Journal of Entomological and Acarological Research 2024; volume 56:13181

ENTOMOLOGY

Distributions of agrobiont lady beetles (Coleoptera: Coccinellidae) among crop and non-crop habitats within an agricultural landscape in east-central South Dakota, USA

Louis Hesler, Eric Beckendorf

Integrated Cropping Systems Unit, Agricultural Research Service, USDA, Brookings, SD, USA

Correspondence: Louis Hesler, Integrated Cropping Systems Unit, Agricultural Research Service, USDA, Brookings, SD, USA.
E-mail: louis.hesler@usda.gov

Key words: biodiversity, agroecology, biocontrol, spatial distribution, temporal distribution

Contributions: both authors made a substantial intellectual contribution, read and approved the final version of the manuscript, and agreed to be accountable for all aspects of the work.

Conflict of interest: the authors declare no potential conflict of interest.

Ethics approval and consent to participate: not applicable.

Funding: the study was supported by base funds from USDA-ARS CRIS Project 3080-21220-008-00D. Mention of trade names or commercial products in this publication is solely for the purpose of providing specific information and does not imply recommendation or endorsement by the U.S. Department of Agriculture. USDA is an equal opportunity provider and employer.

Availability of data and materials: data and metadata will be publicly available at AgData Commons (https://agdatacommons.nal.usda.gov/) upon publication of this study.

Acknowledgments: the authors thank Jack Ingemansen, Phil Rozeboom, Adam Varenhorst, John Kleinjan, Danny and Chris Bessler, and Bowes Farms for permission to sample in habitats used in this study. The technical efforts of Riley Honomichl, Kaitlin Schieuer, Bradley McManus, and Darrell McKeown were greatly appreciated. Sara Duke provided statistical advice. Lauren Hesler and Sharon Schneider reviewed drafts of this paper.

Received: 29 September 2024.
Accepted: 13 October 2024.

Journal of Entomological and Acarological Research 2024; 56:13181
doi:10.4081/jear.2024.13181

Abstract

Alternative habitats to predominant corn and soybean fields may help to stem declines of native lady beetles in central North America, but their relative values to native lady beetles have not been directly compared. The goal of this 2-year study was to compare the abundance and species composition of native agrobiont lady beetles among habitats such as corn, winter grains, prairie, and arboreal tracts across three seasons (late spring, summer, and autumn) in eastern South Dakota, USA. Yellow sticky traps were used to sample a total of 797 individuals and 13 species of lady beetles. *Coleomegilla maculata lengi* Timberlake was the most abundant species and found predominantly in corn and arboreal habitats. *Hippodamia convergens* Guérin-Méneville was the second-most abundant species and found mainly in prairie and crop habitats. *Harmonia axyridis* (Pallas) was sampled only in 2023 in low numbers but preferred arboreal habitat to other habitats. *Hippodamia parenthesis* (Say) preferred winter grain and prairie habitats over corn and arboreal habitats. *Cycloneda munda* (Say) preferred corn to other habitats. This study was designed to include habitats that would optimize detection of *Hip. tredecimpunctata tibialis* Timberlake, which has declined in recent years, but it was not sampled from any of the habitats. Prospects are discussed for conserving native agrobiont lady beetles that prey on crop pests among habitats within agricultural landscapes in eastern South Dakota.

Introduction

Lady (=ladybird) beetles (Coleoptera: Coccinellidae) provide agroecosystem services as major predators of the pests of field crops (Pervez *et al*., 2020). Their prey includes various hemipteran pests, plus the eggs and larvae of beetles and moths (Evans, 2009; Obrycki *et al*., 2009; Pervez *et al*., 2020). Individual agroecosystems typically host a few core species of lady beetles, with many species occurring among different crops within a region (Honěk, 2012; Pervez *et al*., 2020). For example, about 10 lady beetle species form an assemblage across field crops such as corn, soybean, wheat, and alfalfa in central North America (Elliott and Kieckhefer, 1990; Gardiner *et al*., 2009; Hesler and Beckendorf, 2021a). Common agrobiont species of lady beetles may also be found in neighboring non-crop habitats (Rand and Louda, 2006; Hesler and Kieckhefer, 2008; Lamb *et al*., 2019; Samaranayake and Costamagna, 2019).

The lady beetle assemblages of field crops in central north

America have changed both quantitatively and qualitatively over the last few decades (Harmon *et al*., 2007; Lamb *et al*., 2019; Hesler and Beckendorf, 2021b). For instance, a 14-year survey in eastern South Dakota showed declining trends in the annual abundance of lady beetles in field crops and restored prairie, with significant declines in their annual abundance in corn and soybean (Hesler and Beckendorf, 2021a). Declines have been more marked for native than non-native lady beetles (Elliott *et al*., 1996; Lamb *et al*., 2019; Hesler and Beckendorf, 2021a). In eastern South Dakota, four species have declined, including *Coccinella transversoguttata richardsoni* Brown, *Coccinella novemnotata* Herbst, *Adalia bipunctata* (L.), and *Hippodamia tredecimpunctata tibialis* Timberlake (Elliott *et al*., 1996; Hesler and Beckendorf, 2021a). Reasons for the declines are unclear, but factors may include decreases in the prey of lady beetles (Hutchinson *et al*., 2010; Crossley *et al*., 2021), intraguild competition that favors non-native lady beetles (Bahlai *et al*., 2015; Tumminello *et al*., 2015), and consequences of reduced agricultural landscape diversity, such as the predominance of corn and soybean plantings (Gardiner *et al*., 2009; Gardiner *et al.*, 2021).

Crop and land management that promotes alternative habitats to counter the dominance of corn and soybean in the north-central U.S. may be important for conserving lady beetles (Gardiner *et al*., 2009; Samaranayake and Costamagna, 2019; Hesler and Beckendorf, 2021a). These practices may include planting a more diverse set of crops that extend periods of prey availability, adding cover crops, and preserving natural and semi-natural areas that may provide alternative prey and serve as refuges for lady beetles (Olson, 1971; Hesler and Beckendorf, 2021a).

While alternative habitats to corn and soybean fields may help to stem the declines of native lady beetles in mid-central North America (Samaranayake and Costamagna, 2019), particular habitat types may be more valuable than others. For instance, diversifying agricultural habitat with alternative crops such as winter grains can extend the period of available prey beyond that of corn and soybean, and be readily exploited by native species of agrobiont lady beetles, including *Hip. tredecimpunctata tibialis* (Say) (Hesler and Beckendorf, 2021a). Winter grains (typically wheat and rye) are planted and emerge in autumn, undergo winter dormancy and resume growth through spring until maturation and harvest in early summer.

Non-agricultural habitats may also be useful. For example, perennial grasslands support the abundance of native lady beetles over non-native ones (Gardiner *et al*., 2009; Diepenbrock and Finke, 2013), although native agrobiont species comprise only a small proportion of lady beetles in these habitats (Diepenbrock and Finke, 2013). Alternatively, prairie plantings that incorporate native grasses and forbs and situated within and around agricultural fields have been found to increase the abundance and diversity of wildlife and pollinator communities (Robertson *et al*., 2017; Schulte *et al*., 2017; Werling *et al*., 2014), and various prairie plants may host prey that serve as alternate food sources for lady beetles when pest levels wane within crop fields (Olson, 1971). In contrast, while arboreal habitat also offers many environmental benefits to wildlife within an agricultural landscape (Asbjornsen *et al*., 2013), a higher proportion of forested habitat in the landscape may favor the abundance of non-native over native lady beetles (Gardiner *et al*., 2009).

