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Research on the Community of Tallgrass

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RESEARCH ON THE COMMUNITY OF TALLGRASS PRAIRIE BUTTERFLIES 1988-1993

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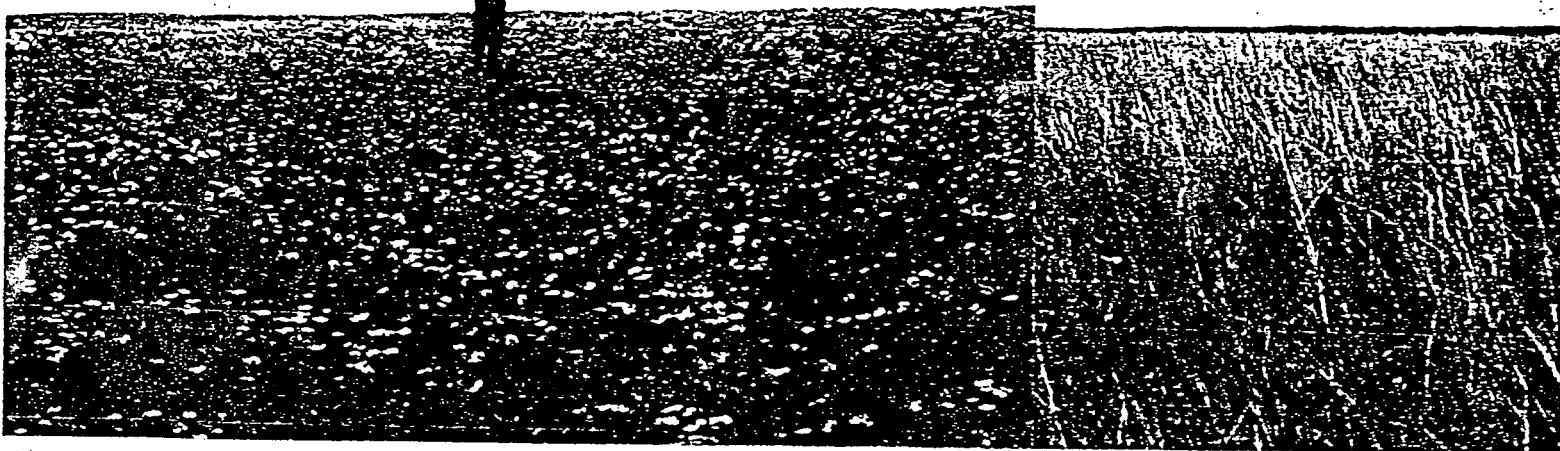
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Little Osage, MO 14 Jun 93

Niawatha, MO - unhayed area 15 Jun 93



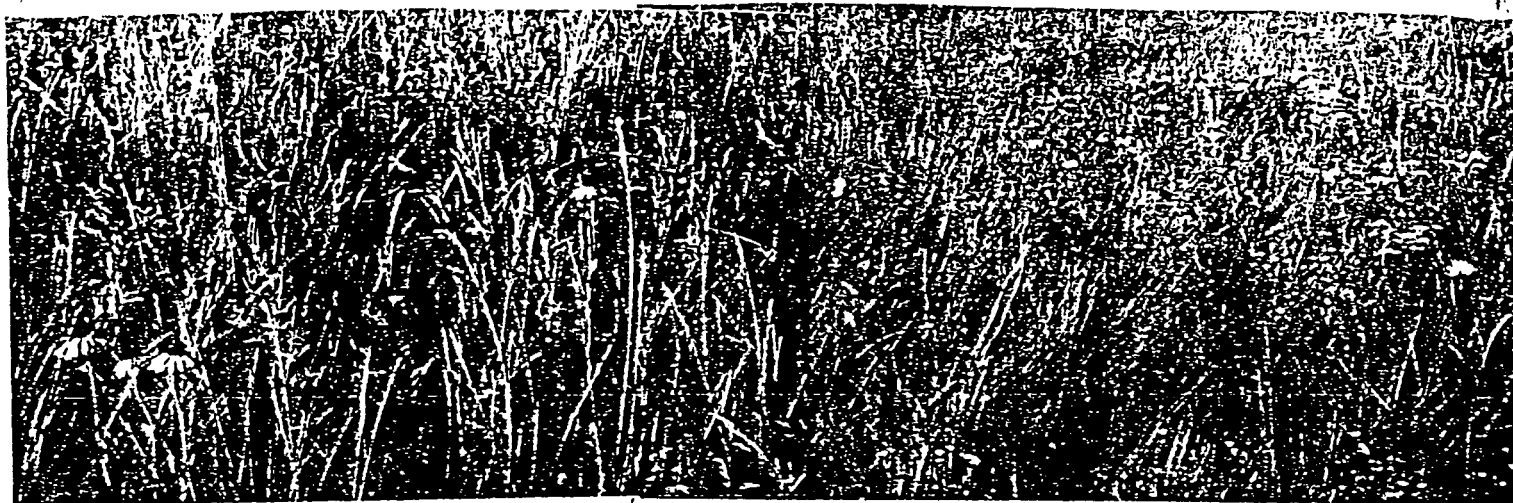
Osage, MO unharvested areas 14 Jun 93

Taberville, MO 16 Jun 93



Hayden, IA 10 Aug 93
woody invasion in burned areas

Prairie Lake, MN 10 Aug 93
monotypic grassy area post-fire



Bicentennial, MN: unburned

left 19 Jul 90

right 8 Aug 91



Bicentennial, MN: 0-1 year postfire

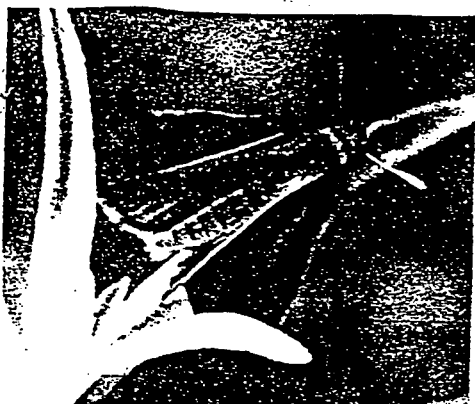
left 9 Jul 93 with dense sweet clover

right 19 Aug 93 with dense brush resprouting

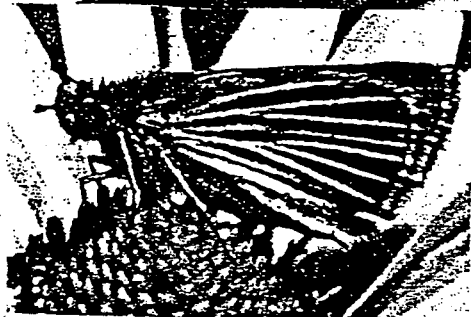


Crawford County, WI grazing prairie 11 Aug 93

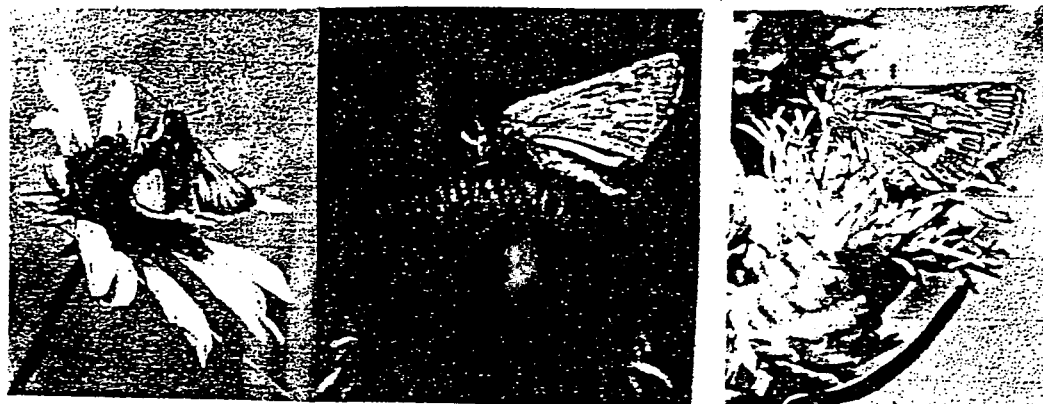
Greater Thomson, WI fallow pasture 11 Aug 92



Ottoe Skipper (female above, female below, male below)



Above: Poweshiek Skipper
Below: Arogo Skipper



Dakota Skipper (male above, female below), Leonard's Skipper



Right and lower right:
Gorgone Checkerspot

Below: Regal Fritillaries
mating (male on left,
female on right)

Below: Regal Fritillary
(female above)



ABSTRACT

We counted 65,390 individuals of 87 butterfly species 1988-92 (90 species and an estimated 75,000 individuals through 1993) in transect surveys at 86 prairies in Illinois, Iowa, Minnesota, Missouri, and Wisconsin and in brief point scans at 7 private hay prairies in Missouri (Map 1). The text details the timing of flight periods, sex ratios, nectar selection, and annual variability of prairie-specialist species, although I do not attempt to address population trends within my dataset. Weather conditions showed surprisingly little effect on butterfly variability, so that sampling in suboptimal weather was more useful than expected. The biogeography, habitat preferences, and management responses are provided for these prairie-specialist species: Poweshiek, Ottoe, Leonard's, Pawnee, Dakota, and Arogos Skippers; Regal Fritillary and Gorgone Checkerspot.

While each butterfly species has its own individual response to fire, multiple analyses agree that specialists have a pronounced and significant aversion to fire for 3-5 or more years. Species with the broadest habitat niche (invaders=immigrants and migrants) are most overrepresented in recently burned units and least represented in longer unburned units. Species of intermediate niches (grassland, generalist) showed mild intermediate patterns. Ordinating observations by family reveals no patterns but at the order level indicates overrepresentation of butterflies in recently burned units, which common species entirely account for. A model explains that butterflies respond to fire based on habitat niche breadth, voltinism, location during fire, vagility, and response of associated plants to fire. Specialist (and to a milder extent grassland) numbers are much higher in hay than fire prairies, while invaders and generalists do not necessarily decline with haying. Limited tests of light grazing show that it also serves Regals better than fire. All available data from other butterfly observers are consistent with these results, which not only strongly contradict the "short-term loss, long-term gain" hypothesis of prairie butterfly response to fire, but also dispute the validity of the fire paradigm, which explains the openness of prairie habitats with frequent prehistoric fire. Since prairie-specialist butterflies are clearly not adapted to fire but are to other conservative managements, they and their habitats must be adapted instead to other process(es), e.g. megafauna herbivory.

Like butterflies, birds are usually reduced after fire, especially ones most specialized to the habitat. Unintensive grazing and mowing can be productive management for birds. The rare and declining Henslow's Sparrow is near absent from the Upper Midwest study sites but abundant in unburned areas in southwestern Missouri, especially hay prairies. In other studies, it occurred abundantly on lightly to moderately grazed and cut farm grasslands, averaging about 5-8 times more abundant than in unburned Kansas prairie surrounded by frequently burned prairie.

The overwhelming destruction of prairie habitat (99% loss since precontact) has disastrous consequences for prairie-specialist species. Prairie loss continues deliberately today but at varying degrees of threat regionally; it is lost passively because the near total disruption of previously prevailing processes allows unnatural floristic releases. An extensive review of the scientific evidence indicates that these processes were primarily megafauna herbivory and climate, rather than the chimera of presumed prehistoric fires, so that to ameliorate the current absence of processes to the benefit of native biodiversity, the right processes must be restored in a way mimicking prehistoric conditions and effects.

While current preserve management with fire is entrenched and troubling, it is also completely correctable within the conservation community. No known prairie butterfly species has gone extinct, and these species have persisted on habitat remnants, so that favorable management changes should translate into readily measurable successes, especially at the study sites identified in this report as

highest priority. Management recommendations include the minimization of fire, substantial reliance on mowing/haying, diversity of management types, setting aside (even small) never-burn management areas, and monitoring biodiversity on an ongoing basis. Current and proposed statuses for the specialist study species are provided. Insects serve as fine-tuned and numerous ecological indicators; declines and extirpations of prairie-obligate insects are indicative of an already existing degradation of a site.

Principles resulting from this research: Design research to make fair comparisons among management types. Invertebrate conservation is not at odds with other conservation objectives. Conserve ecosystems from the top trophic levels down instead of bottom up. Opt for diversity in management approach and appearance within and among sites rather than the notion of a single "best management approach" and appearance for prairie everywhere. Apply "sustainable development" to prairie. Invertebrate surveys are feasible and as important as management. Tallgrass prairie is a biodiversity conservation hotspot that is not adequately recognized for sociopolitical rather than scientific reasons.

EXECUTIVE SUMMARY

INTRODUCTION

Tallgrass prairie is at least 99% destroyed from its occurrence before pioneer settlement so that prairie-obligate butterflies are now rare and primarily restricted to prairie preserves. Prairie requires ecological processes (disturbances) to exist, with fire at a point frequency of several per decade, whether natural (from lightning) or anthropogenic (set by native peoples), usually considered the dominant natural process. Thus, management for tallgrass prairie in most states relies primarily on frequent cool-season fires. Other theories assert that climate primarily causes grasslands or that prairie was primarily a grazing system like the Serengeti in Africa. By the reasoning that organisms must adapt, move elsewhere, or become extinct in response to frequently occurring phenomena, many have assumed that prairie butterflies must be adapted to or even dependent on fire to persist. Others assert that too frequent or large fires may extirpate prairie-obligate butterflies so that diversified and/or alternate management would be better. The main purpose of my research is to provide data on biogeography, status, management effects, and habitat adaptations for immediate application to the conservation of prairie-specialist butterflies. I also wanted to test the theory on adaptedness of the prairie butterfly community to fire to see what their degrees and types of adaptations indicate about the sorts of processes that could or could not have been happening in prehistoric prairie.

METHODS

Study sites and units

The 93 study sites in Illinois, Iowa, Minnesota, Missouri, and Wisconsin (Map 1) vary from 3-1100 ac in prairie patch size and include 7 private hay prairies in Missouri briefly sampled. Most sites are managed principally with cool-season fire, with burns averaging about 25% (range 0->99%) of the prairie patch. Some Missouri sites are managed apparently primarily with summer haying with a little burning and cattle grazing. I designated a new unit within each site whenever the habitat along the route varied by most recent management (type and timing of last treatment), vegetation type, and/or habitat degradation. "Diverse" sites contained prairie types both wetter and drier than mesic; otherwise the site was "uniform."

Transect methodology

At 86 sites we conducted transect survey counts of butterflies along routes that were similar over the years and crossed rather than followed ecotones and edges of management treatments. At 7 private hay prairies in Missouri, we surveyed by brief binocular point scan to count only Regal Fritillaries (*Speyeria idalia*). If possible, we sexed the prairie-specialist species and noted their behavior, and flower species if they were nectaring, when first detected. For each unit, we assessed nectar abundance on a simple relative scale. I coded each unit's weather as good, intermediate, or poor for butterfly observation with a graduated scale consistently applied to all units based on objective weather measures. I used relative (not absolute) population indices to identify which units had relatively greater densities of particular species and which factors might account for this variation. I applied multiple analytical methods that used somewhat different subsets of the data to test the relative efficacy of the analytical methods and to test for replications of results.

Study species

Any species observed 100+ times 1988-92 (or specialist species observed 100+ times 1988-93) is a study species. I classified them according to voltinism (number of generations per year) and habitat niche breadth: prairie specialist,

grassland, generalist, and invader (immigrant or migrant). To standardize the surveys among years onto approximately the same phenological calendar, I adjusted the survey dates to phenological Julian dates ranging from 165 (14 June) to 254 (11 September). I converted each species' numbers in each unit into observation rates of individuals per hour in the unit to allow valid comparisons among units. To determine the prime period of each species' flight (i.e. time when in adult life stage), I plotted their rates against phenological date. If a species was found only or primarily in a particular region or small set of sites, I used this geographical selection for their analysis.

Analysis of variable effects (Mann-Whitney analysis)

This analysis tested for a species' differential abundance in units relative to recent fire (burned or not since last growing season) after testing and controlling the effects of other variables. With flight period and geographical selection (and the Upper Midwest and Missouri done separately), I tested the observation rates of individuals per hour per unit for statistical significance with the Mann-Whitney U test in this predetermined order, controlling significant variables before testing for subsequent effects: 1. weather conditions, 2. year, and 3. four habitat and site variables each tested independently: vegetation, site diversity, and site size (2 codes). 4. recent fire (2 codes). This conservative methodology allows numerous factors other than management to account for a species' variability first and favors producing a random (i.e. non-significant) management effect.

