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Insect Responses to Prairie Management

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Summary

This report summarizes published and unpublished information on the effects of burning, grazing and haying on prairie insects. The presettlement tallgrass prairie was maintained by wildfire and grazing by native herbivores. Changes in the prairie since settlement are based in massive habitat loss, species loss and fragmentation. Prairie remnants are isolated and in some cases have been grazed, hayed, invaded by woody plants and by alien weeds, and protected from fire: all these factors influence their insect communities. Genetic changes may accompany fragmentation.

Studies of the effects of a single burn on insect communities frequently produce inconsistent results, but generally spiders leave the burned area; millipedes tend to be more numerous on burned areas compared to unburned controls; collembola populations are reduced on burned areas; grasshoppers emerge earlier on burned areas and are generally well adapted to burning; Hemiptera and Homoptera are initially reduced in population but tend to invade recently burned areas where the vegetation is regrowing; beetles, Lepidoptera and flies vary among families in their responses to burning; ants tend to survive burning well except for above-ground nesters. Few statistically significant observations were made on other insect groups.

Studies of managed areas indicate that burning causes mortality among many species, and that recolonization from unburned areas is necessary to reestablish populations. Prairie obligate Lepidoptera and leafhopper populations are reduced on sites burned annually, while prairie obligate Orthoptera increase in abundance and species richness on annually burned sites. Many insect species are attracted to recently burned areas or to areas burned one or two years previously. Insects use sites in a very patchy manner; usually any species uses only a fraction of any site, and is absent from some suitable sites. Grazing and haying have received little study as conservation methods.

Site history influences the response of any site to management: the effects of a burn persist for several years, and over the long term species are lost from a site or persist on it in response to local conditions including management. Insect species vary in their responses to management based on their life history (those which pass a dormant period underground are likely to be fire tolerant), mobility and host specificity.

Many areas require additional research: basic biology of prairie insect species and their responses to management, characteristics of sites showing high insect species richness, identification of prairie obligate species, and larger issues of insect population biology on a regional scale are among the most urgent.

Management recommendations differ among authors, with botanists generally urging frequent and thorough burns to enhance prairie vegetation and butterfly specialists urging minimal if any burning to prevent mortality among butterflies. There is no single management program to protect all insects: a three year burn cycle leaving ample unburned areas at any time is recommended for conservation of fire tolerant and intolerant species on midwestern tallgrass sites. Sites should be monitored to determine the effects of management.

Introduction

Prairie management in northern tallgrass areas has emphasized maintenance of prairie plant communities and prevention of woody plant and Kentucky bluegrass invasion using controlled burning as the primary management tool. Recently, concerns have been raised that burning may threaten the survival of prairie obligate insect species, especially on the small isolated sites which comprise the majority of prairie remnants. Plant and animal populations of the presettlement prairie were maintained by wildfire and grazing by native herbivores. Much has been learned about these processes, but the effects of post-settlement fragmentation, fire protection, loss of native herbivores and introduction of alien plants and animals on prairie sites and populations has made the duplication of presettlement processes as management tools impossible. This review surveys general studies of prairie management and insect biology and studies which specifically address the effects of prairie management methods on insects.

Reports and articles on the effects of prairie management fall into several categories: studies of single species' responses to burning, studies of the effects of a single or a series of controlled burns or wildfires on a single site compared with an unburned site, long-term comparisons of burned and unburned sites and historical descriptions of the pre- and post-settlement prairie. Most burn papers focus on plants. Papers dealing with prairie grazing also emphasize plants, and many of those including information on insects are written from a pest control perspective. Little information is available on haying and grazing for prairie management. Ecological and natural history studies of insect-environment relationships and the effects of fragmentation on ecosystems and populations supply a theoretical framework for the development of further studies of management, while many gaps remain to be filled by well-designed research projects.

Forces Maintaining the Pre-settlement Prairie

Fire, drought, increasing aridity and warming trends favor grasslands over forest (Vogl 1974). As grasslands become larger, lightning fires spread unimpeded by firebreaks. Grassland fires tend to be flashy and pass rapidly without damaging basal portions of plants, and leave cool ash rather than burning coals behind them. Fires that occur during droughts may burn roots, dried organic matter and peat. Generally fires increase grassland productivity by removing litter and releasing nutrients; too frequent burning, burning at the wrong season or during drought can reduce productivity and damage the soil. Fire is necessary to cycle nutrients back into the system due to the slow decomposition rates in grasslands. Fires prevent the invasion of woody plants; in areas which support both grassland and forest, areas with the most frequent and intense fires have the fewest woody species. Repeated burning of native grasslands usually does not reduce plant species richness and may increase species richness in some cases. Anderson (1990) observed that in central Illinois fire acted to stabilize sand prairie, savanna and open forest communities, but to destabilize closed forests.

Collins and Gibson (1990) state that the persistence of tallgrass prairie is a function of the interaction of several large-scale disturbances, coupled with small-scale disturbances due to animals. In the absence of fire, grasses will rapidly be replaced by shrubs. The prairie is dominated by the matrix species (the large grasses), and the interstitial species, such as forbs, grow in the remaining space. Grazing reduces the dominant species, enhancing diversity, while fire may increase the dominance of some matrix species and kill some interstitial species, which reduces plant species richness and diversity. Small-scale disturbances such as gopher mounds may destroy matrix species and open small areas of soil for invasion. The tallgrass prairie is composed of many species because of presence of patches in various stages of succession. Plant species richness increases in the year following a fire, and changes are generally due to changes in the number of forb species, not grass species. Maximum plant species richness and diversity will occur in areas with periodic but not annual burning; annual fire tends to decrease patchiness. Grazing increased species richness on both burned and unburned sites in their study. Addition of buffalo wallows further increases species richness.

In a model developed by Risser (1990), the plant species composition of North American grasslands will remain relatively unchanged under conditions of light grazing, mesic climatic conditions and occasional burning.

Herbivores were significant in presettlement grasslands: Swengel (1993) states that the presettlement prairie was maintained by herbivores, which occurred in very high densities and maintained the vegetation in an extremely patchy state; fires were rare, small and did not often occur in early spring. Browsing by elk and moose as well as white-tailed deer were also important in preventing woody plant invasion, and pocket gophers, ground squirrels and prairie dogs were present in much greater numbers than now. When fires occurred, they were patchy due to the herbivore-caused patchiness of the vegetation. Schlicht (1993) notes that before drainage was done, prairie areas contained more sloughs and potholes: these would have reduced the areas of fires. In contrast, Schramm (1992) states that pre-settlement grazing probably had minimal effect on the prairies (compared to fire) due to the migratory and nomadic movements of the animals. Finck et al. (1993) suggest that pronghorn antelope were important herbivores in the tallgrass prairie; their past range was broader than previously thought.

Changes Since Settlement and their Implications for Management

Habitat loss leading to fragmentation, substitution of grazing for natural herbivory or exclusion of grazing and fire suppression have occurred since settlement of the tallgrass prairie. Invasion of alien plants such as bluegrass, brome, purple loosestrife and leafy spurge, and of native woody plants especially aspen in the northern part of our area, and oaks and _Juniperus virginiana_ in southern part have been significant (Vogl 1974). Changes due to fire suppression can't be separated from changes due to loss of grazers or change in grazing species.

The loss of habitat in itself is a serious consequence of fragmentation; smaller fragments can support smaller populations: though it seems obvious that a large population is in less danger of extinction than a small one, there are few if any practical demonstrations of this idea, especially for insects whose populations fluctuate wildly under most conditions. Insect species frequently occur as metapopulations, or populations of populations: it is normal for a population to die out on a site, and the site will later be recolonized from other sites. (Ehrlich and Murphy 1987). As fragmentation occurs, sites may be too far apart to allow recolonization to occur, and repeated local extinctions will lead to species extinctions. This is a serious concern for habitat-restricted insect conservation, and is discussed below in connection with many prairie insect groups, especially Lepidoptera and leafhoppers. The smaller the area, the higher the ratio of edge to interior: small fragments are vulnerable to invasion of generalist species due to their contact with other habitats along their edges.

The loss of habitat diversity, or types of habitat within a fragment is also significant for insects (Murphy and Wilcox 1986). Fragmentation is made more damaging to insect populations as the non-habitat areas between fragments may act as barriers to mobility. Roads and fences may also be barriers for some insect species (Mader et al. 1990).

Fragments (remnants) may have poor soils, atypical topography and atypical assemblages of plants. Ecosystem fragmentation results in fragments of different species composition depending on the geographical distribution of various species through the original ecosystem; the distribution of species is usually non-random, so some fragments will contain certain species while other fragments will be lacking them. At the same time, preservation is non-random; areas of low agricultural value are likely to remain as fragments, so species which are found in these areas are more likely to be maintained. Species which require large areas will be lost from small fragments, while other species may repeatedly recolonize areas following local extinctions. The mobility of any species determines whether fragmentation will divide it into separate populations or leave it as a single interbreeding population. The relation of the species richness of fragments to fragment area is unclear; the number of habitats in a fragment may be a better indicator of fragment species richness than the area of the fragment. Some fragments are much richer in species than others; conversely some species are confined to restricted habitats which may or may not be common in fragments, while other species are found over wider ranges (Usher 1987).

Genetic changes may occur in populations following fragmentation, including increased inbreeding, loss of heterozygosity, founder effects, genetic drift and possibly changes in mutation rates. These are the consequences of small population size and may have unpredictable effects on the viability of the population. Overall, decreased genetic variation is expected to result from fragmentation. This may leave a population unable to adapt to changing circumstances, including management changes (Usher 1987).

In general, insects tend to occur in localized patches (Comer et al. 1995). Ballard and Greenlee (1994) note for Missouri Orthoptera that a single site cannot represent the orthopteran community of a specific community type. They found that faunal composition and diversity were highly divergent among tracts with different fire history and site quality, even among the same community type. Reed (in press) observed similar patchiness among prairie bees: of 125 bee species, only 8 were found on all 8 prairie sites, while 39 were found on one site only. Each site had at least one bee species found on no other site.

Mobility of organisms following fragmentation is important as the balance between local extinction and recolonization will determine total species richness on any fragment (Usher 1987). A population may become less mobile following fragmentation, as more mobile individuals are lost from the population by emigration and are not replaced by mobile immigrants (Dempster 1991).

Mutualistic relationships may be interfered with when fragmentation occurs, and species which are highly specialized for mutualistic partnerships appear to be at high risk of local extinction when fragmentation occurs, because the loss of one species will doom its mutualist to extinction also. Pollinator abundance and diversity decline with fragmentation (Rathcke and Jules 1993). Many bees are highly host specific (Moldenke 1979): loss of their plant from a site will cause local extinction of the bee species. Native bee populations are slow to recover when reduced (Tepedino 1979); their populations remain small for long periods (up to 3 or 4 years for bumblebees). The generalist pollinator species which are able to persist following fragmentation may not be adequate pollinators of all plant species (Rathcke and Jules 1993; Strickler 1979); even generalists do not visit all the available plant species (Tepedino and Stanton 1981). Hendrix (1992) found that population size of Dalea purpurea on Iowa prairie remnants was significantly related to the percentage of seeds fertilized and flowers attacked by seed predators; he suggested that these results were due to the inability of small plant populations to attract pollinators and support seed predators (alternatively, inbreeding depression could be the cause of reduced seed set).. Where pollinators are lost, plants are under severe selective pressure to become self-fertilizing (leading to a loss of genetic variation, a risky situation in a changing environment), wind-pollinated, or to change their floral morphology to be more attractive to the surviving pollinators: the alternative is extinction (Tepedino 1979).

Likewise, competitive, predator-prey, and plant-herbivore relationships may be altered by fragmentation. Bison generally prefer grasses to forbs (Collins and Gibson 1990); Swengel (1993) states that since buffalo prefer grasses more than do cattle, the presettlement prairie was richer in forbs than are existing grazed remnants. Uresk (1986) also notes that cattle do not prefer forbs.

Responses of Plants to Burning

The physical effects of fire at the soil level are increased soil temperature, increased light intensity, heat of fire, and changes in soil nitrogen; these affect all soil organisms, not just plants. There is little penetration of heat more than a centimeter below the soil surface (Anderson 1990). Burning influences plant productivity and biomass, litter depth on the ground, plant community species richness and diversity, and the presence or absence of species from sites. Timing, extent and frequency of burning, as well as the vegetation and topography of the site, are important in determining the effect of a burn.

Ehrenreich and Aikman (1963) documented earlier plant growth (2-3 weeks), faster development, more flowers (on grasses and most forbs) after burning. Litter accumulation reached a maximum in 4-6 years. Burning increased available phosphorus in soil and increased pH. Soil water was depleted earlier on the burn. Burned areas generally had higher yield of grass than clipped areas. Some of their quads were burned once, others twice, others 3 times, others not at all after 9 years of complete protection; another area was mowed twice.

Hulbert (1988) studied the effects of burning on warm-season grasses (most of our native prairie grasses): they start growth earlier in the spring, grow faster and stem tiller density is higher. When burned in late spring, warm-season grasses are more productive than when unburned. Briggs et al. (1994) observed maximum increase in biomass in response to burning in sites which had not been burned for 12 years or more. There were no significant differences in grass biomass in among the groups (1-2, 3-5, 6-12 and more than 12 years since the last fire), but forb biomass showed the greatest increase following burning on sites previously unburned for 6-12 years. Thus aboveground plant biomass may be maximized by infrequent fires.