Lady beetles move among habitats within an agricultural landscape (Figure 1) as mobile adults seeking prey and shelter (Honěk, 2012). Knowledge about favorable alternative habitats for agrobiont lady beetles can be applied toward developing recommendations for the management of agricultural landscapes with respect to their relative values as habitats for lady beetles (Magagula and Samways, 2001; Burgio *et al*., 2006). However, the relative values of various alternative habitats to native lady beetles have not been directly compared in the north-central U.S. In this study, lady beetles were sampled among four habitat types (corn, winter small grain, restored

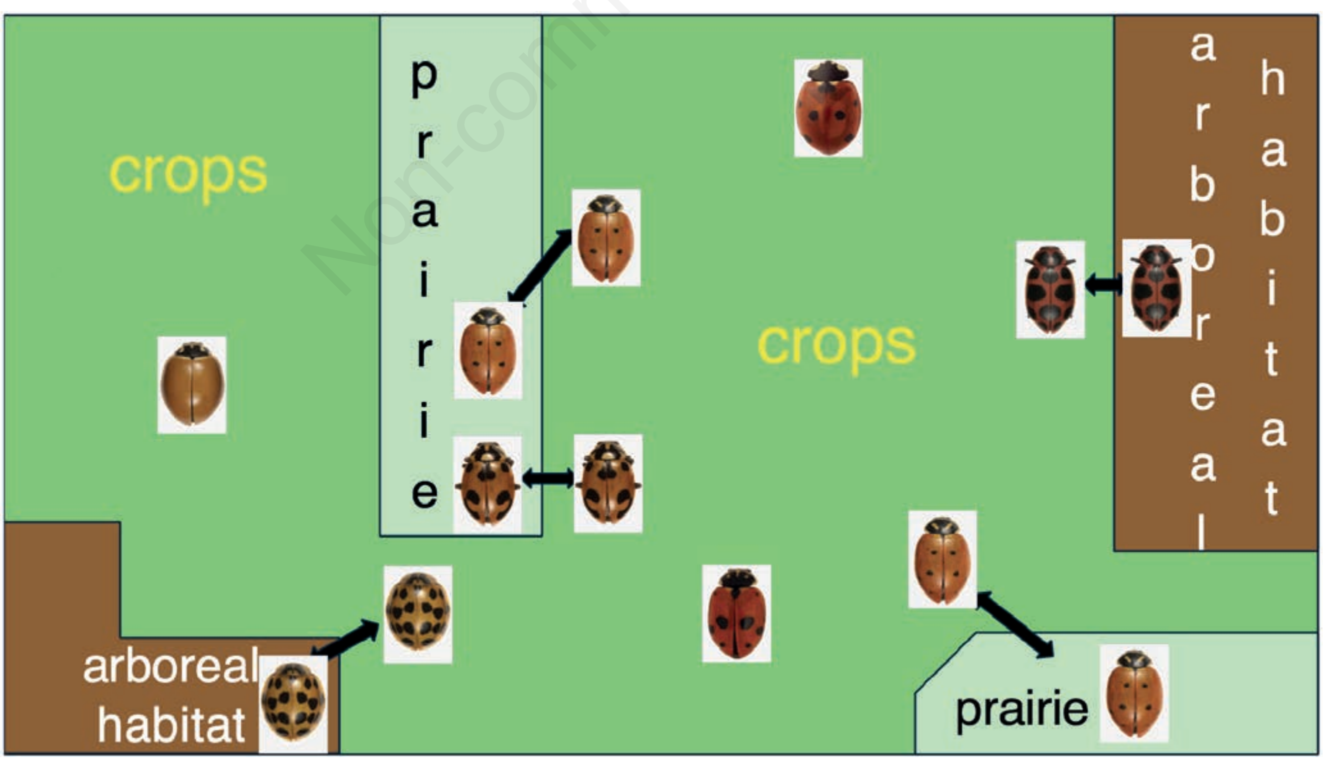

Figure 1. Schematic depicting the presence and movement of adult lady beetles among habitats within an agricultural landscape.

prairie, and wooded tracts) in eastern South Dakota, USA. A common assemblage of lady beetle species may be found among these four habitats, although their rank abundance among these habitats is distinct (Hesler and Kieckhefer, 2008; Hesler and Beckendorf, 2021a). Yellow sticky traps have commonly been used as an effective means for sampling and comparing lady beetle assemblages among the four habitat types (Boiteau *et al*., 1999; Finlayson *et al*., 2008; Hesler and Kieckhefer, 2008; Lamb *et al*., 2019, Hesler and Beckendorf, 2021a). Thus, we used sticky traps to sample lady beetles among habitats and determine the favorability of alternative habitats to native agrobiont lady beetles.

Materials and Methods

Experimental approach

The study was conducted during the spring, summer, and autumn of 2022 and 2023 in Brookings County, South Dakota, USA. Sampling sites included three habitat types: annual field crops, and perennial habitats of restored prairies and groves (=arboreal habitat), with four replicate sites per habitat type in a given season. For field crops, winter small grains (rye and wheat) were sampled in spring and autumn, and corn was sampled in summer (Figure 2). Field crops were planted within a crop rotation sequence. Consequently, sites of individual crop fields differed between years, for a total of 24 field-crop sites. The four prairie and four arboreal sites were perennial habitats and used both years.

Altogether, 32 unique sites were sampled (Figure 3), with sites chosen based on availability, proximity (*i.e.*, within a 30-km radius), and accessibility (in terms of driving to and walking into). Individual sites ranged in size from 0.2 to 60.3 ha. The composition of non-crop vegetation at each site was determined using local botanical guides (Ball and Graper, 1995; Johnson and Larson, 1999). Arboreal habitats that were sampled were typical of those in east-central South Dakota, consisting mainly of green ash (*Fraxinus pennsylvanica*) and an understory of the shrub, buckthorn (*Rhamnus cathartica*), with three of the four arboreal sites in our study having a few additional woody species. Prairies consisted of a mix of native grasses and forbs, except those of the four sties were predominantly native grasses with light incursions of weedy broadleaf species. Details of the plant composition of prairies, arboreal habitats, and crops and sites in our study will be available at Ag Data Commons (https://agdatacommons.nal.usda.gov/) upon publication.

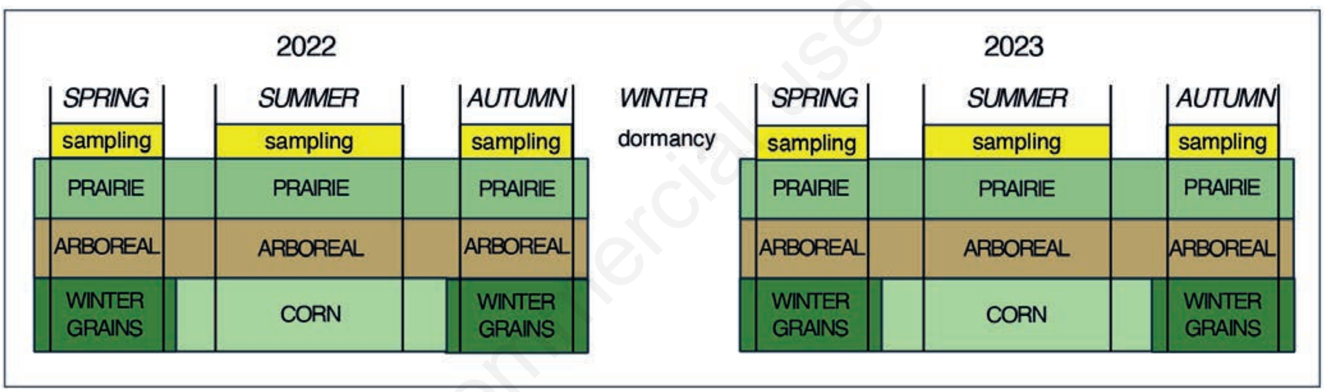

Figure 2. Seasonal timeline of sampling lady beetles within four habitat types, 2022-2023.

