	2	0	0
Hippodamia tredecimpunctata	39	0	0	51	0	0
Brachiacantha ursina	0	1	0	0	0	0
Cycloneda munda	2	0	0	1	0	0
Scymnus spp.	0	0	5	0	4	3
Stethorus spp.	0	1	0	0	0	2
Hyperaspis binotata	0	7	1	0	0	0
Hyperaspis proba	0	3	0	0	1	2
Psyllobora vigintimaculata	0	4	0	0	22	3

between alfalfa and grass. None of the habitats had significantly dissimilar assemblages of coccinellids.

Set 2: commercial maize fields and wooded habitats: Altogether, 239 coccinellids, comprising 12 taxa, were collected on sticky traps in the two commercial maize fields and two wooded habitats in 2001 and 2003, but *Coccinella transversoguttata richardsoni*, *C. novemnotata*, and *A. bipunctata* were not collected (Table 7). Assemblages of coccinellids in maize fields and wooded habitats were independent of one another, with no species in common except for one *H. axyridis* captured in maize and one at the South Slope wooded site. Six species of coccinellids, comprising 185 individuals, were collected from maize. Five of 6 species found in maize [*H. axyridis*, *C. septempunctata*, *Coleomegilla maculata*, *Hippodamia convergens*, *H. parenthesis* (Say), and *H. tredecimpunctata tibialis*] are typically associated with maize, and adults of *Cycloneda munda* are occasionally collected from maize (Kieckhefer *et al.*, 1992; Hesler *et al.*, 2004). Seven coccinellid taxa [*H. axyridis*, *Scymnus* spp., *Stethorus* spp., *Brachiacantha ursina*, *Hyperaspis binotata* (Say), *H. proba* (Say), and *Psyllobora vigintimaculata*], comprising 52 individuals, were collected from the two wooded habitats, and these taxa are typically found in arboreal habitats in North America (Gordon, 1985; Koch, 2003).

Set 3: maize field, relict prairie, and woods: Thirty-six coccinellids, consisting of 7 species, were collected on sticky traps from the Oakwood Lakes area (Table 8). Twenty of the 36 coccinellids were *Psyllobora vigintimaculata*, all from wooded habitats. Five *C. septempunctata* were collected from relict prairie. The remainder of coccinellids consisted of *Coleomegilla maculata*, *Hippodamia convergens*, *H. tredecimpunctata tibialis*, *Hyperaspis binotata*, and *Anisosticta bitriangularis* (Say). *Coccinella transversoguttata richardsoni*, *C. novemnotata*, and *A. bipunctata* were absent from samples.

Anecdotal Observations and Collections

Additional distribution records: Collections of *A. bipunctata* and *H. axyridis* were made from Butte County in western South Dakota. *Adalia bipunctata* was collected

Table 8. Number of adult coccinellids caught on 5 yellow sticky traps per habitat, Oakwood Lakes area, Brookings County, South Dakota, 2003.

Species	Maize field		Relict prairie		Deciduous woods	
	3–12 July	21–28 August	3–12 July	21–28 August	3–12 July	21–28 August
Anisosticta bitriangularis	0	0	1	0	0	0
Coccinella septempunctata	0	0	5	0	1	0
Coleomegilla maculata	0	3	0	0	0	0
Hippodamia convergens	1	1	0	1	0	0
Hippodamia tredecimpunctata	2	0	0	0	0	0
Hyperaspis binotata	0	0	0	0	1	0
Psyllobora vigintimaculata	0	0	0	0	8	12

at a house near the town of Nisland on 5 May 2004, 15 March 2005, and 2 February and 11 March 2006. An additional *A. bipunctata* was collected from a city park in Belle Fourche on 5 April 2006. All *A. bipunctata* collected had multiple maculations or banding on their elytra. Perusal of coccinellid specimens housed at South Dakota State University revealed only a single specimen of *A. bipunctata* collected on 11 July 1994 at Oakwood Lakes State Park that is the last curated since 1971.

Harmonia axyridis was also found at a house near Nisland in 2004 (2 February, 30 October, and 8 and 11 November) and 2005 (10 and 17 February, and 19 March). A few other *H. axyridis* were present but not collected on those dates. These are the first *H. axyridis* recorded from western South Dakota.

