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ABUNDANCE OF COCCINELLIDS AND THEIR POTENTIAL PREY IN FIELD-CROP AND GRASS HABITATS IN EASTERN SOUTH DAKOTA

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ABSTRACT

A rich fauna of coccinellids occurs in eastern South Dakota, but the abundance of some species has declined in association with the establishment of an exotic lady beetle, *Coccinella septempunctata* (L.) (Coleoptera: Coccinellidae), in the mid-1980s. In this study, coccinellids were sampled within field-crop and grass habitats in eastern South Dakota from 1990 to 1995 to survey for various coccinellid species and to determine any effects of habitat management on abundance. Field crops (maize, wheat-alfalfa intercrop, and alfalfa) were subjected to high, intermediate, or low crop-management intensity (CMI), and grass habitats were managed for stands of warm season, cool season, or mixed species. A total of 1,306 adult and 155 larval coccinellids were collected. Four native species (*Coleomegilla maculate* (DeGeer), *Hippodamia convergens* Guerin-Meneville, *Hippodamia parenthesis* (Say), and *Hippodamia tredecimpunctata tibialis* (Say)) and *C. septempunctata* comprised over 96 percent of all coccinellids collected. Of declining species, four *Coccinella transversoguttata richardsoni* Brown were collected from alfalfa, but *Coccinella novemnotata* Herbst and *Adalia bipunctata* (L.) were not found during the study. Coccinellid abundance was seldom affected by CMI. Coccinellids were more abundant in wheat-alfalfa in 1995 under high than low CMI. Coccinellid abundance in maize and alfalfa did not differ with CMI. A prey species, *Empoasca fabae* (Harris) (Heteroptera: Auchenorryncha: Cicadellidae), was more abundant in alfalfa in 1995 under high and intermediate than under low CMI. Coccinellid abundance was not correlated with that of *E. fabae* in 1995, and showed inconsistent association with *E. fabae* during the study. In grass, adult coccinellids (total across species), adult *H. tredecimpunctata tibialis*, and aphids were more abundant in warm-season grasses than in cool-season or mixed grass stands in one of three years. Our results provide further evidence that *C. septempunctata* has become relatively abundant in eastern South Dakota, whereas *C. transversoguttata richardsoni*, *C. novemnotata*, and *A. bipunctata* have become rare or absent.

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A rich fauna of coccinellids inhabit and reproduce within field habitats in eastern South Dakota (Elliott and Kieckhefer 1990a, 1990b, Royer and Walgenbach 1991, Kieckhefer et al. 1992, Elliott et al. 1996). However, recent population declines in two native species of coccinellids (Coleoptera), *Coccinella transversoguttata richardsoni* Brown and *Adalia bipunctata* (L.) have been associated with the establishment of an exotic species, *Coccinella septempunctata* (L.), in the late 1980s in eastern South Dakota (Elliott et al. 1996). These two coccinellids and a third native species, *Coccinella novemnotata* Herbst, were not collected from fields of intercropped wheat and alfalfa in eastern South Dakota in the early 1990s (Hesler et al. 2000), providing further evidence that these previously common coccinellids (Kirk and Balsbaugh Jr. 1975) are in decline in eastern South Dakota. The results from South Dakota parallel trends in the declining abundances of *C. novemnotata* in eastern North America (Wheeler and Hoebeke 1995) and *C. transversoguttata richardsoni* in central Canada (Turnock et al. 2003).

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Wheeler Jr. and Hoebeke (1995) and Ellis et al. (1999) have called for North American entomologists to monitor populations of coccinellids, and to thoroughly document the results of monitoring efforts in order to assess the status of indigenous coccinellids. We have been involved in projects to monitor coccinellids in eastern South Dakota (Hesler et al. 2000), and our monitoring efforts include two further years of sampling in intercropped wheat-alfalfa and additional sampling in maize, alfalfa, and grasses. These samples provide further information on the status of indigenous coccinellids and the effects of habitat management on coccinellid communities. In this paper, we report the results from additional sampling of coccinellids and their potential prey from field-plot habitats in eastern South Dakota.

MATERIALS AND METHODS

Sampling was conducted from 1990 through 1995 in field-crop or grass habitats at the Eastern South Dakota Soil and Water Research Farm, located about 1.5 mi N of Brookings, South Dakota, USA. Insects were sampled from one to eight times per crop or grass per year from late May to early September (Table 1).

