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Differences in ground beetles (Coleoptera: Carabidae) of original and reconstructed tallgrass prairies in northeastern Iowa, USA, and impact of 3-year spring burn cycles

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Abstract

Ground beetle assemblages were monitored at four tallgrass prairie sites burned on 3-year cycles in northeastern Iowa. The objectives of this study were to quantify differences in carabid communities between original and reconstructed tallgrass prairies, and to determine the responses of ground beetles to 3-year cycles of early spring fire commonly used to manage tallgrass prairies. Using pitfall traps, ground beetle assemblages in two original and two reconstructed tallgrass prairies were compared between 1994 and 1998, where beetles were sampled annually (0-, 1-, and 2-year post-fire conditions) from plots burned every 3 years. When burned, the greatest abundance, activity density, and species richness of carabid beetles occurred the year immediately following a spring burn, with abundance declining steadily with increased time since burning. Overall ground beetle diversity as determined by Shannon's diversity index was greatest in original tallgrass prairies several years after a fire. Some species of ground beetles were found only in original prairies, while others were found primarily in reconstructed prairie. Similarly, some species were more abundant the year immediately following a burn, while others were found in greater abundance with increased time since fire. NMS ordination and indicator species analysis clearly show differences in carabid species between original and reconstructed tallgrass prairies, but did not show differences among burn treatments.

Introduction

Prairie grasslands covered approximately 162 million ha of the Great Plains region of the United States prior to Euro-American settlement in the mid-1800s (Samson and Knopf 1994). Since then, it is estimated that areas of tallgrass prairie have declined by more than 82% (Samson and Knopf 1994). This loss of tallgrass prairie may be the largest landscape change of any North American ecosystem. In Iowa, located both in the heart of the Great Plains and the only state located entirely within the distribution of tallgrass prairie, less than 0.1% of presettlement prairie remains (Smith 1998). Thus, the preservation and conservation of the remaining original tallgrass prairie is urgent, and efforts to reconstruct this endangered ecosystem are widespread and sometimes extensive (Smith 1998).

Historical processes such as fire and grazing are crucial to the successful preservation of original prairie and reconstruction of this ecosystem (Samson and Knopf 1996). Reintroduction of large grazers such as bison can be problematic in the highly fragmented and populated landscape that exists today, so fire is now the primary natural process (Towne and Owensby 1984; Hulbert 1988; Anderson 1990; Collins 1990) that managers use to maintain and restore tallgrass prairie. However, the use of prescribed fire in tallgrass prairies continues to generate considerable debate among prairie managers and insect ecologists over its perceived impact on prairie-specialist invertebrates. Recently, Swengel (1996), Orwig and Schlicht (1999) and Panzer (2002) documented negative impact of fire on prairie-specialist butterflies (Lepidoptera), such as the Ottoe skipper (*Hesperia ottoe*), Dakota skipper (*H. dacotae*), and Regal Fritillary (*Speyeria idalia*). In contrast, studies have also shown leafhopper (Homoptera: Cicadellidae) and butterfly abundance and species richness is greater in fire-managed than in fire-excluded prairie sites (Panzer and Schwartz 2000; Panzer 2002).

This study determines the impact of frequent fires on ground beetles (Coleoptera: Carabidae) living in tallgrass prairies. Carabids are primarily predaceous (Larochelle 1990), and one of the most common and abundant beetle families (Lövei and Sunderland 1996). The objectives of this 5-year study were (1) to quantify differences in the carabid assemblages of original and reconstructed tallgrass prairies to see how effective prairie reconstructions are in restoring native prairie insect fauna, and (2) to quantify the impact fire occurring at 3-year intervals is having on ground beetle assemblages.

Management of both original and reconstructed tallgrass prairies in much of the Upper Midwest region of the United States commonly uses a 3-year burn cycle. Given the historical role of frequent fire in the maintenance of tallgrass prairie ecosystems (Collins 1990), we hypothesized that prairie specialist species of ground beetles would be preadapted to frequent fire disturbances and, therefore, would be most abundant and diverse following the occurrence of fire.

Methods

Original prairies have evolved over hundreds or thousands of years (Samson and Knopf 1994) and are composed of diverse plant communities of 350–500 plant species (Samson and Knopf 1996). In contrast, reconstructed prairies are often limited to several dozen species of native prairie grasses and forbs because of limited availability of seed. In addition, very few prairie reconstructions have been established for more than a few years or decades. As prairies are reconstructed, the focus is necessarily on establishing the plant communities rather than on insect communities that are a crucial component of tallgrass prairie. Even in the preservation of original prairie, managers rarely consider insects such as butterflies (Opler 1981) in their management decisions.