Hulbert (1986) summarized the effects of burning on tallgrass prairie plants: earlier plant development, earlier flowering of warm-season grasses, and increased stem density. Production of vegetation on burned areas can be double that of unburned, unmowed and ungrazed areas where the standing dead vegetation is thick. Above-ground plant biomass appears to reach its maximum in about six years if no burn occurs. Mowing and removal of vegetation has the same effect on productivity as burning does. Late spring burning results in fewer forbs but greater grass production than fall or early spring burning. Hulbert states "It is now clear that fire is necessary to keep woody plants from replacing tallgrass prairie...". In presettlement days fires probably occurred once to several times per decade. Without fire, Kentucky bluegrass increases on the Konza, especially in grazed areas. In most cases the combination of vigorous native plants and burning prevents invasion by alien plant species. Gibson (1989) continued observations from Hulbert's study and noted additional general effects on plants. On the Konza, annual burning in March or November resulted in the highest total cover of warm-season grasses and forbs, while late April burning led to a comparatively lower cover of these types of plants. With more frequent burning, growth of warm-season grasses was favored. Cool-season grasses and species richness increased with less frequent burning. Perennial forbs did not show a clear response to burning frequency. Annual and biennial forbs, especially sweetclovers (Melilotus spp.) were favored over perennial forbs by mowing; in the absence of mowing, annuals were most abundant on sites disturbed by animals.

Kentucky bluegrass and smooth brome decreased with spring burning, while big bluestem increased; forbs increased after a single burn, and decreased after a second burn on a tallgrass prairie remnant in eastern South Dakota. In general, warm-season native species were stimulated by burning (Blankespoor 1987). Henderson et al. (1983) burned two Wisconsin prairie remnants during early spring, late spring or late fall for three years and compared vegetation on burned sites to control sites. Cool-season grasses were unaffected by early spring burns but their flowering was greatly reduced by late spring burns. Flowering of the warm-season grasses was stimulated by all burns with the late spring burn having the most effect. In the same study, Lovell et al. (1983) found early-blooming forb species to be damaged by late spring fire (which occurred while they were growing vigorously and had begun to flower), while their flowering and fruit production was enhanced following fall and early spring burns. Midsummer blooming species showed positive or neutral results to all burns. Late blooming species were variable in their response to fire. Number of leaves, flowers and fruits per individual were measured.

Howe (1994a and b) and Swengel (1993) note that choice of burn season influences plant community composition on surviving prairie areas; these areas are then incorrectly considered to be representative of the presettlement prairie. Howe states: "Management practices that employ dormant-season burns may produce quite different communities than those maintained by midsummer burns that simulate the timing of lightning fires." Swengel (1993) states that fire-sensitive invertebrates and plants which grow and flower early in the spring have been lost from current remnants due to spring burns: we should not use managed prairie areas as models or goals for management of areas which have not been disturbed in this way.

Howe (1994b) planted a prairie reconstruction in 1986 in Wisconsin, using the same species and equal numbers of seeds on all plots and sampled plants in 1988 and 1990. Seven plots were burned 31 March, 7 were burned 15 July, 1989. Dormant-season fires (early spring) favored warm-season grasses and forbs, the same plants found in ungrazed prairie remnants. The July burn favored mid- and early-season plants. Howe states that mid-summer fires represent pre-settlement conditions better than dormant season: a "rich" array of burn seasons will allow greater plant species diversity than "monotonous dormant-season fire regimes".

Howe (1994a) states that current conservation methods (dormant-season fire and grazer exclusion) have a weak scientific base (due to being based on studies of remnants and restored areas), are based on poor history, and threaten prairie biodiversity. Pre-settlement is too recent: we should try to recreate earlier conditions under which these species evolved. Both plant and animal communities were far more diverse and varied before the last glaciation. Current species lists show many mid- and early-season flowers; however, we perceive the prairie as being late-flowering. In prehuman days, all fires were lightning fires--most of these occurred in midsummer (July or August). Historically, grazing suppressed dominant plants and allowed higher plant biodiversity. "...Tallgrass assemblages should be diverse, different from each other, and dynamic." Early-season native plants should be included in prairie reconstructions, otherwise early-season exotics will invade under grazing or summer fire.

Fire and fire frequency definitely have important effects on plant species diversity. Leach (1991) compared two prairie remnants managed by burning to three unmanaged remnants in Wisconsin and found that the burned remnants had maintained 12-15 species per m2, while the unburned remnants had only 4 to 6 plant species per m2, a loss of about 6 species per m2 since these remnants were described in the 30s, 40s or 50s by Curtis. Legumes were especially likely to be lost from remnants: lack of competitive ability, browsing by white-tailed deer, or loss of advantage due to nitrogen fixing abilities in the presence of nitrogen pollution should be studied as possible causes of legume loss.

Schwegman and Anderson (1986) described the effect on vegetation of 11 years of fire exclusion from a southern Illinois barren: frequency of prairie forbs and ragweed declined, while woodland herbs, Japanese honeysuckle, tree density and tree dominance increased. Succession from barren to deciduous forest was proceeding. Twenty years of data from the same site (Anderson and Schwegman 1991), with four burns between 1969 and 1988 (fifteen years since the last burn) indicate that irregular fire intervals act as stabilizing forces in barrens vegetation, allowing plant species with different responses to fire to coexist on a single site. Species diversity tended to be highest after cessation of burning, when fire-adapted plants were decreasing and woodland plants were increasing. Competition between annual prairie species which appeared following fire, and perennial prairie species which gradually replaced them, also influenced species diversity. Periodic fires are likely to stimulate increases in annuals. In the absence of fire, the site would undergo succession to a closed forest community.

Collins et al. (1995) found that plant species richness on sites decreased with increased burn frequency on Konza: long-term unburned sites always had higher average species richness than annually burned sites. When the effect of burn frequency were removed statistically, species richness peaked 5-9 years following fire, then decreased and remained steady for the next 10 years (studies of single plots showed surprising year-to-year variation in species richness, and there was wide variation among plots in species richness also). The Konza as a whole has had a long history of very frequent burning.

Studies of individual plant species give some information on the mechanisms by which fire influences plant species richness. Davis et al. (1987) noted that burning reduced stem density, number of flowers per stem and seed production in *Monarda fistulosa*, but had little effect on growth and reproductive effort by *Ratibida pinnata*. They suggest that *R. pinnata* may have evolved in tighter association with prairie fire than did *M. fistulosa*; the presence of *M. fistulosa* in many prairies today may be due partly to fire suppression in the past. In contrast, Hartnett (1991) on the Konza, found that columnar coneflower, *Ratibida columnifera*, from sites not burned for many years were larger and produced more flower heads with greater numbers of seeds than did plants from recently burned sites. Reproductive effort was lowest on annually burned prairie. Hartnett suggested that annual burning may harm mid-season forbs by altering the competitive advantage in favor of warm-season grasses. Glenn-Lewin et al. (1990) list *Amorpha canescens*, *Coreopsis palmata*, *Ratibida pinnata* and *Solidago canadensis* as species which increase their flowering after spring fire, while Dodecatheon media, Helianthus grosseratus, Monarda fistulosa, Petalostemum spp and Vernonia baldwinii decreased flowering following spring burning. The effects of spring burning on flowering varied with habitat for both grasses and forbs. Year-to-year differences also occurred.

Olear et al. (1994) noted that burning increased the rate of wood decay in tallgrass prairie soils. The increase appeared to be due to both direct and indirect effects of fire: for example, termite activity appeared to be more prevalent in annually burned areas.

The effects of a burn on plants varies within and among sites: no two fires are alike; pre- and post-burning conditions are also unique. Fires are likely to damage grassland in arid or marginal sites or on sites which have been heavily grazed. Mesic, ungrazed sites are rarely damaged by burning. Grazing after burning can alter the response of the vegetation to fire due to consumption of new growth and trampling, which may cause soil erosion. Fire following years of fire exclusion may be hotter than frequent fires due to the greater litter accumulation, and lack of wind may produce hotter fires than fires on windy days (Vogl 1974).

Pemble, Van Amburg and Mattson (1981) noted that the flowering response of Minnesota prairie plants following a single spring burn varied among site types (wet, mesic or dry, and differing in flatness). Differences in the completeness of litter removal may have influenced plant response to burning. Generally, flowering activity increased following the burn.

Responses of Plants to Grazing

As noted above, authorities agree that grazing was an important factor in the maintenance of the pre-settlement prairie; in a tallgrass prairie site, grasses are able to compenstate for light to moderate grazing by increasing their biomass (when all plant species were considered.) (Risser 1993). Under mesic conditions, moderate grazing usually enhances plant species diversity (West 1993). However, overgrazing by domestic livestock is destructive to the native plant community and is noted as a threat to the habitats of many prairie insects. For example, Nyboer (1981) noted the damage to Illinois hill prairies resulting from grazing. Grazed prairies showed reduction in native species presence, frequency and diversity. Cattle paths were prime sites for invading species and increased erosion. Invasion by Juniperus virginiana and other woody plants was also increased in grazed areas.The vast majority of studies on the relationships between grazing and vegetation, or between grazing and insect populations have been done from a range management perspective, with the goal of maximizing cattle production with minimum damage to future vegetation productivity. In Europe, grazing has been managed to conserve the semi-domesticated grasslands which have developed along with humans and cattle over many centuries: in the US, grazing is rarely done for conservation purposes.

Grazing animals are selective at several scales: they choose a plant community from those available in the habitat; a patch within the habitat; a feeding station within the patch, and a plant from those within reach at the feeding station. Grazer choices and movement patterns are influenced by herd behavior, presence of landscape feature such as water and shelter, topography and memory (habit), as well as by the presence of preferred food plants. Grazers tend to forage on only a fraction of their habitat, leaving part of an area grazed and other parts ungrazed, and making trails and trampled areas (Stuth 1991). Grazers influence the distribution of nutrients as they deposit urine and dung, and carry seeds internally and externally. When grazing animals are introduced onto a site, preferred plants will tend to decline, and less preferred plants to increase as their competitors are removed. Habitat heterogeneity tends to increase due to physical disturbances and plant community changes, so that when an area is burned the burn will be patchy. Grazing (unlike fire) can reduce flowering (Anderson 1990).

Trampling supplies disturbed areas which are invaded by alien plants whose seeds are carried in by livestock. Selective grazing of alien plants by cattle reduced their ability to compete with native plants; however, cattle droppings and trampling favored alien invasion in selected sites in California (Ehrlich and Murphy 1987).

Interactions occur between fire and grazing. Mammalian herbivores seek out recently burned sites (Vogl 1974; Collins and Gibson 1990). Pfeiffer and Hartnett (1993) found that burning favored *Schizachyrium scoparium* under ungrazed conditions, but burning was detrimental to it under grazed conditions (when grazed by bison). On unburned prairie, bison preferred *Andropogon gerardii* over *S. scoparium*, but the two grasses were grazed with equal frequency on burned sites. Burning removed the dead tillers which deterred grazing when present, and increased mean *S. scoparium* size in the absence of grazing. Hartnett et al. (1994) observed that cool season grasses increased, and warm season grasses decreased in areas grazed by bison, five years after bison were reintroduced to Konza. Plant species diversity was increased by bison grazing at all spatial scales; this was ascribed to the greater microsite diversity generated by bison. Diversity increases associated with grazing were greater on annually burned areas than on areas with less frequent burning. Vinton et al. (1993) on Konza found that bison grazed burned areas during the spring and both burned and unburned tracts during the autumn and winter. They preferred patches dominated by big bluestem and avoided patches dominated by forbs.

Cattle grazing for conservation of meadows in the Netherlands is aimed at a low to moderate grazing level which will result in areas of short herbaceous cover where grazing occurs, with long grass and woody plants in the areas which cattle avoid. This pattern arises because previously grazed areas are revisited as palatable new shoots sprout (Thalen et al. 1987). Similar patterns were reported in England by Kirby (1992). Kirby advocates grazing for grassland management to increase habitat heterogeneity. In contrast, Curry (1994) notes that grazing can decrease habitat heterogeneity on a smaller scale, especially by removal of flowering stems of plants.

Grazing combined with haying and burning is used for conservation management in Missouri (Toney 1989). Haying during the first three weeks in July maintains a balance between grasses and broadleaved plants; later haying tends to favor broadleaves and weaken grasses. Cutting height must be monitored. Initiating grazing when the bluestem is greening up produces the most uniform grazing throughout the season; if grazing is started later, cattle will concentrate on grasses. Burning is the only effective way to control agressive alien grasses and is done at the time of bluestem greenup. Only half of a site should be burned in any year. Summer or fall fires tend to increase erosion and damage winter wildlife habitat; summer fires are best for controlling woody invasion. Burning may be used in conjunction with haying or grazing. The stocking ratio must be manipulated depending on the type and condition of the site. All sites should be inspected annually.

Smith (1992) observed horse grazing on an 0.8 hectare prairie in Ohio. The horses tended to ignore the forbs and graze on the grasses.

White-tailed deer (Odocoileus virginianus) populations have increased, especially in preserves (Miller and Bratton 1992) while many native plant populations have been reduced. Though they are certainly not managed, except in cases where populations are reduced, deer are an important influence on plant communities in the northern tallgrass prairie. Miller and Bratton identified 98 threatened and endangered plant species in 36 families which were disturbed by white-tailed deer herbivory, based on reports by managers and other professionals. Ochids, lilies and legumes were the families most affected: Asteraceae had few affected species, and no grasses were reported. Possible effects on insect populations may be through their consumption of food plants, especially larval food sources for butterflies and removal of flowering stems which supply butterflies, bees and wasps with nectar. Recently burned areas appear to be most attractive to deer.

Deer are browsers and tend to eat young woody sprouts as well as young forbs. Hopkins Vanzant and Miyanishi (1993) observed deer completing browsing all oak sprouts on burned sites; in the absence of fire, deer had no significant effect on oak sprout mortality. Nelson and Anderson (1993) oberved that white-tailed deer are highly selective browsers on prairies in Illinois. Among the preferred plants were Amorpha canescens, Commandra richardsiana, Eryngium yuccifolium and Oxalis stricta. Englund and Meyer (1986) observed deer preferences among 24 species of prairie forb seedlings for two years in Hennepin County, Minnesota. Aster azureus (=oolentangiensis), A. laevis, Helianthus giganteus, Helianthus rigidus and Potentilla arguta were browsed most often, while Amorpha canescens, Anemone cylindrica, Asclepias tuberosa, Aster sericeus, Corepsis palmata, Echinacea angustifolia, Penstemon gracilis, P. grandiflorus, Dalea purpurea and Ratibida columnifera were not browsed at all. Only white-tailed deer were observed browsing in the test plots, although eastern cottontails and 13-lined groundsquirrels were also present.