Field plots. Field plots were established in 1990 and arranged according to a split-plot design. Main plots (91.5 × 30.5 m) consisted of continuous maize (i.e., planted and harvested annually), a four-year rotational series of field crops (maize, soybeans, intercropped wheat-alfalfa, and alfalfa) that were grown in sequence with each crop present each year, and perennial grasses (cool season grasses: intermediate wheatgrass, *Elytrigia intermedia*; orchardgrass, *Dactylis glomerata*; and creeping foxtail, *Alopecurus arundinaceus*; warm season grasses: big bluestem, *Andropogon gerardii*, and switchgrass *Panicum virgatum*; or a mixture of these cool and warm season grasses; Johnson and Larson 1999). Main plots were arranged as a randomized complete block, and each main plot was split into three, 30.5 × 30.5-m subplots. For continuous maize and sequential field crops, each subplot was randomly assigned one of three different intensity levels (i.e., high, intermediate and low) of crop-management intensity (CMI). For perennial grasses, subplots were randomly assigned one of three grass types: cool season, warm season, or a mixture of cool and warm season grasses. Perennial grasses were perpetuated within the same plots during the six years of study. Each CMI level or grass treatment was replicated three times.

Details on planting dates and agrichemical use in each crop or grass type are given in the Appendix. Briefly, CMI levels of field crops differed in amounts and placement of agrichemical inputs and in intensity of tillage operations. Agrichemicals were generally applied to high- and intermediate-intensity treatments, and applications were made before 15 June. High intensity plots were characterized by soil test-based rates of N-fertilizer application designed to achieve high yield goals, specifically 8.15 and 3.0 Mg ha^{-1} in maize and wheat, respectively, and by pre- and post-emergent herbicides broadcast over plots at labeled rates. Tillage in high CMI plots consisted of fall moldboard plowing, spring disking, and two field cultivations of corn in late spring.

Intermediate CMI plots used half the rate of fertilizer applied to high CMI plots. Herbicides were broadcast in spring wheat-alfalfa plots and banded along rows of corn and soybean crops, and no insecticides were applied. Intermediate CMI plots received fall moldboard plowing in odd-numbered years and fall chisel plowing in even-numbered years, and spring disking and two field cultivations of corn each year.

Low CMI plots usually received no agrichemicals, and were hand-weeded. They received fall chisel plowing, and maize plots also received spring disking and two field cultivations annually.

Table 1. Dates of insect sampling within field crops and grasses, Eastern South Dakota Soil and Water Research Farm, Brookings, SD, 1990-1995.

Crop	Year	Sampling dates
Maize	1990	2 Aug., 8 Aug., 16 Aug.
Wheat – alfalfa intercrop	1994	28 Jun.
	1995	16 Jun., 28 Jun., 25 Jul.
Alfalfa	1991	10 Jun., 5 Jul., 31 Jul., 15 Aug., 21 Aug.
	1992	28 May, 2 Jun., 22 Jun., 8 Jul., 20 Jul., 4 Sep.
	1993	11 Jun., 19 Jul., 26 Jul., 23 Aug., 10 Sep.
	1994	26 May, 2 Jun., 12 Jul., 15 Aug., 7 Sep.
	1995	12 Jun., 12 Jul.
Grass	1991	13 Jun., 20 Jun., 27 Jun., 15 Jul., 23 Jul., 31 Jul., 15 Aug., 21Aug.
	1993	4 Aug., 14 Aug.
	1994	2 Jun., 16 Aug., 8 Sep.
	1995	11 Jul.

Insect and plant samples. Sampling of coccinellids and their potential prey occurred in maize, intercropped wheat-alfalfa, alfalfa, and perennial grasses. Maize was sampled only in 1990, because in subsequent years the plots were used for research on corn rootworms, *Diabrotica* spp. (Coleoptera: Chrysomelidae), which imposed additional, confounding treatments. The wheat-alfalfa inter-crop was sampled from 1990 through 1995. Results from 1990-1993 have been published (Hesler et al. 2000), and additional sampling from 1994 and 1995 is described in this paper. Alfalfa and perennial grasses were sampled for insects one year after they were planted. In 1991, grass habitats, particularly warm-season plots, became heavily infested with weeds (*Convolvulus arvensis* L., *Setaria* spp., and *Ambrosia* sp.). Because of this, all grass plots were burned and re-planted in spring 1992. Soybean, a major field crop in the region, lacked significant insect pests and associated natural enemies, such as coccinellids, until recent establishment of *Aphis glycines* Matsumura (Hemiptera: Aphididae) (Wright and DeVries 2000, Catangui 2002). Therefore, sampling of this crop was omitted.