Analysis of adjacent like units

This analysis compared a species' abundance in adjacent pairs of units with very similar vegetation and topography but contrasting recent burn history, if surveyed on the same day in very similar weather. I categorized pairs according to most recent management: recently burned (since last growing season) vs. burned last year, recently burned vs. unburned 2+ years ago, burned last year vs. burned 2+ years ago, and both units burned 2+ years ago. If a species was observed in one or both units of a pair, I calculated an expected number observed in each unit based on even distribution throughout both units per time spent in both units. I used the Chi-square goodness of fit test to test for random (expected) distribution in each category of units. A response index (RI) quantified the varying responses among species: when $RI < 1$, the species was overrepresented in more recently burned units; when $RI > 1$, the species was overrepresented in longer unburned units. For the category of unburned-unburned pairs, if I knew how long ago each was burned, I assigned the more recently burned unit to the "burned" values in the RI equation.

Relative representation in management age classes

This analysis tracked the relative distribution of each species in groups of units classified as year 0 since last treatment (i.e. burned/hayed since last growing season), year 1, 2, or 3+. With flight period and geography selection, I tabulated for each species the totals of survey time and number of individuals in each age class and the proportions of time and individuals represented in each age class. Assuming a random distribution of individuals in an age class when the proportion of individuals equalled the proportion of time there, I calculated the percentage each proportion of individuals deviated from random distribution in each age class. The Upper Midwest and Missouri analyses were done separately; it was only possible to track years 0 and 1 in Missouri. I tested for significant differences in relative representation in these age classes by habitat niche breadth, voltinism, and family with the Kruskal-Wallis one-way analysis of variance and Spearman rank correlation.

Absolute levels in management age classes

With flight period and geography selections, I selected the variable control

from the analysis of variable effects (above) that captured the biggest sample size for comparing a species' numbers in burned and hayed prairies. I calculated the mean observation rates per time of the specialist and selected other species through management age classes up to 5+ years since last treatment in Minnesota 1988-93 (where the only Upper Midwest hay prairies were sampled) and Missouri 1992-93. In Wisconsin, I compared observation rates of the Regal Fritillary and several other non-specialist species in the management age classes at three sites.

NATURAL HISTORY OF SPECIALIST STUDY SPECIES

Summaries are provided for the Poweshiek (Oarisma poweshiek), Dakota (Hesperia dacotae), Ottoe (H. ottoe), Leonard's (H. leonardus leonardus) Pawnee (H. l. pawnee), and Arogos (Atrytone arogos) Skippers, Regal Fritillary, and Gorgone Checkerspot (Charidryas gorgone).

RESULTS

Study species

We counted 65,390 individuals of 87 species 1988-92, 90 species through 1993 with an estimated 75,000 individuals counted, with 28 species observed at least 100 times 1988-92. Since I discuss the Karner Blue (Lycaeides melissa samuelis) elsewhere (Swengel 1993x), I excluded it here, resulting in 27 study species. Two more specialists, the Dakota and Pawnee, exceeded 100 individuals with 1993 data. Descriptive information is provided on the Gorgone Checkerspot, a specialist with only 32 individuals observed.

Behavior: feeding

The Poweshiek particularly nectared at daisy-type composites (90% of visits). In Minnesota, the Ottoe most frequently visited pale purple coneflower. Ottoes in Illinois-Wisconsin and Dakotas in Minnesota visited several species frequently and a number of others rarely. All Leonard's nectar visits were at rough blazingstar. While the Pawnee also most frequently visited a blazingstar (dotted), its nectar selection was not so strongly skewed as the Leonard's. The Arogos overwhelmingly chose purple coneflowers in both Minnesota and Missouri. The Regal Fritillary strongly and consistently tended to select pink-purple flowers (75-100% of visits).

Flight period - Average, peak, annual variability

For most species, a better alignment of flight periods and peaks among years occurred with phenologically adjusted than unadjusted date but not for Leonard's and Pawnee, the only univoltine late summer flyers, so I used unadjusted dates for these skippers. See text for flight periods and annual variability of specialist species, although I do not attempt to address population trends within my dataset.

Flight period - Dissociation among congenics

The Poweshiek and Dakota strongly overlap, while the Arogos and Ottoe similarly overlap in a slightly later and longer flight. The Leonard's/Pawnee dissociates well from the other skippers. Temporal dissociations of sympatric skippers might be an adaptation to reduce competition for adult food, since the superabundance of their larval food (grasses) precludes this as a limiting factor. The Great Spangled (Speyeria cybele) and Aphrodite (S. aphrodite) Fritillaries dissociate somewhat from the Regal in time.

Flight period - Sex ratio

For each species adequately sampled (Ottoe, Dakota, Regal), I computed % males of sexed individuals per unit. All species declined in % males with increasing phenologically adjusted date, Dakotas more so than Ottoes, Regals somewhat more in the eastern than western Upper Midwest. The % males correlated negatively and significantly with phenological date except for the Ottoe, which showed the least

pattern. In all species, the observation rate of all individuals correlated significantly and positively with male rates and likewise with female rates except for a nonsignificant result for Regals in the eastern Upper Midwest. Male and female rates also correlated significantly and positively for all except eastern Regals.

Population variability by habitat and geography

Within the variability of our sample, weather showed relatively little effect on butterfly variability, so that sampling in suboptimal weather was more useful than expected. The Poweshiek occurred at only 16 sites only in Minnesota and was clearly most abundant in diverse sites and in high-quality, dry prairie. We've only found a few Ottoes in Minnesota; most occurred at six Wisconsin sites, with one in 1993 at Harlem Hills, Illinois; all were in dry prairie. The Leonard's and Pawnee occurred at 9 sites in Illinois-Wisconsin and only 4 in Minnesota respectively, only in dry prairie. The Dakota occurred at 12 sites in Minnesota in all prairie types but significantly more in dry, large, diverse prairies, with a possible preference for high quality. Occurring at only seven sites in Minnesota, more (13) in Missouri, the Arogos was absent in wet prairie, with most individuals in dry, diverse prairie. Degradation is likely more important than apparent in this analysis for both the Ottoe and Arogos as this may explain why they are found at so few sites. Occurring widely in Minnesota and southwestern Missouri but rarely in Illinois, eastern Iowa, and Wisconsin, the Regal strongly and significantly peaked in dry, diverse prairies, with a minor second peak in wet and an area effect in the western Upper Midwest. Regal and Aphrodite observation rates correlated positively and strongly, although Regals peaked in dry and Aphrodites in wet prairie. Great Spangled and Regal rates did not correlate. Many more Gorgones occurred in Wisconsin barrens than in our prairie surveys (only in dry units) with none in Missouri probably for phenological reasons. Many Upper Midwest sites abounded in sunflowers (the larval foodplants), yet this species was rarely found.

RESPONSE TO MANAGEMENT

Analysis of variable effects (Mann-Whitney analysis)

In the Upper Midwest, 3 of 4 specialists and 2 of 12 grassland species significantly decreased in recently burned units but none of the 8 generalists and 3 invaders did; 0 specialists, 1 grassland, 3 generalists, and 2 invaders significantly increased. The only significant effect in Missouri was a decrease in 1 of 2 specialists but considerable agreement occurred within species between the Upper Midwest and Missouri.

Analysis of adjacent like units

This analysis used 62 surveys of pairs of units and statistically tested 16 study species, counting the Monarch twice as early- and late-season observations. The specialists had the most significant decreases from fire, which frequently persisted at least two growing seasons, while grasslands showed a milder similar trend. If affected, generalists and invaders usually increased significantly after recent fire. I graphed the response indices (Fig. K1-4) logarithmically for clarity of scale, but here >0 =underrepresentation in burned and <0 =overrepresentation in burned. A consistent strong trend from fire decreasing to fire increasing occurred from the specialists to the invaders within each category of management comparison, especially so in the most recently burned units. This also occurred among categories--the specialists reversed from very fire averse in most recently burned to most and mildly increasing in longest unburned units, while the invaders showed the most marked reverse response. Abundance of blazingstar (Liatris) flowers, at which late-season Monarchs particularly nectar, correlated positively and significantly with Monarch abundance: most abundant in recently burned units vs. burned 1 and 2+ years longer ago, but least abundant in units burned last year.

Relative representation in management age classes

The species varied considerably but showed these trends consistently (Fig. L1-2). Specialist numbers shifted nearly uniformly from most underrepresented in most recently burned units to most overrepresented in longest unburned, while invaders showed the opposite pattern. The intermediate niche groups had less pronounced patterns--grasslands and generalists showed milder versions of the specialist and invader patterns respectively. Likewise, either extreme of the voltinism groups showed significant but opposite trends in year 0--univoltine species were most underrepresented and trivoltine species most overrepresented--with a rather consistent pattern of reversal in representation through the years. Species of intermediate voltinism had a mild pattern, if any. Family group showed no significant effect. Haying in year 0 had a similar effect on relative representation (Fig. L3) but absolute numbers were much higher in both age classes of hay prairies than in fire prairies (Fig. L4), caused mainly by much greater numbers of specialists in hay prairies.

Absolute levels in management age classes

All specialists for which comparisons are possible (Pawnee, Dakota, Regal in Minnesota; Arogos, Regal in Missouri) clearly had more individuals in hayed than burned in comparable age classes, and four of five had more individuals in all hayed age classes than in any burn age class (Fig. M1-3, N1-2). Aphrodites (a grassland) in Minnesota showed a similar but less marked trend. The Great Spangled (a generalist) and Monarch (an invader) had less consistent patterns. In limited comparisons of Regals in Wisconsin, fire was distinctly the most harmful treatment; light grazing was most favorable, but even degraded fallow pasture (i.e. no treatment) was better than fire (Fig. O-1).

Response of individual specialist species to fire

The Poweshiek, Ottoe, Leonard's, and Gorgone declined sharply after recent fire but I have no good tests of alternate management. The Pawnee skewed to greater abundance in longer unburned units within fire prairies and clearly responded better to conservative haying than fire. The Dakota's response to fires would appear to fit the expected pattern of the "short-term loss, long-term gain" hypothesis, except that Dakota numbers were much higher in all hay age classes than in any burn age class (Fig. M1). The Arogos appeared averse both to recent haying and fire, but much more so to fire than to haying, since it had higher numbers and recovered more quickly in hay than fire prairies (Fig. N1). The Regal consistently showed major declines postfire with slow multiyear recovery but responded very favorably to haying (Fig. M2, N2, O1).

Summary of management effects on butterflies

While each species has its own individual response to fire, all analyses agree that specialists have a pronounced and significant aversion to fire which persists 3-5 or more years. Species with the broadest habitat niche (invaders) are most overrepresented in recently burned units and least represented in longer unburned units. Species of intermediate niches (grasslands, generalists) showed milder trends. Ordinating observations by family reveals no patterns, while classifying at the order level indicates overrepresentation of butterflies in recently burned units, which common species entirely account for. Specialist (and to a milder extent grassland) numbers are much higher in hay than fire prairies, while invaders (and generalists to a milder extent) do not necessarily decline. Limited tests of light grazing show that it serves Regals better than fire. Other researchers' observations are consistent with these results, which not only strongly contradict the "short-term loss, long-term gain" hypothesis of specialist response to fire, but also dispute the validity of the fire paradigm. Since specialist butterflies are clearly not adapted to fire, but are to other

conservative managements, it is not unreasonable to suppose that they and their habitats are adapted instead to other process(es), e.g. megafauna herbivory.

Factors affecting response to fire

Although I have not directly studied the mechanisms causing differential abundance of butterfly species relative to fire (e.g. differential mortality, forage quality and availability), my results are consistent with a model that butterflies respond to fire based on habitat niche breadth, voltinism, location during fire, vagility, and response of associated plants to fire.

LITERATURE REVIEW - EFFECTS OF FIRE ON BUTTERFLIES

All available data from other observers agree with my results that frequent fire favors generalists and immigrants and reduces specialists and that specialists (even butterflies in general) are much less abundant in fire prairies than in hay, grazing, and fallow prairies. Since our methods differed considerably, only crude comparisons are possible between Dana's (1991) data 1979-81 and ours 1988-93 from his Minnesota study site, which has experienced frequent fire over increasing areas since his study, but both the Dakota and Ottoe have declined greatly (about 64-98%) since his study. Five 1993 4th of July butterfly counts in southwestern Missouri-northeastern Oklahoma prairies showed strong differences between sites frequently burned (group A) and those not (group B). Group A had almost no specialists while B found at least 50% specialists; A had a minimum of 45% generalists while B found no more than 31%; A had a minimum of 13% invaders while B found no more than 6%; A averaged much lower absolute observation rates of total butterflies (30/hr) than B (126/hr). Surveys for four specialist butterflies in North and South Dakota showed that private property, where grazing and/or haying can be compatible with their maintenance, is important to their persistence. While many northeastern Illinois preserves contain large fire-managed prairies, only a very few specialist populations occur there and even grassland populations can be rare. Several Iowa lepidopterists have independently arrived at conclusions similar to mine regarding prairie fire and its effects on specialist butterflies.

LITERATURE REVIEW - EFFECTS OF FIRE ON INSECTS

The usual response of insects in the immediate (hours during and after fire) and short term (up to two months) after fire is a marked decline, which continues as a "shock phase" from exposure and lack of food for some weeks postfire. The intermediate-term effects (2-12 months postfire) are more diverse, with some taxa persisting in lower numbers, some equilibrating to controls, and some becoming more abundant; sometimes different studies of the same taxon produce conflicting results. Most studies identified at the family or order level, so that only very general tendencies among taxa can be demonstrated and these usually reflect only the trends of the most abundant species. The few studies identifying at the species level found reduced diversity postfire as a result of mortality and niche reduction (simplification). My and others' results indicate that it is the specialist butterflies that are most likely to be eliminated through simplification because they are most underrepresented in the most recently burned areas.

EFFECTS OF MANAGEMENT ON BIRDS

Birds, especially ones most specialized to the habitat, are usually reduced after fire--e.g. in tallgrass prairie, sageland, chaparral, forests, and Australian habitats--and fire eliminates most nesting in the first growing season postfire. Grazing can be productive management for birds. Although grassland birds native to prairie had only prairies (not old fields) for habitat until European immigration, they are now often found more abundantly in fallow or unintensively farmed land. The rare and declining Henslow's Sparrow (Ammodramus henslowii) is a prairie specialist that is near absent from our Upper Midwest study sites but abundant in

unburned units, especially hay prairies, in southwestern Missouri. In other studies, the Henslow's occurred abundantly on lightly to moderately grazed and cut farm grasslands in northern and western Missouri, averaging about 5-8 times more abundant than in unburned Kansas prairie surrounded by frequently burned prairie.

CONSERVATION PROGNOSIS AND PRIORITIES - PRAIRIE SPECIALIST BUTTERFLIES

Status, trends, threats for specialist species

The overwhelming destruction of prairie habitat has disastrous consequences for prairie-specialist species. Prairie loss continues deliberately today by plowing, extreme overgrazing, and development but at varying degrees of threat regionally; it is lost passively because the near total disruption of previously prevailing processes allows unnatural floristic releases. The evidence indicates that these processes were primarily megafauna herbivory and climate, rather than the chimera of presumed prehistoric fires, so that to ameliorate the current absence of processes to the benefit of native biodiversity, the right processes must be restored in a way mimicking prehistoric conditions and effects. There is cause for optimism, for while current preserve management with fire is entrenched and troubling, it is also completely correctable within the conservation community. No known prairie butterfly species has gone extinct, and these species have persisted on habitat remnants, so that management changes should translate into readily measurable successes. I identified the highest priority study sites for management compatible with specialist butterflies (App. 19); see App. 5-8 for the highest priority sites for individual species. Current and proposed statuses for each specialist study species are in App. 20.

Site-specific recommendations

Management favorable for prairie biodiversity, including specialist butterflies, should occur at all preserves, but especially at these sites, for which I provide specific comments: Illinois: Byron, Harlem Hills, Nachusa; Iowa: Freda Haffner, Hayden; Minnesota: Bicentennial, Blazing Star, Bluestem, Hole-in-the-Mountain, Prairie Coteau, Staffanson; Missouri: public prairies; Wisconsin: Dewey Heights, Muralt-Oliver, Spring Green, Thousand's-Thomson complex.