Browsing did not significantly affect seedling survival under the study conditions of limited plant competition and adequate moisture. Anderson et al. (1994) found that deer reduced reproductive success of some prairie species in Illinois. Amorpha canescens, Baptisia leucantha and Phlox pilosa had significantly fewer, or in some cases no flowering stems in a control plot, compared to a deer exclosure.

Although rabbits may be a nuisance for the prairie restorationist (Roy Robison, pers comm), I have have found no studies of their effects on prairie plants or insects.

Responses of Plants to Haying

Haying (mowing followed by removal of the plant material) is similar to grazing in that light to moderate haying maintains or increases plant species richness, while frequent haying may reduce species richness and encourage invasion by alien plants. As with burns, timing of haying is important.

Dale (1983) found mowing of a recently reconstructed prairie in Arkansas to stimulate better growth of prairie grasses, and less weed growth, than burning; the effect was increased in plots with mulch left on them. Burning stimulated weed growth. Burn plots showed less prairie grass growth than unburned plots two years after the burn, despite increased grass growth in burned areas shortly after the burn occurred.

Boettcher and Bragg (1989) on ten eastern Nebraska prairie remnants found that frequent mowing caused major reductions in plant species diversity, decreased total vegetative cover and encouraged disturbance species including aggressive introduced species: this is compared to the sites which were mowed only once per year. Early summer mowing favored warm-season plants (vs. cool season) compared to mowing later in the season.

Ross and Vanderpole (1991) observed a frequently mowed hay meadow next to a prairie restoration in Illinois. When mowing ceased, prairie plants flowered on the formerly mowed site, but were not seen in an adjacent never-mowed area. Apparently the frequent mowing had allowed prairie plants to become established from seed. However, mowing did not prevent alien weeds from invading paths in the prairie restoration itself.

Kettle and Fitch (1983) studied a 27-year-old prairie restoration in Kansas which had been managed for 22 years. The annually mowed or burned tracts had prairie grasses in good condition, while the grazed and protected areas showed loss of grasses with invasion of weedy forbs, shrubs and trees. Dougan et al. (1990) found an increase in prairie plant species diversity in a mowed wet prairie in Ontario compared to an unmanged area. A single autumn mowing maintained the prairie plants.

Effects of Burning, Grazing and Haying on Insect Communities

Warren et al. (1987) reviewed the responses of grassland arthropods to burning from a pest management perspective: prescribed burning can be used to systematically manipulate arthropod populations on rangeland. Interactions of the environment, habitat (vegetation, soil and microclimate) occur during the preburn, combustion (the burn itself), shock (time until the vegetation starts regrowth) and recovery phases (time until the system returns to the preburn state or reaches a new steady state). Acute fire impacts occur during the combustion and shock phases, chronic impacts occur into and beyond the recovery phase. Mortality, natality, immigration and emigration of populations can occur during most phases. Fire characteristics, the arthropod species itself, timing of the burn relative to arthropod phenology, host/parasite and predator/prey ratios following the fire, post-burn weather and the direction and degree of habitat restructuring all can influence a species' response to burning and must be understood in order to predict this response.

Arthropods and non-arthropod predators may be attracted to the burn. Other insects may leave the burned area seeking prey or forage. As recovery begins, arthropod and other herbivores may be attracted to the lush growth, some bringing parasites. Conditions following a burn are usually more xeric than before; some insects may emerge earlier than usual due to higher temperatures. Interactions will continue until a new equilibrium is reached.

Several studies have been done in which an area is subjected to a prescribed burn or mowing, and the insect populations are compared to an untreated control area. These studies vary widely in their quality and thoroughness. Some general patterns emerge, but many conflicting results occur among studies (Table 1). Differences may be due to a variety of factors, including different site histories (an additional burn of a regularly burned site will probably show few differences from its "unburned" control, while a site protected from fire for many years will more likely show major changes following fire), differing taxonomic breakdown (most insect orders appear to contain both fire tolerant and fire-intolerant groups, so lumping a whole order may obscure changes at the family level), and variation between years (for example, the effects of fire may be more pronounced in a dry year than a wet year). The time elapsed between the burn and the start of data collection also varies from study to study.

Cancelado and Yonke (1970) compared burned and unburned areas after a late March burn for one summer, April through October, starting 2 weeks after the burn. They collected Hemiptera and Homoptera in east central Missouri at Tucker Prairie using malaise traps and sweep nets. There were more Homoptera (approximately twice as many) on the burned area. Cicadellidae were most common. Results were similar for Hemiptera though not as pronounced: Lygaeidae and Miridae were most common and showed the most differences. June and July collections accounted for the burned, unburned differences: later in the season, differences were not apparent.

Nagel (1973) observed insects following a single spring burn on a lightly to moderately grazed area in Kansas. There were 2 plots 100 m apart, 100 m in diameter; one was burned 10 April. Collections were made every 2 weeks from 6 June to 27 August using night and day sweeps. Biomass was determined for herbivores, non-herbivores and mixed feeders. Most taxa had approximately equal frequency on both sites: Tettigoniidae, Acrididae and Cicadellidae made up approxmately 74% of the herbivores by number, and Tettigoniidae made up approximately 85% of the herbivore biomass. Diptera and Araneida were 87% of number and 77% of weight of non-herbivore, ants and wasps were 68% of mixed feeders by number and 12% by weight. Most of the increase on the burned area was due to Cicadellidae plus Tettigoniidae, most of the increased weight by Acrididae & Tettigoniidae. In non-herbivores, the greatest increase on the burned area was in Diptera, while Araneida decreased; Hymenoptera and Gryllidae had the greatest increase of mixed feeders on the burned area. Coleoptera, especially Chrysomelidae (85% of beetles) were numerically important on both burned and unburned areas. The damselfly population was somewhat reduced on the burned area. The burned site produced significantly greater numbers and biomass in all categories except herbivore number and non-herbivore weight. Night samples had lower numbers but higher biomass. Weight increased with date.

Halvorsen (1981; Halvorsen and Anderson 1980) compared insect populations on one burned and one unburned site following a single spring burn in the same year on the Buena Vista marsh in Central Wisconsin. The study area was a drained marsh. Few prairie plants were present on the site, which was dominated by bluegrass and some goldenrods with invasive aspen and <u>Spiraea</u> <u>alba</u>. Arthropods were collected by sweep-netting, and their biomass and density on the burned and unburned areas were not significantly different. One hundred sweeps were taken monthly May through October 1978. Burning significantly reduced spider populations in May and leafhopper populations in May, June and July. Spiders increased in June on the burned area and approached control levels thereafter. Leafhoppers (Homoptera) peaked in July on the unburned plot and thereafter there were no significant differences. Beetles were more numerous on the burned grassland (significantly in May). Flies were significantly higher on the burned area in June, ants and bees higher on burned areas in June and July--otherwise there were no significant differences in flies or ants plus bees. Burning had no effect on Heteroptera, Lepidoptera or grasshopper numbers. Overall there were no significant differences in numbers between burned and unburned sites, and no effect of burning on dry weight of insects overall. The monthly average dry weight of individual orders was not significantly affected by burning, nor was total biomass, although biomass was lower on the burned plot just after burning. Insect biomass peaked in September.

Tester and Marshall (1961) studied the Waubun Prairie Research Area in Mahnomen County, Minnesota. They had 2 control plots: one plot burned fall 1957, two plots burned spring 1958, one plot grazed 1958 and 1959. (They attempted to hay one plot but technical problems prevented this; it was mowed but not hayed.) Insects were collected by sweeping in mid-August. Grasshoppers had an optimum litter depth of a light to moderate amount of litter: the litter was too deep in the unmowed and in the grazed plots, too sparse in burned plots; the mowed area had highest grasshopper populations. They suggest that beetles preferred sparse litter as beetle populations were higher in burned areas than in unburned areas.

Anderson et al. (1989) monitored insect abundance and biomass on an Illinois sand prairie for 3 years following a single spring burn. The abundance of all insects combined was lower on the burned site in the first year post burn, but not later. Ants were more abundant on the burned site than the unburned site during the first year, but not the second or thrid. The pattern was reversed for Homoptera (the opposite to expectations--probably due to a lack of green plant response to the burning). Grasshopper numbers showed no differences, but grasshopper biomass was higher on the unburned site during the first year postburn only. The results indicate that these species are adapted to burning, since none showed a severe decline in abundance following fire. The site had been burned in 1976 and 1980 before the experimental burn of half the site in 1984; previous burn history is unknown. Insects were sampled using sweep nets. Insects which were significantly less abundant on the burned section during the first year were Hemiptera, Diptera, Hymenoptera (except ants) and Homoptera. Formicidae and Coleoptera were more abundant on the burned section during the first year. Hemiptera were more abundant on the unburned site in the third growing season after the burn. These were the only significant differences found.

Hansen (1986) sampled insects on burned and unburned sites in Utah (a sagebrush area) following a range fire. More insects were collected on the burned area; the numbers of species collected were equivalent on the areas by one month after the fire. Entomophagous flies such as pipunculids, chamaemyiids and tachinids preferred the unburned site. Mosquitoes and phytophagous lygaeid bugs, leafhoppers, pompilids and sphecids, and moths were more common at the burned sites. Flying insects showing no preference were sciarids, phorids and leafminer flies (all Diptera), also many parastic Hymenoptera. Ground survivors of the burn (collected using pitfall traps) were gryllacridids, carabids, tenebrionids and ants; they were also found on the unburned sites. Silphids and buprestids moved into the burn area. Plant regrowth was evident 3 weeks after the fire. Not all these results are expected based on ecology; for example, Hansen questions why predaceous and parasitic Hymenoptera were found on the burned area at a time when few flowers and host insects were present.

Seastedt et al (1986) studied soil arthropods at Konza. Annual burning for two years resulted in increased biomass of cicada nymphs (which feed on root xylem), while mowing and raking three times a year resulted in increased biomass of white grubs (root chewers). Millipedes were more abundant on burned plots. Chrysomelid larvae, predaceous beetle larvae (mostly soldier, carabid and staphylinid beetles), and detritivores (mostly Diptera larvae) were most abundant on unburned plots. Microarthopods, mostly mites and collembolans, were also more abundant on unburned sites; they feed mainly on litter and fungi. Overall, arthropod biomass was higher on burned plots, but arthopod densities were not significantly different among treatments. Generally the biomass of soil arthopods increases as plant productivity increases, with some time lag. Seastedt (1984) compared the biomass of belowground macroarthropods (belowground arthropod biomass is 2-10 times that of aboveground arthropods) on annually burned and unburned tallgrass prairie at Konza. The increased biomass on the burned area was largely due to increased adults and larvae of Phyllophaga (Coleoptera: Scarabaeidae). Chilopoda (centipedes) were more common on the unburned area (one site only).

Van Amburg et al. (1981) studied the response of arthropods to a single spring burning of a tallgrass prairie in northwestern Minnesota. Ninety-three taxa (mostly families) were collected, of which 75 showed no change by three months after the May 2 burn. Mites showed higher numbers on the burned plots, ticks on the unburned plots. Collembola increased more on the unburned plots. Carabidae, Coccinellidae and Staphylinidae (predaceous Coleoptera) and Meloidae (a herbivorous coleopteran family) were more abundant on the burned plots, while Cantharidae and Elateridae were more numerous on the unburned plots. Among the Diptera, Acroceridae and Bombyliidae were more numberous in the unburned plots, while Anthomyiidae and Syrphidae were in greater numbers in the burned plots. Among Homoptera, only Delphacidae had a significant response to burning (an increase on burned plots). Sphecidae (Hymenoptera: predaceous wasps) were significantly more abundant in the burned plots. Among Lepidoptera, Danaidae were more numerous in the burned plots and Pieridae more numerous in the unburned plots. Mantispidae, a predacious family in the order Neuroptera, occurred in significantly greater numbers in unburned plots. Among grasshoppers, Tettigoniidae were more numerous on the unburned plots. Odonata (dragonflies and damselflies) were slightly more numerous on burned areas. Millipedes (Spirobolida) were in greater numbers on the burned plots. The authors urge study of individual species in order to determine the causes of these responses.

Rice (1932) burned 2 prairie sites in Illinois; one was burned twice, and both were compared with unburned areas. Animals, especially spiders, were present in lower numbers on the burned area. Some animals left to seek cover in unburned grasses.

Two studies compared mowing and burning. Bulan and Barrett (1971) mowed and burned half of an experimental oat field in Ohio and mowed the other half. The effects of mowing persisted two weeks, while the effects of burning lasted for 3 months. Herbivorous Coleoptera species diversity was significantly reduced, while carnivorous Coleoptera species diversity was not affected by the burn on a long-term basis. In general, Diptera, Homoptera and Hymenoptera densities on the burned grid remained significantly below those on the unburned grid until the end of the season, when densities became similar. Hemiptera densities recovered about a month earlier. Arachnid densities on the burned area did not reach those of the unburned area during the study. Mowing caused an immediate decline in density of the above groups, and among Thysanoptera, which were not found anywhere after August 15. In contrast, Coleoptera and Collembola did not decline following mowing. Collembola in the unburned grid increased much more following the burn; the burn population never reached the size of the unburned population. Biomass of all insects increased rapidly following the mowing decline on the unburned area, but at a much slower rate on the burned area. Post fire and post-mowing vegetation on the areas are not described.

Dunwiddie (1991) studied aboveground arthropods in burned, mowed and untreated sandplain grassland sites in Nantucket. The sites had not been burned or mowed for at least 10 years previously. Treatments were conducted in 1983 and 1985 and sampling was done during 1985. Spider numbers were reduced throughout the growing season following the burn. Orthoptera were more abundant on both burned and mowed plots, from one month to two years after the burn. Homoptera, especially Cicadellidae, were more common in both burned and mowed plots one month after treatment. Hymenoptera, mainly Platygasteridae, were abundant on plots mowed or burned 2 years or 4 months previously, but declined following August mowing or burning. Most platygasterids are parasitic on gall midge larvae. Coleoptera, Diptera and Lepidoptera showed no consistent trends. Collembola were more abundant in the mowed plot than in the control or burned plots. Mowing and burning gave similar results in this study, except for the different effects on Collembola.