Insect sampling occurred midday between 0945 and 1515 hours, with temperatures between 20 and 33 ºC with calm to light winds. In maize, sampling occurred from late whorl to blister stage, and coccinellids were sampled by searching two rows (roughly 40 row-m) for about 20 minutes per plot. Coccinellids were identified and tallied within maize plots. In other habitats, coccinellids were sampled by taking 60 pendular sweeps with a 38-cm diam. sweep net along two transects in each plot (30 sweeps per transect). Insects collected along each transect were treated with chloroform in the net, transferred to containers, and taken to the laboratory for identification and counting. Coccinellid adults were identified to species, and larvae were identified to genus or species.

In addition to coccinellids, phytophagous insects that could serve as potential prey for coccinellids were counted or their abundance was estimated within sweepnet samples. In alfalfa, counts were made of potato leafhopper, *Empoasca fabae* (Harris) (Heteroptera: Auchenorryncha: Cicadellidae). The number of aphids (mainly *Acyrthosiphon pisum* (Harris) (Hemiptera:Aphididae)) per 60-sweep subsample was estimated as a necessity to reduce sampling time.

In wheat-alfalfa, the number of cereal-aphid (Hemiptera: Aphididae) infested tillers out of 15 tillers per plot (five randomly selected groups of three consecutive tillers) was recorded on the same dates that sweepnetting occurred. In grass, the number of Lepidoptera larvae per 60-sweep sample was counted in 1991, and the number of aphids per sample was estimated.

Plant growth was measured in alfalfa plots on each date that insects were sampled in plots. Measurements were made at three locations systematically chosen to be near each end and the center of sweepnet transects. Maximum height (cm) and canopy coverage of alfalfa, grassy weeds, and broadleaf weeds was measured at three arbitrarily selected sites within each plot. Canopy coverage was scored within a 20 × 50 cm quadrat using the following scale: 0 = 0-5%, 1 = 5-25%, 2 = 26-50%, 3 = 51-75%, 4 = 76-95%, and 5 = greater than 95% coverage (Daubenmire 1959, Elliott and Michels Jr. 1997).

Statistical Analyses. Statistical analyses were used to detect any effect of sampling date or treatment (crop-management intensity or grass type) on insect abundance. A separate analysis was performed for each habitat each year, as timing of sampling dates differed among habitats and years (Table 1). Data from each crop were analyzed as a randomized complete block design. Data were subjected to a repeated measures analysis (PROC MIXED, Littell et al. 1996), with treatment and sampling date as non-random independent variables. A spatial covariance model was used in analyses, because sampling dates were unequally spaced. Treatment means were separated by using the LSMEANS option (Littell et al. 1996). Analyses were limited to taxa whose means were > 0.2 individuals (per life stage) per sample across all sampling dates and treatments within a year. Pearson's correlation coefficients were calculated for abundances of predatory and phytophagous taxa for alfalfa and wheat-alfalfa within each year (PROC CORR, SAS Institute 1988). The level of significance was set at $\alpha = 0.05$ for all statistical tests.

RESULTS

General trends. A total of 1,306 adult coccinellids (Table 2) and 155 larval coccinellids were collected (Table 3). More adults than larvae were collected in all habitats. Four native species [*Coleomegilla maculata* (DeGeer), *Hippodamia convergens* Guerin-Meneville, *Hippodamia parenthesis* (Say), and *Hippodamia tredecimpunctata tibialis* (Say)] and *C. septempunctata* collectively comprised over 96 percent of all coccinellids collected. Adults of *H. convergens* and *H. parenthesis* were relatively abundant in alfalfa, and *H. convergens* was the most abundant coccinellid in warm season grasses. Adults and larvae of *C. maculata* and *C. septempunctata* were often relatively abundant in intercropped wheat-alfalfa, and *C. maculata* was the most abundant coccinellid in maize. An additional six native species — *C. transversoguttata richardsoni*, *Cycloneda munda* (Say), *Hyperaspis undulata* (Say), *Brachiacantha ursina* (F.), and *Psyllobora vigintimaculata* (Say) — were collected occasionally from various habitats, but only as adults. We also collected 11,107 *E. fabae* in alfalfa, and over 100,000 aphids from alfalfa, intercropped wheat-alfalfa, and grasses.