Study sites

From 1994 to 1998, ground beetles were intensively sampled from four tallgrass prairies managed with 3-year spring (usually early April) burn cycles in northeastern Iowa. Each site was divided into at least three burn units, with typically no more than one-third of a given site burned in a given year. Chipera Prairie is a 31.2 ha original tallgrass prairie located in Winneshiek County (UTM Zone 15, 580825 E, 4775593 N). Hayden Prairie, a 97.2-ha original tallgrass prairie, is located in Howard County (UTM zone 15, 550105 E, 4809715 N). Anderson Prairie was planted with 20 species of forbs and six species of grasses in May 1988 using a drill seeder, is a 9.4-ha reconstructed tallgrass prairie located on the Luther College campus in Decorah, Winneshiek County (UTM Zone 15, 597396 E, 4796283 N). Effigy Mounds National Monument, located on the border of Allamakee and Clayton Counties (UTM Zone 15, 647536 E, 4774137 N), has 25 ha of reconstructed prairie. The Effigy Mounds reconstruction was seeded using drill and broadcast seeders with 65 species of forbs and six species of grasses in 1992 and 1993. Additional details on these sites can be found in Larsen et al. (2003) and Larsen and Williams (1999). In any given year at each prairie site, all three burn treatments (0, 1, and 2 years post-fire) were sampled. No unburned areas were available within any of the four sites.

Ground beetle sampling

Ground beetles were collected using pitfall traps for one-week-long periods in early-June, mid-July, and late-August from 1994 to 1998. Each trap was constructed from one 473 ml plastic cup (9 cm diameter) placed into the ground so the top edge was at or slightly below the ground surface. Each cup was fitted with a funnel constructed from a

207 ml casual cup insert (Sweetheart® Cup Company, Chicago, Illinois) to prevent beetle escape. Approximately 50 ml of 50% propylene glycol was then added as a preservative.

At each site during each trapping period, 12 pitfall traps were placed at approximately 10 m intervals within each prairie burn treatment (0, 1, or 2 years post-fire). If there were several different burned areas within a site in a given year, the 12 traps were divided equally among those areas. After each trapping period, traps were removed and holes refilled. Traps that were damaged and apparently disturbed by large vertebrates were noted and excluded from the analysis. Samples were then washed and stored in 70% ethanol. Ground beetles were identified to species using keys presented in Lindroth (1961–1969) and Noonan (1991), and names standardized using Bousquet and Larochelle (1993). Voucher specimens are housed in the reference insect collection in the Hoslett Museum of Natural History, Luther College, Decorah, Iowa.

Ground beetle faunal analysis

The total abundance of ground beetles and species richness was determined for each prairie and each burn treatment with years combined. Because of some variation among sites and years in the number of recovered traps and length of trap exposure in the field, abundance data were transformed to an activity density of number of beetles captured per trap per day. As a measure of community diversity, species richness, Shannon's diversity (H'), and Pielou's evenness (J') indices using log base e were calculated for the ground beetle fauna of each burn treatment (Krebs 1989). To test for significant differences among Shannon diversity values, we used a pairwise comparison test by Hutcheson (1970) as described by Zar (1999).

Statistical comparisons among the three burn treatments were performed for species richness, and activity density (average number of ground beetles caught per trap per day) for each site and year using the non-parametric analysis of variance Kruskal–Wallis test (Zar 1999).

Differences in carabid community composition between tallgrass prairie sites and the three burn treatments were initially compared using non-metric multidimensional scaling (NMS) ordination. All samples for each burn treatment at each site were pooled during each year. NMS is a non-parametric ordination technique that performs well with data sets where the underlying species response patterns cannot be specified *a priori* (Clarke 1993). For this analysis, Sorenson's distance (also referred to as Bray–Curtis distance) was used and significance of ordination axis was evaluated by comparing the solution stress of the observed data to the stress observed in 50 randomizations of the observed data. All multivariate analyses were completed using the software package PC-ORD, version 4.14 (Anonymous 1999).

Preferences of individual beetle species for original and reconstructed prairies were evaluated using indicator species analysis (Dufrêne and Legendre 1997). Indicator species analysis is a randomization-based test that compares the relative abundance and the relative frequency of individual species across different sampling areas, and expresses a species' affinity for a sampling area as % indication of a particular sampling area (Dufrêne and Legendre 1997). All samples for each burn treatment at each site were pooled for each year.

Accumulation curves were generated using EstimateS software (Colwell 1997). Curves generated compare cumulative species number and sampling effort for all annual samples from each site and burn treatment.

Results

Overall, 7781 ground beetles representing 90 species were collected during the study (Appendix), with 39 of these species (43%) being prairie specialists found primarily or exclusively in tallgrass prairie in northeastern Iowa (Larsen et al. 2003).

Original and reconstructed prairie comparisons

Significantly more beetles (Table 1) were collected from both the Anderson and Effigy Mounds reconstructed prairies than from the Chipera and Hayden original sites ($H = 11.14$; d.f. $= 3$; $P = 0.011$). Species richness was also significantly greater in the reconstructed prairies than in the original prairies ($H = 8.23$; d.f. $= 3$; $P = 0.042$). However, diversity indices such Pielou's evenness

Table 1. Total number, number of species, Shannon diversity index (H'), Pielou's evenness index (J'), and activity density (beetles/trap/day) for ground beetles (Coleoptera: Carabidae) collected from four tallgrass prairies each with 3-year burn cycles in northeastern Iowa from 1994 to 1998. 0 YPF indicates the year of a spring fire, 1 YPF indicates 1 year after a spring fire, and 2 YPF indicates 2 years after a spring fire

