Conservation Value of Roadside Prairie Restoration to Butterfly Communities

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Abstract: *It has been suggested that restoration of roadsides to native habitat can benefit wildlife by adding habitat and restoring connectivity between fragmented reserves. In Iowa, which has one of the highest road densities in the United States, roadside vegetation has traditionally been managed to maintain a monoculture of exotic grass. Recently, several Iowa counties have begun integrated roadside vegetation management, a program that both restores roadsides to native prairie vegetation and restricts the use of herbicides and mowing. We evaluated the effect of this management regime on butterfly populations along central Iowa roadsides. We surveyed 12 separate prairie roadside areas, comparing the abundance and species richness of disturbance-tolerant and habitat-sensitive butterflies in roadside prairies with those of nearby roadsides dominated by either weeds (primarily non-native legumes) or non-native grasses. We found that management of roadsides profoundly affected the butterfly community. Species richness of habitat-sensitive butterflies showed a two-fold increase in prairie compared with grassy and weedy roadsides ($p < 0.0001$), and abundance increased almost five times more on the prairie than on grassy roadsides ($p < 0.02$). Species richness of disturbance-tolerant butterflies showed no response to roadside management, although abundance was slightly higher in weedy and prairie roadsides than on grassy roadsides ($p < 0.01$). Of all habitat variables explored, the species richness of plants in flower showed the strongest effect on mean richness and abundance of both disturbance-tolerant and habitat-sensitive butterfly species. Although there were higher concentrations of road-killed butterflies near weedy and prairie roadsides than on grassy roadsides, relative numbers indicated that mortality risk was more than twice as high on grassy roadsides ($p < 0.0001$). Tracking studies showed that butterflies were less likely to exit prairie roadsides, indicating that their mortality rates may be lower and offering preliminary evidence that roadsides have the potential to be used as corridors. Overall, our results indicate that roadside restoration benefits butterfly populations. More detailed demographic data are necessary, however, to explore the possibility that roadsides are acting as sink habitat for some habitat-restricted species.*

Valor de la Conservación de la Restauración de Praderas Ruderales para Comunidades de Mariposas

Resumen: *Se ha sugerido que la restauración del hábitat nativo de los bordes de caminos puede ser benéfica para la vida silvestre al añadir hábitat y restaurar la conectividad entre reservas fragmentadas. En Iowa, con una de las densidades de carreteras más alta en los Estados Unidos, la vegetación ruderal tradicionalmente se ha manejado para mantener un monocultivo de pasto exótico. Recientemente, varios condados en Iowa han iniciado un programa de manejo integrado de la vegetación ruderal enfocado tanto a restaurar la vegetación de pradera nativa en los bordes de caminos como a restringir el uso de herbicidas y podas. Evaluamos el efecto de este régimen de manejo sobre poblaciones de mariposas a lo largo de carreteras en Iowa central. Examinamos 12 áreas de praderas ruderales separadas y comparamos la abundancia y la riqueza de especies de mariposas tolerantes a la perturbación y sensibles al hábitat en praderas ruderales dominadas por hierbas (principalmente leguminosas introducidas) o por pastos exóticos. El manejo de bordes de caminos afectó significativamente a la comunidad de mariposas. La riqueza de especies de mariposas sensibles al hábitat fue el doble en praderas que en bordes dominados por hierbas ($p < 0.0001$) y la abundancia fue casi cinco veces mayor en praderas comparadas con bordes con pastos ($p < 0.02$). La riqueza de especies de mari-*

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posas tolerantes a la perturbación no mostró respuesta al manejo de bordes de camino, aunque la abundancia fue ligeramente mayor en bordes con hierbas y con praderas comparados con bordes con pastos ($p < 0.01$*). De las variables del hábitat analizadas, la riqueza de especies de plantas con flor tuvo el mayor efecto sobre la riqueza y abundancia promedio de especies de mariposas tanto las tolerantes a la perturbación como las sensibles al hábitat. Aunque hubo mayor concentración de mariposas muertas por colisión cerca de bordes con hierbas y con praderas en comparación con bordes con pastos, los valores relativos indicaron que el riesgo de morir fue más del doble en los bordes con pastos (*$p < 0.0001$*). Estudios de localización mostraron que la probabilidad de que las mariposas salgan de los bordes con pradera es baja, lo que indica que las tasas de mortalidad pueden ser menores y ofrece evidencia preliminar de que los bordes de camino tienen el potencial de ser utilizados como corredores. En general, nuestros resultados indican que la restauración de bordes es benéfica para las poblaciones de mariposas. Sin embargo, se requieren datos demográficos más detallados para explorar la posibilidad de que los bordes de camino actúan como hábitat receptor para algunas especies de hábitat restringido.*

Introduction

Since the development of island biogeography theory (MacArthur & Wilson 1963), the ability of an increasingly fragmented system of natural reserves to support viable populations or retain species diversity for extended periods has been questioned (Diamond 1975). The problem is not just loss of habitat but isolation, which puts populations at greater risk of local extinction (Brown & Kodric-Brown 1977; Lande 1988; Saccheri et al. 1998). Roadside vegetation, which occupies approximately 8 million ha of land (Adams & Geis 1983) bordering nearly 6.4 million km of road in the United States (U.S. Department of Transportation 1998), has been suggested as a resource to both add habitat and restore connectivity between fragmented reserves (Bennett 1991; Spellerberg 1998).