Repeated Measures Analyses. Sampling date often affected abundance of various taxa. This was expected, as the taxa (in their different life stages) vary in abundance throughout the season in field habitats (Kieckhefer and Miller 1967, Elliott and Kieckhefer 1990a, Elliott et al. 1991). However, we were interested primarily in treatment effects (i.e., crop-management intensity or grass type) on insect abundance, and the results that follow are restricted to instances in which CMI or grass type affected the abundance of coccinellids and their prey.

Alfalfa. CMI did not affect the abundance of coccinellids or aphids. Abundance of *E. fabae* in 1995 varied by CMI ($F = 9.24$; df = 2, 4; $P = 0.032$) and sampling date ($F = 397.4$; df = 1, 6; $P < 0.001$), but interaction between these

Table 2. Number of adult coccinellids collected from various field-plot habitats in eastern South Dakota.

Habitat	Year	n[1]	Hippodamia convergens	Hippodamia parenthesis	Hippodamia tredecimpunctata tibialis	Coleomegilla maculata	Coccinella septempunctata	Coccinella transversoguttata richardsoni	Cycloneda munda
Maize	1990	3	2	0	7	39	3	0	0
Wheat-alfalfa	1994	1	1	0	1	0	0	0	0
	1995	3	6	1	18	24	1	0	0
Alfalfa	1991	5	44	103	64	57	60	2	10
	1992	6	135	43	7	25	11	1	7
	1993	5	6	11	106	2	18	1	1
	1994	5	36	150	12	18	45	0	2
	1995	2	3	43	5	23	13	0	0
Grass									
Cool season	1991	8	16	2	2	2	1	0	0
Mixed	1991	8	1	1	4	1	0	0	0
Warm season	1991	8	52	4	20	1	10	0	0
All grasses	1993	2	0	0	0	0	1	0	0
	1994	3	4	4	2	0	0	0	0
	1995	1	0	0	0	0	0	0	0

[1] Number of sampling dates per year. For each sampling date: maize, three, 20 min. searches per sampling date; other habitats, three sets of 60 sweeps per sampling date. Other coccinellids collected included *Brachiacantha ursina* (alfalfa: 1 and 2 adults, 1991 and 1992, respectively; cool season grass: 1 adult, 1991), *Hyperaspis undulata* (alfalfa: 1 adult, 1995), and *Psyllobora vigintimaculata* (alfalfa: 2 adults, 1991, and 1 adult, 1992).

Table 3. Number of larval coccinellids collected from various field-plot habitats in eastern South Dakota.

Habitat	Year	n^1	Hippodamia convergens	Hippodamia parenthesis	Hippodamia tredecimpunctata tibialis	Coleomegilla maculata	Coccinella spp.
Maize	1990	3	1	0	0	14	0
Wheat-alfalfa	1994	1	0	0	0	0	0
	1995	3	3	0	0	4	0
Alfalfa	1991	5	1	26	9	14	4
	1992	6	1	13	3	1	0
	1993	5	0	8	1	1	0
	1994	5	4	15	2	3	17
	1995	2	0	0	0	0	0
Grass							
Cool season	1991	8	0	1	2	1	0
Mixed	1991	8	0	0	2	0	0
Warm season	1991	8	0	1	2	1	0
All grasses	1993	2	0	0	0	0	0
	1994	3	0	0	0	0	0
	1995	1	0	0	0	0	0

[1] Number of sampling dates per year. For each sampling date: maize, three, 20 min. searches per sampling date; other habitats, three sets of 60 sweeps per sampling date.

two factors was not significant ($F = 0.30$; df = 2, 6; $P > 0.05$). Means (± SE per 60 sweeps) for high (38.0 ± 11.0) and intermediate CMI (39.0 ± 10.8) did not differ, but were greater than that of low CMI (27.8 ± 10.1). Populations of *E. fabae* were much greater on July 12 ($\bar{x} \pm SE = 58.3 \pm 2.7$ per 60 sweeps per plot) than on June 12 ($\bar{x} \pm SE = 11.6 \pm 1.8$ per 60 sweeps per plot). The heights and canopy coverage of alfalfa, grassy weeds, and broadleafed weeds did not vary with CMI.

Coccinellids varied in their association with aphids and *E. fabae* in alfalfa during the study, as indicated by correlation analysis (Table 4). Coccinellid abundance was correlated with aphid abundance in alfalfa in 1993 and 1994, but not in other years. Coccinellid abundance was correlated with *E. fabae* abundance in 1993, but negatively correlated in 1992 and 1995.