LITERATURE REVIEW - NATURAL MAINTENANCE/FUNCTIONING OF GRASSLANDS

Introduction

The fire paradigm states that the more frequent the fires, set by lightning and/or Native Americans, the more woody plants were reduced and native herbs favored. Since frequent fire management is widely used and advocated in tallgrass prairie but the response of prairie butterflies is contrary to the fire paradigm, my questions are (1) What is the evidence for prehistoric fire frequency in this biome; (2) What other process(es) were occurring simultaneously; (3) What conservation effects do fire and other processes have today? Discussions of fire ecology sometimes border on religion. While I do not belittle religion (belief in things unproven/unprovable by science), science-based ecology and management requires the interpretation of observable and measurable evidence and the study of testable hypotheses. Fervency of belief and adherence to orthodoxy (traditional/established beliefs) do not strengthen scientific substantiation. It is not disrespectful--indeed it is crucial--to science for researchers to review each others' studies. It is disrespectful for established scientists to ignore legitimate counterevidence or to disparage challengers rather than addressing the substance of their challenges.

Evidence advanced for the fire paradigm

Pioneer diaries are eyewitness accounts of horrifying blazes, but are an incomplete, skewed sample for which unanswerable questions are daunting--e.g. how much area actually burned vs. how much area was observed. Scientific interpretation of eyewitness accounts requires an assessment of the account's

accuracy, objectivity, and historical context. When so done, researchers found no evidence for frequent large fires set by natives, but some evidence for infrequent prairie fires that could harm the natives' prey base, causing famine. I question pioneers' credibility because of possible exaggeration and intense white hostility and cross-cultural misunderstanding toward natives. Pioneer accounts occurred in the historical context of settlement, which was not a time when prairie was nearly pristine. European contact well preceded settlement, and contact alone dramatically and negatively affected both native societies and native ecosystems. Thus, settlers' reports of fires may not closely correspond to precontact conditions. Natives used fire, aside from domestic purposes, to drive game and in agriculture, but not for habitat management per se. Native activities could have significant but local impacts on the environment that does not imply the ecosystem as a whole experienced or adapted to it.

Modern fires mostly occur in dry seasons which are sparse or lacking in lightning. An abundance of highly flammable material can burn only if a spark is provided, but apparently lightning doesn't ignite things very often--modern man does. This implies much modern fire suppression is not unnatural but compensates for unnatural man-caused damage. Since suppression cannot prevent lightning from starting fires but can only reduce the area subsequently burned, we should be able to estimate roughly historical lightning ignition rates (not area burned) by current observation. Most successful lightning ignitions burn small areas, many dying out before any suppression occurs. Lightning can and does ignite fires--even large ones--on occasion, nearly always in trees. This contradicts the fire paradigm that burns should be less frequent the more the trees. Even when managers justify fire in their sites on the basis of lightning, they do not conduct burns during lightning season, but during the dry season. This not only questions the naturalness of such management but further implies that it's a lot easier for man to get fires going in the dry season than for lightning to during thunderstorm season.

Increased woody canopy in the absence of fire does not necessarily occur, although usually another non-fire process is occurring at unburned unshrubby prairies. While fire may control some brushy species, others increase dramatically, and sometimes an awful lot of fire is required to get a little result. While intense tree-topping fires (which is what prescribed burns usually are not, being confined instead to the herb layer) may kill cedars and pines, numerous other species may topkill during fires but rarely rootkill, so that they vigorously resprout post-fire. Fires I've observed not only don't reduce, but don't even stabilize extent of canopy. Warm-season fires may reduce a few species but not others, and what I've seen of non-management summer fires certainly wouldn't encourage me to pursue this further. While in the absence of fire and other processes, brushing in is a likely outcome, I cannot find evidence that fire at credible natural frequencies creates and maintains open habitats.

Extensive subsurface biomass and buds of prairie flora are called adaptations to fire but are just as explicable as adaptations to herbivory. While often claimed, fire-obligate plants (species that must experience fire to persist) are elusive. Management (cool-season) fires favor dominant native warm-season grasses, but since prairies also have native forbs and cool-season grasses, a decline in floristic diversity results. Warm-season fires dramatically increase cool-season grasses--skewing the flora toward another grass component. Fire also increases vegetative biomass. Having more rather than less seems beneficial, but not if it's more of dominants at the expense of diversity and rarities, which it is. Increased flowering of certain forbs occurs short-term postfire, but since forbs decline in the long term, the short-term burst of flowers is at the expense of flowers later, burned or not. The botanical effects do not endorse fire as ecologically sound or necessary for the floristic biodiversity of prairie. That fire should control weeds, especially exotics, doesn't make sense for weeds ought to be well adapted to fire, since they are adapted to disturbance, especially human-caused, and humans

cause a lot of fires. Numerous studies confirm this. Often fire can only be considered effective if one accepts only reduction rather than elimination and/or tolerates frequent treatments, which I would find more acceptable if highly restricted as spot treatments to infested areas. These are rather lax standards for success not necessarily applied to alternatives (e.g. spot herbiciding).

Nutrient cycling is called a fire benefit, but the ash has no demonstrable effect on prairie flora, most nutrients vaporize in fires, and much of what remains leaches away in precipitation. Even if rapid, efficient nutrient turnover were occurring, this could be harmful, for increasing nutrients can degrade grasslands and greatly reduce floristic diversity. Periodic complete litter removal by burning not only eliminates cover but also niches (habitat) for animals. Since fire stimulates dominant grasses, it only briefly alleviates litter buildup, for fire actually causes greater litter problems in the future by increasing production.

Contrary to claims in the popular press of animal adaptations to fire, examples of mass animal mortality in both wild and management fires in prairie and elsewhere are numerous. Because of variable fire behavior and ethological characteristics, animals' responses are not adequate to assure survival of fire and its aftermath. A vertebrate "shock phase" occurs postfire as with insects. Typically the generalist and invader vertebrates benefit while specialists decrease postfire. "Natural" for its own appearance is a culturally biased aesthetic, although "natural" in terms of biodiversity is scientifically quantifiable. Fire management relies heavily on advanced ("natural"?) machinery to imitate (how accurately?) natural fire and requires unnatural landscape features (e.g. firebreaks, uniform burns). Alternate treatments may also look highly unnatural yet they may actually mimic a natural process at least as well as fire and appear more beneficial to biodiversity. While I do not deny that prairies burned, I conclude that convincing evidence for prairie fire has not yet appeared to substantiate that they either were frequent prehistorically or are beneficial today for biodiversity and a disturbingly large body of contrary evidence exists.

Precontact prairie fauna

The diversity of native prairie mammals extirpated or seriously reduced since contact is amazing (Maps 2-5). Of primary relevance to tallgrass prairie are beaver, porcupine, elk, and bison. While one can quibble about the abundance of particular species, one cannot but conclude that the prairie mammal fauna has been profoundly reduced in postcontact. Immense nutrient cycling occurred in prehistoric prairie via megafauna. Fur and dung also created niches on which truly obligate invertebrates (in the strictest sense of the word) depend. The Serengeti in Africa is an analogous grazing system similar to tallgrass prairie in length of growing season, large ungulate biomass, and plant productivity. There ungulates create a "grazing lawn," yet their herbivory stimulates 80% greater plant production, increases floristic diversity, and improves forage quality, with so little litter remaining as to preclude nearly all fires while maintaining a very open landscape.

The prairie megafauna clearly had significant vegetative effects, with ecological release of the flora resulting in their absence. Bison not only very heavily grazed the prairie but also tore up trees and could convert savannas into prairies. They nearly exclusively graze on grasses, so that the exceeding dominance of grasses in most prairies today at least in part results from ecological release from bison grazing. As bison may have helped prairie persist eastward, their extirpation may have allowed forest and savanna to expand westward. Since bison can climb hills so steep people cannot follow and will traverse extensive forests, no prairie site was inaccessible to them. The browsers and granivores native to prairie eat most plants that fire managers are constantly battling. E.g. white-tailed deer are apparently at about the same density in Wisconsin as around 1800 and are therefore not more abundant today than precontact. Thus, extirpated ungulates had herbivory effects additive to those now seen here for deer. Else-

where, studies demonstrate that browsers in normal densities can control brush effectively. We can proceed with an understanding that herbivory was pervasive precontact, resulting in considerably reduced canopy and fuel load, and seek ways to "restore" these effects today in ways demonstrated to benefit what lives there now.

I question the terms "disturbance" and "damage" in reference to native herbivorous megafauna at (sub)normal densities, since these terms usually are not applied to feeding by other herbivores nor are these or comparable terms used to describe other exchanges between trophic levels, e.g. carnivory, decomposition, soil converted to plant biomass. "Disturbance" implies a discrete (and possibly unnatural) event, whereas herbivory by prairie fauna is a continuous phenomenon of varying intensities through time by native species. The concept of "damage" derives from horticulture, in which humans and other animals may compete for plant yields. But preserves are not for maximizing harvest (biomass) but maintaining biodiversity. By the very reasoning (adapt, leave, or die) that fire managers have assumed the adaptation of prairie butterflies to fires assumed (I believe incorrectly) to have been frequent, the prairie flora must assuredly be adapted to herbivory and research has borne this out. Thus, absence of herbivory may be more "damaging" to the flora than its presence. One's image of prehistoric prairie determines what one will seek to produce in prairie preserve management. Most apparently imagine the prehistoric prairie as vast expanses of tall grasses, a result of postcontact animal extinctions. Although most managers would apparently be horrified to have the "grazing lawn" anywhere at any time in a prairie preserve, megafauna herbivory was immense in prehistoric prairie.

The claim of some fire managers that they are mainly concerned with restoring natural processes (as opposed, apparently, to the conservation of biota) would ring truer if they were equally zealous for all processes by including now reduced or absent megafauna herbivory in management, whether by reintroductions or other methods of biotic or mechanical grazing at a site. While one may argue that herbivory pressure comparable to that precontact might be "damaging" on today's fragmented preserves, it is disingenuous to assert that the ecosystem is not adapted to an herbivory process known to have prevailed precontact but at the same time to aspire to restore another process (fire) at precontact frequency, even though this is currently unknown even to an order of magnitude and occurs seemingly regardless of effects on extant animal populations. While mechanical and faunistic cutting share many similarities, cutting is more discrete and uniform while grazing is a more constant, gradual process leading to higher diversity of impact.

Climate/soil

Paleontological evidence shows that climate determines general vegetation characteristics. Prairie occurs in areas with a certain range of precipitation-evapotranspiration ratios, so that even on a small scale, the prairie-forest border moves back and forth in response to wet and dry periods. While ecological inertia slows the migration of plant communities in response to climate change, fire resets vegetational communities to current climatic conditions. Since Wisconsin has been wetter but not hotter in the past 12 years, current climatic conditions have become more favorable for forest, which may explain why management fires are so ineffective at controlling brush.

Applications to biodiversity/ecosystem conservation

Conservation of biodiversity encompasses that of ecosystems and landscapes. The rarest aspects of biodiversity are targeted for conservation action, as these are most likely to be permanently lost. While the prairie flora has the greatest biomass, it contains relatively little of this biome's biodiversity. No grasses are endemic to prairie but some forbs and much more fauna are; the fauna is much more diverse than flora. Insects serve as fine-tuned and numerous ecological indicators; declines and extirpations of prairie-obligate insects are indicative of

an already existing degradation of a site. Science does not substantiate that either the floristic or faunistic diversity of tallgrass prairie is adapted to fire as a dominant or prevailing ecological process nor that they benefit from frequent fires today. Since mechanical cutting and light grazing effectively maintain weedfree, woodfree, diverse prairies--indicating an ecosystem adaptation to prehistoric herbivory--this should have a primary role in modern prairie management.

Many fire managers may disagree with my review, although I drew on the data (not necessarily the opinions and conclusions) of the citation classics. BUT the extent to which we disagree only reinforces my point that the benefits and efficacy of fire management are by no means established. Therefore, this management should not be discussed as if it were efficacious, and should not be applied pervasively and constantly in prairie preserves. I will gladly receive scientific communication and refutation, but reject emotional and personal attack as inappropriate. If fire is so obviously essential to ecosystems, then science should have no difficulty substantiating it, and there is no need to invoke "religion" and emotion.

CONCLUSIONS

Principles

Study what is most important to know, not what is easiest to measure. Design research to make fair comparisons among management types. Discard the idea that fire prairies are the baseline for prairie biota. Conservation of flora and fauna need not conflict. Invertebrate conservation is not at odds with other conservation objectives. Conserve ecosystems from the top trophic levels down instead of bottom up. Maximizing plants may not benefit associated insects; it is management, not preservation status of land, that determines whether these insects persist. Management diversity favors biodiversity. Opt for diversity in management approach and appearance within and among sites rather than the notion of a single "best management approach" and appearance for prairie everywhere. Emphasize results over fashion. Apply "sustainable development" to prairie. Do not assume that floristic diversity and endemism reflect faunistic diversity and endemism. Invertebrate surveys are feasible. Surveys are as important as management. Re-examine the benefits of single-species conservation. Tallgrass prairie is a biodiversity conservation hotspot that is not adequately recognized for sociopolitical rather than scientific reasons.

Management recommendations

Scott Swengel:

1. Institute haying on large percentages of previously burned prairies.
2. Reduce fire dramatically: no 1994 fires at sites with any fire in 1993; $\leq 10\%$ area burned/year/site.
3. Graze hilly sites hard to hay.
4. Continue the management that maintained the prairie (light grazing, haying) before preservation.
5. Control brush with mowing and heavy brushing equipment: handcutting too labor-intensive.
6. Apply the same rules to management of private prairies. They should be preferentially grazed/hayed to be more cost-effective for owners.

Ann Swengel:

Minimize fire in the management regime to be the least used option. Use mechanical treatments first to accomplish as many management goals as possible. Set aside (even small) never-burn management areas for other treatments, especially mechanical cutting. Diversify types of management treatments (i.e. not just fire).

Doing nothing is a viable alternative, especially until adequate surveying and monitoring have been established.

INTRODUCTION

In central North America between the eastern deciduous forest and the Rocky Mountains, prairie comprises a plant community dominated by grasses intermixed with diverse non-grassy herbs ("forbs") and some woody shrubs and occasionally tree seedlings (Curtis 1959). Prairie is classified into three types by rainfall and consequent grass composition. The easternmost and moistest division is the tall-grass prairie, where all sites in this study occur (Risser et al. 1981 as cited in Wendt 1984, Runkel and Roosa 1989). Tallgrass prairie is estimated to be at least 99% destroyed from its occurrence before settlement by pioneers, who converted it to agricultural uses (Betz 1986, Solecki and Toney 1986, Hands et al. 1989). As a result, like other prairie specialists, prairie-obligate butterflies and skippers ("butterflies") are now primarily restricted to prairie preserves and are rare to some degree, with varying statuses on state and federal lists of endangered, threatened, and candidate species (Opler 1981, 1983, Opler and Krizek 1984, Opler and Malikul 1992, Johnson 1986). Although the timing and sites of this research were selected primarily to study factors affecting the abundance of prairie-specialist butterflies and methods for improving their conservation on preserves, all butterflies encountered were tabulated to study the entire butterfly community.

The prairie ecosystem is considered to require periodic disturbances (i.e. ecological processes) to exist (Vogl 1974, Anderson 1982, Reichman 1987). On the basis of some botanical research, fire at a point frequency of several per decade (Bragg and Hulbert 1976, Hulbert 1973, 1986, Reichman 1987), whether natural (from lightning) or anthropogenic (set by native peoples), is usually considered the dominant disturbance that caused prairie to exist (Sauer 1950, Stewart 1956, Curtis 1959, Vogl 1974, Pyne 1986). Indeed, while fire is called a disturbance, some propose that the absence of fire is the actual perturbation of this ecosystem (Reichman 1987). Because of this fire paradigm, prevailing management for tallgrass prairie in most states relies primarily on prescribed fire treatments in the cool season (predominantly spring) in a rotation of management units of one to about five years. Such management is widely discussed in radio and television programs, magazine and newspaper accounts, speeches, and letters to me as the only, primary, and/or best management method for prairie.

With little research clarifying individual species response of prairie butterflies to fire management, hypotheses have developed about how prairie butterflies, particularly the specialists, ought to respond. Based on the reasoning that organisms must adapt, move elsewhere, or become extinct in response to a frequently occurring phenomenon (Reichman 1987), prairie butterflies are assumed to be adapted to or even require fire to persist. Hypothetically, even if they die during the fire or are adversely affected in the immediate aftermath (and if so, a management resulting in an extreme short-term decline should be avoided), they subsequently benefit because of the necessity of long-term habitat maintenance. It is even asserted that in the absence of fire, these species would eventually die out because of lack of habitat maintenance (Panzer 1988, Dana 1991, Stolzenburg 1992).