Figure 3. Grid map and county-scale map highlighting sampling sites in Brookings County, east-central South Dakota, USA.

Adult lady beetles were sampled by deploying 5 yellow sticky traps (Pherocon AM, Trecé, Adair, OK, USA) weekly per site each season. The sticky traps were deployed on 0.88-m-tall stakes 15 m apart in a linear transect at least 15 m from the edges of each habitat. Traps were initially placed lower in winter grains and prairie and progressively raised with increasing canopy height, whereas traps in corn and arboreal habitats were consistently placed at the top of the stakes. Traps were recovered every 7 days and replaced with a fresh set of traps during each sampling period. Upon removal, traps were covered with cellophane and stored in a freezer until processed. Lady beetles on traps were identified as species using keys in Gordon (1985) and then counted.

Sampling for lady beetles was conducted during three discrete periods each year, with breaks in trapping between spring, summer and autumn. Winter grain fields were sampled in spring and autumn, corn fields were sampled in summer, and prairie and arboreal habitats were sampled in all three seasons. Trapping began each spring when temperatures were consistently above freezing, and winter grain plants had greened up and lasted 5 weeks in 2022 and 4 weeks in 2023 until winter grains had senesced. Summer trapping began just before flowering (tasseling) of corn plants and persisted for 9 weeks until corn plants senesced. Autumn trapping began when winter grain plants had emerged to a height of approximately 5 cm and ended with the onset of sustained cold weather and nighttime freezing temperatures, resulting in 3 weeks of trapping in 2022 and 5 weeks in 2023. Thus, traps were deployed for a total of 8 and 9 weeks, respectively, across the winter grain periods of 2022 and 2023. Two individual traps were razed by white-tailed deer, *Odocoileus virginianus* (Zimmermann), and thus, counts were absent for 1 week from each of the two traps. See Table 1 for specific trapping dates. Potential prey items of lady beetles within the sampling sites were not quantified.

Data analysis

Counts of lady beetles on individual traps were summed across weeks for individual sampling sites each season within a year. The sums for individual habitats varied widely among sites within a season each year, so the sums were pooled seasonally. The sums for habitat type were pooled for spring and autumn each year so that trapping periods were comparable between the cropping cycles of winter grain and corn.

Counts were analyzed separately across lady beetle species and for individual species with the highest abundance. The Cochran-Mantel-Haenszel (CMH) procedure (McDonald, 2014) was used to test the null hypothesis that the relative proportions of lady beetles in various habitat types were independent of season and year. Specific follow-up tests for independence of proportions for habitat-by-year and habitat-by-season were conducted by using Pearson chi-square analysis (McDonald, 2014). For species with zero-counts in some habitat-by-season-by-year combinations, counts were collapsed to habitat and tested by Pearson chi-square analysis. All analyses were performed with JMP v. 17 software (JMP, 2022). Mosaic plots (Friendly, 1994) were used to graphically represent proportions and counts of lady beetles by habitat and seasons.

Results

Trap catch of various lady beetle species

The traps sampled 797 lady beetles, with 396 caught in 2022 and 401 in 2023. Six species of lady beetle comprised 96.8% of all individuals (Table 2). *Coleomegilla maculata lengi* Timberlake was predominant, accounting for 514 (64.5%) of lady beetles sampled, followed by *Hippodamia convergens* Guérin-Méneville (146, 18.3%), *Harmonia axyridis* (Pallas) (55, 6.9%), *Cycloneda munda* (Say) (30, 3.8%), *Hippodamia parenthesis* (Say) (17, 2.1%), *Psyllobora vigintimaculata* (Say) (14, 1.8%), and *Coccinella septempunctata* L. (10, 1.3%); the remaining species each comprised <1% of lady beetles sampled. *Hip. tredecimpunctata tibialis* was not sampled.

Proportions of trap catch across all species

When summed across species, the relative proportions of lady beetles differed among habitat types, with higher counts in arboreal (303, 38.0%) or crop habitats (396, 49.7%; corn: 297, 37.3%; winter grains: 99, 12.4%) than in prairie (98, 12.3%). Overall, the proportions were independent of season and year (CMH χ^2=3.38, df=2, p=0.11). However, when counts were subdivided by year and examined graphically, patterns in counts by seasons and habitats appeared to differ between the two years (Figure 4) (suggesting that pooling the counts across years may have obscured statistical differences between them; McDonald, 2014). Within each year, the proportions of lady beetles among habitats varied by season (2022: Pearson χ^2=10.41, df=2, p=0.006; 2023: Pearson χ^2=31.91, df=2, p<0.001), but with distinct differences between years. Specifically, trap counts of lady beetles in prairie were greater in 2023 than in 2022, particularly in summer. In addition, overall counts in arboreal habitat were greater in 2022 than in 2023, but with seasonal nuances. That is, counts in the arboreal habitat were relatively high in the summer and low in the spring-autumn periods of 2022, but counts were slightly higher in the spring-autumn period than in the summer of 2023. The counts of lady beetles within crop habitats were similar between years, with corn having roughly three times as many lady beetles as winter grains.

Proportions of trap catch for individual species

Coleomegilla maculata lengi

This species was trapped predominantly in crop fields (276) and arboreal habitats (235), with only 3 individuals caught in prairie (Pearson χ^2=252.98, df=2, p<0.001). Counts of *Col. macu-*

Table 1. Sample dates in which yellow sticky traps were used to sample adult lady beetles in field crop, restored prairie, and arboreal habitats in east-central South Dakota, USA.

Year	Season	Dates	Habitats sampled
2022	Spring	19 May - 23 June	Winter grain, prairie, arboreal
	Summer	14 July - 15 September	Corn, prairie, arboreal
	Autumn	20 October - 10 November	Winter grain, prairie, arboreal
2023	Spring	2 May - 30 May	Winter grain, prairie, arboreal
	Summer	12 July - 13 September	Corn, prairie, arboreal
	Autumn	4 October - 8 November	Winter grain, prairie, arboreal

lata lengi were disproportionately higher in summer (426) than in spring and autumn (88) (Pearson χ^2=202.91, df=1, p<0.001, adjusted for trap days). Accordingly, the distribution of *Col. maculata lengi* between field crop habitats was skewed toward corn (250) *versus* winter grains (26) (Pearson χ^2=168.76, df=1, p<0.001, adjusted for trap days).

Because of the preponderance of *Col. maculata lengi* in crop and arboreal habitats, additional contingency analysis was limited to those two habitats. The proportions of *Col. maculata lengi* caught in crop and arboreal habitats were not independent of season and year (CMH χ^2=39.91, df=2, p<0.001). The lack of independence was due to higher proportions of *C. maculata lengi* in arboreal habitat in spring 2023 than spring 2022 and higher proportions in arboreal habitat summer 2022 than summer 2023 (Pearson χ^2=80.41, df=2, p<0.001); however, the proportions among habitats did not differ between seasons in 2022 (Pearson χ^2=2.42, df=2, p=0.12) (Figure 5).

The distribution of *Col. maculata lengi* was consistent between years, with 125 trapped across all 9 sample dates in corn fields each year (non-random pattern, p<0.001), overlapped by peaks in trap catch in arboreal habitat on the last two sampling dates of summer each year (non-random pattern, p<0.001), although as noted previously, counts were considerably lower in arboreal habitat in summer 2023 (Figure 6).