Davis et al. (1987) observed an increase in infestation rates of seed heads of Ratibida pinnata by Gelichiid (a microleopidopteran) larvae on burned areas following a single spring burn (this did not reduce seed producution or viability). Seed production by Monarda fistulosa was reduced equally in burned and unburned areas by seed predation by a Pyraloidean microlepidopteran. Hill (1973) observed the effects of burning on pollination and seed predation in the prairie legume Astragalus canadensis on Cayler prairie in Iowa. Milkvetch is pollinated by bumblebees and its seed predator is a snout weevil (Curculionidae: Tychiinae); the weevil is a specialist on this plant species. A single spring burn was conducted on April 10. Burning produced no significant differences in either pollination or seed predation; this is presumably due to the high mobility of both bees and weevils between the burned and unburned areas, and because the beetles pupate underground at the base of the host plant while queen bumblebees overwinter undergound. Weevils were present on the host plants one week prior to anthesis during the first week of July. Hill notes that fire during late summer might harm the weevils because they are present as larvae in the milkvetch seed pods at this time.

Overgrazing can be harmful to insects, just as it is harmful to plants, while light grazing may influence insect populations through its effect on the plant community or on the physical heterogeneity of the habitat. Ehrlich and Murphy (1987) noted that checkerspot larvae were often found exclusively on cattle terraces on north-facing slopes in winter: the terraces received greater insolation than the slopes. Direct mortality of butterflies occurred due to being stepped on or buried in cow pats. Sugden (1985) listed the possible impacts on grazing on bees including destruction of potential nest sites by trampling (bumblebees are expected to be most susceptible to this), and destruction of nests and their contents; most susceptible will be ground-nesting bees which have shallow burrows and stick-nesters above ground. Cavity nesters such as Osmia are at little risk as they nest in logs or standing trees. Removal of food resources would be especially important for smaller bees with limited foraging range. Direct trampling is also a risk to many bees that rest above ground in vegetation in cool nights or mornings. The impact of grazing can be predicted from knowledge of species biology, and the timing of grazing relative to bee phenology is also important. Soil disturbance by sheep may enhance seed germination or establishment; also, competitive interactions among plants may be altered. Sugden observed an increase in bee density on his Great Basin site when nearby areas were grazed, then a complete loss of bees when the site itself was suddenly and intensively grazed by sheep.

Miller and Onsager (1991) found that grazing intensity had little effect on adult grasshopper densities even though grazing reduced vegetation cover and increased areas of bare ground. They subjected 3 sites in western Montana to high intensity short-term grazing, low intensity summer-long grazing, and no grazing, and sampled grasshoppers during the summer of 1985. Livestock dung is a food and thermal resource for rangeland grasshoppers, especially where cattle have removed most of the standing vegetation; grasshoppers may be significant in recycling nutrients contained in dung back into the soil (O'Neill 1994). Many more studies of grasshoppers are noted below.

Table 1. Responses of Insects to a Single Burn or Mowing

Order, Family, Subfamily,	Response and Reference
Araneae (spiders)	1. Lower on burn (B and B) 2. Lower on burn (Rice) 3. Lower on burn (Hal) 4. Lower on burn (Dun) 5. Lower on burn (Nagel)
Acari (mites, ticks)	1. Mites higher on unburned (Sea) 2. Mites higher on burn, ticks higher on unburned (Van A)
Pseudoscorpiones (pseudoscorpions)	1. N. S. burn and unburned (Van A)
Diplopoda (millipedes)	1. Higher on burn (Sea) 2. Higher on burn (Van A) 3.Lower on burn year 1, higher on burn year 2 (Rice) 4.Higher on burn (Nag)
Chilopoda (centipedes)	1. N.S. burn and unburned (Van A) 2. Lower on burn (Nag) 3. Lower on burn (Sea)
Protura (proturans)	1. N.S. burn and unburned (Van A)
Collembola (springtails)	1.Density and biomass increased in unburned area; remained low in burn (B and B) 2. Sminthuridae numbers increased in unburned; Entomybryiidae and Isotomidae N.S. (Van A) 3. Higher following mowing; burn N.S. (Dun) 4. N.S. burn and unburned (Rice) 5. Higher on burn (Nagel)
Diplura (diplurans)	1. N. s. burn and unburned (Van A)
Archaeognatha (bristletails)	
Thysanura (silverfish)	
Ephemeroptera (mayflies)	1. N.S. burned and unburned (Van A)
Odonata (dragonflies and damselflies)	1. Damselflies reduced on burned area (Nag) 2. Aeshnidae, Coenagrionidae, Libellulidae N.S. burn and unburned (Van A)

Grylloblattaria (grylloblattids)	
Phasmida (walkingsticks)	
Orthoptera (grasshoppers, crickets, katydids) burn and mowed vs. control(Dun)	1. Higher numbers on both 2. Burning N.S. on grasshopper numbers (Hal) 3. Grasshoppers higher in mowed--burn results inconsistent (T and M) 4. No difference in grasshopper numbers on burn and unburned--biomass higher on unburned (year 1). *Conocephalus* *strictus* (Tettigoniidae) higher on burn; *Melanoplus* *flavidus* (Acrididae) higher on unburned (both for 2 y, not in year 3) (And) 5. Tettigoniidae more numerous on unburned; Acrididae, Gryllidae, Tetrigidae no difference (Van A) 6. Tettigoniidae and Gryllidae increased numbers and Tettigoniidae, Gryllidae and Acrididae increased biomass on burn (Nag) 7. Gryllacridids survived burn (Han)
Mantodea (mantids)	
Blattaria (roaches)	
Isoptera (termites)	
Dermaptera (earwigs)	
Embiidina (webspinners)	
Plecoptera (stoneflies)	1. N.S. burned and unburned (Van A)
Zoraptera (angel insects)	
Psocoptera (barklice and booklice)	
Phthiraptera (lice)	

Hemiptera (bugs)	1. More numerous on burned area, esp. Lygaeidae and Miridae (C and Y) 2. Density and biomass decreased following mowing, then unburned increased, burn remained low on both (B and B) 3. Less abundant on burn in year 1; more abundant on unburned in year 3, otherwise N. S. (And) 4. N.S. burn and unburned; predators higher on burn, plant bugs lower (Nag) 5. Coreidae, Lygaeidae, Miridae, Nabidae, Pentatomidae, Phymatidae, Reduviidae all N. S. burn and unburned (Van A) 6. N.S. burned and unburned (Hal) 7. Lygaeids higher on burn (Han) 8. Higher on burn (Rice)
Homoptera (cicadas, hoppers, psyllids, whiteflies, aphids, scales)	1. More numerous on unburned, year 1 only (And) 2. Delphacidae more numerous on burn; Aphidae, Cicadellidae, Dictyopharidae, Margarodidae, Membracidae, Psyllidae n.s. (Van A) 3. Increased after mowing and after burning, esp. Cicadellidae (Dun) 4. Higher on burn, esp. Cicadellidae (C and Y) 5. More on burn, esp. Cicadellidae (Nag) 6. Higher on unburned (Hal) 7. Lower on burn until late in season (B and B) 8. Cicada nymphs higher on burn (Sea) 9. Cicadellidae higher on burn (Han)
Thysanoptera (thrips)	1. N.S. burn and unburned (Van A) 2. N.S. burn and unburned (Nag) 3. Lower on burn (B and B)

Neuroptera (alderflies, dobsonflies, fishflies, lacewings, snakeflies, antlions, owlflies)	1. Mantispids higher on unburned: chrysopids N.S. (Van A) 2. Hemerobiidae lower on burn (Hans)
Coleoptera (beetles)	1. Carabidae, Coccinellidae, Meloidae and Staphylinidae higer on burn; Cantharidae, Elateridae higher on unburned; Cerambycidae, Chrysomelidae, Cicindelidae, Curculionidae, Dytiscidae, Endomychidae, Lampyridae, Mordellidae, Pselaphidae, Scarabaeidae and Silphidae N.S. (Van A) 2. Inconsistent on burn and mowed (Dun) 3. Inconsistent on burn and unburned (Nag) 4. Higer on burn (Hal) 5. Higher on burn (T and M) 6. No decrease following mowing; herbivore species diversity decreased after burn; no change in carnivore species diversity (B and B) 7. Chrysomelid, soldier, staphylinid, and carabid larvae higher on unburned (Sea) 8. Higher on burn during first year (And) 9. Carabids and tenebrionids N.S. on burn and unburned; silphids and buprestids moved into burn area (Han) 10. Lower on burn (Rice)
Strepsiptera (twisted-wing parasites)	
Mecoptera (scorpionflies)	
Siphonaptera (fleas)	

Diptera (flies)	1. Higher on burn (Nag) 2. Lower on burn (B and B) 3. Lower on burn, year 1 only (And) 4. Pipunculids, chamaemyids, bombyliids and tachinids higher on unburned; mosquitoes higher on burn; sciarids, phorids and leafminer flies N.S. (Han) 5. Detritivore larvae higher on unburned (Sea) 6. Anthomyiidae and Syrphidae higher on burn; Acroceridae and Bombyliidae higher on unburned; Asilidae, Bibionidae, Caliphoridae, Cecidomyiidae, Chironomidae, Dolichopodidae, Empididae, Otididae, Sarcophagidae, Schizomyidae, Sciaridae, Tabanidae, Tachinidae and Tipulidae N.S. (Van A) 7. No consistent trends (Dun) 8. Higher on burn (Hal) 9. N.S. burn and unburn (Rice)
Trichoptera (caddisflies)	
Lepidoptera (butterflies, moths, skippers)	1. Danaidae higher on burn; Pieridae higher on unburned; Ctenuchidae, Gelechiidae, Hesperiidae, Lycaenidae, Noctuidae, Nymphalidae, Papilionidae, Satyridae N.S. (Van A) 2. No consistent trends (Dun) 3. No effect of burning (Hal) 4. Moths, esp. Noctuidae, higher on burn (Han) 5. Noctuid larvae lower on burn (Rice) 6. N.S. burn and unburned (Nag)

Hymenoptera (wasps, bees, ants)	1. Lower density on burn (B and B) 2. Ants higher on burn, year 1 only; others lower on burn in year 1 (And) 3. Pompilids, sphecids and mutillids higher on burn; parasitic Hymenoptera N.S. (Han) 4. Sphecidae higher on burn; Andrenidae, Apidae, Braconidae, Chalcidoidea, Cynipoidea, Formicidae, Halictidae, Ichneumonidae, Megachilidae, Tenthredinidae, Tiphiidae, Vespidae N. S. (Van A) 5. Platygasteridae lower following mowing or burning; recovered quickly (Dun) 6. Ants and bees higher on burn (Hal) 7. Ants higher on burn; others n.s. (Rice) 8. Higher on burn (Nag)
All insects combined	1. Lower on burn year 1; later n.s. (And) 2. Higher on burn (Han) 3. Herbivores higher on burn; non-herbivores n.s. (Nag) 4. Lower on burn (Rice) 5. Lower on burn (B and B) 6. Soil macroarthropods higher on burn (Sea4)

References:
B and B: Bulan and Barrett 1971
Van A: Van Amburg et al. 1981
T and M: Tester and Marshall 1961
Nag: Nagel 1973
Hal: Halvorsen 1981
Dun: Dunwiddie 1991
C and Y: Cancelado and Yonke 1970
And: Anderson et al. 1989
Sea: Seastedt et al. 1986
Han: Hansen 1986
Rice: Rice 1934
Sea4: Seastedt 1984 N.S. No signficant differences
Authority for names: Borror et al. 1989

Effects of Burning, Grazing and Haying on Single Species or Groups

In these studies, scientists have attempted to identify factors, including management methods, which may affect these insects' survival and interactions.

Spiders

Reichert and Reeder (1970) studied the effects of burning on spider populations and distribution in two prairies in Wisconsin, the restored Curtis prairie, and the remnant Oliver prairie. Both areas had been burned at least twice a few years before the study. Spiders which were active on the surface were eliminated by the burn, while spiders in burrows, sacs under rocks or in clumps of dense vegetation escaped thermal damage. Spiders moved around following the burn: those with high moisture requirements and those needing structural support for webs sought the unburned areas. Other species moved into the burned area, but no movement from prairie onto the surrounding agricultural lands was detected. Some of the increase in spider numbers on the burned area may have been due to emergence of spiders from diapause due to the increased temperatures following the burn. The spider community on Oliver prairie appeared to be adapted to the effects of periodic burning as the species composition of this community was relatively constant over the two years of the study.

Cutler (1988) proposed 8 species of jumping spiders for Minnesota listing as endangered, threatened, or special concern; six of these are prairie species. Tutelina formicaria is found on sand prairie where it is associated with the forb Penstemon grandiflorus; Habronattus rutherfordi has been collected from dry prairie; Sassacus papenhoei is found on forb-rich sand prairie, and Metaphidippus arizonensis is also a sand prairie species associated with forbs. Phidippus apacheanus and P. pius are restricted to unplowed prairie sites. Habitat loss is the major threat to these species. Cutler notes that many parts of the state have not been surveyed for jumping spiders.

Orthoptera (Grasshoppers, Crickets and Katydids)

Grasshoppers compete with cattle for grass, so many studies have been done from a pest control and range management perspective. Evans (1984) sampled grasshoppers during the summer of 1982 on the Konza prairie. The highest grasshopper species richness and diversity occurred on the watershed burned every fourth year ("intermediate frequency of fire"); the lowest richness and diversity occurred on the annually burned sites. Sites not burned for ten years showed similar species richness to those burned every two years. From five to 11 species were found per site. Sites previously unburned for ten years showed the greatest change in species composition when subjected to fire due to the susceptibility of forb feeders to fire: sites which had been burned annually in the past showed little change following an additional experimental burn--the grass feeders on these sites were resistant to spring burning. Forbs make up a small fraction of the biomass on Konza compared to grasses, even in infrequently burned areas.