	Total number of beetles	Species richness	Shannon diversity (H')	Pielou evenness (J')	Activity density (beetles/trap/day)
Original prairies					
Chipera	1408	58	2.556 a	0.629	1.668
Hayden	1685	37	2.588 a	0.717	1.629
Reconstructed prairies					
Anderson	1799	44	2.117 b	0.559	1.658
Effigy mounds	2889	50	2.064 b	0.528	3.607
Burn treatments					
0 YPF	3205	65	2.453 c	0.588	0.888
1 YPF	2766	65	2.681 d	0.642	0.787
2 YPF	1810	64	2.625 d	0.631	0.662
Total	7781	90	–	–	0.789

Shannon (H') diversity indices comparing prairie sites or burn treatments followed by the same letter are not significantly different ($P = 0.05$) as determined by a paired t-test (Hutcheson 1970).

index (J') and Shannon's diversity index (H') that accounts for both heterogeneity and evenness revealed higher overall diversity ($P < 0.05$) in the original prairies than in the reconstructed prairies that were dominated by relatively few species (Table 1). Some species, such as *Oxypselaphus pusillus*, *Pterostichus commutabilis*, and *Agonum palustre* were found only in original prairies. Conversely, other species such as *Chlaenius platyderus*, *Cyclotrachelus seximpressus*, *Dyschirius globulosus*, and *Amara rubrica* were found primarily in reconstructed prairies (Appendix).

Site-specific differences in carabid community composition between reconstructed and original tallgrass prairies correspond to axis 1 of the nonmetric scaling ordination, explaining 49.4% of the total variance (Figure 1). Observed compositional differences between reconstructed and original tallgrass prairies from the NMS ordination are driven in part by differences in four generalist and one prairie-specialist species. Reconstructed tallgrass prairies were characterized by the generalist species, *Chlaenius platyderus* and *Galerita janus*, and the specialist *Anisodactylus rusticus*. Original tallgrass prairies were characterized by two generalist species, *Poecilus lucublandus* and *Agonum fidele*. Abundances of these species were at least moderately correlated with axis 1 of the NMS ordination ($r^2 > 0.20$). Further comparisons of reconstructed and original tallgrass prairies using indicator value analysis showed an additional nine species found predominately in reconstructed prairies and an additional 12 species found predominately in original tallgrass prairie (Table 2).

Site-specific differences between the reconstructed tallgrass prairies at Effigy Mounds and Anderson Prairie were apparent along axis 2 (explaining 29.6% of the variance), although differences in carabid composition were not apparent between the original sites Hayden Prairie or Chipera Prairie (Figure 1). This pattern was driven by two generalist species found almost exclusively at Effigy Mounds, *Calathus gregarious* and *Pterostichus stygicus*, which were negatively correlated with axis 2 ($r^2 = 0.35$ and 0.21 respectively).

Impact of fire

Although activity density (beetles/trap/day) showed ground beetles were most abundant the summer immediately following a fire (0 year post-fire), and decreased in abundance each subsequent year after a burn (Table 1), this trend combining all sites and years was not significant ($H = 1.34$; d.f. $= 2$; $P = 0.51$). The year immediately following a burn (0 YPF) did have a significantly lower Shannon's diversity index (H') than occurred 1 or

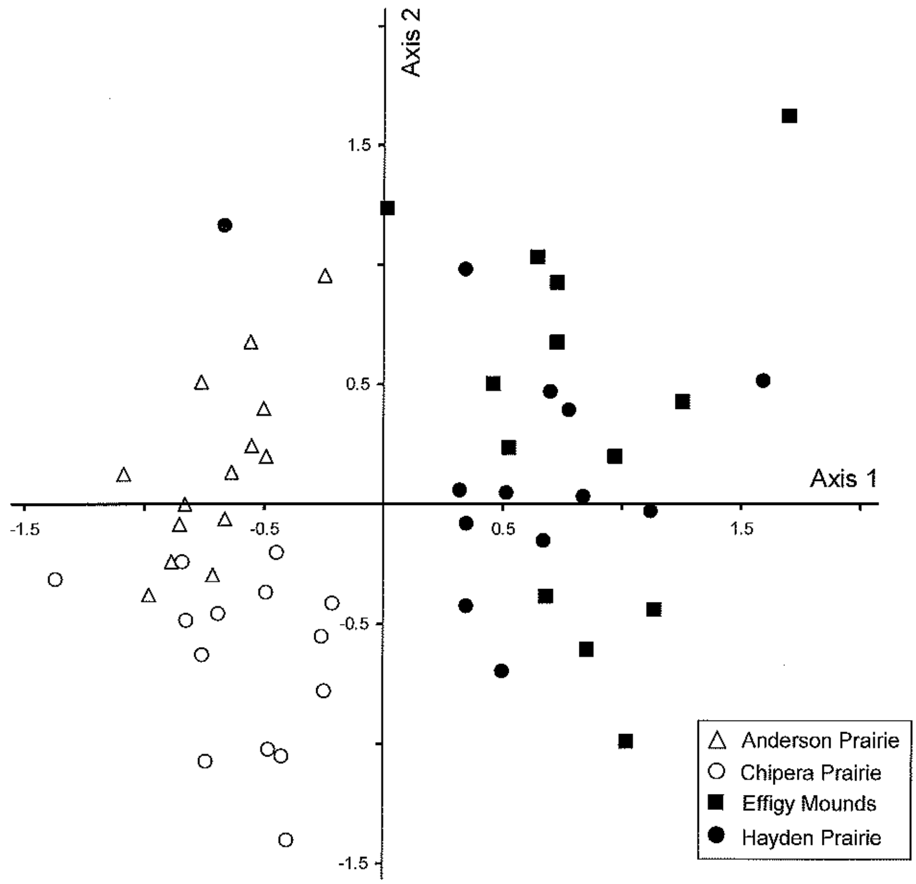

Figure 1. NMS ordination of 54 samples from two original and two reconstructed tallgrass prairies in northeastern Iowa. Solid symbols represent original prairie, while open symbols represent reconstructed prairie.