Those who espouse the predominance of fire may admit a role for other processes such as megafauna herbivory and of other factors such as climate in the maintenance of prairie (Reichman 1987). An alternate theory, described by Clements (1916) and supported by Transeau (1935) and Borchert (1950), asserts that climate primarily causes and maintains grassland, or that climate is a major contributing factor (Weaver 1968, King 1981, Pielou 1991). Others propose that prairie was primarily a grazing system (Larson 1940, England and DeVos 1969, Moore 1988), like the Serengeti in Africa (McNaughton 1983, 1985). A third theory proposes an interaction of climate, grazing, and fire (Anderson 1982).

Furthermore, some evidence contradicts the fire paradigm. Direct current and historical evidence for frequent and large prairie fires is sparse, and there are inherent difficulties applying what evidence there is to prehistoric times and conditions (Higgins 1984, 1986b). Cutting (mowing or clipping) and burning have

many similar effects on flora (Daubenmire 1968, Hover and Bragg 1981, Hulbert 1988), so that fire has not been demonstrated to have caused all of these effects by itself. Fire is not obligatory to keep trees out of all prairie sites over a long time period (Weaver 1968, Anderson 1982). Conventional management fires cause a shift in the flora favoring warm-season over cool-season growers (Daubenmire 1968, Hill and Platt 1975), yet native prairie vegetation includes both types. Plant diversity continues to increase 28 years postfire (Gibson and Hulbert 1987) and when grazing and other disturbances are added to the fire regime (Collins 1987, Collins and Glenn 1988, Collins and Gibson 1990).

Many have suggested that butterflies, particularly the specialists, may be sensitive to fire management (McCabe 1981, Opler 1981, Panzer 1988, Orwig 1990, Schlicht and Orwig 1990). A survey of Australian entomologists revealed a belief that fire was second only to land clearing as a conservation threat to butterflies (New 1992). An alternate hypothesis proposes that fires too frequent or too large (relative to habitat patch size) may extirpate the rarer and more specialized butterfly species that are restricted to the habitat on preserves (McCabe 1981, Orwig 1990). In this scenario, neither lack of management (resulting in habitat change and degradation) nor sole reliance on fire management (resulting in butterfly population decline) benefit these species; diversified management (less fire but addition of other treatments) or alternate management would be more beneficial.

The main purpose of our research is to provide scientific findings on biogeography, status, and habitat adaptations for immediate practical application to the conservation of prairie-specialist butterflies. I was especially mindful to design the research and analysis to study butterfly response to preserve management, since abundant experience indicated that it is not land ownership (i.e. "unprotected" vs. "preserved" land) but land management (i.e. compatible management vs. incompatible land uses) that determine whether specialist butterfly populations persist or die out (New 1991, Warren 1992). Secondly, I wanted to test the theory regarding the adaptedness of the prairie butterfly community to fire to see what their degree and type of adaptations indicate about the sorts of processes that could or could not have been happening in prehistoric prairie.

METHODS

Study sites and units

Of the 51 study sites (App. 1, Map 1), all but 3 in conservation status, in the Upper Midwest, 6 are in Illinois, 7 in Iowa, 21 in Minnesota, and 17 in Wisconsin, from 41.9 to 47.2° N and 89.2 to 96.5° W and 3-1100 ac in prairie patch size. The Illinois sites are in the northwest corner of the state, adjacent to southwestern Wisconsin, where all its sites are. The Iowa sites are in the northern tier of that state, close to either the Illinois-Wisconsin sites or the Minnesota sites, which are in western Minnesota. The 2 sampling sites in private unposted hay prairies in Minnesota are near preserves. In southwestern Missouri from 37.0 to 38.5° N and 93.8 to 95.9° W, the 42 prairie study sites vary in prairie patch size from 14-1410 ac; 35 are preserves; 7 private hay prairies were briefly sampled. Most Upper Midwest and some Missouri sites are managed principally with cool-season fire, with the burned area averaging about 25% (range 0-99%) of the prairie habitat patch. Other Missouri sites are managed apparently primarily with summer haying with a little burning and cattle grazing. I designated a new unit within each site whenever the habitat along the route varied by most recent management (type and year since last treatment), vegetation (wet, wet-mesic, mesic, mesic-dry, dry, "extra-dry" sand prairie), and/or habitat degradation (undegraded, semi-degraded, highly degraded). Data from each unit were kept separate. I called a site diverse if it contained prairie types both wetter and drier than mesic; otherwise the site was rated uniform.

Transect methodology

At 86 sites we conducted surveys similar to the butterfly walk (Pollard 1977, Opler and Krizek 1984). While walking along parallel routes at a slow pace, my co-researcher and I working together as one party looked ahead and to the sides, both nearby and further, to the limit at which a species could be identified, sometimes with binoculars. Routes were similar over the years, sampled representative sections of the site, and crossed rather than followed ecotones and edges of management treatments. At 7 private hay prairies in Missouri, we surveyed by brief binocular point scan, either from the road/ditch edge or the top of the car, to count only Regal Fritillaries (*Speyeria idalia*). We sexed prairie-specialist species if possible and noted their behavior, and flower species if they were nectaring, when first detected. Occasionally subsequent behaviors were also noted, if the subsequent behaviors had not been recorded before during the study for that species and/or related to the original behavior and/or included nectaring, pursuit/evasion, or mating. For each unit, we assessed abundance of nectar flowers by visual scan on a scale measuring relative density on an order of magnitude ratio of flowers per area, with the following ratio: superabundant (100,000), abundant (10,000), common (1,000), uncommon (100), rare (10), and absent (0). We recorded weather (wind, temperature, cloud cover, percentage of time the sun was shining), route distance, and time spent on route for each unit. I coded each unit's weather as good for butterfly observation ($>16^{\circ}$ C, very warm or mostly sunny--usually $\geq 70\%$ sun; wind < 25 km/hr), intermediate (partly to mostly cloudy with some sunshine; or wind > 25 km/hr), or poor (mostly cloudy with little or no sunshine, or worse). This scale was graduated, requiring less sun at warmer temperatures within a weather code, and consistently applied to all units based on objective weather measures. Since butterflies are poikilothermic animals that bask in sunshine to warm their bodies, they are usually active only when it is sunny or warm (Opler and Krizek 1984).

I selected an unintrusive transect survey method because more intrusive methods, e.g. mark-release-recapture, have been found to perturb butterfly behavior (Singer and Wedlake 1981, Morton 1982, 1984, Gall 1984) and may even cause injury or mortality (Benson and Emmel 1973, Murphy 1988). Unintrusive sampling techniques such as transect surveys are nearly always adequate and may be superior to more intrusive methods to study distribution and relative density of butterflies among sites and years, and should especially be used for threatened or endangered species (Pollard 1977, 1984, Morton 1984, Gall 1985, Murphy 1988). I did not attempt to determine the actual (absolute) number of any species per area, although such may be the goal of others even when using transect surveys (Nielsen and Monge-Najera 1991). Rather, I wanted to generate relative population indices to identify which areas of which sites had relatively greater densities of particular species and which factors might account for this variation. I then applied multiple analytical methods that used somewhat different subsets of the data to test the relative efficacy of the analytical methods and test for replications of results.

Study species

Any species observed 100 or more times during the study 1988-92 (or specialist species observed 100 or more times 1988-93) was designated a study species. Based on my observations and the literature, I classified these species according to voltinism (number of generations per year) and habitat niche breadth in our study region: specialist (exclusively restricted or nearly so to prairie), grassland (inhabiting prairie and old field), generalist (inhabiting grassland and other habitats, or edge habitat between forest and grassland), and invader, lumping both immigrant (possible although irregular breeder; study region is outside regular overwintering range) and migrant (regular breeder each year in study region but overwinters regularly in another area outside study region).

The flight periods (times when in the adult life stage) of butterflies vary among the species as to time of year, length, and number of times per year. Some

JUNE				JULY					AUGUST					SEPTEMBER				
14	19	24	29	4	9	14	19	24	29	3	8	13	18	23	28	2	7	11
165	170	175	180	185	190	195	200	205	210	215	220	225	230	235	240	245	250	254

Analysis of variable effects (Mann-Whitney analysis)

Before testing for significant effects of recent fire, I tested numerous other variables first to see if they could account for the variability in the dataset. If significant ($P < 0.05$ two-tailed between any pair of variates), I controlled these variables before testing for subsequent effects. I performed the test for significance only if the samples for both subsets of the test were >5 units; if one or both were <6 units, statistically significant results would be improbable even with powerful real differences (i.e. Type II statistical errors were likely). I tested in this predetermined order: 1. weather conditions (3 codes), 2. year (1990-93 only, since data from earlier years were inadequate to test for a year effect), and 3. four habitat and site variables each tested independently: vegetation (3 codes: wet, mesic, dry), degradation (3 codes), site diversity (2 codes), and site size (2 codes: small and large; break point at 100 or 200 acres or occasionally another value, whichever divided the sample more evenly). 4. Controlling all of the previous variables, if significant, I then tested recent fire (2 codes) with as many subsets of the data as produced testable samples.

This is a conservative methodology that allows numerous factors other than management to account for a species' variability first and favors producing a random (i.e. non-significant) result because a rather conservative test (Mann-Whitney U) was used with the P value set rather low ($P < 0.05$ two- rather than one-tailed). To check for the sample size needed to avoid Type II statistical errors in the test samples for specialist species' response to recent fire, I employed an unsophisticated but objective method of bootstrapping by replicating the entire sample for a test up to 4 times, thus increasing sample size but not altering the nature of the values in the dataset.

Analysis of adjacent like units

This analysis compared a species' abundance in adjacent pairs of units with very similar vegetation and topography but contrasting recent burn history, if surveyed on the same day in very similar weather. I categorized the pairs according to most recent management in each: recently burned (burned since last growing season) vs. burned last year, recently burned vs. unburned 2+ years ago, burned last year vs. burned 2+ years ago, and both units burned 2+ years ago. All study species that produced at least one statistically testable pair of results were analyzed. If a species was observed (obs) in one or both units of a pair, I calculated an expected (exp) number observed in each unit based on even distribution in both units per time spent in both units. With ABstat 6.01 and 7.02 software (1989, 1993 Anderson-Bell Corp., Parker, Colorado), I used the Chi-square goodness of fit test to analyze randomness of distribution for each species between both units in each pair and on the sums of observed and expected values for each category of units, if both expected values were ≥ 5 . For the statistically tested sums, I calculated a response index (RI) to quantify the varying responses among species ("unburned"=the longer unburned values, "burned"=more recently burned values):

$$RI = (\text{unburned obs} / \text{unburned exp}) / (\text{burned obs} / \text{burned exp})$$

When $RI < 1$, the species is overrepresented in the more recently burned units. When $RI = 1$, the species is equally represented in both units. When $RI > 1$, the species is overrepresented in longer unburned units. For the category of unburned-unburned pairs, if I knew how long ago each was burned, and there was a difference, I assigned the more recently burned unit to the "burned" values in the RI equation. I didn't segregate multivoltine species into different flight periods, but I did separate Monarchs (Danaus plexippus) into those observed early and late in the growing season (phenological dates < 215 and > 214 respectively), with the breakpoint determined by the flight period analysis.

Relative representation in management age classes

This analysis tracked the relative distribution of each species in groups of units classified as year 0 since last treatment (i.e. burned/hayed since last growing season), year 1, 2, or 3+ (sample size precluded dividing 3+ into more single years). Restricting the sample for each species to their flight period and geography designations, I tabulated the total survey time and number of individuals in each age class. Next I calculated the proportions of total time and individuals represented in each age class. I assumed a random (expected) distribution of individuals in a management age class when the proportion of individuals equalled the proportion of time we spent in that age class. Lastly, I calculated the percentage each proportion of individuals deviated from random distribution in that age class. The Upper Midwest and Missouri analyses were done separately, with the former restricted to 1988-92 data since lack of time prevented the addition of 1993 data by report deadline. The Missouri analysis tracked butterfly representation in burned and hayed prairies only for years 0 and 1 since we have only 2 years of data and therefore haven't identified enough units in age classes longer since last management; I eliminated those study species observed only in very low numbers in only one type of management rotation. I tested for significant differences in

patterns of relative representation in these age classes by habitat niche breadth, and in the Upper Midwest also by voltinism and family, with the Kruskal-Wallis one-way analysis of variance and Spearman rank correlation. If voltinism was variable within a species, I coded it as the mean of the extremes.

Absolute levels in management age classes

In conjunction with flight period and geography selections, I selected the variable control indicated in the analysis of variable effects (Mann-Whitney analysis) (see above) that captured the biggest sample size for comparing a species' numbers in burned and hayed prairies. Data from the Upper Midwest 1988-93 (restricted to Minnesota where the only hay prairies in this region were sampled) and Missouri 1992-93 were tabulated separately. I calculated the mean observation rates per time of the specialist and selected other species through management age classes up to 5+ years since last treatment. In Wisconsin, I compared observation rates of the Regal Fritillary and several other non-specialist species in the management age classes of the three sites where Regal populations occur.

NATURAL HISTORY OF SPECIALIST STUDY SPECIES

For this I referred to the following: Ebner 1970, Irwin and Downey 1973, Ferris and Brown 1981, Pyle 1981, Opler 1981, 1983, Opler and Krizek 1984, Sedman and Hess 1985, Scott 1986, Tilden and Smith 1986, Heitzman and Heitzman 1987, Shull 1987, Coffin and Pfannmuller 1988, Ferge 1988, Royer 1988, Dana 1991, Iftner et al. 1992, Opler and Malikul 1992, Royer and Marrone 1992a-d, Stanford and Opler 1993.

Poweshiek Skipper

This skipper (Oarisma poweshiek) inhabits fen wetlands in Michigan (Leni Wilsman, pers. comm.), where its larval foodplant is reported as sedges. In Wisconsin it lives in low prairies, but in Minnesota, it occurs in prairie from wet to dry types, with larval host(s) as yet unreported, and apparently tolerates moderate habitat degradation and fragmentation. In southeastern North Dakota, it is found usually in moist, but sometimes in dry prairies, as well as sedgy ditches, again with sedges reported as larval food. The Poweshiek overwinters as a fifth instar larva, and adults have a single flight from mid- to late June into July.

Dakota and Ottoe Skipper

The Dakota (Hesperia dacotae) and Ottoe (H. ottoe) Skippers are typical of the genus, having one generation per year with adults in summer. Shortly after eggs are laid, larvae commence development, constructing shelters on their food plants--major prairie grasses, especially big (Andropogon gerardii) and little (A. scoparius) bluestems, side-oats grama (Bouteloua curtipendula), and (Dakota only) prairie dropseed (Sporobolus heterolepis). The larvae overwinter in an intermediate instar in shelters in the basal areas of bunchgrass clumps and pupate the following spring. Where sympatric, the Dakota adults emerge 1-2 weeks ahead of the Ottoe and have a somewhat shorter flight. The Ottoe typically begins flight in late June, peaking sometime in July, but continuing until the beginning of August, although in Kansas and Missouri, the flight predominantly occurs in June. The Dakota's historic range was restricted to northern prairie from southern Manitoba and northwestern North Dakota southeastward through western Minnesota and northernmost Iowa to Illinois, where the Dakota is known from only three specimens 1895-1940. The Ottoe's range broadly but spottily encompasses the prairie and plains from lower peninsula Michigan west through southern Wisconsin and Minnesota to southern Manitoba and eastern Montana and southwest through southwestern Missouri to northern Texas and eastern Colorado. Both species typically inhabit relatively undisturbed prairie, the Dakota in wet-mesic tallgrass and dry-mesic mid-grass prairies and the Ottoe in well-drained short-, mixed-, and tallgrass prairie, often on upland slopes and barrens.

Leonard's-Pawnee Skipper

The Leonard's (Hesperia leonardus leonardus) and Pawnee (H. l. pawnee) Skippers are considered to relate clinally over their range, which occurs broadly from the northern half of the eastern U.S. westward to southeastern Saskatchewan, Montana, and Colorado. The more eastern Leonard's has a rust-red background ventrally while the more western Pawnee is bright yellow, with intermediate forms in western Wisconsin and Minnesota. I have referred all individuals observed in Illinois-Wisconsin to Leonard's and all in western Minnesota to Pawnee. At a few sites in western Minnesota, a few Assiniboia Skippers (H. [comma] assiniboia) may have been misidentified as Pawnee, but I believe that most or all individuals were Pawnee. The natural history of these skippers is similar to the Dakota-Ottoo, but the flight period is later (mid-August to early October) and first instar larvae overwinter. Larval hosts are dominant grasses such as bluestems, needlegrasses (Stipa), and dropseed. The Leonard's may inhabit wet grasslands, apparently more so east and northeast of this research's study region, but both subspecies also live in dry prairie/savanna habitat, especially westward.