Evans (1988a) studied the effect of fire frequency, topography and vegetation on grasshopper assemblges of the Konza Prairie in Kansas. Spring burning alters the environment for grasshoppers by changing the environment into which the nymphs hatch: they are underground during the actual burn. Some are forb and mixed feeders, some are grass feeders. He collected 25, 987 grasshoppers from 38 sites sampled in from 1-5 years between 1982-86. The sites had been managed consistently since 1972. A greater number of grasshopper species were found on sites left unburned or burned every 4 years than on sites burned annually or biennially; the unburned and burned every 4 years sites also had the highest forb biomass (more frequently burned sites had more grass biomass). The relative abundance of grass vs. forb feeders did not vary between the upland and lowland sites, though some individual species showed preferences. Evans concluded that fire and topography affect grasshopper assemblages by changing the plant community and noted that the effects of plant species and the effects of the physical structure of the plant community, such as the amounts of litter and standing dead vegetation, were not separated.

Evans (1988b) on Konza 1982-86 found that species richness, diversity and composition of grasshopper communities did not vary in a regular fashion with the four-year fire cycle. Periodic fire tends to set broad limits on possible species composition of communities. Local comunities tended to return to some characteristic species composition when displaced. For all sites combined, the relative abundance of grass-feeders increased after a fire and declined in subsequent years.

Capinera and Sechrist (1982) monitored grasshopper populations 6 shortgrass prairie pastures in northeastern Colorado subjected to different grazing intensities for 2 years. Total grasshopper numbers were significantly higher in the ungrazed or lightly grazed pastures, which had higher biomass. Members of the subfamily Oedipodinae were more numerous in the moderately or heavily grazed, low biomass pastures. Gomphocerinae and Catantopinae numbers, the phytophilous subfamilies, were postitively correlated with grass and forb biomass, while Oedipodinae, a geophilous group, were negatively correlated with all biomass measures. The authors suggest that grasshopper abundance could be modified by regulating cattle grazing intensity, and that these changes in abundance would be accompanied by shifts in the grasshopper species present. They also suggest that arthropod responses to grazing are site-specific, depending on the arthropods present, the plant species, and grazing intensity.

Welch et al. (1991), in Colorado, compared grasshopper populations on a lightly grazed pasture to those of a pasture heavily grazed, both for 20 years. Species composition was similar to that described by Capinera and Sechrist (1982), and more grasshoppers were found on the lightly grazed area than on the heavily grazed area.

Fielding and Brusven (1993 a and b) in southcentral Idaho observed that areas which had been severely disturbed by wildfires and exotic plant invasion had significantly higher grasshopper densities than less severely disturbed areas with sagebrush. Factors involved in habitat selection by grasshoppers may include availability of preferred foods, interspecific competition, predation, vegetative structure, microhabitat preferences and oviposition sites; some of these variable may be affected by management. They suggest that rehabilitation of annual grasslands with perennial grasses and shrubs, and protection of endemic plant comunities could contribute to more diverse grasshopper populations with lower proportions of pest species.

Areas burned in early spring had higher grasshopper populations than heavily grazed areas (Higgins et al., no date).

Bock and Bock (1991) found that most grashopper species declined temporarily following a wildfire in ungrazed Arizona grassland. A few species increased after the fire--these are known to prefer bare ground and/or herbaceous foods. The differences disappeared by the second year after the fire. The authors conclude that the community is highly fire-tolerant but not fire-dependent.

Ballard and Greenlee (1994) studied orthopteran abundance and species diversity in 30 sites including Missouri prairies, woodland/savannas, glades and fens. Degraded sites such as parking lots, closed canopy woodlands and lawns were used as comparison sites. Prairies showed the highest orthopteran diversity: annually burned prairies and woodlands showed consistently higher abundance and diversity than comparable unmanaged sites. Burning produced a different and more diverse grasshopper community than haying. Ballard and Greenlee ascribed these results to the higher diversity and health of the grasses and forbs, and the lack of a heavy thatch layer in the burned areas. Microhabitat features such as the presence of rock outcrops were required for certain species, while other species require tall grasses. They compared orthopteran species in high-quality and degraded habitats and defined those species requiring high floristic quality as conservative (11 of 58 species). These were prairie and glade species, while most woodland species were also found in degraded or cultivated sites. Those species which were potentially susceptible to fire damage due to inability to fly or above-ground oviposition, among other factors, were defined as sensitive. Both conservative and sensitive species were more diverse in fire-managed sites than in unburned sites. Ballard and Greenlee collected 132 species of Orthoptera, including 5 species new to the state. They recommend crude numerical methods such as a one-hour timed-meander through each area to give semi-quantitative data on grasshopper diversity and abundance. Species presence-absence data gave an adequate representation of the differences among community types; within-community type differences were revealed by quantitative methods. They conclude that there is no evidence that frequent or even annual burning poses a threat to orthopteran species in Missouri habitats. Orthoptera may be used as indicators of high-quality prairie sites due to the close relationship of the conservative species with habitat quality.

Homoptera (Cicadas, hoppers, aphids, whiteflies, scale)

Hamilton (1994) surveyed leafhoppers and piglet bugs on 148 northern tallgrass prairie sites in the US and Canada. He classified sites based on the number of endemic species, and noted those which were "frequently-burned or recently burned". Of 28 burned sites, 23 were classified as depauperate (0-3 endemic species), 3 as fair (4-6 endemic species), 1 as good (7-10 endemic species) none as very good, and 1 as excellent (more than 15 endemic species). Of the 120 sites not listed as frequently or recently burned, 43 were depauperate, 33 fair, 26 good, 12 very good and 6 excellent. The basis of the burned/unburned classification was not stated.

Coleoptera (Beetles)

Rickard (1970) found the same 4 ground beetle species in 3 sampling areas each in an unburned area and an area burned 6 years previously in shrubsteppe vegeation in southeastern Washington. Two species were more common in pit traps in the unburned than burned areas. Neither area had been grazed during the previous 25 years. McCoy (1987) found little difference in species richness of ground beetles in plots which were unburned for more than 20 years vs. burned every 1, 2, 5 or 7 years in a Florida sandhills area. No clear patterns emerged, possibly due to the confounding of the site burn history and the time since last burning variables. (The paper does not indicate exactly when the burns were done relative to the time of the study.) From 23 to 28 species of ground beetles were collected by pit trapping from each plot.

Huber (1988) explained that tiger beetles (Coleoptera: Cicindelidae), are near the top of the invertebrate food chain and thus face the same problems as mammalian and avian carnivores; they are similar in importance to the functioning of their ecosystems as are the mammalian and avian carnivores on a larger scale. Their extreme habitat restriction also places them in danger of extinction. Huber proposes half of Minnesota's tiger beetle species for listing as endangered, threatened, or special concern. Cicindela macra macra is found in sandy areas within the prairie ecosystem in southeastern Minnesota. These beetles may be harmed when grazing animals trample their larval burrows, but the main threat is development of their open sandy habitat.

Lepidoptera (Butterflies, moths and skippers)

Vander Schaff (1984) studied the Oregon Silverspot butterfly (Speyeria zerene hippolyta) on the Cascade Head Preserve in Oregon. The butterfly's habitat is grassland which was maintained by fire in presettlement days, then by grazing for the last 100 years. Controlled burns during 1983 tended to increase the larval food, Viola spp. but the butterflies were scarce on the burned area. The scarcity may have been due to high winds in the burned area, a scarcity of nectar plants there, or death of larvae or eggs during the burn.

Schlict and Orwig (1992) noted the temporal sequence of habitat use by prairie obligate skippers in the Loess Hills of Western Iowa. Flight periods occurred between April 19 and October 2, so that at least one species was present in a vulnerable life stage (unable to fly) at all times during the management season. They recommend the use of multiple management techniques at different times and on small portions of the patches of plants used by prairie obligate invertebrates.

Karner blue butterfly, Lycaeides melissa samuelis, has received substantial study leading to and resulting from its placement on the federal endangered species list (Andow et al. 1994a). Karner blue is found in pine barrens in the east and oak savanna in the midwest, or in their remnants, and it is in rapid population decline. These habitats are similar to prairie in that they require disturbance to prevent succession to woodland, yet the butterfly itself appears to be susceptible to mortality from fire at any time during its life cycle. Eggs and larvae are more likely to be killed by fire than are adults and pupae. Fires during especially dry years may be especially harmful to butterflies.

Despite extensive study, many factors related to Karner blue survival are not yet understood. How far individuals can disperse, and through what types of habitat, remain unknown. The butterfly is dependent on lupine as its larval food, yet many areas with large lupine populations do not support the butterfly. Landscape-level dynamics of the butterfly and its habitat may not be receiving adequate study for long-term management.

Dana (1991) studied the prairie skippers Hesperia dacotae and Hesperia ottoe in southwestern Minnesota. Higher fuel loads and later timing of burns increased larval mortality: in early spring larvae are in burrows, later they move to surface shelters. Early spring burns with light to moderate fuel loads will not produce enough mortality to be of concern. Also, late spring burns can delay the flowering of nectar plants. Fall burning may pose a greater risk than spring burning. Dana noted that the ambush bug Phymata, probably a significant predator on the skippers, showed nearly total mortality in the spring burns; its population did not recover until later, when the skippers' flight period was almost complete. Crab spiders were not affected by the burn. Moderate grazing appears to maintain the grass at a suitable height for the skippers, and some of the favored nectar plants respond well to grazing. Male skippers used trampled areas by stockponds for "puddling".

Swengel (1993) surveyed butterflies and skippers in 93 study sites in Illinois, Iowa, Minnesota, Missouri and Wisconsin during 1988-1993. The sites were divided into units according to most recent management (not stated how this was determined), vegetation type or degree of habitat degradation. The report does not indicate how many sites were divided into units, nor exactly how this was done. Lepidoptera species were classified as specialist (restricted to prairie), grassland (prairie and old field), generalist (grassland and other habitats) and invader (overwinters outside of study area); 90 species were observed. Abundance of each species for each site or unit was determined by walking a single transect through the area and counting the individuals observed.

Presence/absence of species on recently burned (burned since last growing season) vs. not recently burned units was noted. Twice as many individuals as expected from random distribution, mainly Monarchs, were found on the recently burned units.

Transect counts were converted to individuals per hour, and comparisons were adjusted to account for differences in weather, year of observation, and site vegetation, degree of degradation and size. Butterfly populations were then compared for each species for units with recent fire (burned since the last growing season) vs. units without recent fire. In the Upper Midwest sites, of the 4 specialists, 3 showed lower numbers in recently burned units; of 12 grassland species, 2 showed lower numbers in recently burned units and one showed higher numbers. Of the 9 generalists, none showed lower numbers and three species showed higher numbers on the recently burned units; of the 4 invaders, 2 species were found in higher numbers on the burned units, none in lower numbers.

Adjacent units which varied in recency of burn were compared for numbers of butterflies observed per hour. The report does not describe how the date of the most recent burn was determined. Sixty-two pairs of units in 36 sites and 17 species were available for analysis: 4 specialists, 4 grassland, 5 generalists and 4 invaders. Chi-square analysis showed lower numbers among specialist and grassland species, and higher numbers in 1 generalist and 3 invaders when units burned since the last growing season were compared to adjacent units unburned for 2 or more years. When units which were burned last year were compared to units unburned for two or more years, of 12 species which could be compared, one specialist and one grassland were present in higher numbers on the unburned areas, and one generalist was present in higher numbers on the recently burned area: a similar pattern to that observed when units which had both been unburned for two or more years were compared pairwise.

When management age classes were compared over all, specialists as a group were most common on units one year since burn, less common on units burned 2 and 3 plus years previously, and least common on units burned since the last growing season. Invaders showed a pattern almost opposite to this. Grassland species abundance increased with years since burn, and generalist abundance declined with years since burn. When individual species populations could be compared in units of different time since burn, specialists tended to be present in the highest numbers in units which had been burned one or two years previously, lowest in units burned since the previous growing season, and intermediate in units burned 3 or 4 years ago. Invaders tended to be highest on units burned since the previous growing season, and to decline thereafter. Grassland and generalist species showed intermediate patterns. A derived term, relative rank, was used as an index of abundance: this is the proportion of total observations found in each management class for the group as a whole, so the four groups are being compared with each other, not with themselves from year to year. A low number indicates a lower number of observations than would be expected if the group was evenly distributed among the management units. Differences in populations on adjacent units may indicate population changes within each unit, or movement of insects into preferred areas.

Comparison with of burned prairies with prairies managed by haying in Missouri were limited by the small number of sites, but hay prairies generally showed more individuals present than burned prairies, especially when areas just hayed were compared to areas just burned. Individual specialist species varied in their presence on sites following fire, haying and grazing to the extent that these could be observed. Haying appeared to benefit the Dakota skipper and Arogos skipper, and grazing and haying to benefit the Regal fritillary.

Swengel (1991) studied the regal fritillary on 35 sites in Minnesota, Wisconsin, Iowa and Illinois during its flight period in 1990 and 1991. She found topography (both upland and lowland prairie present on site), prairie size (areas of more than 250 acreas had the largest populations) and burn management since the last growing season (units burned since the last growing season had fewer regals) to be important factors in determining the number of regals observed. Larval food (violet) abundance did not appear to be an important variable. Swengel (1994) continued to survey prairie areas for the regal fritillary and the Ottoe skipper in Illinois, Iowa and Wisconsin. Regal populations in Wisconsin were generally low and tended to be located on private farmland or combinations of preserve and private farmland, in sets of nearby fragments with grazing history. The Ottoe skipper was restricted to high quality dry prairie and sand prairie, and was found on 7 sites in Wisconsin, with only one site each in Iowa and Illinois. Some of the Wisconsin populations have persisted at very low numbers for several years; they were formerly larger.