Predation on non-target aphids: On 8 September 2003, a single adult *H. axyridis* was found preying upon *Stegophylla quercicola* (Monell) on bur oak at Scout Peninsula, Oakwood Lakes State Park, Brookings County. Several other adult *H. axyridis* were observed in association with (though not feeding upon) *S. quercicola* on bur oak.

Several adults and larvae of *H. axyridis* and adults of *C. septempunctata* were observed preying upon mealy plum aphids (*Hyalopterus pruni* (Geoffroy)) on common reed (*Phragmites australis* (Cav.) Trin. ex Steud.) at Oakwood Lakes State Park on 8 September 2003. Adults of both coccinellid species were also found in the park among common reeds preying upon *H. pruni* on 24 September 2003.

On 14 September 2003, adult *H. axyridis* were found feeding upon *Aphis asclepiadis* Fitch within several patches of milkweed (*Asclepias* sp.) that were growing in roadside ditches and uncultivated land near Lake Goldsmith (about 16 km west of Brookings).

On 24 and 28 September 2006, several adults of *H. axyridis* and *C. septempunctata* were observed feeding on honeydew from oleander aphids (*Aphis nerii* Boyer de Fonscolombe) that were infesting butterfly weed (*Asclepias tuberosa* L.) in the city of Brookings. On 1 and 2 October 2006, several adult *H. axyridis* were observed feeding on oleander aphids on the same butterfly weed plant.

Discussion

One of the objectives of this study was to determine the extent to which *C. septempunctata* and *H. axyridis* dominated coccinellid assemblages in South Dakota, and the results were mixed. With regard to larvae, *C. septempunctata* and *H. axyridis* composed the majority collected from field crops and were manifold greater in abundance than other species in three instances. However, adults of *C. septempunctata* and *H. axyridis* occurred in at least low numbers in many habitats, but were prevalent in only a few.

Reasons were not clear with regard to the discrepancy in the relative abundance between larvae and adults of *C. septempunctata* and *H. axyridis*. The preponderance of larvae of invasive species in the limited number of instances in this study might be atypical of habitats throughout South Dakota, or their prevalence might be offset by success of native larvae at other sites. Alternatively, some factors might disproportionately favor other life stages of native species relative to invasive species (e.g., overwintering success of adults), but comparative studies to evaluate such factors are lacking. Interspecific interactions may occur in each life stage of coccinellids, but competition between species may be most intense during the immature stages (Cottrell and Yeargan, 1998; Snyder *et al.*, 2004; Yasuda *et al.*, 2004; LaBrie, *et al.*, 2006). Habitats in which coccinellid larvae are abundant may be places to determine the relative success of invasive coccinellids (Obrycki *et al.*, 2000; Marco *et al.*, 2002), and additional studies are needed in such habitats.

Two other objectives of our study were to determine if populations of *A. bipunctata*, *C. transversoguttata richardsoni*, and *C. novemnotata* had recovered and to survey habitats as potential refuges for native coccinellids. None of the three previously common, native species was found among samples from habitats in eastern and central South Dakota. Thus, there is no support for the hypotheses a) that these species have recovered their abundance in field-crop habitats, or b) that populations of these species exist in refuge habitats in eastern and central South Dakota. The results from South Dakota parallel trends in the decreased abundances of *C. novemnotata* and *C. transversoguttata richardsoni* in several regions of North America (Wheeler and Hoebeke, 1995; Elliott *et al.*, 1996; Turnock *et al.*, 2003; Alyohkin and Sewell, 2004; Hesler *et al.*, 2004; Snyder *et al.*, 2004). Further studies are needed to define the status of *C. transversoguttata richardsoni* and *C. novemnotata* throughout North America and to develop plans for conserving these native species.

Despite the absence of *A. bipunctata* from eastern and central South Dakota, several *A. bipunctata* were recorded from Butte County in far western South Dakota over several dates in 2004 through 2006, indicating an extant population in that region. Specimens of *A. bipunctata* were collected from a house and a park, and thus it was not clear which habitat(s) in western South Dakota were suitable for production of *A. bipunctata*. Follow-up studies are needed to characterize such habitat(s) and also to develop plans for conservation of *A. bipunctata*.