2 years post-fire (paired *t*-test (Hutcheson 1970); $P < 0.05$).

Although the overall species richness found within burn treatments did not fluctuate from 64 to 65 species, there was a shift in the species composition of beetles present over time following fire. Related to this shift in community composition, there were a number of species that declined in abundance with increased time since burning. In particular, *Chlaenius platyderus*, *Cyclotrachelus sodalis*, *Cyclotrachelus seximpressus*, *Harpalus pensylvanicus*, and *Oxypselaphus pusillus*, were most abundant the year immediately following a burn and declined in subsequent years. In contrast, other species such as *Amara impuncticollis*, *Chlaenius emarginatus*, *Bembidion graciliforme*, *Agonum nutans*, and *Pterostichus femoralis* increased in abundance with increased time since burning. Other species showed variable responses in their abundance to fire over time.

When time since most recent burn was overlaid on the NMS ordination, no consistent pattern in carabid composition was apparent within reconstructed or original tallgrass prairie sites (Figure 2). Likewise, comparisons using indicator value analysis between sites that had been sampled immediately following burning, 1 and 2 years post-fire revealed only three species, *Agonum cupripenne* ($IV = 48.2$, $P = 0.047$), *Amara cupreolata* ($IV = 48$, $P = 0.029$), and *Bembidion versicolor* ($IV = 0.027$, $P = 0.027$), had a significant time since burn effect.

Rarefacted estimates of species richness showed little difference among plots that were sampled immediately following burning, 1 year since burn

Table 2. Habitat preferences (from Larsen et al. 2003), indicator values, and Monte Carlo Simulation mean ± SD of indicator values of carabid beetles collected from original and reconstructed tallgrass prairies in northeastern Iowa

Species	Habitat preference	Indicator value	Monte Carlo simulation mean ± SD of indicator value	*P*-value
Original tallgrass prairie				
Pterostichus commutabilis	Prairie	80.8	28.4 ± 6.44	0.001
Pterostichus femoralis	Prairie	79.5	28 ± 5.61	0.001
Oxypselaphus pusillus	Grassland	50	18.3 ± 5.26	0.001
Agonum gratiosum	Prairie	34.6	13.8 ± 4.55	0.001
Bembidion praticola	Prairie	30.8	12.2 ± 3.78	0.001
Amara impuncticollis	Prairie	49.4	30.3 ± 6.44	0.002
Agonum fidele	Generalist	37.9	17.5 ± 4.68	0.002
Agonum palustre	Generalist	30.8	12.2 ± 4.11	0.002
Poecilus lucublandus	Generalist	69.9	53.3 ± 4.89	0.004
Pterostichus permundus	Generalist	72	54.5 ± 7.32	0.012
Amara cupreolata	Grassland	54.2	34.3 ± 7.47	0.013
Agonum nutans	Prairie	18.2	10.2 ± 3.8	0.024
Carabus maeander	Prairie	19.2	8.7 ± 3.32	0.027
Pterostichus melanarius	Generalist	30.8	18.8 ± 5.44	0.029
Reconstructed tallgrass prairie				
Chlaenius platyderus	Generalist	95.1	42.5 ± 5.29	0.001
Calathus gregarius	Generalist	85.7	51.9 ± 7.82	0.001
Galerita janus	Generalist	80.6	29.9 ± 5.57	0.001
Cyclotrachelus seximpressus	Generalist	79.3	35.3 ± 6.24	0.001
Anisodactylus rusticus	Prairie	52.7	20.9 ± 4.99	0.001
Amara rubrica	Prairie	50	19.2 ± 5.34	0.001
Dicaelus elongatus	Prairie	35.7	14.8 ± 4.48	0.001
Harpalus herbivagus	Generalist	43.1	25.3 ± 5.43	0.006
Dyschirius globulosus	Grassland	28.6	13.7 ± 4.89	0.006
Harpalus pensylvanicus	Agricultural	34.2	20.6 ± 4.96	0.023
Anisodactylus harrisii	Prairie	42.9	29 ± 5.54	0.024
Sphaeroderus stenostomus lecontei	Generalist	17.9	9.1 ± 3.64	0.043

and 2 years since burn (Figure 3). Sites sampled 2 years after burning were different from other burn treatments only as randomizations approach the maximum number of individuals in the 2 years since burn treatment. This likely represents a statistical artifact rather than a biological effect of burning because of the decrease in sampling units used in the randomization procedure necessarily created smaller error terms.