Wheat-Alfalfa Intercrop. Coccinellid abundance did not vary with CMI in 1994, but, in 1995, abundance of adult coccinellids varied with CMI ($F = 7.59$; df = 2, 4; $P = 0.044$), sampling date ($F = 18.62$; df = 2, 12; $P < 0.001$), and their interaction ($F = 5.06$; df = 4, 12; $P = 0.013$). This was manifested as a greater abundance of adult coccinellids in high CMI plots on June 28 ($\bar{x} \pm SE = 7.0 \pm 1.5$ per 60 sweeps per plot) than on other CMI-sampling date combinations ($\bar{x} \pm 2.3$ per 60 sweep per plot). The pattern of coccinellid abundance in 1995 was driven largely by that of adult *Coleomegilla maculata*, which varied by CMI ($F = 9.10$; df = 2, 4; $P = 0.033$), sampling date ($F = 13.14$; df = 2, 12; $P < 0.001$), and their interaction ($F = 7.03$; df = 4, 12; $P = 0.004$). Adult *C. maculata* were also greater in high CMI plots on June 28 ($\bar{x} \pm SE = 5.7 \pm 1.7$ per 60 sweeps) than in other CMI-sampling date combinations ($\bar{x} \leq 0.7$ per 60 sweeps). The percentage of aphid-infested tillers did not vary with CMI in 1994 and 1995, and coccinellid abundance was not correlated with aphid levels.

Maize. Abundance of coccinellids in maize did not vary with crop-management intensity or sampling date in 1990.

Grass habitats. Grass treatment, sampling date, and their interaction affected abundances of total adult coccinellids, adult *H. tredecimpunctata tibialis*, and aphids in 1991 (Table 5), but insects occurred in low numbers in subsequent years and grass treatment was not significant ($P < 0.05$). In 1991, adult lady beetles (especially *H. tredecimpunctata tibialis*) were more abundant in warm-season grass on the last two sampling dates (Fig. 1). Aphids also were generally more abundant in warm-season grass than in cool-season or mixed plots in 1991 (Fig. 1). Total adult coccinellids ($r = 0.64$), adult *H. tredecimpunctata tibialis* ($r = 0.62$), and adult *H. convergens* ($r = 0.56$) were correlated with aphid abundance in perennial grass in 1991. The abundances of total adult coccinellids and adult *H. convergens* were correlated (each $r = 0.55$) with the abundance of larval lepidopterans (Fig. 1), which was not affected by grass treatment (Table 5).

DISCUSSION

The preponderance of adult coccinellids in our samples was expected, because sweepnet sampling was used in all habitats except maize, and this method is more efficient in sampling adult than larval coccinellids (Elliott et al. 1991, Elliott and Michels Jr. 1997). Among adult coccinellids, the collection of three previously common, but declining coccinellid species (*A. bipunctata*, *C. transversoguttata richardsoni richardsoni*, and *C. novemnotata*) was limited to four *C. transversoguttata richardsoni richardsoni*. These four individuals were collected from alfalfa on different dates over three years (10 June and 21 August, 1991, each in intermediate CMI plots; 2 June 1992, and 19 July 1993, each low CMI), and these samples were associated with plots containing between 25 and 257 aphids per 60-sweep sample. No other parameters measured (e.g., crop or weed height) were common to the samples. The location of our study plots near

Table 4. Pearson correlation coefficients, *r*, between adult coccinellids and prey in alfalfa.

Prey	1991 (df = 45)	1992 (df = 54)	1993 (df = 45)	1994 (df = 45)	1995 (df = 18)
Aphids	0.18	0.11	0.67*	0.57*	0.09
Empoasca fabae	0.24	-0.30*	0.69*	0.12	-0.78*

Correlation coefficients followed by the symbol * are significant, $P < 0.05$.

Table 5. *F* values of repeated measures analyses in which grass treatment was significant for various insect taxa in grass habitats, 1991.

Taxon	Life stage(s)	Grass type (GT) df = 2, 4	Sampling date (SD) df = 7, 42	GT X SD df = 14, 42
Aphids	adult + nymph	17.02*	5.04*	4.07*
Lepidoptera	larvae	3.60	3.92*	2.33*
Coccinellids	adult	11.70*	9.61*	3.93*
Hippodamia tredecimpunctata tibialis	adult	13.02*	14.77*	4.96*

F values followed by the symbol * are significant, $P < 0.05$.