Arogos Skipper

This skipper (Atrytone arogos) has two subspecies: the eastern arogos spottily occurs in dry grasslands and sand prairies of the Atlantic and Gulf coastal plains, while iowa in the Great Plains ranges widely in prairies (usually undisturbed) from Minnesota and North Dakota south to eastern Colorado, Texas, Missouri, and only one county (Mason) in central Illinois. It has one generation per year in midsummer, two southward (June and September). The larvae, which feed on dominant grasses such as big and little bluestem, overwinter in the fourth instar.

Regal Fritillary

Regals are typical of large fritillaries (Speyeria), with one generation each year and adults during a long summer flight, with males emerging ahead of females, a week or more for the Regal. In the Upper Midwest, Regals usually fly from late June/early July until late August/early September but further south from May to October with main male flight mid-June to mid-July and main female flight early July to mid-August. Female Regals, like some other large fritillaries, may enter diapause, an adaptation possibly restricted to dry climates (I have never noticed this), and delay egg-laying until late summer. Large fritillaries usually lay eggs, which hatch the same season (laid, haphazardly on or near violets (Viola) but the larvae overwinter unfed, feeding the following spring violets at night and hiding diurnally away from the host. While birdfoot violet (V. pedata) is most often cited, it is sometimes rare or absent at sites with Regals, so that at least several kinds of violets must be used. The Regal formerly occurred from coastal southeastern Canada south in the Appalachian and Piedmont Mountains to North Carolina, westward across the midwestern USA from Ohio to southwestern Missouri and lower peninsula Michigan and Minnesota; in the Great Plains, southward to northern Oklahoma, westward to eastern Colorado and Montana, and straggling north to Manitoba. In the northeast USA, Regals inhabit(ed) damp meadows and dry grasslands; in the Midwest and Great Plains, wet to dry tallgrass prairie and wetter types of mixed- and short-grass prairie.

Gorgone Checkerspot

This species (Charidryas gorgone) has a very broad range centered on the Great Plains of the central USA and southern Canada. It inhabits open areas, especially prairie/savanna but also wastelands and old fields, where the larvae feed on composites, mainly sunflowers (Helianthus). The third instar larva overwinters. The number of adult flights per year varies with length of growing season.

RESULTS

Study species

We counted 65,390 individuals of 87 species 1988-92, 90 species through 1993 with an estimated 75,000 individuals counted (not yet tabulated because of time constraints). 28 species were observed at least 100 times 1988-92 (App. 9,10), accounting for almost 94% of all individuals. Common and scientific terminology follow Hodges et al. (1983) and NABA (1993). The remainder included both species infrequently encountered and unidentified individuals, particularly pierids, crescents (Phyciodes), and ladies (Vanessa). Since I discuss the Karner Blue (Lycaeides melissa samuelis) in detail elsewhere (Swengel 1993a), I excluded it as a study species here, resulting in 27 study species. Two more specialist species, the Dakota and Pawnee, exceeded 100 individuals with 1993 data. Some descriptive information is provided on the Gorgone Checkerspot, since it is a specialist of conservation concern but only 32 individuals were observed. Since only a few individuals of the Byssus Skipper (Problema byssus), another specialist, were observed each year in Missouri only at Gama Grass, I cannot analyze its occurrence.

Behavior: feeding

The rate of nectaring instances per total individuals observed varied considerably, with very high frequencies for Arogos (59% in Minnesota, 94% in Missouri) and Dakota (53%) Skippers, probably because a very good, close look at these individuals is necessary to identify them, and nectaring individuals are relatively easy to find and examine.

Poweshiek Skipper. This species particularly nectars at daisy-type white/yellow/pink composites (90% of visits) (App. 2).

Ottoe Skipper. Dana's (1991) data agree with ours (App. 2) for Ottoes in Minnesota that pale purple coneflower is most frequently visited, but our dataset is too limited for more comparisons. His data agree with ours from Illinois-Wisconsin that several species are frequently used, while a number of others are visited rarely. In our data, the top two nectar choices by males and females are the same.

Leonard's Skipper. All nectar observations were at a single species, rough blazingstar (App. 2), which agrees with my experience of this species in Wisconsin barrens, where it also visits dwarf blazingstar. Most individuals of the rust-red morph I have seen have been associated with Liatris. By contrast, the yellow morphs I observed at Blue River, Wisconsin (not on formal surveys of this research) perched on goldenrod flower stalks and lichens.

Pawnee Skipper. While the most important nectar source is also a blazingstar (dotted), its nectar selection was not so strongly skewed to a single plant genus as the Leonard's (App. 2). Although I have not collected data on perch selection, this species frequently perches on yellow surfaces (perhaps for camouflage?).

Dakota Skipper. Our top nectar item (blanketflower) is rare or absent (now at least) at Dana's (1991) study site while his top nectar item (pale purple coneflower) was important but third in our study, with vervain rather important in his dataset but unrepresented in ours (App. 2). These differences are partly explained by phenology, for most of our observations were in 1992-93 with visits before peak coneflower bloom, and partly by the variability of our more numerous sampling sites. Nevertheless, our datasets generally agree on relative importance of particular species, and on the pattern that a few species visited frequently but many species are visited rarely.

Arogos Skipper. Purple coneflowers were overwhelmingly chosen in both Minnesota and Missouri, but the sample is small (App. 2). Very few were sexed because this requires a very good look at the above side.

Regal Fritillary. Although flowers of other colors are widely available, this species shows a strong tendency to select pink-purple flowers: in Illinois 100% of visits were to flowers of such colors, Iowa 75%, Minnesota 97%, Missouri 77%, Wisconsin 89% (App. 2). This behavior occurs consistently throughout the flight period and is obvious in the field, as when a Regal passes over drifts of mountain

mint to visit the one ironweed patch or passes over abundant black-eyed susans to visit the first open floret of prairie blazingstar. Thistles are a particular magnet; while these flowers are usually rare and scattered in the prairie landscape, Regals often fly from thistle flower to flower, seeming to orienteer by them and use them for mate-finding. One mating pair was observed on purple coneflower in Missouri, suggesting the female was found and/or courted there.

Gorgone Checkerspot. We didn't take data on their nectar visits.

Flight period - Average, peak, annual variability

These results are restricted to the Upper Midwest, since I lack adequate time depth from Missouri. The phenological adjustment worked well for most species by producing a better alignment of flight periods and peaks among years than with unadjusted date (e.g. Regals at Muralt, Fig. E1-2); all subsequent discussion of these species uses phenologically adjusted dates. This adjustment was not valuable for the Leonard's and Pawnee, the only univoltine late summer flyers. Only a few of these skippers were found in 1991, while in 1992-93 we found more at an earlier phenological date but later calendar date than in 1991. This suggests that the flight periods for these species may be calibrated backward from the arrival of fall rather than from phenological progress since spring. I therefore used unadjusted dates to define these skippers' flights. For those cases where annual variability cannot be attributed to the survey's timing relative to flight period, I can only speculate about why the abundance of species varies annually, although weather factors seem quite important, with different components potentially relevant to different species and potentially affecting different species in different ways. Immediate and cumulative effects, positive and negative, of management may also be a factor. However, I'm not attempting to address general population trends within my dataset, since this requires a longer time horizon.

Poweshiek Skipper. In western Minnesota, this species primarily flies in the last half of June to early July; in this study, we covered this phenological period in 1988-89 (at Hole-in-the-Mountain only) and 1992-93. Some have implied that relatively high densities of this species are occasional and somewhat unpredictable. We have observed high numbers (defined arbitrarily as >50/hr) in unit(s) at Hole-in-the-Mountain especially in 1988-89 and in 1992 (but somewhat lower) but not in 1993, Ordway and Prairie Coteau in 1992 but not 1993, and Staffanson 1992-93. Overall, observation rates averaged significantly lower in 1993 than 1992 (App. 3). Thus, although with some variability, each year we've sampled in the appropriate phenology, we've also experienced abundant densities somewhere at predictable times and places.

Ottoe Skipper. The main flight in our Illinois-Wisconsin sites spans early July to early August, usually peaking early to mid-July, with strong overlap of males and females, consistent with the literature (Fig. A1-3). Numbers were higher in 1990-91; 1992 and especially 1993 were lower.

Leonard's Skipper. Main flight in our Illinois-Wisconsin sites was on/after August 20. We surveyed much at sites with this species at this time only in 1993.

Pawnee Skipper. The main flight in western Minnesota occurs on and after August 10, which we sampled in 1992-93, with many more observed in 1992.

Dakota Skipper. Prime flight in western Minnesota was the last half of June with a few individuals from early to late July (Fig. B1-3). Dana's observations (1991) were slightly later in unadjusted dates but in the same general period.

Arogos Skipper. In Minnesota, the main flight occurs from late June to late July. Although not significant (possibly because of low numbers overall), a steady decline occurred from 1990-92; in 1993, we apparently missed the flight period. I believe our mid-June Missouri sampling, while producing observations each year, have been early in the flight, especially in 1993.

Regal Fritillary. In the eastern Upper Midwest (i.e. northeastern Iowa, northern Illinois, and southern Wisconsin), the main flight lasts from late

June/early July to mid-August, starting in mid/late June southward (Fig. C1-3). In the western Upper Midwest (longitude $>94^{\circ}$, i.e. northwestern Iowa and western Minnesota), the main flight occurs from early/mid-July to late August (Fig. D1-3). Timing and duration of peak may be affected by population size. In 1990, the year we found the most individuals at Muralt, the phenologically adjusted peak (early August) occurred well later than in 1991-93 (Fig. E-2), when the peak was similarly timed (early to mid July). In 1993 at three Wisconsin sites (Fig. E-3), Muralt and Thomson had a similarly timed early peak (early July adjusted) while the site with the most individuals had a later peak (early August) with a longer period of high numbers prepeak. Our data in the eastern Upper Midwest generally agree with Iftner et al. (1992) that numbers drop rather sharply after peak. We had no significant year effect 1990-93 in the Upper Midwest and 1992-93 in Missouri (App. 3). While we found slightly higher levels in Missouri in 1993 than 1992, I assume we were earlier in their flight in 1993 since we found many fewer females.

Gorgone Checkerspot. To increase sample and seasonal coverage, I used data from this study's prairie sampling and from our Wisconsin barrens research (Swengel 1993a). This multivoltine species showed some tendency to build in numbers as generations progressed during the growing season, more so in the prairie research whereas in the barrens, spring seemed a more predictable time to find this species more widely (Fig. F1-2). Although previously mapped as two generations with a long period of late-season stragglers (Swengel 1991a), I see three relatively discrete flights in these graphs (Fig. F1-2): May-early June (data from barrens only but surely occurring in prairies too), early-late July (data from barrens and prairies), and mid-late August (prairie data only; unknown whether this occurs in the more northern barrens). Although the graphs of multiple-year data imply a fair spread of dates per brood, within a single year each brood's span was usually quite narrow, except in prairies in midsummer 1992, with a fair spread between Rush Creek and Dewey Heights, two southwestern Wisconsin sites. I have also noted brief peak flights at sites near our home that we observe frequently. Since we've seen none in Missouri, I assume we've been between flights during our sampling there.

Flight period - Dissociation among congenetics

The Poweshiek and Dakota strongly overlap, while the Arogos and Ottoe similarly overlap in a slightly later and longer flight. See Dana (1991) for direct comparisons of the Dakota and Ottoe for the Ottoe is near absent in our Minnesota surveys. The Leonard's/Pawnee Skippers dissociate well from the other specialist skippers. Schlicht and Orwig (1990) noted a similar series of somewhat overlapping skipper flight periods. Clench (1967) suggested that temporal dissociations of sympatric skippers might be an adaptation to reduce competition for adult food; the superabundance of larval food (grasses), as in prairies, precludes this as a limiting factor. While I've not quantified degree of nectar dissociation among these species, it does seem that each species has slightly different menu selections.

The Great Spangled (Speyeria cybele) and Aphrodite (S. aphrodite) Fritillaries dissociate somewhat from the Regal in time and also habitat niche breadth (generalist, grassland, and specialist respectively) and habitat preferences (see "Population variability by habitat and geography" below). The Spangled's main flight in the Upper Midwest spans mid-June to mid-August (Fig. G-1) while the Aphrodite's main flight in the Eastern Upper Midwest (longitude $<94^{\circ}$) spans mid-June to mid-July (Fig. G-2) and late June/early July to mid-August in the Western Upper Midwest (longitude $>94^{\circ}$) (Fig. G-3). While the Spangled's flight fully encompasses the other two fritillaries (as in the literature, e.g. Iftner et al. 1992, Cech 1993, Glassberg 1993), both it and the Aphrodite peak at rather similar times ahead of the Regal (compare Fig. H-1 and I-1 with E-2; H-2 and I-2 with E-3), as also in the literature: The Aphrodite peaks immediately after the Spangled, mid-July vs. late June/early July (Glassberg 1993) or 27 June-4 July vs. 20-27 June, with Regals peaking 11-18 July (Iftner et al. 1992). Cech (1993) also indicated a second

Spangled peak in early September, possibly explaining the odd increase of this species late in summer 1993 at the Crawford County, Wisconsin site (Fig. H-2).

Flight period - Sex ratio

I analyzed the Upper Midwest data, where I have an adequate time spread. For each species with adequate samples (Ottoe, Dakota, Regal), I computed % males of all sexed individuals per unit. All species declined in % males with increasing phenologically adjusted date, Dakotas much more so than Ottoes, Regals somewhat more in the eastern (longitude < 94°) than western (longitude > 94°) Upper Midwest (Fig. J1-4). The % males correlated negatively and significantly with phenological date except for the Ottoe, which showed the least tendency in this regard (Tab. 1). In all species, the observation rate of all individuals correlated significantly and positively with male rates and likewise with female rates except for Regals in the eastern Upper Midwest, where the correlation was non-significant (Tab. 1). The correlation between male and female rates was also significant and positive for all except eastern Regals. This apparent difference in female Regal behavior/phenology between the eastern and western Upper Midwest cannot be explained simply by phenological differences since both regions were sampled over a long and comparable phenological period; it may be a real phenomenon that females can and do dissociate more from males in the less dense eastern than western populations.

Table 1. Pearson's Product Moment Correlation Matrix of sex ratio patterns.

	r	N	P
% males of sexed individuals with phenological date			
Dakota Skipper - Western Upper Midwest	-0.56762	49	0.0000
Ottoe Skipper - Eastern Upper Midwest	-0.18092	65	0.1492
Regal Fritillary - Eastern Upper Midwest	-0.51856	104	0.0000
Regal Fritillary - Western Upper Midwest	-0.39622	279	0.0000
rates of observation of males and all individuals			
Dakota Skipper - Western Upper Midwest	0.93836	285	0.0000
Ottoe Skipper - Eastern Upper Midwest	0.79306	250	0.0000
Regal Fritillary - Eastern Upper Midwest	0.87064	104	0.0000
Regal Fritillary - Western Upper Midwest	0.85328	451	0.0000
rates of observation of females and all individuals			
Dakota Skipper - Western Upper Midwest	0.88478	285	0.0000
Ottoe Skipper - Eastern Upper Midwest	0.68159	250	0.0000
Regal Fritillary - Eastern Upper Midwest	-0.05028	104	0.6123
Regal Fritillary - Western Upper Midwest	0.44264	451	0.0000
rates of observation of males and females			
Dakota Skipper - Western Upper Midwest	0.72874	285	0.0000
Ottoe Skipper - Eastern Upper Midwest	0.74351	250	0.0000
Regal Fritillary - Eastern Upper Midwest	-0.27656	104	0.0045
Regal Fritillary - Western Upper Midwest	0.26596	451	0.0000

Population variability by habitat and geography

Within the variability of our sample and the constraints of coding weather into three categories, weather showed little effect on variability of butterfly densities (App. 3) although I recognize that weather has obvious effects; thus, we do not sample in dreadful weather and crepuscular periods. Nevertheless, I conclude that sampling in suboptimal weather is more useful than I expected.

Poweshiek Skipper. We found this species at only 16 sites in Minnesota, never in Illinois or Wisconsin, and although we found this species in Iowa in 1989, we have never found it there during this study's surveys (App. 5). Rather small samples for statistical tests apparently caused Type II statistical errors with regard to habitat variables, for some strong patterns are nevertheless apparent. Site size showed no effect, but this species was clearly most abundant in diverse sites

and in high-quality, dry prairie (App. 3). This seems odd since their only reported larval foods are sedges, but may explain the benefit of site diversity.