Although the presence of roads is often considered to have negative effects on wildlife, the amount of land dedicated to roadside vegetation is substantial. For many regions where habitat loss has been severe and human presence is well established, roadside restoration offers an opportunity for extensive additions to the regional system of reserves. Therefore, information on the effects of roadsides on wildlife is crucial. Recently, many states have instituted policies to restore roadsides to native vegetation, often for the primary purpose of weed and erosion control (Henderson 2000). Although several studies have documented the use of roadsides by wildlife, we were not able to find a single study that examined the effect on any animal species of restoring roadsides to native habitat. The purpose of our study was to explore the conservation value of restored and native prairie roadsides to butterflies in central Iowa.

Roadsides as Additional Habitat

Several small-bodied animals, including birds (Laursen 1981; Arnold & Weeldenburg 1990; Cale 1990; Warner et al.1992; Camp & Best 1994), small mammals (Getz et al. 1978; Woodward 1990; Clark et al. 1996; Kirsch 1997), insects (Munguira & Thomas 1992; DeMers 1993; Vermeulen 1993; Eversham & Telfer 1994; Samways et al. 1997), snails (Baur & Baur 1992), and reptiles and amphibians (Way 1977; Seabrook & Dettmann 1996) use roadside vegetation as habitat. Most of the species found in this habitat are common (Bennett 1991), however, and the possibility that roadsides act as population sinks (Pulliam 1988) is rarely explored (Eversham & Telfer 1994). Source-sink dynamics in roadsides may have serious implications for the conservation of species on a regional scale because increasing the amount of sink habitat relative to source habitat in the landscape has the potential to decrease the overall population size, even as the amount of total habitat increases (Danielson 1992).

There are several negative consequences of using roadside vegetation as habitat. Approximately one million vertebrates are killed every day by cars in the United States (Lalo 1987), although some studies suggest that mortality from vehicles is only a minor contributor to overall death rates (Bennett 1991). Little research has focused on invertebrates, but one study found road mortality for butterflies to be high, yet minor compared with other causes (Munguira & Thomas 1992). Roads may be a barrier for dispersal (Mader 1984; Merriam et al. 1989), and culverts have been used to increase permeability (Yanes et al. 1995). Roadsides are also subject to contamination from passing cars, with high concentrations of several heavy metals being found in soil, vegetation, earthworms, and small mammals (Scanlon 1987).

Roadsides as Corridors or Stepping Stones between Habitat

The idea that corridors or "stepping stones" between habitat "islands" can decrease isolation of fragmented habitat has become extremely popular (Noss & Harris 1986; Noss 1987; Mann & Plummer 1993). Stepping stones provide small habitat patches between larger reserves that decrease the average distance between patches and therefore may decrease isolation. Habitat corridors are meant to directly connect habitat, but the idea remains controversial (Simberloff et al. 1992; Rosenberg et al. 1997).

One of the main criticisms of corridors is that the high cost of creating them could be better spent on other conservation priorities (Mann & Plummer 1993). Roadside vegetation is a permanent part of the landscape, however, and is already being actively managed. If corridors are a useful tool for conservation, roadsides may offer a source of corridor habitat that does not take resources away from other programs. Movements of organisms along roadside vegetation have been documented for several species (Suckling 1984; Arnold & Weeldenburg 1990; Bennett 1990; Vermeulen 1994). Roadsides have also been implicated as a factor in range expansion for mice (Getz et al. 1978) and ants (DeMers 1993). As with most proposed corridor systems, however, there is no direct evidence that roadsides accomplish the main goal of corridors: to reduce isolation of populations in larger habitat patches or reserves.

Prairies and Roadside Management in Iowa

Prairie is one of the most endangered ecosystems in the United States (Smith 1981). The tallgrass prairie has suffered the most severe decline, with a total loss of area estimated from 82% to 99%, more than any other major ecosystem in North America. Iowa is one of the most severely affected states, with <0.01% of the original tallgrass prairie remaining (Sampson & Knopf 1994). There are an estimated 179,000 km of roads in Iowa encompassing 243,000 ha of land (Flynn 1994). Traditionally, these roadsides were managed with aggressive mowing and spraying techniques to control invasive weeds. Recently, however, several Iowa counties have begun integrated roadside vegetation management (IRVM) programs that involve restoring roadsides to native vegetation and restricting the use of herbicides (Cramer 1991; Flynn 1994). Although IRVM is generally implemented for the purpose of weed and erosion control, another explicit goal of the program is to benefit wildlife (Cramer 1991). The uneven implementation of IRVM, both within and among counties, has resulted in a great deal of variation in the quality of roadsides in Iowa. Most roadside vegetation in central Iowa remains a uniform monoculture of exotic, cool-season grasses (primarily *Bromus* spp.), but many areas now have thickets of non-native flowers, and a small but growing number of roadsides are now dominated by native prairie grasses and wildflowers.

Status of Grassland Butterflies in Iowa

The health of an ecological system can often be gauged by its assemblage of species. Butterflies are a particularly useful group in this regard because they display a wide range of tolerances to habitat disturbance, are relatively well known, and their host-plant relationships are well described (Scott 1986). Many of the plants included in native seeding projects along Iowa roadsides serve as larval host plants or nectar resources for several species of butterfly.

The Iowa Natural Resource Commission lists 2 species of Iowa butterflies as endangered, 5 as threatened, and 25 as species of special concern. Schlict and Orwig (1998) have expanded this list to include 8 critically endangered species (known in only one to five sites), 15 endangered, and 21 threatened. They also list one butterfly, the Dakota skipper (*Hesperia dacotae*), a prairie specialist, as extinct in Iowa. Of the 44 species included on their list, 21 are considered prairie specialists.