The occurrence of *A. bipunctata* in western South Dakota supports the prediction by Obrycki *et al.* (2000) that low abundance of *A. bipunctata* in eastern South Dakota is a local phenomenon. They suggested that the lack of *A. bipunctata* in eastern South Dakota may be related to the paucity of preferred wooded habitat. The majority of *A. bipunctata* in the current study was collected within a house, so that the beetles' field origin is unknown. However, the house was set in a landscape of open rolling hills dominated by farmland and ranchland with occasional shelterbelts. The large expanse of the forested Black Hills are about 30 km south of where we collected *A. bipunctata*, and the presence of *A. bipunctata* in western South Dakota may be influenced by the proximity of arboreal habitat. Additional surveys among landscapes are needed to determine the effect of wooded habitat on abundance of *A. bipunctata* in adjacent, non-arboreal habitats.

The current study documented the geographic range expansion of one native and one invasive coccinellid in South Dakota. *Scymnus kansanus* is native to North America but had not been reported previously in South Dakota (Kirk and Balsbaugh, 1975; Gordon, 1985), and its collection in this study represents a new **state record**. *Scymnus kansanus* has been recorded from southeastern Nebraska and Wisconsin (Gordon, 1985). *Scymnus* spp. are generalist predators of homopterans such as aphids and scale insects Our study did not determine particular reason(s) for the geographic range expansion of *S. kansanus* into eastern South Dakota, and this may be a goal of future studies.

Harmonia axyridis has expanded its geographic range into central (since 2002) and western South Dakota (since 2004). As *H. axyridis* has not been recorded from western North Dakota (Fauske *et al.*, 2003) or from Wyoming and Montana (Koch *et al.*, 2006), its chronology in South Dakota suggests a westward expansion. The site in western South Dakota where *H. axyridis* was collected lies about 50 km from the eastern borders of Wyoming and Montana and about 200 km from the southwestern border of North Dakota, and its continued expansion into those states is expected. The western South Dakota collection site is also about 30 km north of the Black Hills National Forest. *Harmonia axyridis* is principally arboreal (Coderre *et al.*, 1995), and given its discovery within natural areas in this study, geographic expansion of *H. axyridis* into the Black Hills is likely. Surveys may be conducted to determine its colonization and impact there.

Harmonia axyridis and *C. septempunctata* preyed upon several species of aphids in the current study. In some instances, predation by exotic coccinellids on non-target prey is fortuitous, e.g., predation of cereal aphids by *C. septempunctata* on wheat and by *H. axyridis* on maize in our study. However, *H. axyridis* and *C. septempunctata* are now unprecedented mortality factors for some native aphids (e.g., *S. quercicola*, *A. asclepiadis*) in natural or semi-natural settings, but their impact is yet undetermined. Exotic coccinellids may pose a risk to native insects (Koch, 2003; Koch *et al.*, 2005; Schellhorn *et al.*, 2005), but our study was not designed to test for long-term impacts of *C. septempunctata* and *H. axyridis* on native aphids. Further studies are needed to assess the risk to native aphids and other non-target insects, and to determine other long-term effects of invasive coccinellids (Lodge, 1993; Wheeler and Hoebeke, 1995; Strayer *et al.*, 2006).

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Literature Cited

Alyohkin, A., and G. Sewell. 2004. Changes in a lady beetle community following the establishment of three alien species. Biological Invasions 6:463–471.

Blackman, R. L., and V. F. Eastop. 1994. Aphids on the World's Trees, 2nd ed. CAB International, Oxon, U.K. viii + 987 pp. + 16 plates.

Brown, M. W. 2003. Intraguild responses of aphid predators on apple to the invasion of an exotic species, *Harmonia axyridis*. BioControl 48:141–153.

Brown, M. W., and S. S. Miller. 1998. Coccinellidae (Coleoptera) in apple orchards of eastern West Virginia and the impact of invasion by *Harmonia axyridis*. Entomological News 109:136–142.

Bullock, J. A. 1971. The investigation of samples containing many species. II. Sample comparisons. Biological Journal of the Linnean Society 3:23–56.

Chapin, J. B., and V. A. Brou. 1991. *Harmonia axyridis* (Pallas), the third species of the genus to be found in the United States (Coleoptera: Coccinellidae). Proceedings of the Entomological Society of Washington 93:630–635.

Coderre, D., É. Lucas, and I. Gagné. 1995. The occurrence of *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) in Canada. Canadian Entomologist 127:609–611.

Colunga-Garcia, M., S. H. Gage, and D. A. Landis. 1997. Response of an assemblage of Coccinellidae (Coleoptera) to a diverse agricultural landscape. Environmental Entomology 26:797–804.