Nekola (1990) surveyed the butterfly and skipper fauna of 16 Iowa prairie remnants, ten managed and six unmanaged, during three days in early June 1989. Each site received a visit of 30-90 minutes. The six unmanaged (i.e. unburned; not stated how this was determined) sites had 4, 2 (2 sites) or 1 (3 sites) prairie restricted species, while the ten managed sites had 4, 1 (4 sites) or no (5 sites) butterfly species which were defined by him as prairie restricted. Most of the unmanaged sites were in the northwest corner of the state; the managed sites were more scattered. The sites ranged from 14 to 200 acres in size: five of the managed sites, but no unmanaged sites, were larger than 90 acres. Total butterfly species on sites did not differ between managed and unmanaged sites. Nekola also reports 15 anecdotal site histories, and six of these describe loss of prairie obligate species since burning began. In four of these cases, prairie butterflies of the species lost from the managed area were observed on nearby unburned areas. Schlicht (1993) also gives anecdotal descriptions of unmanaged prairies such as railway rights-of-way, hayfields and pastures with greater prairie obligate butterfly diversity than managed sites.

Dana and Huber (1988) recommended habitat protection for the Uncas skipper Hesperia uncas, the Assiniboia skipper H. assiniboia, Uhler's arctic Oeneis uhleri varuna, and the Ottoe skipper Hesperia ottoe (as well as of the other endangered, threatened, and special concern species in Minnesota); more information is needed on their complete life cycles and food sources.

Hymenoptera (Ants, wasps and bees)

The gall wasp Antistrophus silphii Gillette is vulnerable to spring fires in the stem of its host Silphium integrifolium var. laeve Torrey and Gray. Fay and Samenus (1993) measured heights of 1, 062 galled and ungalled shoots at Konza; galls were most abundant on mid-length shoots. Shoots lodged during the winter, abolishing the height difference and bringing galls lower, where they were vulnerable to fire. A spring burn in this one-year study caused catastrophic mortality of gall wasps at the heights at which wasps were found. Personal observation by Fay indicates that wasps can survive in large, dense, Silphium patches, which are somewhat resistant to fire. The gall wasp appears vulnerable to local extinction in land managed with annual burning. They did not study possible indirect effects, eg changes in host plant quality, on wasps.

Trager (1989; 1990) states "the litter-inhabiting cryptic species and twig-, stem-, and acorn-nesting species which make up a large portion of the woodland ant fauna are virtually lacking in regularly burned prairies, while the prairie is much richer than the woodlands in mound-building and subterranean root-aphid tending species". His research over two years on ants of natural and recreated prairies in Missouri and Illinois near St. Louis suggests that prairie ants, which are all soil-dwelling, are unaffected by burning frequency as long as the open, native-dominated character of the vegetation is maintained. Many prairie ant species have been successful in colonizing recreated prairies.

Kannowski (1994: pers. comm.) noted that fire is detrimental to the thatching ant Formica obscuripes because the thatch covering the nests tends to catch fire and kill workers and brood. Also, fall fires reduce reproduction during the following season as the loss of vegetation in the fall decreases the snow retention capability of the habitat and subjects the nest to greater temperature extremes.

Warren et al. (1987) note that ants are able to survive the combustion phase due to their cryptic habits, their tolerance of dry soil makes them well adapted to the shock phase, and their social habits allow them to recolonize burned areas rapidly.

Descriptions of Preferred Sites

Understanding the basic biology of a species is essential for its conservation, and descriptions of sites which support healthy populations of the species is an important first step toward this understanding. Royer and Marrone (1992a-h) searched for Atrytone arogos, Euphyes dion, Hesperia dacotae, Oarisma powesheik, Poanes massasoit, P. viator, Phyciodes batesii and Speyeria idalia in North and South Dakota during the summer of 1991. The typical habitat of Atrytone arogos (Arogos skipper) is undisturbed bluestem-dominated prairie remnants with a variety of Asteraceae such as coneflowers, black-eyed Susan, and thistles which are nectar sources for the adults. This skipper is typically found in low numbers. The big bluestem, Andropogon gerardii, is its larval food; the fourth-instar larvae hibernate in a leaf cocoon about a meter above the ground. Threats to the species include loss of nectar sources due to aerial herbicide spraying to combat leafy spurge, invasion of the habitat by brome grass and bluegrass, and overgrazing leading to degradation of the habitat. The authors state that the effect of haying or controlled burning on this species are not entirely understood.

Euphyes dion, Poanes massasoit, and Poanes viator are restricted to permanently wet sedge marshlands, and E. dion is found only in the Sheyenne Delta of North Dakota; continuous water turnover seems to be required for these skippers as they are not found in more poorly drained prairie pothole areas. Euphyes dion and P. viator are associated with cattails, bullrushes and the sedge Carex lacustris, their larval food. In nearby similar habitats where alder, birch or willow are dominant, making the area shady (shrub swamps), P. massasoit is more likely to be found (Carex stricta is its larval food). The healthiest P. viator populations are found on sedge marshes with woody shrubs nearby. Both Poanes species are tightly restricted to their habitat and rarely move even from one oxbow to another. Recent oxbows are less suitable for these species than older oxbows, making this a successional habitat. Domestic livestock damage this habitat by trampling. Euphyes dion males appear to require a large territory, up to half an acre per individual; in contrast, Poanes viator individuals are non-territorial and normally occur in high density.

Oarisma powesheik is most often found in sedge plus grass communities forming a transition zone between wetlands and uplands. Hesperia dacotae, *Speyeria idalia* and *Atrytone arogos* share this habitat. *Oarisma powesheik* thrives in healthy tallgrass prairie and “produces blooms of epidemic scope”, for example hundreds of individuals on one six-acre site. In the past, populations were probably continuous over large areas, but now only widely separated remnants remain. This species appears to tolerate some haying but is threatened by wetland drainage, bluegrass and brome invasion, and by herbicide and pesticide use. Dana and Huber (1988) note that this species is less habitat specific than other rare Minnesota Lepidoptera and is able to persist in small remnants, in a wide variety of prairie habitat types, and is able to tolerate moderate habitat degradation.

Phyciodes batesii is associated with moist clearings in natural spen or green ash woodland margins, especially in riparian situations, in the ecotone between forest and prairie. The preferred habitat often occurs where valley-bottom woodland meets undisturbed bluestem prairie. The habitat sometimes occurs at roadsides, where the larval food, *Aster* spp, is threatened by herbicide spraying to control leafy spurge (leafy spurge is a preferred nectar plant for this butterfly). It is not known whether the species is stable or declining in the Dakotas, but there is no reason to believe that it is increasing.

Speyeria idalia is likely to be found in any mid- to tallgrass native prairie site with adequate nectar supplies, in South Dakota and southeastern North Dakota, and may be locally common in these areas. Typical sites contain bluestem and numerous Asteraceae, milkweeds, thistles, bergamots and blazingstars. The larval food, *Viola* spp, is also required. The authors suggest that the species establishes itself and then disappears intermittently on isolated prairie remnants; it is a vagile species that readily colonizes suitable habitat. Females range widely during the late summer for nectaring and oviposition. Late haying may be an alternative to fire in habitat management; the management goal is to prevent drastic changes on habitats where populations are known to occur.

Hesperia dacotae is an obligate resident of undisturbed tallgrass to midgrass prairies, typically undistubed bluestem-dominant remnants with a variety of Asteraceae which are used as nectar plants. The skipper is found in two types of habitats which the authors designate as wet mesic and dry mesic; these habitat types converge in South Dakota, and both are marginal for agriculture, which has protected some skipper populations. The habitat is commonly associated with the margins of glacial lakes. In wet mesic situations, *H. dacotae* may be dominant to the exclusion of other species, while in dry mesic sites the habitat may be shared with *H. ottoe* and *Polites origines*. Where the dry mesic habitat has been degraded by grazing, *H. uncas* typically replaces *H. dacotae*. Dry mesic sites appear to be somewhat resistant to woody invasion; wet mesic sites may be protected from succession with the least damage to the skipper by October haying. The skipper’s historic response to fire and haying is not well understood. *H. dacotae* is not inclined to disperse unless its habitat is disturbed and it must move away to find nectar. The authors state that the dispersive capacity of this species is effectively nil due to the small size and isolation of its remaining sites. Threats to this species include weedy invasion of the habitat and chemical control of weeds (this destroys nectar plants), spraying to control grasshoppers and widespread fire and early haying in fragile and isolated habitats, as well as conversion of habitat to agriculture. Dana and Huber (1988) note that H. dacotae is commonly associated with the purple coneflower Echinacea angustifolia in Minnesota, in undegraded prairie usually with midgrasses. Herbiciding, overgrazing, gravel mining and agriculture threaten this skipper in unprotected areas. Protection of this species in Minnesota is important as a significant number of the surviving populations occur in Minnesota.

Factors which Influence Site Responses to Management

Site history influences the response of the organisms on the site to any managementby two mechanisms: the lasting effects of a single management treatment or incident, and the long-term changes in species composition in response to long-term management practices including no intervention. The effect of a fire on litter depth persists for approximately 5 years in the northern tallgrass prairie (Ehrenreich and Aikman 1963). Gibson (1989) in a compilation of long-term studies on the Konza, noted that six to ten years of experimental treatments were insufficient to remove all effects of prior grazing and burning on plants. Brotherson and Landers (1978) described the Kaslow prairie site in central Iowa, one portion of which had been heavily grazed before acquisition. After 20 years of protection (management techniques were not described in the paper), one-fourth of the species on the adjoining prairie had reinvaded the former pasture and the authors predict that full recovery from grazing will require at least 100 years.

To what extent have plant and animal communities on prairie remnants changed in response to the fragmentation and isolation which have occurred since settlement? Nekola (1990) states that since over a century has elapsed since fragmentation became extensive in Iowa, most species which are intolerant of fragmentation have already become extinct. The surviving species are those which tolerate isolation, small population sizes and small habitat areas, and other conditions associated with life in prairie remnants, including the absence of fire. If this is the case, introduction of fire management may lead to the extinction of some species. In contrast, the Konza prairie in Kansas has been burned annually for many years by ranchers: an additional burn on this area would be expected to cause little change in plant or animal communities. Nagel (1973) suggests herbivore populations could increase where recurrent burning is practiced since herbivorous insect biomass increased on burn areas while parasite and predator biomass did not in his study.

Topography, patchiness of vegetation, and soil moisture influence the heat and completeness of burns. Topography is also an important influence on the choice of grazing areas by herbivores. Weather before and after a burn influences the burn itself and the responses of plants and animals to it. In general, sites which are located further east and south in our area are faster to recover from burns and more prone to woody invasion than the drier western sites.

Factors which Influence Insect Responses to Management and to Vegetation Changes following Management

Life history features, mobility, host specificity, and requirements for multispecies interactions such as predation and mutualisms can potentially influence the responses of insect species to management, and many specific examples have already been given. Lycaenid butterflies were suggested by Cushman and Murphy (1993) as being especially susceptible to endangerment due to their low dispersal ability, the limited geographic range of the subspecies, hostplant specificity, and associations with ants. Swengel (1993) proposed a qualitative model to predict the responses of Lepidoptera species to burning. Widely distributed generalists will be more able to repopulate a site following burn-induced mortality than will narrowly habitat-restricted specialists; multivoltine species will recover from a burn faster than univoltine species because they have more generations to work with; the insect's location during the fire may be important, eg. species burrowing into the ground may be protected from fire; highly vagile insects will be less affected, as a population, than more sedentary insects as they will tend to recolonize burned areas faster. Finally, insects whose host plants tolerate and quickly recover from burning will be faster to recover following fire. Other factors, such as fire effects on mate-finding and on predators may also be important.

Nagel (1973) predicts that species with life stages in soil at the time of burning may be favored by burning, since higher soil temperatures post-burn will speed their development, while those in litter or stalks will be reduced.

Insects frequently become locally extinct, then recolonize areas, so mobility is generally accepted as an important factor in allowing a species to persist. Many species declines and extinctions have been ascribed to low mobility (Dempster 1991).

A high degree of host specificity, whether of a herbivore for its plant, a parasitoid for its host, or a predator for its prey, will limit an insect species to the area where the host is found, and the host's response to management will be significant in the insect's response also.

Few tests have been made of the effects of the factors listed above on survival of insects on managed sites. Ballard and Greenlee (1994) found that low mobility and above ground oviposition were not detrimental to orthopteran survival on fire-managed sites: in fact, species with these characteristics were found in higher abundance and species richness on annually burned sites than in unburned areas.

Management Goals and Recommendations of Authors

The controversy over prairie management methods is in part due to differences in management goals. Management goals may be broadly based on some vision of the pre-settlement or pre-human prairie; they may be derived from present-day sites thought to be of high quality; goals may be narrowly focused against a single threat such as woody invasion, or may emphasize (sometimes by legal mandate), the conservation of a single species-- at present, often prairie chickens or waterfowl. Once goals are set, management methods are limited by the information available: both general information concerning plant and animal species, and specific information on the actual site to be managed. Resources available to managers limit the both the availability of information and the extent of management activities. Conservation of high-quality prairie sites, restoration of degraded areas, and reconstruction of new prairies are related but not identical issues, and definitions of site quality differ among specialists. Conservation of rare species on any site where they occur is valuable: but for long-term survival, all populations of the species must be considered.

Discussions with scientists, managers and others interested in prairie conservation reveal strong opinions about the best conservation methods, coupled with concern on the managers' parts about the necessity of management for a variety of objectives simultaneously, pressures from the public, and lack of knowledge and resources to pursue insect conservation (conservation of insect biodiversity, prairie endemics or certain species) in addition to maintenance of the prairie plants on their sites. Botanists often claim that frequent burning is necessary to prevent woody plant invasion while many lepidopterists argue that burning is harmful or fatal to prairie butterfly species. Some of the authors cited here conclude that burning is useful or even essential for insect conservation, while others do not agree that burning is necessary or even valuable in keeping woody plants out of prairies.