Discussion

Studies of butterflies (Debinski and Babbit 1997) and springtails (Brand and Dunn 1998) show original prairies were more diverse than reconstructed prairies. In our study of ground beetles, Chipera Prairie had the greatest species richness, although Effigy Mounds had the greatest activity density. When both heterogeneity and evenness were evaluated, original tallgrass prairies were more diverse as indicated by greater evenness (J') and a higher diversity index (H') for carabids.

Although tallgrass prairie is dependent upon frequent disturbance such as fire and grazing for maintenance (Samson and Knopf 1996), these disturbances do not destroy the root system and soil structure of original prairies. Disturbances in reconstructed prairies are different from original tallgrass prairies in that they involve a wholesale establishment of a new ecosystem with the growth of a new root system. This establishment phase, that may take as long as decades or centuries (Samson and Knopf 1996), produces significant

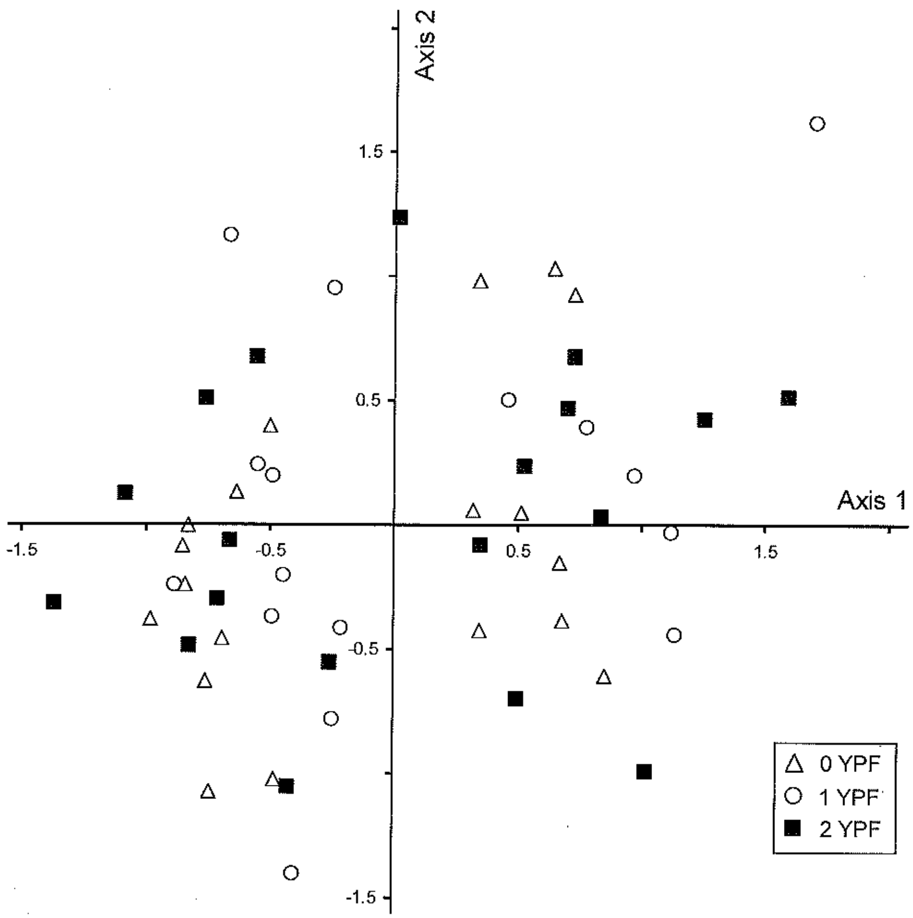

Figure 2. NMS ordination of 54 samples from two original and two reconstructed tallgrass prairies on 3-year burn cycles in northeastern Iowa where 0 YPF = the year immediately following a spring burn, 1 YPF = 1 year after a fire, and 2 YPF = 2 years after a fire.

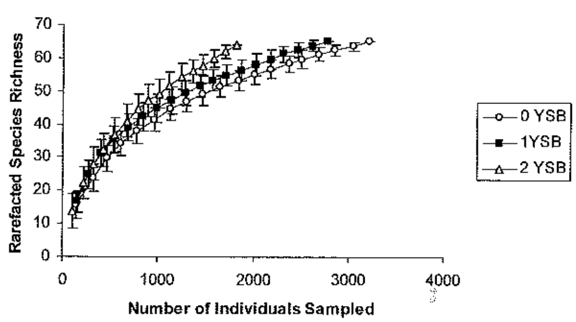

Figure 3. Rarefacted species richness curves of ground beetles sampled from two original and two reconstructed tallgrass prairies on 3-year burn cycles in northeastern Iowa where 0 YSB = the year immediately following a spring burn, 1 YSB = 1 year after a spring fire, and 2 YSB = 2 years after a spring fire.

stress in these reconstructed ecosystems not present in original prairies. Ecosystem stress has been shown to have a negative impact on carabids in prairies (Lavigne and Campion 1978). Both Anderson Prairie and the prairie at Effigy Mounds have much lower plant diversity and continue to become established. This establishment phase seems to provide greater resources for some dominant ground beetle species (resulting in the high abundance of beetles), and may temporarily be offering habitat for more species, many of which may be extirpated from the sites as they stabilize. Hayden Prairie, an original prairie with the lowest species richness of the four sites we sampled, should be stable, but may also be experiencing unusual stress and disturbance. This site has periodically experienced very intense burn treatments with some areas managed for woody vegetation by burning on an annual basis for several years. The affects of intensive burn treatments are thought to have extirpated some species of butterflies such as the regal fritillary, *Speyeria idalia* (Swengel 1996; Swengel and Swengel 2001) and may have negatively impacted ground beetle species richness at Hayden Prairie.