Ottoe Skipper. We've only found a few individuals in Minnesota; most observations come from six Wisconsin sites, but one individual was at Harlem Hills, Illinois in 1993 (App. 6). All individuals occurred in dry prairie, with no apparent size effect (App. 3). Site diversity was untestable as all Illinois-Wisconsin sites in analysis are uniform, but the Minnesota site is diverse. I suspect degradation is a more important factor than apparent in this analysis for this may explain why Ottoes are found at so few sites.

Leonard's Skipper. Although we've not extensively sampled during this species's flight, it was found at nine sites in Illinois and Wisconsin, most or all red morph, only in dry prairie units that were also only in uniform sites (App. 3), although I have also seen Leonard's in central Wisconsin barrens that are diverse. The non-significant higher mean in small sites probably results from some sort of site effect (or sampling error) rather than an actual size-effect. Leonard's seem less sensitive to degradation than the Ottoe, for we know of many more sites with Leonard's (both prairie and barrens) than Ottoes, even though we do much more and wider survey coverage during Ottoe than Leonard's flight.

Pawnee Skipper. We found this species at only four sites in Minnesota (Bicentennial, Bicentennial Hay, Frenchman's Bluff, Seven Sisters), always in dry prairie with no apparent difference between semi-degraded and high-quality units but the possibility (untestable because of small sample) that site diversity might confer some benefit (App. 3). The non-significant but considerably higher mean in larger sites may result from sampling error, site effect, or a Type II statistical error.

Dakota Skipper. We've found this species at 12 sites in Minnesota, in all prairie types but significantly more in dry prairie and large and diverse sites, with an apparent (non-significant) preference for high quality as well (App. 3).

Arogos Skipper. We found this species at only seven sites in Minnesota, more (13) in Missouri (App. 7,8). In both states it was absent in wet prairie and most individuals (non-significantly) found in dry prairie, and it possibly (non-significantly) benefited somewhat from higher habitat quality (App. 3). Site diversity was untestable in Minnesota but we've only observed it in diverse sites. Many more individuals in Missouri were in diverse than uniform sites but this was not significant. As with the Ottoe, I suspect degradation is more important than apparent in this analysis for this may explain why this species is found at so few sites.

Regal Fritillary. This species occurred widely in Minnesota, at all sites except Zimmerman, but only sporadically present at Kettledrummer and Lundblad; Regals were very numerous and widespread in southwestern Missouri prairies, but very rare in the eastern Upper Midwest (Illinois, eastern Iowa, Wisconsin) (App. 6,8). They strongly and significantly peaked in dry prairie in diverse sites in the western Upper Midwest (longitude > 94°) and Missouri (App. 3), and have only been found in dry prairie in Wisconsin. In the western Upper Midwest, a minor but significant second peak occurred in wet prairie, with the lowest numbers in mesic, but Missouri didn't show this effect. Habitat quality (within the range of our sample) had no apparent effect in the western Upper Midwest, consistent with the three studied Regal populations in Wisconsin, where one occurs in a highly degraded fallow pasture (Thomson); habitat quality was not statistically testable in the Missouri data. Regals showed a significant area effect in the western Upper Midwest but not in Missouri, possibly because so much prairie habitat there occurs on private property and this might function to augment the prairie patch sizes at "small" public prairies.

Gorgone Checkerspot. We've found many more individuals in central and northwestern Wisconsin barrens (118 individuals in formal surveys) than in our prairie surveys (32 individuals in the Upper Midwest, only in dry prairie) with none in Missouri probably because we're sampling between flights. A strong preference for dry habitat is also evidenced by the numbers observed in barrens and at Valentine National Wildlife Refuge (30 adults, 2 larvae) and Niobrara Preserve

(4 on the access road, 10 in the preserve), Nebraska on 27 June 1991. From the literature, degradation would seem not to be strongly disfavorable so long as larval food (sunflowers) is available, but most units where Gorgones occurred in our prairie and barrens surveys were high-quality. Many of our sites in the Upper Midwest abound in sunflowers, yet we rarely find this species.

Dissociation among congeners. The correlation of Regal and Aphrodite observation rates is strong, although the more numerous of the species reverses between the eastern and western Upper Midwest:

Region	r	N units	P	N Regals	N Aphro.
E. Upper Midwest (longitude<94°)	0.48866	675	0.0000	519	603
W. Upper Midwest (longitude>94°)	0.25674	450	0.0000	3332	1347

Nevertheless, these species dissociate somewhat in time (see "Flight period - Dissociation among congeners" above) and in habitat. Regals peak strongly in dry while Aphrodites peaked strongly in wet prairie in the western Upper Midwest (but aren't testable in the eastern Upper Midwest); otherwise, Aphrodites were much less marked in habitat trends than the Regal (App. 3,4). This does not mean that Aphrodites displace Regals; I expect that the conservation of Regals does not require disfavoring Aphrodites, but favoring both species over generalists and invaders. There was no correlation between Great Spangled and Regal rates, either in the Upper Midwest (eastern or western) or Missouri.

RESPONSE TO MANAGEMENT

Tabulating 1988-92 data only for Upper Midwest census units where all butterfly individuals were counted (almost all units; time constraints precluded the addition of 1993 data to this tabulation), we found 29,967 individuals (46.2%) in recently burned units (burned since last growing season), twice as many as expected based on time spent in such units (61.1 hr, 23.0%); this is entirely due to extreme overrepresentation of Monarchs late season (phenological dates>215) in burned mesic to wet prairies. The percentage of total numbers of individual species in burned units presents a continuum from extreme under- to overrepresentation, from 0.7 to 86.3%, and corresponds well to the species' results in this report's statistical analyses (presented below). The variability of presence-absence tabulation of individual species in burned vs. all units was less pronounced, ranging from 7.7 to 35.9%, vs. 23.8% of all units being burned. The proportion of burned units a species was present in usually agreed with its tendency to under- or overrepresentation indicated by the proportion of total individuals in recently burned units, but the former proportion varied less than the latter. Thus, presence/absence is a coarser measure of fire effects than indices of abundance.

Analysis of variable effects (Mann-Whitney analysis)

In the Upper Midwest, 3 of 4 specialists and 2 of 12 grassland species significantly decreased in recently burned units, but 0 of the 8 generalists and 3 invaders did; no specialist, 1 grassland, 3 generalists, and 2 invaders significantly increased (App. 9). The only significant effect of recent fire in the Missouri dataset was a decrease in 1 of 2 specialists (App. 10). Selected species analyzed in both regions with 1988-93 data showed similar trends, and considerable agreement occurred within the same species between the Upper Midwest and Missouri (App. 9,10). All but one generalist species shared at least one identical statistical result between regions. Eight of the 11 non-significant analyses of specialists (1988-93 data) became significant via bootstrapping that replicated the data set 2-4 times. The three remaining analyses (Leonard's 1993, Arogos Missouri 1993, Regal mesic-uniform-small Upper Midwest) showed no signs of becoming significant.

Analysis of adjacent like units

I identified 62 surveys of pairs of units that qualified for this analysis, conducted June-August 1989-93 at 4 units in 2 Iowa sites, 24 units in 9 Minnesota

sites, and 8 units in 3 Missouri sites. Sixteen study species, counting the Monarch twice as early- (<215 phenological Julian date) and late-season (>214) observations, were statistically testable by this method, which offers the most stringent control of other variables affecting butterfly abundance.

In recently burned units vs. unburned 2+ years (App. 11), the 4 specialist and 4 grassland species that were statistically testable showed a significant decrease in burned units, while 1 of 5 generalists and 3 of 4 invaders were significantly more abundant in burned units. In recently burned vs. burned last year, 2 of 3 specialists and 2 of 4 grasslands were significantly affected--all underrepresented in the more recently burned, while 1 of 3 generalists and 1 of 2 invaders that were significant were more abundant in the more recently burned. In burned last year vs. unburned 2+ years, 1 of 2 specialists and 1 of 4 grasslands were significantly affected and lower in more recently burned units, while 1 of 4 generalists was significantly affected and higher in more recently burned, but the 1 of 2 invaders significantly affected was underrepresented in more recently burned. In comparisons of units both unburned 2+ years, the 2 testable specialists and 2 testable generalists showed no significant differences, while 2 of 3 grassland species were significant (one lower, one higher) and 1 of 2 invaders was significant (lower in more recently burned). This last category was not a comparison of identical treatments, because I have no substantiation that all management age classes >1 year postfire are identical (indeed, subsequent analyses below show they are not) and I always put the more recently burned of the two units (if known) in the left (more recently burned) column to allow consistent comparisons with previous categories.

Thus, specialists had the most significant decreases from fire, often persisting at least two growing seasons, while grasslands showed a milder similar trend. If affected, generalists and invaders usually showed a significant increase from recent fire. Response indices (>1=underrepresentation after recent fire, <1=overrepresentation after recent fire) clustered by habitat niche breadth and showed a consistently progressing trend among categories (App. 11). I graphed these indices (Fig. K1-4) logarithmically [$\ln(\text{response index})$] for clarity of scale, but note that here, >0=underrepresentation in burned and <0=overrepresentation in burned. A consistent strong trend from fire decreasing to fire increasing occurred from the specialists to the invaders within each category of management comparison, especially in most recently burned units (Fig. K1-2), but also among categories (Fig. K1-4): the specialists reverse from the being very fire averse in recently burned units (Fig. K1-2) to being the most and mildly increasing in longest unburned units (Fig. K4), while the invaders showed the most marked reverse response.

Although Monarchs showed no significant trends early in the season, late-season Monarchs showed an unusual tendency (App. 11): strong overrepresentation in recently burned units, most underrepresentation in units burned last year, and mild increase again in longer unburned units. Abundance of blazingstar (*Liatris*) flowers, at which late-season Monarchs particularly nectar (4483/5205 nectar visits 1990-92 were at *Liatris*), appears important to their late-summer habitat occupation. Restricting my sample to those units surveyed when any blazingstar was flowering in either unit (24 pairs, all in August, 3 in Iowa, 21 in Minnesota), I summed the relative flower abundance of all blazingstar species in each unit as quantified by our nectar abundance scale. Monarch observation rates in these units correlated positively with blazingstar abundance (Spearman rank correlation, $r=0.34465$, $P<0.025$). Furthermore, blazingstar abundance differed significantly among the three burn age groups. They were exceptionally abundant in year 0 (recently burned), exceptionally scarce in year 1 (burned last year), and somewhat more abundant again in year 2+: $P=0.02$ between years 0 ($N=12$) and 1 ($N=8$), $P=0.03$ between years 0 and 2 ($N=27$), and $P=0.11$ between years 1 and 2 (Mann-Whitney U test). Thus, Monarch numbers shifted significantly among these age classes as predicted by changes in blazingstar abundance (App. 11), with Monarchs more abundant in recently burned units vs. those burned 1 and 2+ years longer ago, but

less abundant in units burned last year vs. longer ago.

Relative representation in management age classes

The species varied considerably in the degree and direction of deviation from random distribution in each burn age class in both the Upper Midwest (App. 12) and Missouri (App. 13) but showed the following trends consistently (Fig. L1-2). Either extreme of the habitat niche groups (specialists and invaders) showed marked but opposite responses, both within each niche group from year 0 to 3+ (testable in Upper Midwest only, significantly so, App. 14,15) and between these two niche groups especially in year 0 (significant in Upper Midwest and Missouri, App. 14,15) but also in year 3+ (testable in Upper Midwest only, significantly so, App. 15). Distribution of specialist numbers shifted nearly uniformly from most underrepresented in most recently burned units to most overrepresented in longest unburned units, while invaders showed the opposite pattern (App. 12,13, Fig. L1-2). The intermediate niche groups (grasslands and generalists) had less pronounced patterns: grasslands showed a milder version of the specialist pattern, while generalists showed a milder version of the invader pattern.

In the Upper Midwest, controlling to univoltine species only, habitat niche breadth continued to show the same effect on relative rank but less significantly (App. 14,15). Likewise, either extreme of the voltinism groups showed significant but opposite trends in year 0 (App. 14), with univoltine species most underrepresented and trivoltine species most overrepresented. While voltinism was not significant in any other year, the univoltine and trivoltine groups did show a rather consistent pattern of reversal in representation through the years. Species of intermediate voltinism had a mild pattern, if any, through the age classes. Family group showed no significant effect within year, although nearly significant in year 0 (App. 14). A Mann-Whitney U test of family rankings in year 0 produced only one significant effect ($P < 0.05$) out of 21 pairings tested, which is the number (1/20) of Type I statistical errors expected (i.e. randomly spurious significant values).

In Missouri, haying in year 0 had a rather similar effect in relative representation (Fig. L3), with specialists and invaders showing marked but opposite trends somewhat more symmetrical than in burn (Fig. L2). Grasslands and generalists show virtually no trend--an even milder effect than in burn. However, absolute numbers are much higher in hayed than burned systems (Fig. L4). In both age classes studied, hayed prairies well exceeded burned in absolute numbers of individuals observed per hour, caused mainly by the much greater numbers of specialists in hay prairies. When specialists were excluded from the calculation, hay prairies had far fewer individuals but still more in year 0 than burned. While 11/16 species had higher observation rates in hayed than burned in year 0, this dropped to 7/16 species higher in hayed than burned in year 1, but it was mostly the generalists and invaders (no specialists) that shifted downward with time since haying.

Absolute levels in management age classes

All specialists for which there is a sample to compare, both in Minnesota (Pawnee, Dakota, Regal) and Missouri (Arogos, Regal), clearly had more individuals in hayed than burned in comparable age classes, and 4 of 5 had more individuals in all hayed age classes than in any burn age class (Fig. M1-3, N1-2, App. 16). The one hay prairie sampled during the flight for the Poweshiek and Arogos in Minnesota had very few or no individuals but neither did the nearby similar fire prairie, so I have no good comparison for these species. Aphrodites in Minnesota (Fig. M4) showed a similar trend to Regals (Fig. M2) but burned and hayed in year 0 were less different. The Great Spangled and Monarch showed less consistent trends: in Missouri, Spangleds (Fig. N3) were more numerous in hayed than burned age classes, but showed the reverse in Minnesota (Fig. M3). (Early-season) Monarchs in Missouri (Fig. N4) showed opposite trends in the 1992 and 1993 data; (late-season) Monarchs in Minnesota (Fig. M5), while at higher levels in hayed, also showed less marked

differences between fire and hay prairies than specialists.

In Wisconsin, I have made limited comparisons of fire, grazing (not for conservation but in low-intensity farming), and degraded fallow pasture with a small sample of sites. For the Regal, fire was distinctly the most harmful treatment; light grazing was most favorable, but even fallow pasture (i.e. no treatment) was better than fire (Fig. O-1). The Thomson-Thousand's complex illustrates this well (App. 17): patches of high-quality fire-managed dry prairie (Thomson, Thousand's II) have had few, sporadic Regal records; so also in the fire-managed degraded fallow pasture (Greater Thomson units 3,7), with the population concentrated in the unburned degraded fallow pasture (Greater Thomson units 4-6,8). The Aphrodite, a grassland species, showed a somewhat similar but milder response, with slightly more in grazed (Fig. O3). The Spangled, a generalist, showed the reverse pattern of the Regal (Fig. O2): generally highest numbers in fire management, lowest in grazing, fallow also low. The Monarch, an invader, was variable among sites, but tended had higher numbers in more recently burned areas as well as fallow, with low numbers in light grazing (Fig. O4). The Ottoe was not as well served by farm practices, for it was absent at Thomson (both fallow and burned pasture) and only one was found each year at the lightly grazed site. This does not prove that fire is beneficial for them--many fire prairies have few or no Ottoes, or that grazing (or haying) specifically designed for conservation rather than profit might not serve this species better.

Response of individual specialist species to fire

Poweshiek Skipper. This species declines sharply after recent fire, with by far the highest response index of any tested species (App. 11), but I have no good tests of alternate management. However, my three best populations (App. 5) all had grazing or haying land uses pre-preservation.

Ottoe Skipper. This species' abundance patterns in the burn age classes usually skew toward much greater representation in older age classes (App. 12,16), except in one subset of one analysis (App. 16 1992-93 only), which might appear to fit the pattern expected in the intermediate disturbance curve (Connell 1978 as cited in Hobbs and Huenneke 1992), i.e. low numbers both shortly after fire and long since fire with higher numbers intermediate between fires, but see "Dakota Skipper" below. I do not have a good test of alternate management.

Leonard's Skipper. This species strongly skewed to lower numbers in the first several years postfire, with 0/67 found in a recently burned unit (App 16.).