Brookings is roughly the midpoint to three other locations in eastern South Dakota where *C. transversoguttata richardsoni* were sampled from 1973 to 1985 and 1988 to 1992 by Elliott et al. (1996), who found that abundance of *C. transversoguttata richardsoni* was reduced 20 to 32 times after *C. septempunctata* had established in the area in the late 1980s. In general, our results corroborate the decline in *C. transversoguttata richardsoni* noted by Elliott et al. (1996), and they parallel the decline in abundance of *C. transversoguttata richardsoni* in central Canada (Turnock et al. 2003).

Adult *C. novemnotata* were also absent from our samples. Surveys by Kieckhefer et al. (1992) found low numbers of this species and only from margins of field-crop habitats in eastern South Dakota. Our results provide further evidence that *C. novemnotata* populations have declined greatly in eastern South Dakota and also correspond with declines in *C. novemnotata* in other regions of North America (Wheeler Jr. and Hoebeke 1995).

It is possible that larvae of *C. transversoguttata richardsoni* and *C. novemnotata* were collected, but we were not able to identify species of *Coccinella* larvae, as a species-level key for distinguishing among the larvae of North American *Coccinella* has not been published. However, given low numbers of adult *C. transversoguttata richardsoni* and the absence of adult *C. novemnotata*, it is unlikely that their larvae were collected. A key to distinguish larvae of *Coccinella* species, reference specimens, or perhaps both are needed to quantify accurately the abundance of *C. novemnotata* and *C. transversoguttata richardsoni* in future monitoring efforts.
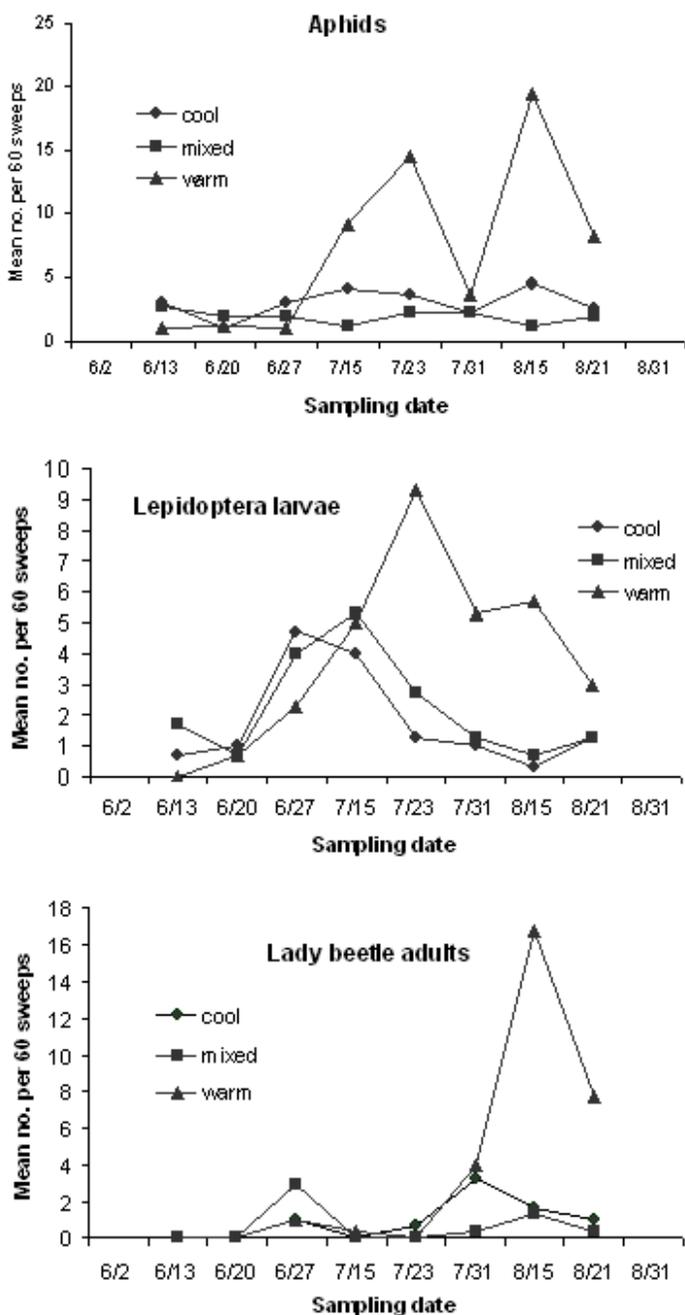
Figure 1. Abundance of aphids, Lepidoptera larvae, and adult coccinellids in perennial grasses, 1991.