Objectives

The goal of this study was to assess the effects of IRVM practices on butterfly communities. Our specific objectives were to (1) determine how IRVM affects butterfly communities, (2) compare butterfly communities in native and restored prairie roadsides, (3) compare butterfly communities in prairie roadsides with those in native, nonroadside prairie remnants, and (4) estimate the effect of butterfly mortality due to collisions with cars in different roadside habitats. We surveyed butterflies that overwinter in Iowa and that are associated with open habitat. Species that don't overwinter in Iowa move great distances during their lifetime and are not as strongly tied to local habitat patches. We divided species into those that are tolerant of highly disturbed habitat (disturbance-tolerant) and those that are not (habitat-sensitive). By focusing on species richness and the abundance of these two groups of butterflies, we show how management techniques may increase the value of roadside vegetation for butterfly populations.

Methods

Site Selection and Description

Each study area was located near a restored or native (never plowed) roadside prairie in central Iowa. We selected prairie roadside locations based on information gathered from county roadside managers in the four counties included in the study. The study included all high-quality restored roadsides that were at least 0.5 km long and well established. The length of restored roadsides varied considerably, ranging from a half kilometer to several kilometers. We also included all known native prairie roadsides located within the study area. In total, 12 study areas were established (Fig. 1), 4 areas with native roadsides and 8 with restored roadsides.

In all areas, each 160-m section of roadside vegetation within 1.6 km of the roadside prairie was classified as weedy (>20% non-native legumes), grassy (<5% forb cover and dominated by non-native grass, primarily *Bromus* sp.), or prairie (dominated by native prairie grasses

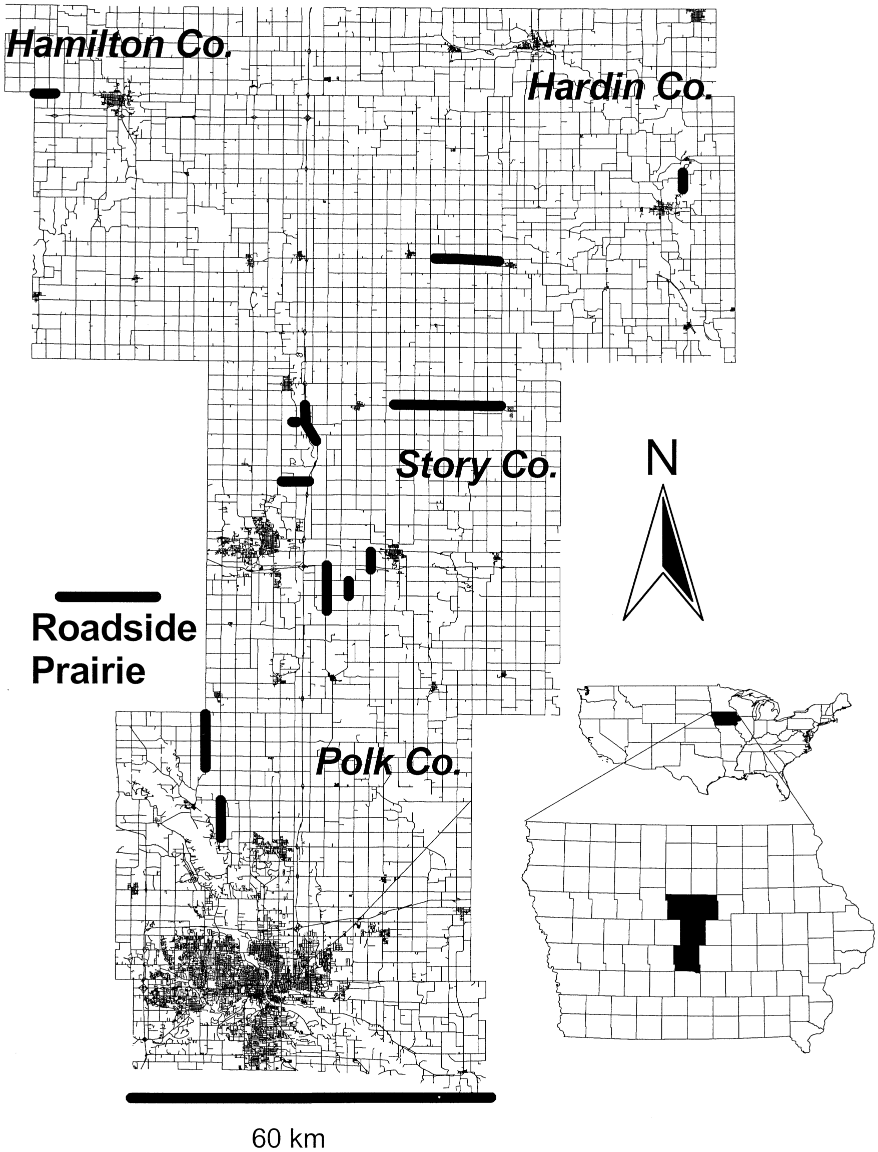

Figure 1. Map of study areas showing locations of roadside prairie restoration in four counties in central Iowa (U.S.).

and forbs). Weedy roadsides were restricted to those dominated by non-native legumes because their presence is tolerated by roadside managers. Other weeds, such as Canada thistle (*Cirsium arvense*), are considered nuisances and are subjected to intensive spot spraying or mowing (Cramer 1991).