Hippodamia convergens

This species was caught on traps primarily in prairie (68 individuals) and crop fields (55 winter grains, 13 corn) and rarely in arboreal habitat (9 individuals). Thus, contingency analysis was conducted using only prairie and crop habitats, which indicated that proportions were not independent of season and year (CMH χ^2=43.16, df=2, p<0.001). Indeed, the proportions of *Hip. convergens* among prairie and crop habitats differed by season in 2022 (Pearson

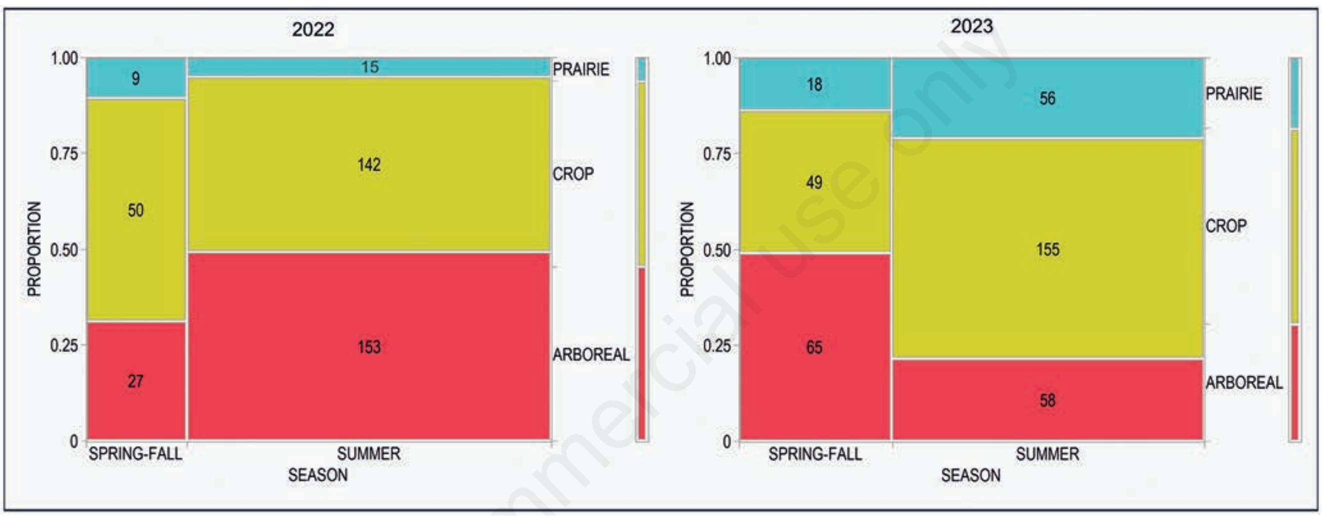

Figure 4. Proportions and counts of adult lady beetles on sticky traps by seasons among various habitats in east-central South Dakota, USA, 2022-2023.

Table 2. Number of adult lady beetles sampled in 2022-2023 from field crop, restored prairie, and arboreal habitats in east-central South Dakota, USA.

Species	*Number sampled*	*Percent*	*Habitats*
Coleomegilla maculata lengi	514	64.5	WG, RP, CO, AR
Hippodamia convergens	146	18.3	WG, RP, CO, AR
Harmonia axyridis	55	6.9	WG, RP, CO, AR
Cycloneda munda	30	3.8	RP, CO, AR
Hippodamia parenthesis	17	2.1	WG, RP, CO, AR
Psyllobora vigintimaculata	14	1.8	AR
Coccinella septempunctata	10	1.3	WG, RP, AR
Brachiacantha ursina	6	0.8	WG, RP, CO, AR
Brachiacantha albifrons	1	0.1	RP
Hippodamia variegata	1	0.1	WG
Hyperaspis undulata	1	0.1	WG
Nephus flavifrons	1	0.1	AR
Scymnus sp.	1	0.1	AR
Total	797		

WG, winter grains; RP, restored prairie; CO, corn; AR, arboreal habitat.

χ^2=7.04, df=2, p=0.008) and 2023 (Pearson χ^2=38.15, df=2, p<0.001). In the spring and autumn of each year, relatively large proportions of *Hip. convergens* (78 and 83%, respectively) were found in winter grains, whereas in summer, equal (2022) or much larger proportions (2023) of *Hip. convergens* were found in prairie compared to corn (Figure 7).

Harmonia axyridis

This species was caught on traps only in 2023. 38 *Har. axyridis* were found in arboreal habitats, 8 in prairie, 6 in corn, and 3 in winter grains. When counts were summed across seasons, their proportions did not vary significantly by habitat (χ^2=2.99, df=2, p=0.22).

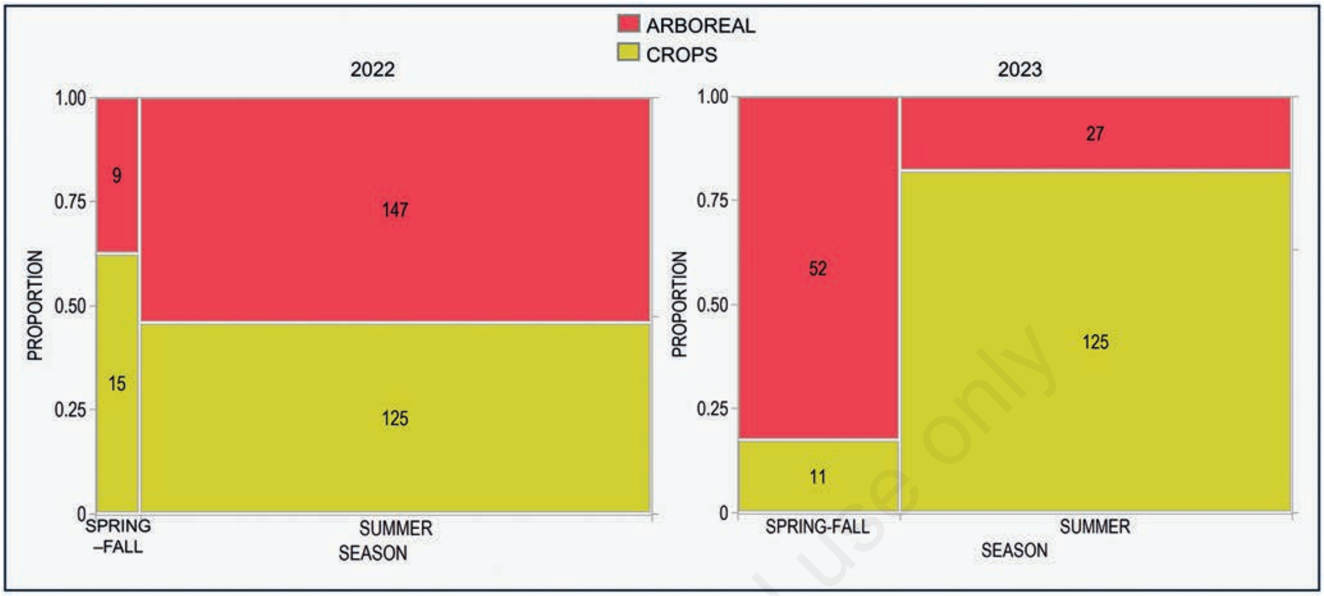

Figure 5. Proportions and counts of *Coleomegilla maculata lengi* on sticky traps seasonally among various arboreal and crop habitats in east-central South Dakota, USA, 2022-2023.