Adult *A. bipunctata*, another species whose abundance has declined in association with establishment of *C. septempunctata* (Elliott et al. 1996), was absent from our samples. Elliott et al. (1996) collected *A. bipunctata* in eastern South Dakota from fields of maize, but did not find it in fields of small grains or alfalfa. The absence of *A. bipunctata* in our study may have been due to a single year of sampling in maize and to the infrequent occurrence of this species in other field habitats in this region.

The influence of CMI on insect abundance was limited in our study. One instance involved an herbivore, *E. fabae*, which was more abundant in high and intermediate CMI plots than in low CMI plots in 1995. It is unclear why *E. fabae* were more abundant in high and intermediate CMI plots. For instance, vegetation factors that were measured (e.g., crop and weed heights, canopy coverage) did not vary with CMI. Coccinellids prey on *E. fabae* (Wheeler Jr. 1977), but coccinellid abundance was negatively correlated with that of *E. fabae* in 1995 and showed inconsistent association with *E. fabae* during the other years of the study.

In a second instance of CMI effects, adult coccinellids, and particularly adult *C. maculata*, were more abundant in high CMI plots of wheat-alfalfa on June 28 than other CMI-sampling date combinations in 1995. These results are generally consistent with previous results showing that higher intensity crop management of intercropped wheat-alfalfa led to greater abundances of coccinellids in some years (Hesler et al. 2000). However, the results contrast with previous studies showing that predator abundance is favored by low crop-management intensity through lack of pesticides (Adams and Drew 1965, 1969, Neil et al. 1997) and by provision of more sources of alternate prey and supplementary food such as weed pollen and nectar (Altieri and Whitcomb 1979). Cereal-aphid infestation levels did not differ with CMI in our study, and other, ephemeral food items (e.g., pollen) might have been responsible for the spike in abundance of coccinellids, especially *C. maculata*, in high CMI plots. High CMI plots had more wheat heads per 0.9 m^{-2} ($\bar{x} \pm \text{SE} = 37.8 \pm 4.9$) on 10 July than low CMI plots (27.2 ± 1.4), but intermediate CMI plots did not differ from high or low CMI plots in the number of heads (30.8 ± 1.7). The lack of relationship to the number of wheat heads suggests that other, undetermined factor(s) contributed to the peak in coccinellid abundance.

Many of the same coccinellids, including *C. septempunctata*, found in field crops were present in perennial grasses in our study, but species known to occur in grass habitats were either rare (e.g., *B. ursina*) or absent (e.g., *H. undulata*) in grass samples. The predominance of species that typically inhabit crop fields may have been due to the proximity of field-crop plots. The lack of grassland species shows that they did not readily colonize small patches of grass habitats that were interspersed within a mosaic of field-crop plots.

Larvae of five species (*C. septempunctata*, *H. convergens*, *H. tredecimpunctata tibialis*, *H. parenthesis* and *C. maculata*) were collected from perennial grass. Their presence indicates that perennial grass may, at least occasionally, be an additional source of coccinellids within an agricultural landscape.

Elliott et al. (1996) noted that no information exists regarding the interactions of native coccinellids with *C. septempunctata* in non-agricultural landscapes of eastern South Dakota. However, predator abundance, species richness, and species diversity may increase with greater amounts of non-cultivated lands and an increasing patchiness in the surrounding landscape (Elliott et al. 1998). Additional studies are needed to understand the role of grass tracts (e.g., relict prairie and land in the US Department of Agriculture's Conservation Reserve Program) and other non-agricultural habitats in the landscape ecology of coccinellids, particularly native species with waning populations, in eastern South Dakota and elsewhere.

Ecologists have questioned the reliability of results obtained with mobile insects (e.g., adult coccinellids) from relatively small, field-research plots, and have also questioned the applicability of such results to larger field or landscape spatial scales (Levin 1992, May 1994). Our study design should have minimized these concerns for the following reasons. First, we sampled plots at frequencies ≥ 5 days, which enabled mobile insects ample time for redistribution and further colonization within plots. Second, collection methods such as sweepnetting are efficient and recommended for sampling coccinellids and mobile prey insects (e.g., leafhoppers) (Pruess et al. 1977, Elliott et al. 1991, Elliott and Michels 1997). The coccinellids and associated herbivores that we collected are representative of those found in agroecosystems in eastern South Dakota (Elliott and Kieckhefer 1990a, 1990b, Royer and Walgenbach 1991, Kieckhefer et al. 1992). Moreover, the size of individual, replicate field-plots in our study (900 m^2) are considered relatively large in agroecology research (Bommarco and Banks 2003), and their size increases the probability that results are directly applicable to larger spatial scales. However, as mentioned above, our collections may have underrepresented grassland fauna, and this underscores the need for more studies to increase our understanding of the roles of grasslands and other non-agricultural habitats in the ecology of coccinellids and their prey (Elliott et al. 1998, Thies and Tscharntke 1999).