Three plots were established within each roadside class (grassy, weedy, and prairie) within each area. Plot locations were randomly selected among plots that met the following requirements: at least 50 m away from all other plots, roadside at least 6 m wide and not dominated by wetland vegetation, grassy plots never adjacent to weedy plots, and both grassy and weedy plots at least 500 m from prairie plots to avoid spillover of individuals. All roadsides were bordered by row crops. Depending on the prevalence of grassy and weedy roadsides, some areas were missing either one or two plots. Of the 12 study areas (Fig. 1), 7 were complete and 5 were missing either 1 or 2 plots, resulting in a total of 101 study plots. The plots were located along a wide range of roads, from county gravel roads to interstate highways. Each survey plot was 50 m long and 5 m wide. To examine the differences between native prairie reserves and prairie roadsides, we established three randomly placed 50 $\times$ 5 m plots in four native prairie remnants ranging in size from 2 to 16 ha.

Butterfly and Flower Surveys

Three rounds of surveys, each lasting approximately 3 weeks, were conducted from 22 June through 22 August 1998. During the three rounds, each plot was visited three times, so over the course of the summer most plots were sampled nine times. Exceptions were plots that were flooded or recently mowed. Within each area and round, the order in which surveys were conducted was random. Surveys were conducted between 1000 and 1830 hours when the temperature was between 21° and 35° C and sustained winds were below 16 km/hour. On partly cloudy days, surveys were started only when the sun was shining. Each transect was walked for 5 minutes in one direction; timers were stopped when a butterfly was seen. We conducted a total of 953 surveys over the summer.

During each survey, we counted all butterflies (including skippers) that overwinter in Iowa. Butterflies were identified on the wing if possible, otherwise they were netted. Due to the difficulty of identification in the field, *Colias eurytheme* and *C. philodice* were identified to genus and were considered one species throughout the analysis. Both species are common in Iowa and have similar host-plant specificity and disturbance tolerance (Scott 1986). The percent cover of flowers was estimated once during each round to determine the amount of nectar available to butterflies. Within each plot, six 5 × 1 m transects perpendicular to the butterfly transect were placed every 10 m. These 5 × 1 m transects were then broken down into 1 × 1 m sections. A visual estimate of the percent cover of the flowers of each species was made in each of the 30 1 × 1 m plots. The values were then averaged over the entire plot. Although somewhat subjective, this allowed us to obtain a relative measure of flower cover between plots in a manner that was not prohibitively time consuming.

Mortality Surveys

Mortality data were collected in two ways: observing movement behavior near roads and collecting dead butterflies along roadsides. Behavioral butterfly surveys were conducted only during the second round of sampling. Butterflies in the plot were observed for successful road crossings. A 50 × 2 m transect parallel to the study plots described previously, but with half the width of the plot extending into the road, was used for observation.

Each entry of a butterfly into the plot was classified either as an approach (butterfly entered the 1 m of vegetation but did not continue into the road); an attempt (entered plot, flew across part of the road or shoulder, but then turned back); or a cross (entered the plot from the vegetation and crossed the road). Individuals that crossed were further classified as to whether they succeeded in crossing the road or were struck and killed by a vehicle. Butterflies that flew perpendicular to the road were not used in the analysis. Seventy-five behavioral surveys were conducted.

Roadkill surveys were conducted after all regular butterfly surveys during the last two rounds. Transects in these surveys were parallel to each survey plot along both sides of the road's edge where the vegetation met the pavement or gravel. Again, only species that overwinter in Iowa were counted in the survey. Butterflies struck by cars rarely stuck in grills; in general, they became caught at the grass' edge within 25 m from the point of collision (personal observation). We conducted a total of 212 mortality surveys.

Data Analysis

For the community analysis, all butterflies observed were classified either as disturbance-tolerant or habitat-sensitive, based on data collected by the Iowa Lepidopterist Project (Nekola 1995) and habitat classifications given by Scott (1986). These categories were relative to the extreme level of habitat disturbance that occurs throughout Iowa, so species classified as disturbance-tolerant were those that survive well on farmland or within cities and towns. Species classified as habitat-sensitive were associated with areas that didn't receive high levels of continual human disturbance, but there was no requirement that they rely on native habitat. To calculate abundance, the mean for each of the three surveys conducted within one round was used to arrive at one value for each plot in each area. Plots of a single type within an area were considered subsamples and were averaged together to arrive at a single mean for grassy, weedy, and prairie roadsides for each of the 12 study areas. We used the same procedure for species richness but used the cumulative richness over three surveys before averaging values from different plots together within a study area. This procedure eliminated the problem of pseudoreplication (Hurlbert 1984).

For most analyses, the response variables examined were the number of species (species richness) and abundance for both disturbance-tolerant and habitat-sensitive butterflies. An analysis of variance (ANOVA) (PROC GLM; SAS Institute 1990) was used to compare abundance and species richness in grassy, weedy, and prairie roadsides. For the main analysis, restored and native roadsides were considered one type (prairie roadsides) because each of the 12 study areas acted as a "replicate" where all three roadside types were present, but no areas had both restored and native prairie roadsides. We used a separate *t* test to look for differences between native and restored roadsides and between prairie roadsides and nonroadside prairie remnants. We used ANOVA to test the effect of restoration size on butterfly abundance and richness using only prairie roadside plots. To examine this variable, we classified all roadsides as either small (<800 m in length), medium (800–5000 m), or large (>5000 m). We used linear regression to test for effects of flower cover and richness, but we analyzed each survey separately because flower abundance and diversity varied within areas and between rounds.

For the mortality survey, the number of individuals found dead along roads was divided by the number counted during the normal butterfly survey to obtain relative mortality rates. We used ANOVA to test for differ-

Table 1. Habitat category and total number of each species of nonmigratory butterflies observed during surveys of roadsides and prairies in central Iowa in 1998.