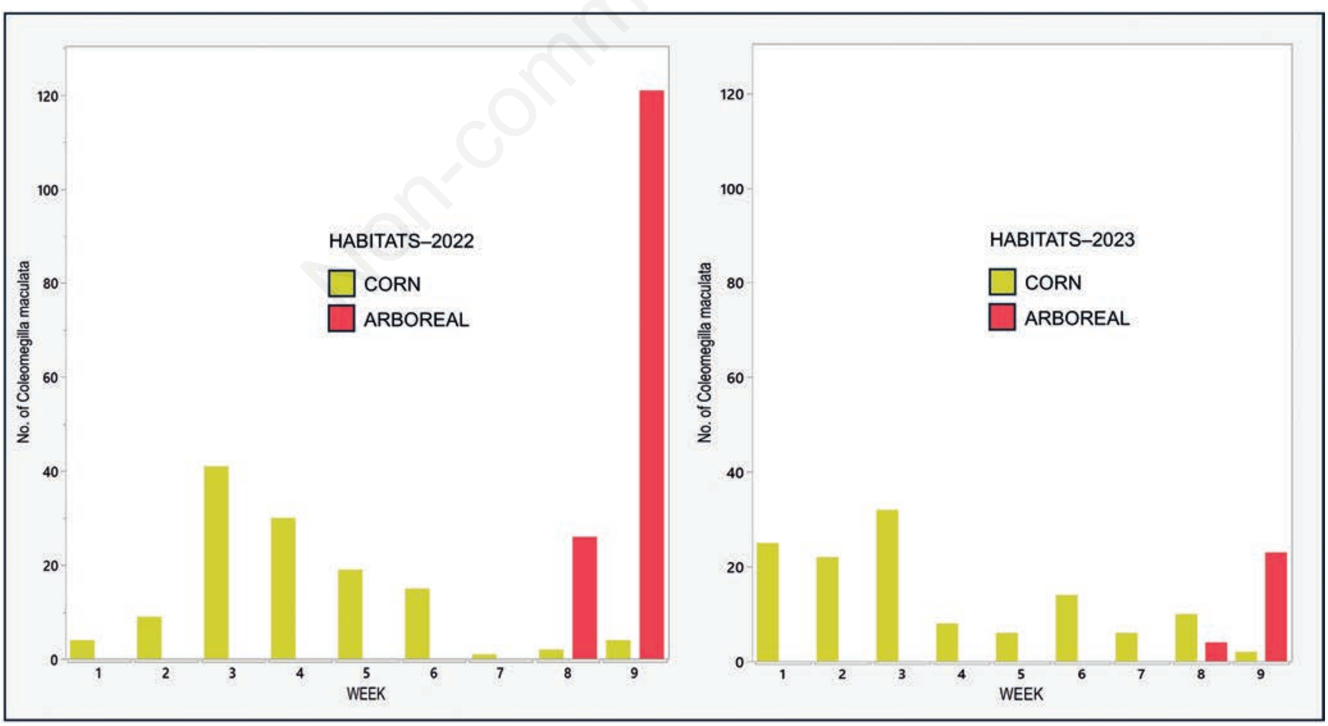

Figure 6. Numbers of *Coleomegilla maculata lengi* on sticky traps by week across four arboreal habitats and four corn habitats in summers of 2022 and 2023 in east-central South Dakota, USA. Weeks run starting from 14 July to 8 September 2022 and from 12 July to 6 September 2023.

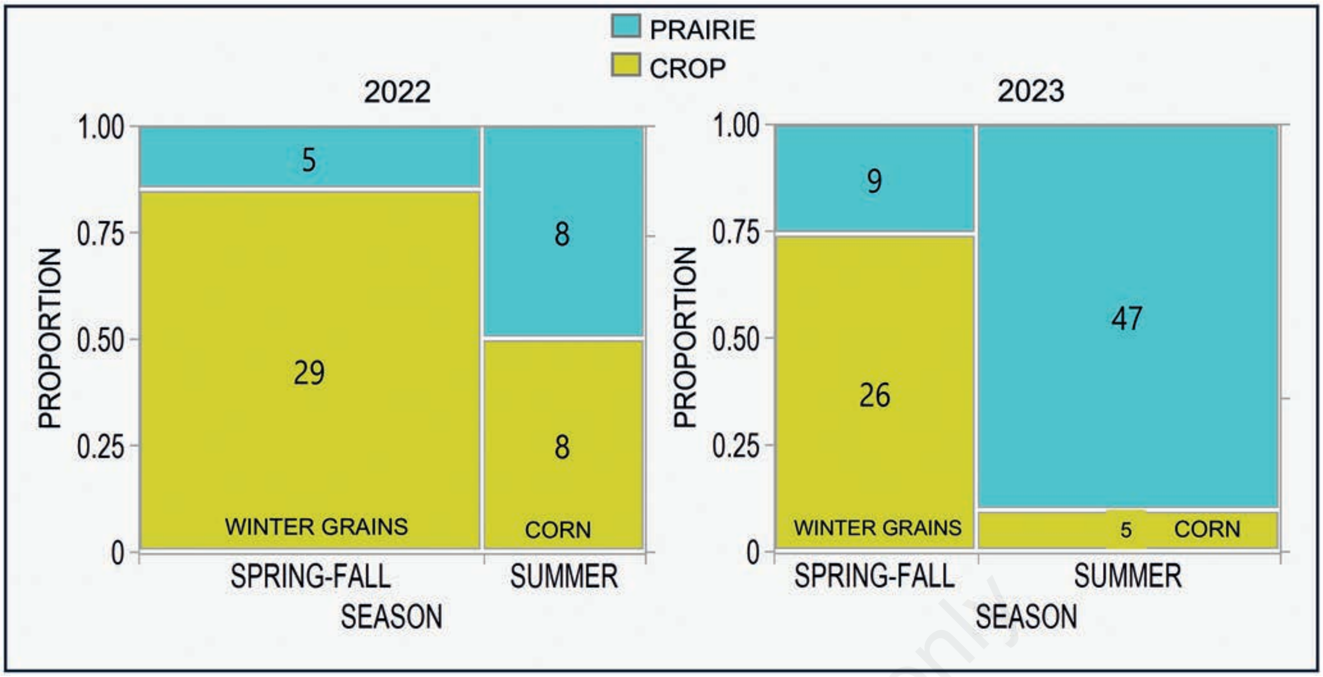

Figure 7. Proportions and counts of *Hippodamia convergens* on sticky traps seasonally across various crop and prairie habitats in 2022 and 2023 in east-central South Dakota, USA.

However, when counts were tested only by habitat, the distribution of *Har. axyridis* in arboreal habitat was skewed significantly from an expectation of no habitat preference (Pearson χ^2=32.16, df=3, p<0.001).

Hippodamia parenthesis

The 17 *Hip. parenthesis* were spread across habitats, with 8 in winter grain fields, 6 in prairie, 1 in corn, and 1 in arboreal habitat. The higher counts in winter grain and prairie habitats showed a distribution that was skewed significantly from the expectation of no habitat preference (Pearson $\chi 2$=14.77, df=3, p=0.002).

Cycloneda munda

Twenty-six of the 30 *Cyc. munda* were found in corn, 2 in prairie, 2 in arboreal habitat, and none in winter grain fields. The relatively high counts of *Cyc. munda* in corn deviated significantly from the expectation of no preference among habitats (Pearson χ^2=106.00, df=3, p<0.001).

Other species

Counts of the remaining species were too low for statistical analysis. Of the 10 *Coc. septempunctata* sampled, six were found in prairie, 3 in winter grain fields, and 1 in arboreal habitat. All eight *Psy. vigintimaculata* were caught in 2022 in arboreal habitats. The 6 *Brachiacantha ursina* (F.) were composed of two individuals from winter grains, two from prairie, and one each from corn and arboreal habitat. The five remaining lady beetle species sampled were represented by one individual each.

Discussion and Conclusions

The results of this study showed the occupancy of two alternative habitats, prairie and arboreal tracts, by various agrobiont species of lady beetles in addition to their use of two standard field crops, namely corn in the summer and small grains in the spring and autumn. In fact, there were slightly more lady beetles sampled in the arboreal habitat (303) than in corn (297). The number of lady beetles sampled in prairie (98) was roughly equal to that in winter grains (99). However, the numbers in arboreal and prairie habitats must be qualified, as sampling occurred in these habitats in spring, summer, and autumn, whereas sampling in corn and winter grains happened only during their respective cropping seasons.