Recommendations may be in conflict due to conflicting management priorities: Schramm (1992) and Schwarzmeier (1994) are most concerned over the loss of prairie plant species as woody plants and exotics invade prairie sites on a large scale; if the prairie habitat is lost, prairie insects will be lost also. Schramm (1992) states that most prairie preserves are not burned often enough, thoroughly enough or at the right time. Many sites are being lost to woody plant invasion due to lack of burning. There is only one time to burn: early spring. Early spring burning leaves winter wildlife cover and stimulates early germination and sprouting to promote prairie plant growth during the time when maximum moisture is available. This lengthens the growing season for warm-season plants. The main outcome of a fire is to stimulate prairie plant species to make them competitive (suppression of exotics is less important). Late spring burns stress the warm-season natives just as they are entering peak growth. For remnants: "How frequently the original prairies burned does not have much bearing on determining frequencies for management." This is due to abuse by grazing, haying and other disturbances--remnants need regular burning to maintain their original quality. Burn half the area each year to leave refugia for possible endemic insects. If improvement is evident after 10 years, burn half every three to four years. Reconstructions should be burned every year for 10 years or so--there are no endemic insects to worry about. After the reconstruction is well established, burn half every three to four years. This advice applies to hill, glade and sand prairies as well as flat mesic areas. Mowing and grazing can't substitute for fire as they result in incomplete litter removal. Pre-settlement grazing probably had minimal effect on the prairies (compared to fire) due to the migratory and nomadic movements of the animals. All this based on his 25 years experience with prairie restoration in Illinois.

Schwarzmeier (1994) also urges major increases in burning (in Wisconsin) based on his observation of increasing brush invasion of prairie and savannah remnants, especially since the cessation of wooded site grazing in central Wisconsin which occurred during the 1960's. Schwartzmeier points out that local savannah and prairie remnants (unlike prairie reconstructions) usually experience patchy burns due to their varied topography and vegetation, so that adequate refuges for invertebrates would be left after large-scale fires. He also notes that smaller burns require land to be used as firebreaks, and the additional preparation time required for numerous smaller burns will result in less acreage being burned per year. Wet areas cannot be mowed because they will not support the machinery, and mowers will also damage thin soils, especially on slopes.

In contrast, Nekola (1990) urges benign neglect rather than careless management. The minimum necessary management should be done, and the smallest sized disturbance patches should be created. Burning should be done no more often than every six to eight years, as mulch buildup reaches its maximum after six years. Spot brush cutting and herbiciding, or light grazing and mowing (which maintained these remnants before they were protected) may be used. He urges management for maximum biodiversity by maintenance of maximum habitat heterogeneity and emphasizes the importance of maintaining internal recolonization sites since prairie remnants are unlikely to receive external colonists. Swengel (1993) and Schlicht (1993) also urge consideration of no management as a management option for Lepidoptera on prairie remnants.

Recommendations may be aimed at increasing biodiversity, preserving species which are prairie obligates, or protecting single prarie insect species or groups of species. Ecosystem management for multiple land use, in which conservation of the habitat or species is only one of many purposes of management of the area may be required.

Opler (1981) recommends surveying and mapping of sensitive insects on prairie remnants on a regionally coordinated basis, followed by monitoring of presence and relative population levels. Additional preserves, as large as possible, should be secured, and untilled land adjacent to small or medium prairie reserves should also be managed for prairie species. Prairie wetlands should be well represented as they have obligate species. Reserves should be connected by corridors along railway or highway rights-of-way planted to native plants of local ecotypes. Burning and mowing should be done on a rotational scale, and the entire range of an insect's host or nectar plant should not be burned or mowed simultaneously. Nectar plants may be reintroduced if they are absent from a site or present at low levels. Management of insects which are dependent on vertebrates, such as dung-feeding scarabs and tenebrionids which use animal burrows as shelters, will be more difficult. Healthy vertebrate populations must be maintained, and if vertebrates are reintroduced, their insects should be included also.

Ehrlich and Murphy (1987) give "lessons" based on their 27-year study of of checkerspot butterflies (Euphydryas spp). Of special relevance to prairie insect conservation are these: 1) movement of individuals between habitat patches or reserves does not necessarily mean that gene flow is occurring: nor does it mean that in the case of extinction, one patch will recolonize the other. 2) Topographic heterogeneity or other aspects of habitat diversity may be key determinants of habitat suitability for the maintenance of insect herbivores. Ehrlich (1992) adds: the favorability of microclimates varies from year to year--a complex interaction between rainfall, host plant, slope and exposure determines which areas are suitable for checkerspot larval survival. 3) Under severe environmental conditions, the degree of oligophagy (food specialization) may be a crucial determinant of extinction proneness. 4) Recolonization of empty patches may not occur in most years; many populations may be re-established in rare years of explosive dispersal (note: this may apply to establishment of new populations on prairie reconstructions as well) and, 5) The ease of maintaining a metapopulation or re-establishing extinct metapopulations by introducing insects into "empty" habitat is difficult to predict. 6) Environmental stochasticity, especially variation in host quantity, quality and phenology, is the major cause of extinction, particularly in small populations; reserves may need to be larger than predicted from a species use of the area in non-extreme years. 7) Introduced mammalian herbivores may have complex impacts on endangered herbivorous insects. Especially discouraging lessons are: 8) Habitat patches and metapopulations are difficult to protect and 9) Endangered populations of insects may be "studied to death". "We probably should make a best guess about the habitat area required to preserve a species, and then at least double that area to reach a recommended minimum reserve size." Studies must be long-term. We must focus on the conservation of populations, not species.

Should prairie remnants be managed? Swengel (1991) notes that there are biodiversity costs of management; some species may be lost with any management. She urges setting of common-sense management goals for the long-term health of the whole community without compromising short-term needs of individual species.

How should we choose areas for intensive management? Swengel (1994) makes a distinction between sites requiring conservation action (those where the animal is rare), and sites which are most suitable for conservation research: those where the animal is most abundant.

Swengel (1991) distinguishes among high-quality prairie, semi-degraded areas, and degraded areas. In high-quality areas, management aims at maintaining the plant and animal species already present: management should be conservative. “Degraded areas may be managed in the most cost-effective--i.e. intensive ways, since the results are more beneficial than the methods are costly.” Semi-degraded area should be managed more intensively than high-quality areas. For regal fritillary conservation, improving a degraded site to semi-degraded is more beneficial than improving a semi-degraded site to high quality, in terms of the relationship between management costs and benefits to the butterfly population. Swengel suggests that it is more important to prevent woody invasion than to eradicate herbaceous aliens. For regals, suggests a 4, 5 or longer year burn interval with a maximum of 20-25% of the site burned per year--but do not let unburned units become too small for the species to maintain its population. Rather, include no-burn years.

Kirby (1992) recommends grassland management by cattle grazing to maintain habitat heterogeneity, hence biodiversity, on ancient grasslands in England. Traditional management practices should be maintained on sites where they have been practiced for a long time. Cutting can also be used if it is done on a rotational basis to allow different turf heights, is done late in the year, and if the cut material is removed to prevent litter buildup. Burning is recommended only as a method of last resort on overgrown sites, not as a consistent management method. The whole site should never be burned at one time. Some shrubs may be left to increase habitat heterogeneity and and provide nectar and pollen, shelter and resting places for insects. Grassland communities in the British Isles have not been maintained by fire historically, nor are they threatened by exotic plant species.

Swengel (1993) recommends managing for maximum biodiversity by using different management methods. Fire should be minimized, used as rarely as possible and only when mechanical treatments fail. Never-burn areas should be set aside. Doing nothing is appropriate when assessment and monitoring of the site have not been completed. Her focus is rare butterflies; she states that management for forbs, prairie birds and butterflies need not conflict; however, sites should be managed “from the top down” with focus on higher trophic levels (herbivores and carnivores) rather than plants. It is not valid to assume that an intact plant community ensures an intact animal community. Swengel (1993) and Schlicht (1993) generally concur on management recommendations: fire should be used as rarely as possible; if burning is done, a 5-10 year, or at most 3-year fire cycle should be used. Adjacent units should not be burned in consecutive years. Burn units should be long and narrow to maximize edge, and should be designed to ensure that no habitat patch or type is completely burned in any year. Small areas of critical habitat should be protected from burning. No burn should be done without a compelling reason.

Moffat and McPhillips (1993) state “A sound management plan should combine control methods such as fire, mowing, grazing, and spot-herbiciding and spot-brushing to maintain biodiverse grassland communities... reserves should be treated in carefully laid out sections...based on invertebrate species presence, nectar and host plant distribution, and total reserve size." Their goal is promotion of biodiversity and native prairie species; they consider that management to benefit butterflies will help to conserve all native species. Small reserves need special care.

Panzer (1988) is specifically concerned with prairie obligate insects on prairie remnants. He notes that habitat deficiencies, excessive levels of competition and predation, and intensive burning regimes can contibute to the extinction of insects from prairie remnants: management should minimze these problems by restoring habitat diversity, eliminating unnatural habitat features, and burning with restraint. Opportunistic predators including robins, crows, starlings, raccoons, opossums, skunks and domestic cats enter preserves and prey on invertebrates in recently burned prairies; tree-lined ditches, utility corridors and weedy trails are often their entry corridors. Non-prairie landscape features, especially shrubs and trees, support ecologically tolerant insects which may compete with prairie specialists on sites where prairie areas are small. Thus, non-prairie features should be eliminated or reduced. Many insects require habitat mosaics, different parts of which are used during different parts of the life cycle. Habitat diversity (i.e. a range of habitats from wet through dry prairie, typically lowlands and uplands) should be maintained and restored; frequently uplands are badly degraded while wetlands may be in better condition on the same site. Resources, such as nectar for butterflies, may shift through these ranges from year to year.

Many species are known to be fire-sensitive during at least part of their life cycle, yet they have managed to persist on fire-managed remnants studied by Panzer (although Swengel (1993) states that more Lepidoptera species should be present on these sites than have been observed). Thus burning need not be eliminated, but should be done cautiously. Fifty to 75 percent of the intact plant community should be spared from burning each year, while severely degraded areas should be burned intensively to expand and restore prairie plant communities. Burn units should include samples of each habitat type. Unburned skips should be left as they occur, and fires should be cool. The abundance of fire-sensitive species should be monitored annually. The loss of species which has been documented over the last several decades can be expected to continue, and direct intervention will be necessary to prevent further species loss. Rare insect species should be reintroduced to sites within their former range to establish additional protected populations on the largest available sites; Goodman (1987) also recommends reintroduction of species into geographically dispersed reserves which experience mutually independent environmental variation.

Schlict and Orwig (1992) recommend the use of multiple management techniques at different times and on small portions of the patches of plants used by prairie obligate invertebrates. Orwig (1992) notes the need to prevent or reduce invasion by leafy spurge (Euphorbia esula) which is highly tolerant of burning. He recommends careful use of herbicides, mowing, grazing and brush-hogging, and longer fire intervals. Patchiness and biodiversity must be emphasized, because we don't know much about which species are present, or their requirements for survival.

Issues related to single-species management of the Karner blue butterfly, which is present on many sites with different sized populations, are discussed by Schweitzer (1994) and by Andow et al. (1994b). Both papers note the importance of whole population rather than single-site conservation. Schweitzer states that tiny populations have little prospect for survival (this includes most of the known Karner blue sites), and that limited resources might best be applied to sites with larger populations; also, protection efforts should be biased toward sites where a functioning barrens or savanna community could be restored. Conversely, Andow et al. state that population size is not necessarily a good predictor of population persistence in Karner blue; at this time, the information is not available to predict which populations are likely to persist with or without management. Andow et al. explicate the conflict between two conservation philosophies: triage versus spread the resources. In a triage system, only populations considered likely to recover and persist receive management attention. Spreading the resources implies that all populations receive some management resources. Theoretical advantages of spreading the resources are based on the greater genetic variability among a larger group of populations located in different geographical areas and somewhat different habitats compared to the variation in a few larger populations located in only a few areas.

Andow et al. note that Karner blue appears to be able to coexist with humans--thus its recovery could be linked with anthropogenic disturbance as well as with habitat restoration and preservation. Ecosystem management for multiple uses could result in the loss of some Karner blue to allow alternative uses of savanna and barrens.

Other authors have made specific recommendations for their study areas or groups. Ballard and Greenlee (1994) emphasize the need for well-managed buffers around high quality prairie sites to prevent invasion by "weedy" Orthptera. Small sites may be inundated by edge species. Nearby pesticide use may also affect reserves. Frequent to annual burns should be done. Ballard (1992) recommends that prescribed burning be used only as emergency management where the open character of a site is in danger of being completely lost on the Newaygo, Michigan sand prairies which he studied. This recommendation is based on the very restricted local distributions of many of the sand prairie insect species, including some species which have high conservation priority. In most cases the distributions are not well known, and additional surveys are needed to determine these. Widespread use of fire could potentially eliminate populations of some of these species; many of the leafhoppers and planthoppers have low vagility. Carefully planned burns may be conducted once the distributions of fire-sensitive insects are known, and once insects' responses to fire are better understood. The greatest long-term threat to these areas is encroachment on open areas by oaks (ORVs actually the worst immediate threat).

Vander Schaff recommends controlled burns to increase the larval food plant, Viola, for the Oregon Silverspot butterfly. Areas which have violets on their periphery should be burned: this will increase the violet population without putting larvae or eggs at risk of mortality from burning. Burns should be small scale.

Dana (1991) for prairie skippers recommends early spring burns to produce at least one unit with no more than three growing seasons since the last burn. If skipper populations decline, controlled grazing could be tried. This refers to the Hole-in-the-Mountain site, where populations are relatively high; in other sites where numbers are lower, fire may not be advisable. Mowing may be used to reduce litter accumulation, but does not suppress exotics. Any procedure which favors midgrasses over tallgrasses will favor skippers.

Metzler and Zebold (1993) recommend a 4-year burn rotation with no more than 25% of Huffman Prairie (in Ohio) to be burned in any year. Probably natural burns did not occur more frequently than every five years; fire kills insects (though too little is known about the responses of individual species to fire), so refuges must be left. Inventory should be continued, and invertebrate biology (host plants of insects, insect fauna of plants, life cycles and microclimatic differences) should be studied.