Pawnee Skipper. This species had greater numbers in longer unburned units within fire prairies but clearly responded better to haying than fire (App. 16).

Dakota Skipper. This species' response to fire appears to fit the expected pattern of the intermediate disturbance curve (see "Ottoe Skipper" above), seeming to support the "short-term loss, long-term gain" hypothesis of prairie butterfly response to fire, except that Dakota numbers are much higher in all hay age classes than in any burn age class (Fig. M1, App. 16).

Arogos Skipper. This species appeared averse both to recent hay and fire, but much more so to fire than to haying (App. 16). The species had higher numbers and recovered (i.e. increased) more quickly in hay than fire prairies (Fig. M1).

Regal Fritillary. I have by far the largest and geographically widest sample for this species, which illustrates well the consistent spatiotemporal replications of specialist response to fire: major declines postfire with slow multiyear recovery (Fig. M2, N2, O1). My results summarize the average species response, but at a given site in a given year, a range of responses better or worse than average is possible. For example, Muralt and Nachusa showed impressive recoveries in 1993 from 1991-92 fires, although these populations remain quite small and vulnerable to future population stressors (App. 17, Fig. E3). However, Thomson showed continued decline in 1993 from 1992 fire (App. 17). Thus, while the average response reported here provides predictive power for results from average management at

average sites, to increase the probability of persistence of specific population(s) at particular sites, managers must allow for worse than average responses--i.e. be conservative in management and expectation. Regals responded very favorably to haying (App. 16, Fig. M2, N2), probably not just because of differential direct and indirect mortality between burning and haying, but also because conservation haying is favorable for forbs (both the spring flora their larvae require and the long season of summer nectar the adults need). Light grazing is also beneficial (as at Crawford County site, Fig. E3). In fact, past and/or present grazing is an important component of all known current Regal populations in Wisconsin. I don't have direct comparisons to determine which of haying and grazing is better for Regal, but fire is worst and even fallow (no treatment) is better than fire (Fig. O1) although lack of all processes may not be long-term stable for the habitat.

Gorgone Checkerspot. While I lack an adequate sample for analysis, distribution of individuals observed in this and our barrens surveys (Swengel 1993a) follow the pattern of other specialists: 146/150 (97%) individuals were in unburned units; 4 of 32 prairie Gorgones were in recently burned units, half that expected based on survey effort, while 0 of 118 barrens Gorgones were in burned units (10 expected based on effort). Gorgones seemed to increase indefinitely with time since fire; rates were very high in units burned 15+ years ago, and second highest in units burned 5+ years ago (App. 16).

Summary of management effects on butterflies

While each butterfly species has its own individual response to fire, all analyses agree that the specialists have a pronounced and significant aversion to fire, and this effect persists 3-5 or more years. Species with the broadest habitat niche (invaders) are most overrepresented in more recently burned units and least represented in longer unburned units. Thus, these two extremes of the habitat niche spectrum show opposite trends through the fire rotation. Species of intermediate classifications (grasslands, generalists) tend to show milder trends. Ordinating observations by family reveals no patterns, while classifying at the order level indicates overrepresentation of butterfly individuals in recently burned units, which common species entirely account for. By contrast, in haying management specialist numbers (and to a milder extent grasslands) are much higher than in fire, while invaders (and generalists to a milder extent) did not necessarily show an opposite effect. I have only limited tests of grazing as a conservation treatment, but it serves Regals (the only specialist tested) better than fire. Other researchers' observations are consistent with these results (see "LITERATURE REVIEW - EFFECTS OF FIRE ON BUTTERFLIES" below).

These results strongly contradict the "short-term loss, long-term gain" hypothesis of specialist response to fire. From comparisons between fire and other treatments, it appears that specialists are losing both short- and long-term in fire management but fare better both short- and long-term in alternate conservation management. These results are also contrary to theoretical expectations about the effects of fire management on prairie butterflies. The specialist species, those most adapted to live in this habitat and most dependent on prairie preserves to exist, show the least benefit and adaptation (if any) to fire and most benefit from alternate management while the most ecologically flexible and widespread species--the invaders--show the reverse trend.

Specialist butterfly response to fire is disturbingly similar to effects of clearcutting forests (long considered "renewable resources"--i.e. ecosystems that can recover completely from disturbance) on spring flora (Duffy and Meier 1992), salamanders (Petranka et al. 1993), and beetles (Niemelä et al. 1993). Although the time scale is different, the graphs of their decline and recovery is strikingly similar; recovery, if it occurs, takes longer than the management interval allows. Generalist beetles thrived postcut but some mature-forest specialists apparently never recolonized regenerated stands. Conservationists would not propose that

these species are adapted to clearcutting nor that the short-term loss is warranted because they may recover to some degree later on. While timber managers objected to Duffy and Meier's (1992) assertion that the ecosystem hadn't recovered (Elliott and Loftis 1993, Steinbeck 1993) because only a component of the flora was studied, Duffy (1993) responded that regardless of how the rest of the ecosystem fares (and no researcher studies everything in the ecosystem), if the native spring flora hasn't recovered, then the ecosystem cannot be considered fully recovered.

My results not only dispute that fire management is beneficial (even neutral) to the conservation of specialist butterflies, but also whether the fire paradigm is correct. If current fire treatments are mimicking prehistoric prairie phenomena, why aren't prairie specialists adapted to them? One response to my results would be to study how long it takes for specialists to recover from fire (if they do) in order to determine how to manage a prairie primarily with fire yet still maintain specialist populations. While I cannot prove that this can't be done, I do question whether it is the most beneficial approach not only for conservation of butterflies but of the prairie generally. Can fire be infrequent enough to accommodate butterflies yet frequent enough to accomplish other management objectives? Since prairie specialists are clearly not adapted to fire, but are to other conservative management treatments, then it is not unreasonable to suppose that they (and their habitats) are adapted instead to other process(es), e.g. megafauna herbivory. Future research should give specialist butterflies (and their associated flora) more opportunity to demonstrate such adaptations.

Factors affecting response to fire

Although I did not directly study the mechanisms causing differential butterfly abundance postfire (e.g. mortality during and after fire, differential forage quality and availability), my results are consistent with previous studies that demonstrate high mortality for insects present when an area burns (see "LITERATURE REVIEW - EFFECTS OF FIRE ON BUTTERFLIES & INSECTS" below). On this basis, I propose a qualitative model that butterfly species respond to fire management based on habitat niche breadth, voltinism, location during fire, vagility, and response of associated plants to fire. Besides explaining why these factors are relevant, my model adds other factors that in interaction largely explain why each species has its own individual but fairly predictable response to fire.

Habitat niche breadth. To repopulate a burn unit, individuals from unaffected areas must have access to the burned unit. The broader the habitat niche, the more widespread the species would be and the more likely that source populations would exist both on and off the preserve within dispersal distance. Specialists would more likely be restricted to the preserve's habitats; whenever a preserve experiences fire, such species would have smaller reservoirs in the vicinity for recolonization. I suspect another factor as well. As a global generality, specialists tend to be conservative in habitat choice, preferring older-growth (climax) rather than early successional habitats; the diversity of specialist species implies that climax habitats can persist rather stably. Generalists and invaders are more likely to capitalize on early successional seres, which while often abundant are often ephemeral and sporadic in distribution. While most people do not conceive of grasslands as a late (rather than early) successional sere persisting in a stable state, I suspect it is likely when their native abundance and diversity of megafauna occur (see "Precontact prairie fauna" below).

Voltinism. This determines how many generations a population has to recover from one fire before the next occurs, so that multivoltinism would be beneficial.

Location during fire. It is beneficial to be absent when a site burns. Resident butterflies would vulnerably rest in the fuel for the flames unless they have some adaptation to protect themselves from fire. If the animal is present in a burning area but insulated from the fire's destruction by burrowing into the ground, boring into branches, or perching up in shrubs, it may gain some degree of

protection (McClure 1981), but research should test this and the consequences of the subsequent "shock phase" (see "LITERATURE REVIEW - EFFECTS OF FIRE ON INSECTS" below) before management assumes a species is protected from adverse fire effects.

Vagility. The more recolonizers enter the burn unit, the quicker the recovery will be, so the greater the dispersal tendency of a butterfly, the more quickly and thoroughly it should recolonize burned sites. Some butterfly species may be much more sedentary than one might predict for winged animals. In the United Kingdom, about 85% of butterfly species form closed colonies, with some quite sedentary, as measured by their apparent unwillingness to cross unsuitable habitat, even small barriers of non-habitat, to occupy nearby suitable habitat (Thomas 1984).

Response of key plants. Although beyond the scope of this study to measure directly the effects of fire on the study species' larval food and adult nectar sources, the literature provides useful information. A plant's response to fire is partially determined by how actively it is growing when fire occurs (Daubenmire 1968), so that cool-season growers are most likely to be harmed by current fire practices (see "Evidence advanced for the fire paradigm" below). Thus, most violet-feeding species (Aphrodite, Regal, Meadow, and Silver-bordered Fritillaries) are fire averse (App. 9,11,12). Response of nectar sources may also be relevant, as for late-season Monarchs (see "Analysis of adjacent like units" above).

Other possible factors. Fire might enhance natality, if oviposition plants are favored by fire, since a female butterfly might more easily locate more oviposition sites in very recently burned areas because of less obstructing vegetation. Conversely, given fire mortality, mate finding should be less efficient in burn units, since many more females should eclose in unburned units, encouraging males to remain there. Ability to flee the flames is largely irrelevant in my study because management burns occur primarily in the cool season, when few butterflies are in the adult (most mobile) life stage. For some part of the summer, most diurnal Lepidoptera are in the adult life stage, but it is not clear whether they would successfully flee fire, especially since vertebrates can also experience high mortality (see "Evidence advanced for the fire paradigm" below). Summer fires would also be harmful in the short term because charred areas would be devoid of key plants and cover. This is less so following mowing, for some vegetation is still available postcut. Although invertebrate predators may die during fires, I doubt this benefits specialists, slow to recover. At least some of the predators would be generalists that likely respond to fire as generalist butterflies do and would also follow the fire-increasing generalist butterflies into burned areas, so that predator populations probably rebuild faster than specialist butterflies.

LITERATURE REVIEW - EFFECTS OF FIRE ON BUTTERFLIES

Studies of prairie-specialist Lepidoptera include those by Dana (1991) on the Dakota and Ottoe Skippers and Borth and Barina (1991) on Catocala moths whose larvae feed on leadplant (Amorpha canescens). Both document sharp drops in larval abundance and increases in larval mortality in recently burned areas. Since our study methods differed considerably, only crude comparisons can be made between Dana's data and ours from his study site, which has experienced frequent fire management over increasing areas since his study. In Fig. 15 (Dana 1991, p. 38), which presents his data on observation rates, the scale of butterfly rates on the vertical axis is 10 times too high, i.e. move the decimal place one digit left (Dana in litt. 5 Mar 93). Since his rates would have been higher if all his time were devoted to counting (as we do) rather than also to mark-release-recapture effort, he adjusted his rates to conservative estimates of his observation rates counting only observation effort at/near each species' peak (Tab. 2) (Dana in litt. 5 Mar 93). In the decade since his research, both the Dakota and Ottoe have declined greatly, especially in the more appropriate comparison to his adjusted rates (Tab. 2). In 1990, the new acquisition (my units 1-6, Swengel 1992b)

produced our highest Ottoe rate ever at this site (3.6/hr), which dropped 95% in 1991-92 after fire in about a two-year rotation occurred in the new acquisition. Each year we have surveyed at appropriate times for one or both species. I judge this for Ottos from our observations in Wisconsin, which appears slightly faster phenologically than Minnesota; from the few Ottos we've seen at this site, it is unimaginable to find any sort of sample of Ottoe ova on coneflower stalks as Dana did. We have never seen many Dakotas at Hole-in-the-Mountain (App. 5), yet Dana (1991) did, and we've found much higher Dakota numbers elsewhere (Fig. M1), even achieving rates comparable to or exceeding Dana's adjusted rates, evidence we surveyed at appropriate times.

Table. 2. Comparison of Dana's rates in 1979-81, both actual (Dana 1991 corrected in litt. 5 Mar 93) and adjusted (Dana in litt. 5 Mar 93), with ours 1988-93 for two specialist skippers at Hole-in-the-Mountain Prairie, Minnesota.

	-----DAKOTA-----		-----OTTOE-----	
	average rate	% change from 1979-81	average rate	% change from 1979-81
1979-81 actual	3.9/hr		1.7/hr	
1979-81 adjusted	20.0/hr		10.0/hr	
1988-90	2.3/hr	-41% act, -89% adj	2.3/hr	+35% act, -77% adj
1991-93	1.4/hr	-64% act, -93% adj	0.23/hr	-86% act, -98% adj

While not studying management effects, other sources provide relevant data. The only tallgrass prairie area with a number of 4th of July butterfly counts was southwestern Missouri-northeastern Oklahoma in 1993 (Opler and Swengel 1994). Readily sorted by management, these five counts (Tab. 3) differ strongly between sites frequently burned (group A) and those not (group B). Group A (fire prairies) had almost no specialists (<4% of individuals) while B found at least 50% specialists; A had a minimum of 45% generalists while B found no more than 31%; A had a minimum of 13% invaders while B found no more than 6%. Group A also averaged much lower absolute observation rates of total butterflies (30/hr) than B (126/hr); B averaged over 200 times as many specialist individuals/hour than A (fire prairies). This agrees with my results that frequent fire favors generalists and immigrants and reduces specialists and that specialists (and even butterflies in general) are much less abundant in fire prairies than in hay, grazing, and fallow prairies.

Not only were 23,110 acres (70%) of the Tallgrass Prairie burned in spring 1993 (TNC 1993) on a preserve of 33,000 acres (Opler and Swengel 1994), with additional fires on neighboring land, but this area apparently has a history of frequent fire as a local ranching practice (R. Panzer pers. comm. 12/93). At Buffalo Jump, whose center is only 27 miles from the center of the next nearest count (El Dorado Springs), 33-50% of the area has been burned annually, in addition to annual summer mowing (Opler and Brown 1990). In 1993, 66% was intentionally burned but 98% actually burned when control of the fire was lost in a wind shift. The count compiler states, "In spite of a nearly complete burn, species and numbers sighted matches counts of previous years" (Opler and Swengel 1994). This is true, but probably for a reason unanticipated by the observer. Previous fire management had already profoundly affected the butterfly community; it is not an unusual increase in fire size that could substantively affect this community but rather a major decrease in fire, in which case specialists from populations in numerous private/public hay prairies in the vicinity might re-establish themselves here.

Royer and Marrone (1992a-d) reported status surveys for four prairie butterflies in North and South Dakota. Tabulations of those populations confirmed extant in 1990-91 (Tab. 4) showed that Regals were the most widespread species best represented on preserves and refuges, but even so, 53% of populations were on private land; 37% were grazed and 20% hayed. Poweshieks had 6 confirmed sites (83%

Table 3. 1993 4th of July butterfly counts from southwestern Missouri-northeastern Oklahoma that primarily surveyed prairie habitat. Weather is summarized by this study's coding and presented as: temperature (F); cloud cover (MC=mostly cloudy, PC=partly cloudy, mC=mostly clear, C=clear, IR=intermittent rain); wind direction and speed in miles/hour if reported. Spec=specialists, Grass=grasslands, gen=generalists, inv=invaders, unid=unidentified.

Count name	State	Lat-Lon	Date- Weather	Party- Hours	Total individuals-Percentage					
					Spec	Grass	Gen	Inv	Unid	Total
<u>A. Frequent/intense fire management:</u>										
Buffalo Jump	MO	37°46'N	7-04-93	4.75	4	33	62	15	2	116
		93°29'W	poor-good		3.4%	28.4%	53.4%	12.9%	1.7%	
weather: 75-84°; MC then hazy; S 0-5										
Tallgrass Pr	OK	36°50'N	6-26-93	8.00	0	95	131	62	0	288
		96°24'W	poor-good		0.0%	33.0%	45.5%	21.5%	0.0%	
weather: 78-85°; MC then PC; SW 5-15										
<u>B. Infrequent/unintense fire management:</u>										
El Dorado Spr	MO	37°52'N	6-16-93	4.22	518	55	28	17	55	673
		94°01'W	good		77.0%	8.2%	4.2%	2.5%	8.2%	
weather: 87-92°; mC then PC to MC; S 15-25										
Sedalia	MO	38°33'N	6-19-93	5.25	653	107	97	18	0	875
		93°15'W	poor-good		74.6%	12.2%	11.1%	2.1%	0.0%	
weather: 68-86°; MC with IR then C; S to N										
Taberville	MO	38°00'N	6-19-93	7.00	188	43	116	22	0	369
		94°00'W	poor-inter.		50.9%	11.7%	31.4%	6.0%	0.0%	
weather: 77-86°; MC then PC; SW to W 5-15										

Table 4. Summary of site and management information for prairie-specialist species surveyed by Royer and Marrone (1992a-d) in North and South Dakota 1990-91.