Since the completion of this study, another exotic, generalist coccinellid, *Harmonia axyridis* Pallas has recently established in eastern South Dakota (Hesler et al. 2001) and other areas of North America (Koch 2003). Its actual or potential impact on native coccinellids (Cottrell and Yeargan 1998, Michaud 2002, Cottrell 2005) should add impetus to further research.

ACKNOWLEDGMENTS

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APPENDIX

Maize. High- and intermediate-intensity management plots of maize, respectively, received 112 and 53 kg ha^{-1} of 13-33-13 (N-P-K) starter fertilizer each year. These plots also received preemergence applications of herbicides alachlor (4.5 kg ha^{-1}) and cyanazine (1.1 kg ha^{-1}), and postmergence application of either bentazon (1.1 kg ha^{-1}; 1990 and 1993) or bromoxynil (0.6 kg ha^{-1}; 1991 and 1992). Low intensity plots received application of bentazon (1.1 kg ha^{-1}) in 1993. High intensity plots received preplant, banded applications of insecticide terbufos (7.8 kg ha^{-1}, 1990) or fonofos (10.0 kg ha^{-1}, 1991-1993) for control of corn rootworms (*Diabrotica* spp.).

Soybeans. High- and intermediate-intensity management plots of soybean, respectively, received 96 and 53 kg ha^{-1} of 13-33-13 (N-P-K) starter fertilizer in 1990, and 112 and 53 kg ha^{-1} of 13-33-13 (N-P-K) starter fertilizer annually from 1991 through 1994. From 1990-1993, these plots also received preemergence applications of herbicides alachlor (4.5 kg ha^{-1}) and metribuzin (0.6 kg ha^{-1}, except 1992), and postmergence application of bentazon (1.3 kg ha^{-1}, except1993). Low intensity plots were also sprayed with bentazon (1.3 kg ha^{-1}) in 1993. In 1994, high-intensity plots received postemergence applications of herbicides flumetsulam and metolachlor (2.9 liters ha^{-1} combined).

Wheat-alfalfa intercrop. Hard red spring wheat and alfalfa ('Coyote 990,' 12 kg ha^{-1}) were planted simultaneously in 17.6-cm rows using a 16-row John Deere® 750 drill. 'Guard' spring wheat (104 kg ha^{-1}) was planted on 26 Apr., 4 Apr., and 7 Apr. in 1990, 1991, and 1992, respectively; 'Butte' spring wheat (118 kg ha^{-1}) was planted on 20 Apr., 1993. High-intensity wheat-alfalfa plots received 99, 116, 116, 103, 103, and 103 kg ha^{-1}, respectively, of 46-0-0 (N-P-K) starter fertilizer from 1990-1995. Intermediate-intensity wheat-alfalfa plots received 50, 58, 58, 51, 51, and 51 kg ha^{-1}, respectively, of 46-0-0 (N-P-K) starter fertilizer from 1990-1995. The postemergent herbicide MCPA (0.6 kg ha^{-1}) was applied to high and intermediate intensity plots each year.

Alfalfa. In 1990, alfalfa ('Coyote 990,' 12 kg ha^{-1}) was planted in 17.6-cm rows using a 16-row John Deere® 750 drill. Fertilizer (kg ha^{-1}, N-P-K) was applied at planting in high (69, 0-45-0) and intermediate intensity plots (35, 0-45-0), and 0.4 kg ha^{-1} bromoxynil was broadcast over plots after planting. All other alfalfa was established as an intercrop with spring wheat, and received no

fertilizer or herbicide after spring wheat had been harvested. Alfalfa plots received no tillage after their establishment until all were moldboard-plowed after final cutting and baling in early fall.

Grasses. Plots were established in 1990. Management was similar among perennial grasses. In 1990, grass plots were sprayed after planting with herbicide 2, 4-D (2, 4-dichlorophenoxyacetic acid). In subsequent years, grass plots were hand-weeded.