Future Research Priorities

Research at all scales from regional views of the entire prairie to a single plot is needed. Methods and content are both important: many of the studies cited above comparing management methods are difficult to interpret due to poor design. We need more information on prairie insect communities, individual species, attributes of insect-rich prairie sites, and insect population biology.

A research project must be designed specifically to measure the effects of certain variables and to eliminate other variables. It is essential to clarify the research goal (the question to be asked) before designing the project. Glenn-Lewin et al. (1990) noted methodological problems in research on the effects of burning on plants: some studies did not include a control plot, or did not report the initial state of treatment and control plots. Some studies were based on responses to vegetation to an unexpected wildfire, so that burned and unburned areas were not randomly assigned. Every site has a history--thus "unburned" may actually be a treatment, not a control. The larger the plots, the more likely there will be differences between them in addition to the treatments; however, it may be too difficult to work with many small plots.

Another issue is the inherent variability among fires caused by the differences in vegetation patchiness, plant growth form and other site characteristics. There are usually different numbers of individuals of each species in each plot. Also, controlled fires in small plots appear to be more complete and less patchy than natural wildfires. Although some of these problems can be approached statistically, in some cases where individuals are patchily distributed and present in low numbers, statistical analysis is impossible and we must be satisfied to simply describe the patterns observed.

Kirby et al. (1992) give advice on designing studies of the effects of grazing: 1) one or more controls (ungrazed areas) must be available and 2) assignment of the grazing treatment must be done randomly, rather than using an already grazed area as the treatment area and an ungrazed area as control. 3) there must be replication of randomly assigned treatment vs. control combinations. Both spatial and temporal replication are required--ten years at least are needed to determine how long the effect of a management practice persists under a variety of weather and climatic conditions. Control and treatment sites must be compared both before and after treatment.

The above comments apply to insect studies as well as to plant studies, with the additional consideration that insects are significantly more mobile than plants. Differences in the insect populations of adjacent burned and unburned areas may show differing survival on the areas or movement by individuals from one area to the other, so sites must be well separated or very closely monitored to determine whether insects are moving from site to site.

Inventory and monitoring methods which are comparable among sites must be used. Data collection methods must be designed, or statistical techniques used, to equalize collection effort among sites. References such as Coddington et al. (1991), Disney (1986), and Krebs (1989) provide information on sampling methods and collection effort. Original data should be included in reports as well as derived statistics such as averages or percentages.

Once research is complete, it should be reported, preferably by publishing, so that the new knowledge can be put to work. Individuals and agencies should keep copies of reports on file in an accessible manner. Many studies have been lost, after all the work that went into doing them: at least, there are many reports that I have not been able to locate.

More work is need to describe the prairie insect community; the insect species composition of prairie areas is very poorly known.

For example, Henderson (1994) identified Homoptera collected from 8 prairie remnants in south central Wisconsin: of 86 species, 22 were new state records and 3 were newly described. Tepedino and Stanton (1981) collected bees for 2 summers on 2 sites on the shortgrass prairie in Wyoming; they found over 200 bee species in 43 genera; these were 1/3 of the species described for Wyoming. About a third had not been recorded in Wyoming before (new state records), and 9% were undescribed. Ballard and Greenlee (1994), collected 132 species of Orthoptera, of which 5 species were new to the state.

As inventory proceeds, some sites may be identified which are especially rich in prairie insect species. These should be described in systematic ways including management history, plant community, and physical features. We need to know whether some sites are support high species richness of all insect groups, or whether sites rich in some groups are poor in others (for example, Orthoptera appear to be highly fire tolerant, and Lepidoptera highly fire intolerant: can we see high diversity of both on one site?)

When previously unmanaged degraded prairie sites are burned or repeatedly mowed, some prairie plant species which previously were so rare that they went unnoticed become prominent. Whether this phenomenon occurs among insect species also is not known.

Until insect species are better known, they cannot be protected. There were only 51 arthropod species proposed for endangered, threatened or special concern listing in Minnesota in 1994 (Rich Baker, Minnesota Department of Natural Resources): 16 Lepidoptera, 13 caddisflies, 11 tiger beetles, 8 jumping spiders, 2 dragonflies and one leafhopper. The Department of Natural Resources requested recommendations for listing from specialists: in many cases listing is based on the work of a single individual.

How can we determine what species should be the focus of prairie insect conservation efforts? Panzer et al. (1995) in a study of prairie remnants in the Chicago area noted that less than 25 percent of the species they studied were limited to prairie remnants; this proportion varied widely among families. Major work including literature searches, collecting in a variety of habitats and identification of specimens was required to determine this figure. It is the remnant-restricted species that need management: the remaining species were able to survive in disturbed areas, and apparently need no conservation consideration. Much more work is needed to identify species which are prairie obligates, and to use the presence of these species (rather than species richness or diversity measures in general) to evaluate sites and management methods. Existing literature on well-known groups can give some indication of which species are characteristic of prairies.

Insect conservation monitoring could be expedited if one or more insect groups exists whose presence indicates that the prairie insect community is healthy: although specialists have recommended their own groups (Ballard and Greenlee: Orthoptera; Swengel: prairie specialist Lepidoptera; Comer et al.: Papaipema and other specialist Lepidoptera; Hamilton: leafhoppers; Panzer et al.: moths, butterflies and leafhoppers), there is no consensus on how an indicator group might be chosen, or how it might be used. For example, as discussed above, prairie Orthoptera and prairie specialist Lepidoptera may have different responses to management, so an increase in one group may occur along with a decrease in the other on the same site.

For single species, there is no substitute for natural history observations of their basic biology, including all phases of the life cycle. Descriptions of habitats where these species are found in healthy populations are extremely valuable. Life history, larval and adult food sources, mating and oviposition behavior, and overwintering are known for only a few species. For example:

Cuthrell (1991) searched for butterflies and skippers in prairie areas in Kittson and Roseau counties in Minnesota every day (weather permitting) during the summer of 1991. Although his index species, the Dakota skipper, is relatively well known, Cuthrell called for more studies related to its population and habitat requirements before management decisions could be made.

Insect orders, families, genera and even individual species differ in their responses to fire. Prediction of susceptibility of individuals to death from fire, and predictions of responses of populations to fire management, based on obvious life history feature, have not always been successful. How do species which are fire-susceptible throughout their life cycle manage to survive on sites which are burned?

In order to manage populations, we must answer the basic conservation biology question: is the population healthy or declining? This is especially difficult to answer for insects due to their short life cycle and fluctuating populations, and a major issue relating to initiating or changing management. If a population is healthy, management should not be changed; if a population is declining, a change in management may help it persist. Goodman (1987) suggests that the key to long-term population persistence is reduction of the variance of the population growth rate; long-term studies will be needed to test this idea. Is a widespread decline in insect populations occurring? Can we do anything about this locally?

Population structure has important implications for habitat protection and management of any species in all its sites (Andow et al. 1994b). Core-satellite populations need protection of their cores. Metapopulations, where each sub population is a critical component of the whole population, are in danger with the loss of any of their populations. Persistence of single continuous populations does not depend on other populations.

Usually a site will contain only a fraction of the insect species present at a landscape scale for any group (grasshoppers, Kemp 1992; bees, Reed in press). Conversely, distributions of single species often show patches of apparently perfectly good habitat which lack the species. To what extent is this a normal feature of insect populations, and to what extent is this a consequence of fragmentation? This situation is often interpreted as evidence that the habitat is unsuitable, or that the species is in decline, but instead may be a normal feature of the biology of the species. Most status survey reports include several locations not yet investigated, but believed likely to support other possibly extant natural occurrences, and it will be interesting to monitor these sites and see whether they are eventually colonized by the species of interest.

Interactions among species on sites needs more study. Competition of prairie specialists with generalist insects, has been very little studied; in general there is little evidence that insect species compete with each other, but competition, especially at site edges, has been suggested by some observers as a threat to prairie species on small sites. Predator-prey interactions among prairie insects have received little attention.

Some basic management issues still need more work. Very few studies have been made on the use of grazing and haying for conservation management in the northern tallgrass prairie. Interactions of grazing with burning need more study, and even the issue of the tendency of woody species to invade prairie sites, and the extent to which this can be controlled by burning, or by grazing, is still confusing. There are many sites where woody plants continue to invade, despite repeated burning, and whether the answer is more burning, other management methods such as combining burning with grazing, or whether this increase is an inevitable result of long-term climate change, is still unknown. Comparisons of sites where burning is and is not effective with full attention to management history and site features may clarify this.

The insect populations of managed and unmanaged sites, or of sites differing in management methods still need more study. Such a study should include sites of known (not inferred) management history which are near to each other, though distant enough to prevent exchange of individuals in the short term, and similar in all respects except for the management variables being tested. All major insect groups should be included, and the status of each as prairie specialist or not should be noted.

Conclusions and Recommendations

Many insect species suffer substantial mortality during burns, regardless of burn timing, and other species leave the burned area following the fire. Many insect species are immediately attracted to the burned area; some emerge earlier from winter diapause following a burn; others make extensive use of the new vegetation growth which follows burns, and some species are dependent on plant species whose growth is stimulated by burning. For example, many prairie specialist Lepidoptera die or leave an area following a burn: but they are found in high numbers on areas burned two years previously. Leafhoppers are susceptible to fire mortality, but some species quickly colonize the lush growth on recently burned areas. Some characteristic prairie insect species exhibit such low mobility that they are rarely able to colonize new sites The effects of haying are similar to those of burning, but litter removal is less complete, soil warming does not occur as extensively, and plant and insect populations return to their previous state more quickly.

Most insect species use only a small fraction of any site. For example, among the sedge skippers described above, each species selects a subhabitat along the moving water to mesic prairie gradient. Other species are limited to areas containing their larval food or nectar plants. The exact fraction of the site used may vary from year to year depending on weather-, animal- and management-induced changes in microclimate and in plant distibution and senescence.

Ample evidence indicates that management activities, especially fire frequency, have major influence on plant and animal communities. Areas which are burned annually support different plant and animal species than those which are burned less frequently or not at all. An intermediate level of burn frequency (burning every few years) generally produces the highest plant species richness based on a mix of fire tolerant and fire intolerant species, but it has not yet been shown whether insects follow this pattern also.

Complete site surveys should precede any management. Surveys ideally should include information about the insect species present and the ways in which they use the habitat. For example, do insects use the trails created by grazing animals, or the plants which colonize the trails? Are there any site features which may aid the invasion of alien species? Threats to the site should be noted, and an estimate made of how serious they are or how soon they may become serious. Will immediate intervention be needed to counter these threats, or is there time for planning?

Site quality should be assessed: use prairie species presence to evaluate sites regarding insect quality. Determine whether the site is of good quality, to be maintained as it is using past management practices, or of poor quality, to be restored.

Analysis of site history should also be done: past management has allowed persistence of populations on the site so far. If these populations are healthy, there is no need for management change. If they are declining, or if the site is changing in other ways which will cause them to decline, management may help. Monitoring will be needed to determine whether populations are stable or changing.

Develop management objectives and ways to measure whether they have been met. Look at all populations and all sites, rather than trying to have everything on one site: in some cases, management for one rare species may be incompatible with management for another. It is not possible to manage for all plants and animals simultaneously. Annual early spring burning of whole sites will usually lead to reduction in woody plant and Kentucky bluegrass invasion, development of a plant community high in warm-season grasses and relatively high in mid-season forbs, and a fire-tolerant insect community including many grasshopper species. Fire intolerant insects, such as some Lepidoptera and leafhoppers, and spring-flowering forbs, will decrease or be lost from the site, depending on the site topography and the completeness of burns. Changing the burning season to fall may increase the spring forbs and bluegrass, but the effects on insects will be similar to those of spring burning. Decreasing the burn frequency, so that the site is burned every four or five years or less, may enhance Lepidoptera and leafhopper populations and create more balance among spring and summer flowering forbs. Woody plant and bluegrass invasion may not be halted. Insect species which are highly tolerant of burning may decline in populations and diversity.

To benefit most prairie insects, sites should include unburned and recently burned areas, at the spatial scales insects use. To develop a mix of fire tolerant and intolerant insect species, keep each site patchy in terms of time since mowing or burning. Burning can be done on a three year rotation (no unit burned more often than every 3 years) with the usual cautions: do not burn a whole patch of any kind in the same year, do not burn adjacent units in consecutive years, and leave ample refuges for fire intolerant species. More precise management may be used for promotion of a single species, as noted in the reviews above. Mowing may be substituted for burning, especially where mowing has historically maintained a site in good condition: mowing favors insect species which are tolerant of fairly deep litter, such as some Lepidoptera, and disfavors others, such as certain grasshoppers, which do not tolerate deep litter. If grazing is used, the effects must be monitored carefully.

If possible, develop buffer zones between prairie sites and areas of intensive agriculture or development. These zones will decrease alien invasion and reduce edge effects on the site.

Maintain complete records of all management actions, and monitor the results of actions. This information is indispensable both for further management and for research. Willingness and ability to change management techniques, based on the results of monitoring over the short and long term, while maintaining management goals is also essential. Prairie management is not for the fainthearted.

Acknowledgments

I thank all the prairie lovers who shared information with me. See you in the field.

Appendix

People Contacted

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Discussions, Meetings and Networks

- Request for information placed in Restoration and Management Notes
- Prairie Butterfly Research Meeting. LaCrosse, WI. January 4, 1994
- Fourteenth North American Prairie Conference, Manhattan, KS, July 1994
- Regional Meeting on Inventory/Research on Prairie Insect Communities. Dubuque, Iowa, November 10, 1994

Journals Searched back through 1989

- American Midland Naturalist
- Atala
- Conservation Biology
- Great Lakes Entomologist
- Journal of the Kansas Entomological Society

North American (earlier called Midwest) Prairie Conference
Proceedings (all 13)
Prairie Naturalist

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