Common name	*Scientific name*	*Habitat category*[a]	*Number*
Sulpher	*Colias* sp.	disturbance-tolerant	1124
Eastern-tailed blue	*Everes comyntas*	disturbance-tolerant	1124
Pearl crescent	*Phyciodes tharos*	habitat-sensitive	710
Least skipperling	*Ancyloxypha numitor*	habitat-sensitive	170
Black swallowtail	*Papilio polyxenes*	disturbance-tolerant	145
Deleware skipper	*Atrytone logan*	habitat-sensitive	133
Common sootywing	*Pholisora catullus*	disturbance-tolerant	126
Cabbage white[b]	*Pieris rapae*	disturbance-tolerant	103
Common wood nymph	*Cercyonis pegala*	habitat-sensitive	77
Great spangled fritillary	*Speyeria cybele*	habitat-sensitive	48
Great grey copper	*Lycaena xanthoides*	habitat-sensitive	40
Red admiral	*Vanessa atalanta*	disturbance-tolerant	16
Viceroy	*Limenitis archippus*	habitat-sensitive	15
Yellow-patch skipper	*Polites peckius*	habitat-sensitive	14
Tiger swallowtail	*Papilio glaucus*	habitat-sensitive	13
Checkered skipper	*Pyrgus communis*	disturbance-tolerant	11
Two-spotted skipper	*Euphyes bimacula*	habitat-sensitive	10
Regal fritillary[c]	*Speyeria idalia*	habitat-sensitive	8
Tawny-edged skipper	*Polites themistocles*	habitat-sensitive	7
Gorgone checkerspot	*Chlosyne gorgone*	habitat-sensitive	5
Checkered white	*Pieris protodice*	disturbance-tolerant	2
Silver-spotted skipper	*Epargyreus clarus*	habitat-sensitive	2
American painted lady	*Vanessa virginiensis*	disturbance-tolerant	2
Dion skipper	*Euphys dione*	habitat-sensitive	1

[a]Habitat categories are based on response to the high level of disturbance in Iowa. Those categorized as disturbance-tolerant do well in farms and cities; those categorized as habitat-sensitive are restricted to less-disturbed (though not necessarily native) habitat.
[b]Not native to the United States.
[c]Prairie specialist.

ences in relative mortality based on plot type and road-surface type (paved or gravel). For the road-surface type we used only weedy roadsides because there was a relatively even number of paved and gravel roads ($n = 13$ and 16, respectively). Grassy roads were predominantly gravel and prairie roads were predominantly paved. In general, road surface can be a surrogate for traffic volume, gravel roads having low volume and paved roads having high volume. For the behavior study, we used logistic regression (PROC LOGISTIC; SAS Institute 1990) to determine the effect of plot and road-surface type on the probability that an individual approaching the road would cross.

Results

We identified a total of 3906 butterflies of 25 species during 953 surveys over the course of the summer (Table 1). There was no significant interaction of survey round with roadside type for any of the response variables examined; therefore, data from all rounds were combined for analysis.

More habitat-sensitive individuals were observed in prairie roadsides than in grassy and weedy roadsides (Fig. 2a), although only grassy and prairie roadsides were significantly different ($p < 0.02$). Disturbance-tolerant spe-

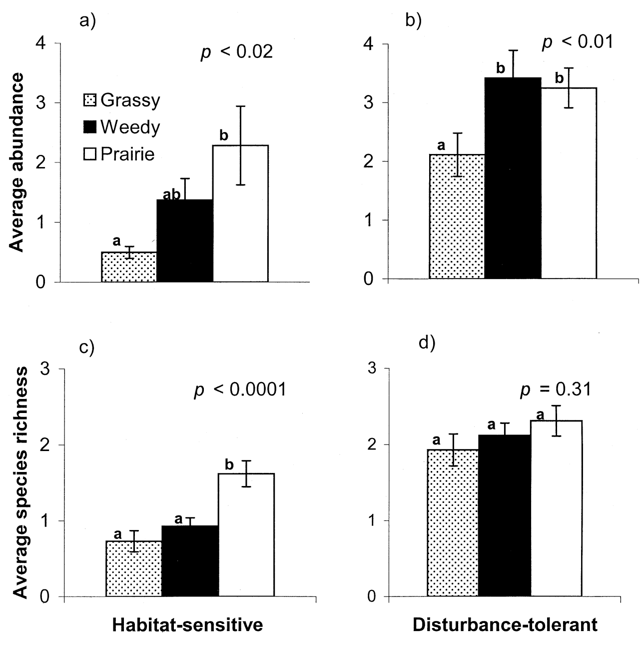

Figure 2. Average abundance of (a) habitat-sensitive and (b) disturbance-tolerant butterflies and species richness of (c) habitat-sensitive and (d) disturbance-tolerant butterflies in grassy, weedy, and prairie roadsides in central Iowa. Values are based on an analysis of variance. Different letters indicate means that are significantly different.

cies had approximately two-thirds the number of individuals in grassy roadsides compared to weedy and prairie roadsides; there was no difference between weedy and prairie roadsides (Fig. 2b). There were about twice as many habitat-sensitive species in prairie roadsides than in grassy and weedy roadsides (Fig. 2c). Species richness of disturbance-tolerant species did not differ among the three roadside types (Fig. 2d).

There were no significant differences in species richness or overall abundance between restored and native prairie roadsides for both habitat-sensitive and disturbance-tolerant species (Table 2). Only richness of habitat-sensitive species showed a trend, with more species in native than weedy roadsides. Although this result was not significant ($p = 0.13$), there were only four native roadsides, so there was little statistical power to detect a difference. Neither richness nor abundance of habitat-sensitive species differed between prairie roadsides (native and restored combined) and nonroadside prairie remnants (Table 2). Disturbance-tolerant species had almost twice the abundance in roadsides than in prairie remnants (Table 2; $p < 0.05$) and a marginally higher richness in roadsides (Table 2; $p = 0.09$).