Cottrell, T. E., and K. V. Yeargan. 1998. Intraguild predation between an introduced lady beetle, *Harmonia axyridis* (Coleoptera: Coccinellidae), and a native lady beetle, *Coleomegilla maculata* (Coleoptera: Coccinellidae). Journal of the Kansas Entomological Society 71:159–163.

Elliott, N. C., R. W. Kieckhefer, and W. Kauffman. 1996. Effects of an invading coccinellid on native coccinellids in an agricultural landscape. Oecologia 105:537–544.

Ellis, D. R., D. R. Prokrym, and R. G. Adams. 1999. Exotic lady beetle survey in northeastern United States: *Hippodamia variegata* and *Propylea quatuordecimpunctata* (Coleoptera: Coccinellidae). Entomological News 110:73–84.

Elton, C. S. 2000. The ecology of invasions by animals and plants. Methuen, London, United Kingdom. xiv + 181 pp. + 32 plates.

Evans, E. W. 2000. Morphology of invasion: body size patterns associated with establishment of *Coccinella septempunctata* (Coleoptera: Coccinellidae) in western North America. European Journal of Entomology 97:469–474.

Fauske, G. M., P. P. Tinerella, and D. A. Rider. 2003. A list of the lady beetles (Coleoptera: Coccinellidae) of North Dakota with new records from North Dakota and Minnesota. Journal of the Kansas Entomological Society 76:38–46.

Foott, W. H., and P. R. Timmons. 1973. Effects of infestation by the corn leaf aphid, *Rhopalosiphum maidis* (Homoptera: Aphididae), on field corn in southwestern Ontario. Canadian Entomologist 104:449–458.

Gagné, W. C., and J. L. Martin. 1968. The insect ecology of red pine plantations in central Ontario. Canadian Entomologist 100:835–846.

Gordon, R. D. 1985. The Coleoptera (Coccinellidae) of America north of Mexico. J. New York Entomological Society 93:1–912.

Gordon, R. D., and N. Vandenberg. 1991. Field guide to recently introduced Coccinellidae (Coleoptera) in North America, with a revised key to North American genera of Coccinellini. Proceedings of the Entomological Society of Washington 93:845–864.

Hesler, L. S., R. W. Kieckhefer, and D. A. Beck. 2001. First record of *Harmonia axyridis* (Coleoptera: Coccinellidae) in South Dakota and notes on its activity there and in Minnesota. Entomological News 112:264–270.

Hesler, L. S., R. W. Kieckhefer, and M. A. Catangui. 2004. Surveys and field observations of *Harmonia axyridis* and other Coccinellidae (Coleoptera) in eastern and central South Dakota. Transactions of the American Entomological Society 130:113–133.

Howarth, F. G. 2001. Environmental issues concerning the importation of non-indigenous biological control agents., pp. 70–99. *In* J. A. Lockwood, F. G. Howarth, and M. F. Purcell (eds.). Balancing Nature: Assessing the Impact of Importing Non-Native Biological Control Agents (An International Perspective). Entomological Society of America, Lanham, Maryland. vi + 130 pp.

Kieckhefer, R. W., N. C. Elliott, and D. A. Beck. 1992. Aphidophagous coccinellids in alfalfa, small grains, and maize in eastern South Dakota. Great Lakes Entomologist 25:15–23.

Kirk, V. M., and E. U. Balsbaugh, Jr. 1975. A list of the beetles of South Dakota. South Dakota Agricultural Experiment Station Technical Bulletin B42.

Koch, R. L. 2003. The multicolored Asian lady beetle, *Harmonia axyridis*: a review of its biology, uses in biological control, and non-target impacts. Journal of Insect Science 3:32. Available online: *http://www.insectscience.org/3.32/Koch_JIS_3_32_2003.pdf*. Last accessed 9 October 2007.

Koch, R. L., R. C. Venette, and W. D. Hutchison. 2005. Influence of alternate prey on predation of monarch butterfly (Lepidoptera: Nymphalidae) larvae by the multicolored Asian lady beetle (Coleoptera: Coccinellidae). Environmental Entomology 34:410–416.

Koch, R. L., R. C. Venette, and W. D. Hutchison. 2006. Invasions by *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) in the western hemisphere: implications for South America. Neotropical Entomology 35:421–434.

LaBrie, G., E. Lucas, and D. Coderre. 2006. Can behavioral and developmental characteristics of the mulitcolored Asian lady beetle *Harmonia axyridis* explain its success? Biological Invasions 8:743–754.