The presence of lady beetles in these four habitat types depended on species, with particular species showing preferences for one or more habitat types. Three species had moderate to relatively high numbers in arboreal habitats. *Col. maculata lengi* was the most abundant lady beetle in arboreal habitats, with peak abundance in late summer (*i.e.*, early September). At the arboreal site where *Col. maculata lengi* was most abundant, we observed aggregations of this species on the non-adhesive fold of traps, at the base of the trap stake, and amid leaf litter and fallen branches on the ground. This type of aggregation behavior is typical for *Col. maculata lengi*, which form overwintering aggregations at the base of prominent objects such as fence posts or in wooded areas at the base of trees (Benton and Crump, 1979). Thus, in this study, arboreal tracts were valuable to *Col. maculata lengi* as overwintering habitat.

Two other species were captured in moderate numbers in arboreal habitat. *Psy. vigintimaculata* was captured on sticky traps in a wooded habitat at low numbers in 2022, whereas *Har. axyridis* was found in modest numbers on traps in autumn 2023 in wooded areas in our study. *Psy. vigintimaculata* is mycetophagous, and it has previously been observed in our area within the arboreal habitat feeding on mycelium growing on vegetative plants within the canopy of woods (Hesler and Kieckhefer, 2008). Thus, its detection in our study was likely due to its foraging on fungi in wooded habitat.

Har. axyridis is non-native in North America and has become one of the predominant predatory lady beetles within field habitats in east-central South Dakota and similar regions in central North

America (Hesler and Kieckhefer, 2008; Samaranayake and Costamagna, 2019; Hesler and Beckendorf, 2021a). It commonly preys on the invasive soybean aphid, *Aphis glycines* Matsumura (Hemiptera: Aphididae) (Hesler and Beckendorf, 2021a). *Har. axyridis* is facultatively arboreal (Honěk, 2012), and it has been observed consuming various prey in arboreal habitats in central North America at various times of the year, including predation of the soybean aphid on its overwintering host, buckthorn, in autumn (Hesler, 2003; Hesler *et al*., 2004; Hesler and Kieckhefer, 2008). Soybean aphid populations had waned in east-central South Dakota since roughly 2017 (Hesler and Beckendorf, 2021b), but resurged in 2023 (personal observations). Concomitantly, numbers of *Har. axyridis* had declined in recent years (Hesler and Beckendorf, 2021a), but its detection in our study only in 2023 was coincident with the resurgence of soybean aphid. Buckthorn was common as an understory shrub in arboreal habitat at our sampling sites, and although we did not quantify prey at these sites, it was likely that *Har. axyridis* was foraging on prey on buckthorn or other plant(s) within arboreal habitat. Its presence in arboreal habitat was likely transitory, as *Har. axyridis* typically overwinters in buildings and rocky edifices (Nalepa *et al*., 2000).

Occupancy within prairie habitat was notable for only two lady beetle species. During spring and autumn, the majority of *Hip. convergens* (55 individuals) was found in winter grain habitats rather than prairie (14 individuals). In summer, occupancy of *Hip. convergens* in the prairie was equal to (2022) or greater in prairie than in corn fields. The presence of *Hip. convergens* in winter grains was expected, as this species has historically been reported as one of the predominant lady beetles in this crop in east-central South Dakota (Olson, 1971; Elliott *et al*., 1996; Hesler and Kieckhefer, 2008; Hesler and Beckendorf, 2021a). The sparsity of *Hip. convergens* in prairie habitats was also consistent with previous, though relatively limited numbers of studies on it in this habitat (Olson, 1971; Hesler, 2013; Hesler and Beckendorf, 2021a). However, our relatively low trap catches of *Hip. convergens* in corn habitats contrasts with previous studies showing that it is often one of the most abundant lady beetles in corn fields of east-central South Dakota (Olson, 1971; Elliott *et al*., 1996; Hesler and Kieckhefer, 2008), though Hesler and Beckendorf (2021a) have noted recent declines. Specific reasons for the low numbers of *Hip. convergens* in corn fields during our study are unknown, but the paucity of prey (*e.g*., aphids, stem-boring, and grain-feeding lepidopterans) may have been a factor (Crossley *et al*., 2021).

Though overall numbers of *Hip. parenthesis* were low, trap counts indicated habitat preferences for prairie and winter grains. Its occupancy in prairie was consistent with previous reports of it being found outside of crop fields on plants common to prairies in east-central South Dakota (Olson, 1971; Hesler and Beckendorf, 2021a). However, *Hip. parenthesis* was one of the most abundant lady beetles in winter grains and corn (Olson, 1971; Elliott *et al*., 1996), and its low numbers in our samples among various habitat types are consistent with a previous report of low relative abundance among lady beetle species (Helser and Beckendorf, 2021a).

Winter grains hosted comparatively low numbers of lady beetles, which ran counter to our hypothesis that this habitat type would extend the period of available prey for agrobiont lady beetles beyond that of summer annual crops such as corn. *Hip. convergens* and *Hip. parenthesis* were the principal species sampled in winter grains. In east-central South Dakota, winter grain is not known to harbor overwintering lady beetles during its dormant season (Elliott and Kieckhefer, 1990), so the occupancy of lady beetles within winter grain fields is dependent on prey availability. Although we did not sample for prey within winter grain habitat, we did not observe any substantial pest levels there when servicing traps in either spring or autumn, and thus one can surmise that low prey availability limited occupancy of lady beetles within winter grain fields.

Roughly half of all lady beetles in this study were sampled from corn habitats. *Col. maculata lengi* comprised the majority of lady beetles within corn habitat, with much lower numbers of *Cyc. munda* and *Hip. convergens*. *Col. maculata lengi* has been reported as one of the dominant lady beetles in corn habitat in east-central South Dakota (Elliott *et al*., 1996; Hesler and Beckendorf, 2021a). The low relative abundance of *Cyc. munda* is also consistent with prior reports, but the low relative abundance of *Hip. convergens* generally contrasts previously studies (Olson, 1971; Elliott *et al*., 1996; Hesler and Beckendorf, 2021a). Individual species may have low (even 0) counts within corn fields within a particular year (Elliott *et al*., 1996), but the low abundance or absence of multiple species of agrobiont lady beetles other than *Col. maculata lengi* within corn fields that we sampled suggest that prey densities were low. Although not quantified, this is supported by our observations made while deploying and servicing traps within fields that indicated no notable evidence of pest infestations of corn plants. The widespread use of pest-resistant corn hybrids has greatly reduced insect pest pressure in the north-central United States (Hutchinson *et al*., 2010) and likely has contributed to reduced occupancy of insect predators such as *Hip. convergens* within corn fields. In contrast, *Col. maculata lengi* can complete its development on corn pollen alone (Smith, 1971), and therefore is not dependent on prey in corn fields.

The main goal of this study was to compare various agricultural and non-agricultural habitats with regard to the occupancy of lady beetles. An impetus for the study was to evaluate alternative habitats for hosting agrobiont lady beetles, particularly *Hip. tredecimpunctata tibialis*, whose numbers have declined considerably in recent studies (Hesler and Beckendorf, 2021a). This agrobiont species is a generalist that historically frequented corn and small-grain fields and is presumed to overwinter largely in arboreal habitat (Olson, 1971; Elliott *et al*., 2002). *Hip. tredecimpunctata tibialis* is still occasionally sampled in very low numbers in our other studies in east-central South Dakota (unpublished data), but alternative habitats in the current study did provide additional venues for its detection. Soybeans, another common crop in eastern South Dakota, typically host other lady beetles such as *Hip. convergens* and *Coc. septempunctata*—but rarely *Hip. tredecimpunctata tibialis*—when soybean aphids are present (Hesler and Beckendorf, 2021a). Future research should investigate other habitat strategies (*e.g*., cover crops, other minor crops, novel crops) for sustaining populations of *Hip. tredecimpunctata tibialis* in east-central South Dakota, and sampling should be undertaken in surrounding areas to obtain a regional perspective on the population status of *Hip. tredecimpunctata tibialis*. Additional hypotheses regarding the decline of *Hip. tredecimpunctata tibialis* besides habitat-related factors (*e.g*., competition, parasites, climate) should also be tested in future studies.