The number of species in flower explained little of the overall variation in butterfly numbers ($r^2 = 0.07$, $p < 0.0001$). There was a clear trend, however, of increase in mean butterfly richness and abundance as flower richness increased; this trend was observed within all three roadside types (Fig. 3). In contrast, percent cover of flowers showed no significant effect on either richness or abundance. There was a marginally significant increase in richness of habitat-sensitive species as restoration size increased (Fig. 4c, $p = 0.08$). Restoration size had no effect on disturbance-tolerant butterflies (Fig. 4b & 4d).

Mortality Study

The survey of road-killed butterflies showed that although the absolute number of butterflies found was lowest near grassy roadsides, the relative mortality rate along grassy roadsides may actually have been higher (Fig. 5a). In addition, relative mortality was about nine times higher on paved than on gravel roads (Fig. 5b). A significantly higher percentage of individuals crossed roads with grassy and weedy roadsides than those with prairie roadsides (49, 44, and 23% respectively, $p < 0.001$). There was no effect of road surface on road-crossing behavior. We observed 108 butterflies cross the road and only 3 were hit by a vehicle, for an overall mortality risk of 2.8%. Mortality risk was higher for paved than gravel roads (7% and 1%, respectively). The low number of individuals hit did not allow for a statistical analysis of mortality risk for any of the factors examined.

Discussion

Our results show that management of roadside vegetation has a profound effect on butterfly communities. The prevalence of grassy, weedy, and prairie roadsides is a direct result of the roadside management practices of each county within Iowa. Both habitat-sensitive and disturbance-tolerant species showed an increase in weedy and prairie roadsides that was not seen in grassy roadsides. Habitat-sensitive species showed a positive response to active prairie restoration, with higher overall abundance and species richness in prairie than in weedy roadsides, indicating that at least some individuals responded to restoration in roadsides. Disturbance-tolerant species showed increased abundance in response to IRVM techniques, but there was no increase associated with active prairie restoration.

Roadsides as Additional Habitat

Butterflies have complex life cycles and need different resources at each stage of development. For roadsides to truly add habitat for a particular species, the habitat must either provide resources necessary for all life stages or be within reasonable distance of required resources. In addition, increases in fecundity must outweigh possible increases in mortality. In other words, habitat should be able to support a population without depending on immigrants from other areas (Pulliam 1988). Under these criteria, it is difficult to rigorously measure the value of habitat to any particular species without collecting de-

Table 2. Comparison of the mean abundance and species richness of both habitat-sensitive and disturbance-tolerant butterflies in different types of prairie habitat in central Iowa.[a]

		Roadside comparison					Prairie comparison				
Dependent variable	*Habitat category*	*restored*	*native*	*df*	t	p > t	*roadside*	*remnant*	*df*	t	p > t
Abundance	habitat-sensitive	2.43 (0.99)	1.99 (0.39)	10	0.305	0.767	2.28 (0.66)	1.59 (0.17)	12.3	1.02	0.327
	disturbance-tolerant	3.24 (0.47)	3.26 (0.53)	10	0.033	0.975	3.25 (0.34)[b]	1.75 (0.51)[b]	14[b]	2.239[b]	0.042[b]
Species richness	habitat-sensitive	1.43 (0.18)	2.00 (0.33)	10	1.649	0.13	1.62 (0.17)	1.70 (0.12)	14	0.235	0.818
	disturbance-tolerant	2.16 (0.27)	2.60 (0.20)	10	1.039	0.323	2.31 (0.20)	1.61 (0.27)	14	1.828	0.089

[a]*Comparisons were made between restored and native prairie roadsides (roadside comparison) and between prairie roadsides and nonroadside prairie remnants (prairie comparison) with a t test. Standard errors are shown in parentheses after mean values.*
[b]*Significance at the 0.05 level.*