It appears that fire affects ground beetles of tallgrass prairie in a number of ways. Overall ground beetle assemblages were more diverse in tallgrass prairies that had not been burned for several years. However, assemblages of prairie-specialist beetle species were more diverse immediately following fire, and became less diverse with increase in time after a burn. Either way, there is a predictable sequential change in the ground beetle community composition over time following a fire.

The overall ground beetle activity density (a measure of abundance) was greatest the summer immediately following a spring burn. This follows the removal of the leaf litter layer the first season after a prairie fire, and results in the production of a dense grass canopy (Mushinsky and Gibson 1991). Increased productivity of grasses following fire has been associated with increased density and biomass of a number of soil arthropods (Lussenhop 1976; Seastedt et al. 1986). Although fire may cause a reduction in the abundance of beetles immediately after a burn due to direct heat mortality (Holliday 1984), the increased carabid activity may be affected more by alteration of the vegetation architecture than by the fire directly (McCoy 1987). Therefore, we believe the increased activity of beetles collected from plots the year they were burned is due to the removal of the dense leaf litter that rapidly builds up in unburned tallgrass prairies and hinders their movement. As pitfall traps are primarily a measure of ground beetle activity (Greenslade 1964), it is likely that the build-up of leaf litter over time after fire inhibits ground beetle activity.

Previous research on the effects of burning prairies on ground beetles is mixed. Rickard (1974) found no significant difference in the abundance of the carabid *Calosoma luxatum* between burned and unburned stands of shortgrass prairie. Van Amburg et al. (1981) found a greater abundance of adult carabid beetles in burned tallgrass prairie plots than in unburned plots. In contrast, Seastedt et al. (1986) found carabid larvae were more abundant in unburned than burned tallgrass prairie plots.

In forests, it has been shown that fire has little affect on carabid species diversity, but species composition may change (McCullough et al. 1998). Habitat alterations after a fire are largely the result of the removal of standing vegetation and leaf litter (Warren et al. 1987). These alterations result in dramatic changes in the microhabitat experienced by epigaeic insects, such as ground beetles, including increased soil temperatures, increased organic matter, increased air movement, decreased humidity, and decreased soil moisture (Warren et al. 1987).

In addition to microhabitat changes, the responses of ground beetles to fire may be determined by plant species composition and habitat complexity (McCullough et al. 1998). Those species which were most abundant the year immediately after a fire likely are not stimulated by fire, but stimulated by the change in habitat structure and composition after a burn. These beetles may be responding to the presence of less leaf litter, which may allow greater activity, or to the effects of the new plant growth stimulated after a fire, which may provide a greater and more nutritious food source for herbivores, ultimately supporting bigger predator ground beetle populations.

One might generally conclude from the relatively high community diversity among prairie specialists immediately following fire, in contrast with the lower community diversity immediately following fire of the overall ground beetle assemblage, that prairie-specialist ground beetles are preadapted to the occurrence of fire better than non-prairie species. However, it appears that some of the non-prairie species also respond positively to fire. Responses to fire within large taxonomic groups such as ground beetles are often diverse, and individual species respond to fire in different ways (Van Amburg et al. 1981; Reed 1997). For example, species such as *Chlaenius platyderus*, *Cyclotrachelus sodalis*, *C. seximpressus*, *Harpalus pensylvanicus*, and *Oxypselaphus pusillus* respond positively to recently burned prairie conditions by becoming more abundant. Both Harris and Whitcomb (1974) and Holliday (1991) found this same response in forest assemblages of ground beetles, with some species becoming more abundant after fire. However, other species of ground beetles have a negative response to fire, and become more abundant with increased time since burning, and both Harris and Whitcomb (1974) and Holliday (1991) found this response in forest assemblages of ground beetles as well. In this study, species such as *Amara impuncticollis*, *Chlaenius emarginatus*, *Bembidion graciliforme*, *Agonum nutans*, and *Pterostichus femoralis* became more abundant in plots several years after burning and least abundant in plots the year of a fire. These species are likely responding to improved habitat conditions, whether it be the increased abundance of some herbivore feeding on a prairie plant that also does not begin to flourish for several years after a fire, or some abiotic characteristic of the prairie habitat caused by a thicker litter layer with its higher humidity and moderated temperature conditions. It is possible that other species may require an even longer post-fire period before they find conditions suitable for their survival. However, the 3-year burn cycle currently used does not permit these species time to respond.

It appears that the main question of whether to burn or not to burn tallgrass prairie out of concern for prairie-insects does not have a simple answer. The contradictory responses of different species of ground beetles to the widely practiced 3-year burn cycle, along with their varying degrees of habitat specialization (Larsen et al. 2003), clearly indicate a need to diversify the management strategies and techniques we use to promote insect species with strong affinities for the tallgrass prairie ecosystem. Although these and other data (e.g., Panzer 1988) show there is no compelling reason to stop the use of fire in maintaining prairie, there is sufficient evidence that the use of fire as a management tool of tallgrass prairie must be both intentional and prudent.