LaMana, M., and J. C. Miller. 1996. Field observations on *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae) in Oregon. Biological Control 6:232–237.

Lodge, D. M. 1993. Biological invasions: lessons for ecology. Trends in Ecology and Evolution 8:133–137.

Marco, D. E., S. A. Paez, and S. A. Cannas. 2002. Species invasiveness in biological invasions: a modelling approach. Biological Invasions 4:193–205.

Maredia, K. M., S. H. Gage, D. A. Landis, and T. M. Wirth. 1992. Ecological observations on predatory Coccinellidae (Coleoptera) in southwestern Michigan. Great Lakes Entomologist 25:265–270.

Michaud, J. P. 2002. Invasion of the Florida citrus ecosystem by *Harmonia axyridis* (Coleoptera: Coccinellidae) and asymmetric competition with a native species, *Cycloneda sanguinea*. Environmental Entomology 31:827–835.

Morrison, L. W. 2002. Long-term impacts of an arthropod-community invasion by the imported fire ant, *Solenopsis invicta*. Ecology 83:2337–2345.

Multi-State Soybean Aphid Survey Protocol. 2003. *http://www.soybeans.umn.edu/pdfs/MultiStateSoybeanAphidSurvey.pdf*. Last accessed 9 October 2007.

Nault, B. A., and G. G. Kennedy. 2003. Establishment of multicolored Asian lady beetle in eastern North Carolina: seasonal abundance and crop exploitation within an agricultural landscape. BioControl 48:363–378.

New, T. R. 2004. Invertebrate Conservation and Agriculutral Ecosystems. Cambridge Press, Cambridge, UK. xiii + 354 pp.

Obrycki, J. J., N. C. Elliott, and K. L. Giles. 2000. Coccinellid introductions: potential for and evaluation of nontarget effects, pp. 127–145. *In* P. A. Follett and J. J. Duan (eds.). Nontarget Effects of Biological Control. Kluwer Academic, Boston, Massachussets. xii + 316 pp.

Omkar, and A. Pervez. 2005. Ecology of two-spotted ladybird, *Adalia bipunctata*: a review. Journal of Applied Entomology 129:465–474.

Putman, W. L. 1964. Occurrence and food of some coccinellids (Coleoptera) in Ontario peach orchards. Canadian Entomologist 96:1149–1155.

Rees, B. E., D. M. Anderson, D. Bouk, and R. D. Gordon. 1994. Larval key to general and selected species of North American Coccinellidae (Coleoptera). Proceedings of the Entomological Society of Washington 96:387–412.

Rhoades, M. H. 1996. Key to first and second instars of six species of Coccinellidae (Coleoptera) from alfalfa in southwest Virginia. Journal of the New York Entomological Society 104: 83–88.

SAS Institute. 2002. SAS, Release 9.1. SAS Institute, Cary, NC.

Schellhorn, N. A., C. P. Lane, and D. M. Olson. 2005. The co-occurrence of an introduced biological control agent (Coleoptera: *Coccinella septempunctata*) and an endangered butterfly (Lepidoptera: *Lycaeides milissa samuelis*). Journal of Insect Conservation 9:41–47.

Siegel, S., and N. J. Castellan, Jr. 1988. Nonparametric Statistics for the Behavioral Sciences, 2nd ed. McGraw-Hill, New York, New York. xxiii + 399 pp.

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

Southwood, T. R. E. 1978. Ecological Methods. Chapman and Hall, London. xxiii + 524 pp.

Strayer, D. L., V. T. Eviner, J. M. Jeschke, and M. L. Pace. 2006. Understanding the long-term effects of species invasions. Trends in Ecology and Evolution 21:645–651.

Turnock, W. J., I. L. Wise, and F. O. Matheson. 2003. Abundance of some native coccinellines (Coleoptera: Coccinellidae) before and after the appearance of *Coccinella septempunctata*. Canadian Entomologist 135:391–404.

Wheeler, A. G., Jr, and E. R. Hoebeke. 1995. *Coccinella novemnotata* in northeastern North America: historical occurrence and current status (Coleoptera: Coccinellidae). Proceedings of the Entomological Society of Washington 97:701–716.

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.

Zar, J. H. 1998. Biostatistical Analysis, 4th ed. Prentice Hall, Upper Saddle River, New Jersey. x + 662 pp. + appendices.