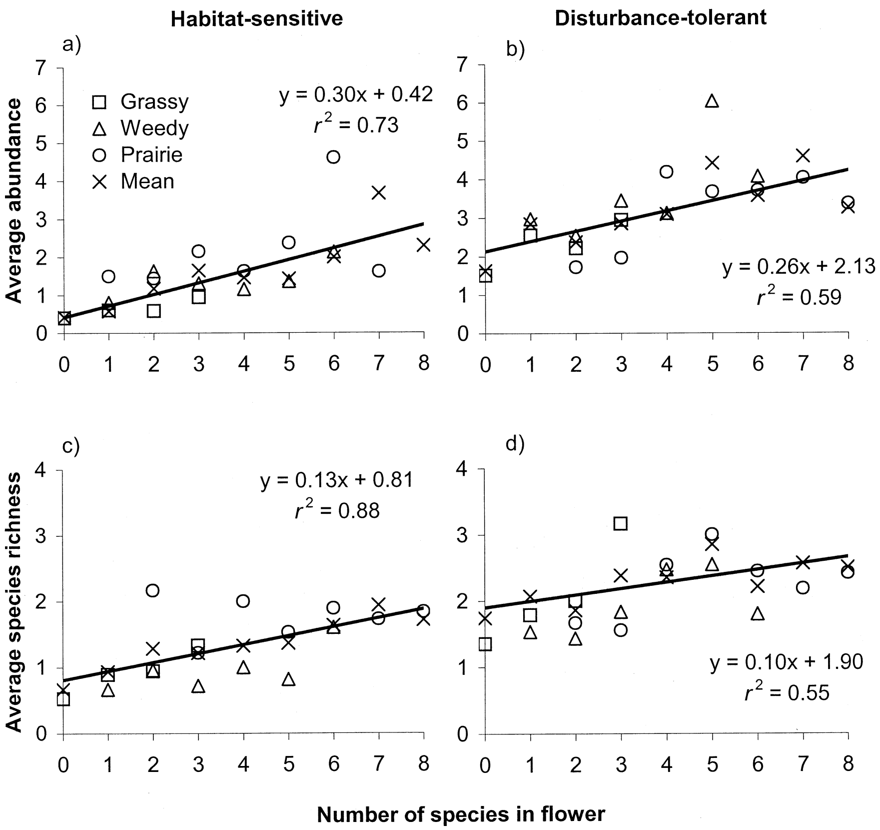

Figure 3. Average abundance of (a) habitat-sensitive and (b) disturbance-tolerant butterflies and species richness of (c) habitat-sensitive and (d) disturbance-tolerant butterflies as the number of species in flower increased in roadside plots in central Iowa. Regressions were performed on mean values, but values for roadsides classified as grassy, weedy, and prairie are also illustrated.

mographic data (Van Horne 1983). The greater density and richness in both weedy and prairie roadsides, however, offers preliminary evidence that IRVM may add habitat for some butterfly species.

By increasing the diversity and amount of forbs in roadsides through direct planting and decreased use of herbicides, IRVM increases both the nectar and host-plant resources in the surrounding landscape for many species. The most common butterflies seen in our surveys (*Colias* sp. and *Everes comyntas*) both use a variety of legumes as host and nectar plants (Scott 1986). Legumes were dominant in weedy roadsides (by design) and often in prairie roadsides. Therefore, it is likely that both weedy and restored roadsides provide habitat for the most common butterflies in Iowa. Disturbance-tolerant butterflies, which are at little risk in Iowa, almost certainly benefit from IRVM practices, but they probably gain little, if anything, from actual prairie reconstruction. In contrast, habitat-sensitive species did respond to active prairie restoration over passive colonization of weeds. For some species, therefore, prairie restoration may be necessary to realize a benefit from IRVM.

Our data suggest that individual mortality risk is highest in grassy roadsides, despite the fact that most are located along gravel roads. This may be because individuals are more likely to exit grassy roadsides than prairie roadsides (49% and 23%, respectively). Being near a paved road greatly increased mortality risk, however, and most restoration projects are located along paved roads. The fact that mortality risk was lowest in prairie roadsides even though these areas tended to be paved may be explained by a reduced tendency of the butterflies to exit the roadside habitat. That overall abundance was higher in prairie roadsides may also indicate either that birth rates are offsetting mortality or that individuals are being drawn into the population from elsewhere. If the latter is the case, then roadsides attractive to butterflies may be acting as a high mortality trap.

Roadsides as Corridors or Stepping Stones between Habitat

Although we did not collect data specifically to test the hypothesis that roadsides can "connect" populations in fragmented habitat, our data offer some preliminary evidence that restored roadsides may be able to link habitat. The IRVM increases nectar resources in the landscape, which provides energy for an individual moving through the landscape searching for a new, suitable habitat patch. For species that can reproduce in roadside habitat, roadsides may function as stepping stones between reserves by decreasing the distance between habitat fragments. Even in situations where roadsides cannot sustain a population, limited reproduction in roadsides could add individuals to the migrant pool, effectively increasing linkage between isolated populations.

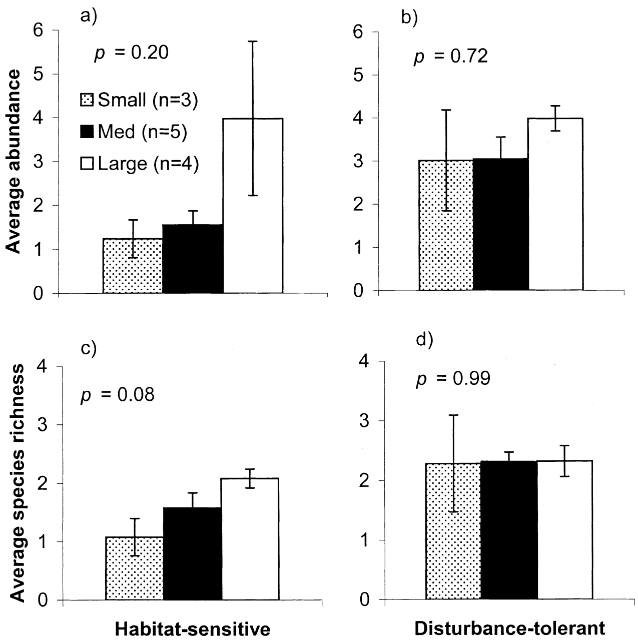

Figure 4. Average abundance of (a) habitat-sensitive and (b) disturbance-tolerant butterflies and species richness of (c) habitat-sensitive and (d) disturbance-tolerant butterflies based on length of roadside restoration in central Iowa. Restoration length was categorized as small (<800 m), medium (800–5000 m), and large (>5000 m). Values are based on an analysis of variance. Different letters indicate means that are significantly different.