This study did not compare burned prairie sites with unburned prairie sites. Nekola (2002) recently found that any history of fire on a prairie site had significant impacts on prairie-specialist land snails. It is very possible that prairie-specialist carabids may also respond very differently in unburned prairie sites. The lack of prairie sites in northeastern Iowa with a long-term absence of fire has so far prevented us from examining this possibility. Thus, the management of tallgrass prairie that may best conserve prairie insect biodiversity could involve a constantly shifting mosaic of treatments on the landscape. Although labor intensive, the ideal management plan for tallgrass prairie likely includes burning annually, short-term burn cycles of 3 or 4 years such as the treatments in this study, and even long-term cycles of many years between burns, while also keeping some unburned areas as refugia incorporating mowing, haying, or grazing into the management plan to maintain these areas. From our results with fire, it would appear that each of these strategies could benefit certain groups of prairie-specialist insects and may possibly extirpate others. As suggested by Panzer (1988), maintaining such an ecologically heterogeneous landscape in the tallgrass prairie by varying management strategies to provide the diverse microhabitats appropriate for different species to flourish is important in successfully maintaining prairie insect biodiversity.

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Appendix. Number of ground beetles (Coleoptera: Carabidae) collected from four tallgrass prairies each with 3-year burn cycles in northeastern Iowa from 1994–1998. 0 YPF indicates the year of a spring fire, 1 YPF indicates 1 year after a spring fire, and 2 YPF indicates 2 years after a spring fire. Habitat specialization as categorized by Larsen et al. (2003) is indicated

		Original prairies		Reconstructed prairies		Burn treatment			
Species ID	Habitat	Chipera	Hayden	Anderson	Effigy Mnds	0 YPF	1 YPF	2 YPF	Total
Chlaenius platyderus Chaudoir	Generalist	0	83	753	992	930	524	374	1828
Cyclotrachelus sodalis (LeConte)	Generalist	252	301	391	394	594	482	262	1338
Poecilus lucublandus (Say)	Generalist	307	311	44	167	229	352	248	829
Calathus gregarius (Say)	Generalist	37	100	113	561	299	222	290	811
Pterostichus permundus (Say)	Generalist	271	224	26	100	252	258	111	621
Pterostichus stygicus (Say)	Generalist	77	143	14	230	176	208	80	464
Cyclotrachelus seximpressus (LeConte)	Generalist	4	19	56	242	175	75	71	321
Agonum cupripenne (Say)	Grassland	39	109	31	9	110	64	14	188
Pterostichus femoralis (Kirby)	Prairie	46	76	0	2	24	53	47	124
Amara cupreolata Putzeys	Grassland	34	66	7	5	11	87	14	112
Oxypselaphus pusillus (LeConte)	Grassland	37	65	0	0	58	40	4	102
Amara impuncticollis (Say)	Prairie	61	19	16	5	29	26	46	101
Pterostichus commutabilis (Motschulsky)	Prairie	80	19	0	0	26	55	18	99
Anisodactylus harrisii LeConte	Prairie	11	4	60	11	14	44	28	86
Galerita janus (Fabricius)	Generalist	0	2	51	27	26	31	23	80
Anisodactylus rusticus (Say)	Prairie	1	0	52	2	17	27	11	55
Harpalus herbivagus Say	Generalist	6	1	33	5	16	23	6	45
Amara rubrica Haldeman	Prairie	0	0	40	4	19	17	8	44
Pterostichus melanarius (Illiger)	Generalist	4	30	5	0	16	21	2	39
Agonum palustre Goulet	Generalist	20	15	0	0	26	5	4	35
Bembidion quadrimaculatum oppositum Say	Generalist	5	8	1	21	19	6	10	35
Poecilus chalcites (Say)	Agricultural	12	0	1	19	13	7	12	32
Agonum fidele Casey	Generalist	17	9	0	3	10	9	10	29
Chlaenius emarginatus Say	Generalist	5	0	22	2	5	11	13	29
Harpalus pensylvanicus (DeGeer)	Agricultural	2	3	14	5	14	7	3	24
Dicaelus elongatus Bonelli	Prairie	0	0	19	4	3	12	8	23
Agonum gratiosum (Mannerheim)	Prairie	7	14	0	0	5	5	11	21
Agonum nutans (Say)	Prairie	7	10	0	1	4	2	12	18
Bembidion praticola Lindroth	Prairie	1	15	0	0	5	7	4	16
Dyschirius globulosus (Say)	Grassland	0	0	6	10	1	12	3	16
Cymindis americanus Dejean	Generalist	1	10	2	2	5	7	3	15
Amara aeneopolita Casey	Prairie	13	0	0	0	2	1	10	13
Chlaenius tricolor Dejean	Generalist	3	0	6	2	2	5	4	11
Syntomus americanus (Dejean)	Prairie	1	0	0	9	1	7	2	10
Agonum placidum (Say)	Generalist	1	1	6	1	5	4	0	9
Anisodactylus ovularis (Casey)	Prairie	1	0	8	0	4	4	1	9
Bembidion versicolor (LeConte)	Agricultural	0	8	1	0	9	0	0	9