Besides lady beetles, the presence of perennial habitat embedded within the agricultural land matrix has benefits for agriculture and other interests (Asbjornsen *et al*., 2013, Kordbacheh *et al*., 2018). For instance, tracts of wooded habitat and prairie within and around agricultural fields have been found to increase the abundance and diversity of pollinators and wildlife, and enhance soil conservation, nutrient retention, and carbon sequestration in central North America (Werling *et al*., 2014; Robertson *et al*., 2017; Schulte *et al*., 2017).

Trends over the last few decades have shown overall that both prairie and arboreal habitats have had a net decrease in central North America, particularly in and around the region in which our study was conducted. This has largely been due to simplification of agricultural landscapes by production of a narrow set of commodity crops (*viz*., corn and soybean), livestock grazing land and feedlots, intensive weed and vegetation management, and the incorporation of peripheral land into field-production areas (Brown and Schulte, 2011; Johnston, 2013; Wimberly *et al*., 2017; Wright and Wimberly, 2013; Wright *et al*., 2017). In addition, stands of green ash, major components of many arboreal tracts (*i.e*., shelterbelts) proximate to agricultural land, have been recently attacked by the invasive emerald ash borer, *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae). The invasion is projected to greatly reduce stands of green ash and related trees due to infestation or pre-emptive culling of trees (Klooster *et al*., 2018). In a recent survey, arboreal habitat constituted 0.8% of agricultural land in South Dakota (USDA-NASS, 2022), and pest infestations, aging, and general deterioration may further reduce arboreal habitat.

However, more recent efforts have been aimed at restoring perennial habitats in central North America. These efforts include restoring land to prairie habitat, planting prairie strips within crop fields, and reestablishing tree belts (Asbjornsen *et al*., 2013; Schulte *et al*., 2017; Kemmerling *et al*., 2022). These efforts are encouraging with regard to several conservation aspects, including insect-mediated ecosystem services such as pollination and biological pest control. Additional research is needed to optimize the design and management of perennial vegetation areas within or adjacent to agricultural fields, particularly with regard to improving habitat for lady beetles and fostering their biocontrol services against agricultural pests.

In conclusion, the numbers of lady beetles sampled in arboreal habitat (303) were comparable to corn (297), and the numbers sampled in prairie (98) roughly equaled that in winter grains (99) in our study. The fact that the respective numbers of lady beetles in arboreal habitat and prairie were comparable to that in corn and winter grains on an annual basis establishes the relative value of these alternative habitats in an agricultural landscape to lady beetles. Moreover, it may be important to conserve arboreal and prairie tracts and perhaps increase their proximity to crop fields. The interactions of agricultural and non-agricultural habitats are complex with regard to lady beetle populations in eastern South Dakota (Elliott and Kieckhefer, 1990; Elliott *et al*., 2002), and consideration of additional complexity may be warranted in future studies to improve recommendations regarding habitats for lady beetles. Additional work focused specifically on *Hip. tredecimpunctata tibialis* and its decline will also be needed.

References

ASBJORNSEN H., HERNÁNDEZ-SANTANA V., LIEBMAN M., BAYALA J., CHEN J., HELMERS M.J., ONG C.K., SCHULTE L.A., 2013 - Targeting perennial vegetation in agricultural landscapes for enhancing ecosystem services. Renew. - Agr. Food Syst. 29: 101-125.

BAHLAI C.A., COLUNGA-GARCIA M., GAGE S.H., LANDIS D.A., 2015 - The role of exotic ladybeetles in the decline of native ladybeetle populations: evidence from long-term monitoring. - Biol. Invasions 17: 1005-1024.

BALL J.J., GRAPER D.F., 1995 - Trees for South Dakota. Extension Circular No. 903, Cooperative Extension Service, South Dakota State University, Brookings.

BENTON A.H., CRUMP A.J., 1979 - Observations on aggregations and overwintering in the coccinellid beetle Coleomegilla maculata (DeGeer). - J. N.Y. Entomol. Soc. 87: 154-159.

BOITEAU G., BOUSQUET Y., OSBORN W.P.L. 1999. - Vertical and temporal distribution of Coccinellidae (Coleoptera) in flight over an agricultural landscape. - Can. Entomol. 131: 269-277.

BROWN P.W., SCHULTE L.A., 2011 - Agricultural landscape change (1937–2002) in three townships in Iowa, USA. - Landscape Urban Plan. 100: 202-212.

BURGIO G., FERRARI R., BORIANI L., POZZATI M., VAN LENTERN J., 2006 - The role of ecological infrastructures on Coccinellidae (Coleoptera) and other predators in weedy field margins within northern Italy agroecosystems. - Bull. Insectol. 59: 59-67.

CROSSLEY M.S., SMITH O.M., DAVIS T.S., EIGENBRODE S.D., HARTMAN G.L., LAGOS-KUTZ D., HALBERT S.E., VOEGTLIN D.J., MORAN M.D., SNYDER W.E., 2021 - Complex life histories predispose aphids to recent abundance declines. - Glob. Change Biol. 27: 4283-4293.

DIEPENBROCK L.M., FINKE D.L., 2013 - Refuge for native lady beetles (Coccinellidae) in perennial grassland habitats. - Insect Conserv. Divers. 6: 671-679.

ELLIOTT N.C., KIECKHEFER R.W., 1990 - Dynamics of aphidophagous coccinellid assemblages in small grain fields in eastern South Dakota. - Environ. Entomol. 19: 1320-1329.

ELLIOTT N., KIECKHEFER R., KAUFFMAN W., 1996 - Effects of an invading coccinellid on native coccinellids in an agricultural landscape. - Oecologia 105: 537-544.

ELLIOTT N.C., KIECKHEFER R.W., BECK D.A., 2002 - Effect of aphids and the surrounding landscape on the abundance of Coccinellidae in cornfields. - Biol. Control 24: 214-220.

EVANS E.W., 2009 - Lady beetles as predators of insects other than Hemiptera. - Biol. Control 51: 255-267.

FINLAYSON C.J.; LANDRY K.M., ALYOKHIN A.V., 2008 - Abundance of native and non-native lady beetles (Coleoptera: Coccinellidae) in different habitats in Maine. - Ann. Entomol. Soc. Am. 101: 1078-1087.

FRIENDLY M., 1994 - Mosaic displays for multi-way contingency tables. - J. Am. Stat. Assoc. 89: 190-200.

GARDINER M.M., LANDIS D.A., GRATTON C., SCHMIDT N., O'NEAL M., MUELLER E., CHACON J., HEIMPEL G.E., DIFONZO C.D., 2009 - Landscape composition influences patterns of native and exotic lady beetle abundance. - Divers. Distrib. 15: 554-564.

GARDINER M.M., PERRY K.I., RILEY C.B., TURO K.J., DELGADO DE LA FLOR Y.A., SIVAKOFF F.S., 2021 - Community science data suggests that urbanization and forest habitat loss threaten aphidophagous native lady beetles. - Ecol. Evol. 11: 2761-2774.

GORDON R.D., 1985 - The Coccinellidae (Coleoptera) of America north of Mexico. - J. N.Y. Entomol. Soc. 93: 1-912.

HARMON J.P., STEPHENS E., LOSEY J., 2007 - The decline of native coccinellids (Coleoptera: Coccinellidae) in the United States and Canada. - J. Insect Conserv. 11: 85-94.