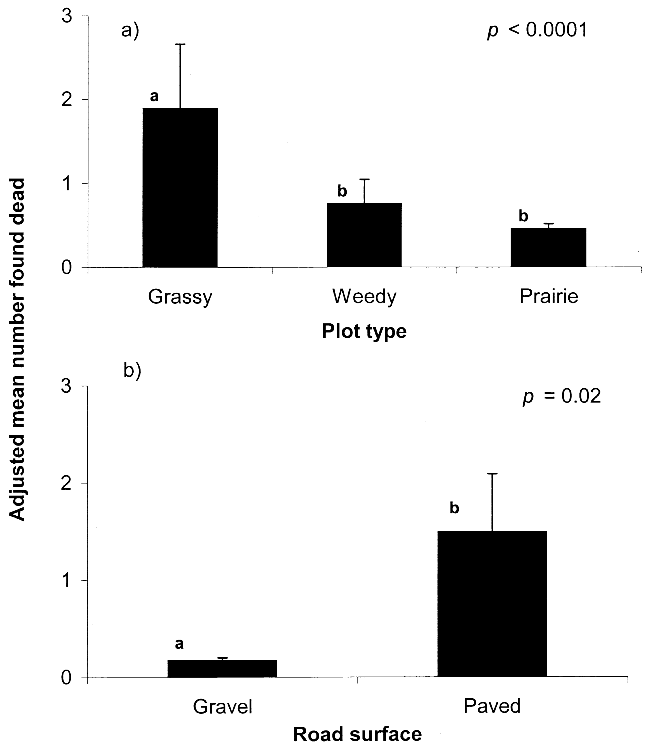

Figure 5. Number of individual butterflies found dead on the road divided by the number seen alive during roadside surveys in central Iowa, based on (a) roadside type and (b) road surface. Values are based on an analysis of variance. Different letters indicate means that are significantly different.

The most rigorous evidence supporting corridor value would be densities higher in connected than in unconnected patches (Beier & Noss 1998), but this type of data is rare (but see Haddad & Baum 1999). With few exceptions, restored roadsides do not exist as a continuous corridor between prairies or any other grassland reserve. At present, therefore, it is impossible to directly test the ability of roadsides to act as corridors between habitat fragments. In lieu of this evidence, two approaches have been taken to gather evidence that linear strips of habitat such as roadsides may function as corridors. The first and most common is to demonstrate that animal richness or density is higher in corridor than in noncorridor habitat, which we have demonstrated for habitat-sensitive species. The second type of data demonstrates that individuals tend to reflect off habitat boundaries, thus increasing the likelihood of moving down a corridor toward a connecting patch (Soulé & Gilpin 1991; Lima & Zollner 1996; Schultz 1998; Haddad 1999). We offer preliminary evidence for this by showing that individuals are most likely to turn at the boundary of prairie roadsides compared with grassy and weedy roadsides (77%, 51%, and 56% respectively).

This preliminary evidence suggests that butterflies may be able to use prairie roadsides as corridors or stepping stones. Butterflies unable to breed in weedy roadsides need to arrive at suitable habitat within their lifetime or the corridor acts as a sink rather than facilitating movement between patches. Even restored and native prairie roadsides may not be able to support populations of some butterfly species, and the only way these species could benefit would be if roadsides functioned to direct movement between habitat patches. As roadside restoration continues, we will be able to explore this issue more rigorously. One factor that needs to be considered is that as restored roadsides become more prevalent, prairie roadsides may become a continuous grid of linear habitat. If this occurs, roadsides may act as new habitat but may not have the ability to connect isolated patches because most roadside prairies will not lead anywhere. Thus, the question of whether reproduction can occur in roadsides will become even more critical.

Roadside Restoration versus Native Roadsides and Remnant Prairies

Richness of habitat-sensitive species was the only variable that showed a trend toward an increase in native compared with restored roadsides (Table 2). Species richness is an important indicator of habitat quality, and our results indicate that native roadsides may be superior to restoration for some habitat-sensitive species. That it was not significant may be due to small sample sizes. But with only four native roadsides surveyed and a highly variable system, it is difficult to draw any strong conclusions. Given the rarity of native prairie remnants, however, preservation of these roadsides should be made a priority.

Our finding that habitat-sensitive species differed little in abundance between actual prairie remnants and prairie roadsides should be interpreted with caution. Butterfly communities vary a great deal among prairies (personal observation). We used only four prairie locations in this study, although they were among the highest-quality prairies in central Iowa. The largest, highest-quality site was mowed after the first round of surveys (data after mowing were not collected), which may have influenced the outcome of the results. Nevertheless, our results indicate that roadside butterfly communities appear similar in structure to a subset of central Iowa prairies. Once again, the lack of demographic data makes it difficult to compare the true value of either habitat type.

Conclusions

Integrated roadside vegetation management likely provides additional habitat for Iowa's most common disturbance-tolerant butterflies. These practices result in roadsides with more nectar sources and an increase in host plants for many of the most common species in Iowa. Yet these butterflies are in little danger, and focus should be placed on habitat-sensitive species. Our data indicate that roadside restoration may add habitat and has the potential to provide corridors for at least some habitat-sensitive species. Our results suggest that larger restoration efforts providing a greater richness of flower species will most benefit butterfly communities. Caution must be taken, however. Roadside restoration may be attracting habitat-sensitive species to areas where they have little hope of reproducing or may be doing little to direct species toward new habitat because no specific effort is being made to restore roadsides between prairie fragments. If roadside habitats do act as sinks for some species, as restoration continues and becomes more prevalent in the landscape, they have the potential to do more harm than good (Danielson 1992). Source-sink dynamics are notoriously difficult to demonstrate but must be understood before the real benefit of roadsides to butterfly communities can be assessed. Although we were not able to consider demographic information, our data indicate a positive effect of roadside restoration on Iowa's remaining sensitive species. As roadside restoration continues in Iowa and throughout the world, there is a need to rigorously assess the effects of restoration on habitat-sensitive species.

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