Elaphropus anceps (LeConte)	Agricultural	3	1	0	5	5	1	3	9
Amara angustata (Say)	Prairie	2	0	1	5	0	7	1	8
Carabus maeander Fischer von Waldheim	Prairie	0	7	0	0	4	3	0	7
Sphaeroderus stenostomus lecontei Dejean	Generalist	0	0	2	5	5	1	1	7
Badister notatus Haldeman	Generalist	4	0	1	1	2	2	2	6
Chlaenius purpuricollis Randall	Prairie	0	0	0	6	3	1	2	6
Dicaelus sculptilus sculptilus Say	Prairie	3	2	1	0	1	2	3	6
Notiophilus aeneus (Herbst)	Generalist	0	0	2	3	3	0	2	5
Pterostichus mutus (Say)	Woodland	0	0	0	5	0	3	2	5
Amphasia sericea (Harris)	Prairie	2	0	1	1	1	1	2	4
Bembidion graciliforme Hayward	Grassland	3	1	0	0	0	1	3	4
Bembidion rapidum (LeConte)	Agricultural	2	1	1	0	1	2	1	4
Synuchus impunctatus (Say)	Generalist	0	0	0	4	3	0	1	4
Calleida punctata LeConte	Prairie	0	0	3	0	1	1	1	3
Chlaenius amoenus Dejean	Prairie	0	0	0	3	3	0	0	3
Chlaenius pusillus Say	Prairie	3	0	0	0	1	0	2	3
Dicaelus purpuratus splendidus Say	Prairie	0	0	0	3	0	2	1	3
Elaphropus granarius (Dejean)	Prairie	3	0	0	0	2	1	0	3
Pterostichus luctuosus (Dejean)	Prairie	1	2	0	0	0	3	0	3
Amara obesa (Say)	Agricultural	1	0	1	0	0	1	1	2
Anisodactylus sanctaecrucis (Fabricius)	Agricultural	1	0	1	0	2	0	0	2
Calleida decora (Fabricius)	Prairie	2	0	0	0	0	0	2	2
Cymindis neglectus Haldeman	Prairie	0	2	0	0	1	0	1	2
Harpalus caliginosus (Fabricius)	Agricultural	1	0	0	1	2	0	0	2
Harpalus compar LeConte	Prairie	1	0	1	0	1	1	0	2
Harpalus somnulentus Dejean	Grassland	1	0	1	0	1	1	0	2
Hartonymus hoodi Casey	Prairie	0	2	0	0	0	2	0	2
Panagaeus fasciatus Say	Prairie	0	0	0	2	1	0	1	2
Platynus decentis (Say)	Woodland	0	0	0	2	1	0	1	2
Scarites quadriceps Chaudoir	Grassland	1	1	0	0	1	1	0	2
Selenophorus opalinus (LeConte)	Agricultural	0	0	1	1	0	0	2	2
Stenolophus ochropezus (Say)	Prairie	2	0	0	0	1	1	0	2
Acupalpus carus (LeConte)	Prairie	1	0	0	0	0	1	0	1
Acupalpus partiarius (Say)	Grassland	0	0	1	0	0	0	1	1
Anisodactylus agricola (Say)	Generalist	0	0	0	1	0	0	1	1
Apenes lucidulus (Dejean)	Generalist	0	0	0	1	0	0	1	1
Brachinus ovipennis LeConte	Woodland	0	0	0	1	1	0	0	1
Bradycellus semipubescens Lindroth	Prairie	1	0	0	0	0	1	0	1
Calosoma calidum (Fabricius)	Prairie	0	1	0	0	1	0	0	1
Carabus goryi Dejean	Woodland	0	0	0	1	0	0	1	1
Chlaenius sericeus (Forster)	Grassland	1	0	0	0	0	1	0	1
Chlaenius tomentosus (Say)	Prairie	0	0	1	0	0	1	0	1
Dicaelus politus Dejean	Woodland	0	0	0	1	1	0	0	1
Diplocheila obtusa (LeConte)	Prairie	1	0	0	0	0	0	1	1

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Appendix Continued

Species ID	Habitat	Original prairies		Reconstructed prairies		Burn treatment			Total
		Chipera	Hayden	Anderson	Effigy Mnds	0 YPF	1 YPF	2 YPF	
Discoderus parallelus (Haldeman)	Prairie	1	0	0	0	0	0	1	1
Harpalus erythropus Dejean	Prairie	1	0	0	0	1	0	0	1
Loricera pilicornis (Fabricius)	Agricultural	1	0	0	0	0	1	0	1
Notiobia terminata (Say)	Prairie	0	0	1	0	0	0	1	1
Patrobus longicornis (Say)	Generalist	1	0	0	0	0	1	0	1
Pterostichus adstrictus Eschscholtz	Woodland	0	0	0	1	1	0	0	1
Pterostichus corvinus (Dejean)	Prairie	1	0	0	0	0	1	0	1
Stenolophus conjunctus (Say)	Grassland	0	0	1	0	0	1	0	1
Stenolophus rotundicollis (Haldeman)	Grassland	0	0	0	1	0	0	1	1

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