HESLER L.S., 2003 - Large summer population of multicolored Asian lady beetle in North Dakota. - Prairie Nat. 35: 287-289.

HESLER L.S., 2013 - Risk to native Uroleucon aphids (Hemiptera: Aphididae) from non-native lady beetles (Coleoptera: Coccinellidae). - Entomol. Am. 119: 14-22.

HESLER L.S., BECKENDORF E.A., 2021a - Declining abundance of Coccinellidae (Coleoptera) among crop and prairie habitats of Eastern South Dakota, USA. - Front. Conserv. Sci. 2: 742036.

HESLER L.S., BECKENDORF E.A., 2021b - Soybean aphid infestation and crop yield in relation to cultivar, foliar insecticide, and insecticidal seed treatment in South Dakota. - Phytoparasitica 49: 971-981.

HESLER L.S., KIECKHEFER R.W., 2008 - Status of exotic and previously common native coccinellids (Coleoptera) in South Dakota landscapes. - J. Kansas Entomol. Soc. 81: 29-49.

HESLER L.S., KIECKHEFER R W., Catangui M.A., 2004 - Surveys and field observations of Harmonia axyridis and other

Coccinellidae (Coleoptera) in eastern and central South Dakota. - Trans. Am. Entomol. Soc. 130: 113-133.
HONĚK A., 2012 - Distribution and habitats. In: Hodek I., van Emden H.F., Honěk A. (eds.). Ecology and behaviour of the ladybird beetles (Coccinellidae) (pp. 110-140). Chichester, UK: Wiley-Blackwell.
HUTCHINSON W.D., BURKNESS E.C., MITCHELL P.D., MOON R.D., LESLIE T.W., FLEISCHER S.J., ABRAHAMSON M., HAMILTON K.L., STEFFEY K.L, GRAY M.E, HELLMICH R.L., KASTER L.V., HUNT T.E., WRIGHT R.J., PECINOVSKY K., RABEY T.L., FLOOD B.R., RAUN E.S., 2010 - Areawide suppression of European corn borer with Bt maize reaps savings to non-Bt maize growers. - Science 330: 222-225.
JMP, 2022 - JMP® 17 Documentation Library. Cary, NC, USA.
JOHNSON J.R., LARSON G.E., 1999 - Grassland plants of South Dakota and the northern great plains. South Dakota State University, College of Agriculture and Biological Sciences, Ag Communications, Brookings.
JOHNSTON C.A., 2013 - Wetland losses due to row crop expansion in the Dakota prairie pothole region. - Wetlands 33: 175-182.
KEMMERLING L.R., RUTKOSKI C.E., EVANS S.E., HELMS IV J.A., CORDOVA-ORTIZ E.S., SMITH J.D., VÁZQUEZ CUSTODIO J.A., VIZZA C., HADDAD N.M., 2022 - Prairie strips and lower land use intensity increase biodiversity and ecosystem services. - Front. Ecol. Evol. 10: 833170.
KLOOSTER W.S., GANDHI K.J.K., LONG L.C., PERRY K.I., RICE K.B., HERMS D.A., 2018 - Ecological impacts of emerald ash borer in forests at the epicenter of the invasion in North America. - Forests 9: 250.
KORDBACHEH F., JARCHOW M., ENGLISH L., LIEBMAN M., 2019 - Productivity and diversity of annually harvested reconstructed prairie communities. - J. Appl. Ecol. 56: 330-342.
LAMB R.J., BANNERMAN JA., COSTAMAGNA A.C., 2019 - Stability of native and exotic lady beetle populations in a diverse landscape. - Ecosphere 10: e02630.
MAGAGULA C.N., SAMWAYS M.J., 2001 - Maintenance of ladybeetle diversity across a heterogeneous African agricultural/savanna land mosaic. - Biodivers. Conserv. 10: 209-222.
MCDONALD J.H., 2014 - Handbook of biological statistics 3rd ed., Sparky House Publishing, Baltimore, USA.
NALEPA C.A., KIDD K.A., HOPKINS D.I., 2000 - The multicolored Asian lady beetle (Coleoptera: Coccinellidae): orientation to aggregation sites. - J. Entomol. Sci. 35: 150-157.
OBRYCKI J.J., HARWOOD J.D., KRING T.J., O'NEIL R.J., 2009 - Aphidophagy by Coccinellidae: Application of biological control in agroecosystems. - Biol. Control 51: 244-254.
OLSON G.A., 1971 - Field populations and flight activity of three Hippodamia species in eastern South Dakota. Available from: https://openprairie.sdstate.edu/etd/5304.
PERVEZ A., OMKAR HARSUR M.M., 2020 - Coccinellids on crops: nature's gift for farmers. In: Chakravarthy A. (ed). Innovative pest management approaches for the 21st century. Springer, Singapore.
RAND T.A., LOUDA S.M., 2006 - Spillover of agriculturally subsidized predators as a potential threat to native insect herbivores in fragmented landscapes. - Conserv. Biol. 20: 1720-1729.
ROBERTSON G.P., HAMILTON S.K., BARHAM B.L., DALE B.E., IZAURRALDE R.C., JACKSON R.D., LANDIS D.A., SWINTON S.M., THELEN K.D., TIEDJE J.M., 2017 - Cellulosic biofuel contributions to a sustainable energy future: choices and outcomes. - Science 356: eaal2324.
SAMARANAYAKE K.G.L.I., COSTAMAGNA A.C., 2019 - Adjacent habitat type affects the movement of predators suppressing soybean aphids. - PLoS One 14: e0218522.
SCHULTE L.A., NIEMI J.B., HELMERS M.J., LIEBMAN M., ARBUCKLE J.G., JAMES D.E., KOLKA R.K., O'NEAL M.E., TOMER M.D., TYNDALL J.C., ASBJORNSEN H., DROBNEY P., NEAL J., VAN RYSWYK G., WITTE C., 2017 - Prairie strips improve biodiversity and the delivery of multiple ecosystems services from corn-soybean croplands. - P. Natl. Acad. Sci. USA 114: 11247-11252.
SMITH B.C., 1971 - Effects of various factors on the local distribution and density of coccinellid adults on corn (Coleoptera: Coccinellidae). - Can. Entomol. 103: 1115-1120.
TUMMINELLO G., UGINE T.A., LOSEY J.E., 2015 - Intraguild interactions of native and introduced coccinellids: The decline of a flagship species. - Environ. Entomol. 44: 64-72.
USDA-NASS, 2022 - Census of agriculture. Available from: https://www.nass.usda.gov/AgCensus/.
WERLING, B.P., DICKSON T.L., ISAACS R., GAINES H., GRATTON C., GROSS K.L., LIERE H., MALMSTROM C.M., MEEHAN T.D., RUAN L., ROBERTSON B.A., ROBERTSON G.., SCHMIDT T.M., SCHROTENBOER A.C., TEAL T.K., WILSON J.K., LANDIS D.A., 2014 - Perennial grasslands enhance biodiversity and multiple ecosystem services in bioenergy landscapes. - P. Natl. Acad. Sci. USA 111: 1652-1657.
WIMBERLY M.C., JANSSEN L.L., HENNESSY D.A., LURI M., CHOWDHURY N.M., FENG H., 2017 - Cropland expansion and grassland loss in the eastern Dakotas: New insights from a farm-level survey. - Land Use Policy 63: 160-173.
WRIGHT C.K., WIMBERLY M.C., 2013 - Recent land use change in the Western Corn Belt threatens grasslands and wetlands. - P. Natl. Acad. Sci. USA 110: 4134-4139.
WRIGHT C.K., LARSON B., LARK T.J., GIBBS H.K., 2017 - Recent grassland losses are concentrated around US ethanol refineries. - Environ. Res. Lett. 12: 044001.