Species- site status	N sites	OWNERSHIP					
		private	TNC	state	federal	Indian	
Poweshiek-present	6	5	1				
-absent	2			1	1		
Dakota -present	26	19		3	3	1	
-absent	8	6	2				
Arogos -present	6	5			1		
-absent	2	1	1				
Regal -present	51	27	4	8	10	2	
-absent	n/a						
<u>Management/Land use of extant sites:</u>							
		priv.	pres.			semi-hay	
	rec. pre-	fal-	prai-	duck	semi-	semi-	school
	graze hay game area serve NWR low rie prod. graze WPA ROW graze ? land						
Powes.	2 2			1			
Dakota	8 9 1	1	1		1 2	1 1 1	
Arogos	1 4	1					
Regal	18 10 7	4 4 1 2	1		1 2 1		

private), 2 grazed and 2 hayed. Dakotas had 26 confirmed sites: 73% private, 31% grazed, 35% hayed. All but one of four sites rated abundant were private (1 grazed, 2 hayed); the fourth was a state waterfowl production area. This is consistent with McCabe's (1981) preference for late-season mowing for Dakota management. Arogos Skippers also had only 6 confirmed sites (83% private), 1 grazed and 4 hayed. Management was not listed for most public sites; some of them might be grazed or hayed, too. It is clear that private property is very important to the continued existence of these species in this region and that grazing and/or

haying can be compatible with their maintenance.

Some have noted that R. Panzer has espoused fire management recommendations that are not as conservative as many others, e.g. Opler, Schweitzer, Swengel (all reviewed in Moffat and McPhillips 1993). I have not seen a scientific analysis of fire effects on any insect group by Panzer, although Panzer (1988) has published a compilation of anecdotes on species, including prairie specialists, known to have survived to any degree at least a decade of fire management at selected sites. This approach, commonly used to defend fire management, is comparable to noting that Northern Spotted Owls (*Strix occidentalis*) still exist in northwestern forests in clearcut timber management. While one is glad the owls persist, their mere existence in no way endorses the current management--one must track the populations to see how many persist and at what trend over time. Panzer's set of anecdotes, while certainly valuable, is a highly skewed sample. Since fire management started well before Panzer's surveys at some (probably most or all) sites, fire-decreasing species could easily have been lost prior to any attempts to detect them, and I can neither prove nor Panzer refute this possibility. By this approach it is virtually impossible to obtain anything other than positive data (i.e. fire survivors). It is not an endorsement of fire that no data exist to prove it has extirpated species when such data are virtually unobtainable.

It is an odd conservation approach to use extirpation as the method and standard. Presence/absence data are a much weaker measure of response than abundance indices (see "RESPONSE TO MANAGEMENT" above). The more appropriate questions are whether rare species are declining, whether any such trends at a number of sites correlate with any factors, and what might conservationists do to arrest any such declines. Panzer (1988) stated that no populations were extirpated by fire at his study sites during his 3-7 years of surveying. Specifying proximate cause of extirpation at a particular site is difficult; just as fair a question is whether fire can be proven not to have caused or contributed to any population losses, but this probably can't be answered definitively either. However, with great sadness I note that sites in Panzer's region contain very few prairie specialists, although some sizable preserves there could plausibly support such populations. While I have not visited any of these sites and cannot comment on prairie quality and extent, ten Illinois nature preserves ranging from 70-829 acres in six counties around Chicago (Cook, DuPage, Kane, Kendall, McHenry, and Will Counties) protect large prairie patches. Yet Panzer (1992) reported that on a minimum of 23 sites in the Chicago region, only a few populations occur of specialists as I defined them in this report (1 Byssus, 0 Ottoe, 0 Leonard's, 1 Regal, 1 Gorgone). Even grassland populations can be rare (e.g. 5 Delaware and 3 Crossline Skippers; 2 Aphrodite, 2 Silver-bordered, and 4 Meadow Fritillaries). While neither I nor anyone else can prove site-specific causes, these preserves are not protecting many prairie specialists and certainly do not endorse fire management for them. The specialists' paucity is consistent with my and others' data on the effects of frequent fire on butterflies.

After extensive observations over long periods, several Iowa lepidopterists have independently arrived at conclusions similar to mine regarding prairie fire and its effects on specialist butterflies. They have asserted that fire burned less frequently in ancient prairies than in modern management, grazers were important in prehistoric prairie management and affected how fires burned (i.e. making them patchier), and management should be diversified, not relying primarily or solely on fire (Orwig 1990, Schlicht and Orwig 1990). Schlicht (1993) reported that prairie-obligate butterflies usually do worse on fire-managed sites than on unmanaged (i.e. non-preserve) sites, plot size is less important than management regime for obligate survival, grazed plots are often more diverse in obligates than fire-managed plots, and that, given insects can have dramatic population fluctuations naturally, excess disturbance (i.e. fire reducing their numbers) could extirpate local populations. He asks what is less dangerous than fire for

obligates; he answers: habitat fragmentation, linear habitat, occurrence in rights-of-way of actively used highways and railroads, grazing, and being ignored.

LITERATURE REVIEW - EFFECTS OF FIRE ON INSECTS

The usual response of a variety of insects in the immediate (hours during and after fire) and short term (up to two months) after fire is a marked decline (Rice 1932, Bulan and Barrett 1971, Lamotte 1975, Morris 1975, Anderson et al. 1989, Samways 1990). Thus, fire can be effective in the control of a variety of undesirable insect populations (Miller 1979) and can eliminate food for insectivorous birds (Daubenmire 1968). Since the decline can continue for some weeks postfire, several authors proposed that not only mortality during the fire occurs but also a "shock phase" afterward from exposure and lack of food (Rice 1932, Lamotte 1975, Warren et al. 1987). The intermediate-term effects (2-12 months postfire) are more diverse. Some taxa persist in lower numbers, some become similar to controls, and some become more abundant; sometimes different studies of the same taxon produce conflicting results (Rice 1932, Cancelado and Yonke 1970, Bulan and Barrett 1971, Nagel 1973, Lamotte 1975, Morris 1975, Van Amburg et al. 1981, Seastedt et al. 1986, Warren et al. 1987, Evans 1988, Anderson et al. 1989). Most of these studies identified individuals at the family or order level, so that only very general tendencies among taxa can be demonstrated, and these differences tend to persist only into the short- or intermediate-term.

Such studies cannot predict how a particular species within the larger taxon might fare; instead, they usually reflect only the trends of the most abundant species. The few studies that identified at the species level have found reduced diversity postfire. Hemiptera and Homoptera diversity was significantly lower in burned than unburned plots in the intermediate term, the only time period studied (Morris 1975). While grasshopper numbers (Order Orthoptera) are usually but not always more abundant in burned plots in the short and intermediate term (Lamotte 1975, Nagel 1973, Warren et al. 1987); grasshopper diversity was lower in more frequently burned plots than in less frequently or never burned plots (Evans 1988).

Several researchers have attempted ecological explanations of these responses. Miller (1979) concluded that insect mortality increased if the population was in a life stage and location (usually on the ground) vulnerable to fire. Another ordination regards feeding adaptation. While herbivorous beetle diversity was significantly reduced up to the intermediate term, carnivorous beetle diversity was unchanged (Bulan and Barrett 1971). In another study (Evans 1988), more frequently burned plots had lower forb cover and forb-feeding grasshopper diversity decreased there. Nevertheless, while grass-feeding grasshoppers dominated the species diversity of more frequently burned plots, their numbers did not correlate with grass density. Thus, the shift in plant cover from forbs to grasses caused by more frequent fire disfavored forb-feeders but did not benefit grass-feeders. Forb- or grass-dependence did not entirely explain grasshopper response, however, since two common grass-feeding species with similar diets had different local distributions, possibly because of variation in amount of litter accumulation.

Lamotte (1975) found that in general those groups adept at flight recovered in the intermediate term from the pervasive immediate and short-term decline postfire and also proposed that fire-induced habitat changes are important in determining insect response. The environment resulting from fire favors a sunloving and mobile fauna dependent on grasses, but disfavors or eliminates species of other niches, since recently burned habitat offers less niche diversity than unburned (Lamotte 1975). We've informally observed that mosquitoes (adept at utilizing ephemeral habitat patches and seres) are more numerous in recently burned areas; the increase in mosquito density is frequently quite sharp when we move from unburned to burned wet to mesic prairie. The process of niche and diversity reduction has been termed "simplification" (Bulan and Barrett 1971) and hints at the possibility of permanent effects, at least if fire is frequent or pervasive, as does the finding of distinct

grasshopper communities segregated by fire frequency (Evans 1988).

My results indicate that if/when simplification of the prairie butterfly community occurs after fire, specialists are most likely to be eliminated because they are most underrepresented of any group in the most recently burned areas. Others' observations of fewer or no specialists the more frequently burned the site agrees with this scenario. Given the conservation concern for specialist species, such an outcome is undesirable. Rare species have been found to respond differentially more poorly to other lethal management treatments as well. For example, while overall species richness of nontarget Lepidoptera showed no significant difference between a site treated with a microbial insecticide and the untreated site, richness of uncommon species was significantly lower in the treated site (Miller 1992).

EFFECTS OF MANAGEMENT ON BIRDS

I will only cursorily examine this issue, leaving more detailed treatment to my co-researcher, an ornithologist. Birds, especially ones most characteristic (i.e. specialized) to the habitat, are usually reduced after fire: tallgrass prairie (Volkert 1992, Zimmerman 1992, our unpubl. data), sageland (Petersen and Best 1987), chaparral (McClure 1981), forests (Apfelbaum and Haney 1986), and Australian habitats (Smith 1977, McFarland 1988). Austrian dry grasslands and their birds are considered threatened by fire (Kollar 1991). Fire management eliminates most nesting in the first growing season postfire (R. Johnson in litt., Kruse and Piehl 1986), so that populations can recover only if relatively higher nesting success and density occurs in future years (Johnson and Temple 1986). Grazing can be a good way to manage birds including waterfowl and prairie grouse (Skinner 1975, Kantrud 1981, Barker et al. 1990). The two greatest success stories (i.e. population increases) we've found for the management of Greater Prairie Chickens (Tympanuchus cupido) and Sharp-tailed Grouse (T. phasianellus) are attributable to haying in Missouri (Christisen 1985) and a combination of grazing and a little fire in North Dakota (Bjugstad 1988), respectively.

Although grassland birds are native to prairie, and until European immigration, had only prairies for grassland habitat (few or no old fields were available), they are now often found more abundantly in fallow or unintensively farmed land (Skinner 1975, Zimmerman 1982, Howe and Rossa 1984), especially in the Conservation Reserve Program (CRP). While I am glad that CRP, enacted in 1985 to reduce soil loss on highly erodable farmland, has had beneficial conservation consequences such as reversal of landscape fragmentation, maintenance of regional biodiversity, and creation of wildlife habitat (Dunn et al. 1993), some people have developed the peculiar notion that grassland birds really aren't prairie species because they are more abundant in old field than high-quality prairie preserve vegetation. The important point is not so much that they live abundantly in fallow farm fields, but that they are so scarce in preserves--where they ought to be and where something is clearly going wrong.

The Henslow's Sparrow (Ammodramus henslowii), a federal category 2 (candidate) species considered among those birds most likely to become extinct soon (Butcher 1989), is a prairie specialist. It is near absent from our study sites in the Upper Midwest. We've never confirmed one during our surveys for this research; we found one at Oliver, Wisconsin on 30 April 1991, possibly another at Cayler, Iowa on 5 July 1993, and multiple consistent observations at Pine Island, Wisconsin (but not on surveys for this research). Our observations elsewhere in Wisconsin agree that the Henslow's is rare, now present only in marginal habitats, but surely this apparent habitat "preference" is an artifact, for during most of this species' existence, only native (not exotic) grasslands were available for it to inhabit.

By contrast, Henslow's are abundant in our southwestern Missouri sites that are hayed or unburned. We've found about 540 in 111 transects covering 45 miles, a mean rate per unit of about 14.1/mi (17.4/hr), while only 4 were found in 17 transects covering 4.2 miles in recently burned units--1.03/mi (1.5/hr). This

sparrow is consistently denser in hay prairies than fire prairies; our survey units averaged 1.0/mi (1.5/hr) in year 0 and 19.2/mi (20.7/hr) in year 1 of fire management, but 21.9/mi (27.3/hr) in year 0 and 23.3/mi (25.5/hr) in year 1 of haying management. This is similar to the Regal Fritillary's differential abundance in management age classes, except that the difference in year 1 between fire and haying is much more marked in the Regal. In fact, Regals and Henslow's correlate strongly in Missouri (Pearson's correlation matrix, Regals and Henslow's/mi: $r=0.24707$, $P=0.0053$, $N=126$; Regals and Henslow's/hr: $r=0.20132$, $P=0.0235$, $N=126$). Henslow's have also occurred at 20-35/hr on lightly to moderately grazed and cut farm grasslands in northern and western Missouri, where total bird and nest densities can be enormous (Skinner 1975). The Missouri study in hayed/cut/grazed grasslands averaged about 5-8 times as many Henslow's as the 4.5/mi found by Zimmerman (1992) in unburned Kansas prairie surrounded by frequently burned prairie--the latter lacked Henslow's in burn years. Note that hours is the unit in Skinner's study--bird surveys often progress at slightly less than one mi/hr.

CONSERVATION PROGNOSIS AND PRIORITIES - PRAIRIE SPECIALIST BUTTERFLIES

Status, trends, threats for specialist species

General. The overwhelming destruction of prairie habitat (see "INTRODUCTION" above) has obvious disastrous consequences for prairie-specialist species, many of which were originally restricted to only a part of the prairie biome, so that only portions of what remains is habitat for them. Prairie loss continues deliberately today by plowing, extreme overgrazing, and development but is of varying degrees of threat regionally. Marginal farmlands, while under threat of overintensive use because of economic difficulties for family farms, have also been sheltered by the Conservation Reserve Program (see "EFFECTS OF MANAGEMENT ON BIRDS" above). It is prairie still in unintensive use (e.g. light grazing/haying) on arable land that I perceive to be under greater threat of incompatible farm uses. Development generally depends on human density, thus primarily around cities and suburbs, while in much of the prairie region rural populations are sparse; the increasing trend of rural home-building for urban commuters is a significant threat. Prairie is also lost passively because the near total disruption of previously prevailing processes allows unnatural floristic releases. From the scientific evidence (see "LITERATURE REVIEW - NATURAL MAINTENANCE OF GRASSLANDS" below), I believe the primary processes were megafauna herbivory and climate, rather than the chimera of presumed prehistoric fires, so that to ameliorate the current absence of processes to the benefit of native biodiversity, the right processes must be restored in a way mimicking prehistoric conditions and effects.

Farmland uses have varying impacts on specialist butterflies. Some (Dakota, Regal, Gorgone) benefit more from less intensive farm practices, with farmlands important to their conservation today, than others (Ottoe, Arogos). An uncomfortable question is how much preservation has really benefited specialist butterflies. From the evidence (see "RESPONSE TO MANAGEMENT" and "LITERATURE REVIEW - EFFECTS OF FIRE ON BUTTERFLIES" above), it would apparently have been and remains more beneficial to preserve unintensive farming (i.e. light grazing/haying) than to acquire such land as preserves if this necessarily also means the institution of frequent/intense fire management. I continue to believe, however, that conservationists are able and ought to be willing to conduct a more beneficial mix and type of management program (as in hay-graze-burn management seen in southwestern Missouri), in which case preservation would be preferable to farming. Thus, there is cause for optimism, for while current preserve management is both entrenched and troubling, it is also completely addressable and correctable entirely within the conservation community. Furthermore, no known prairie butterfly species has gone extinct, and these species have persisted long and widely on habitat remnants, so that such changes should translate into readily measurable successes. I assessed my study sites in each state to identify the highest priority areas for management

compatible with maintaining high populations of specialist butterflies (App. 19); see App. 5-8 for the highest priority sites for individual species.

Poweshiek Skipper. This species clearly qualifies for federal listing (App. 20). It is extant in six of the eight states comprising its historic range. In two it already has the threatened/endangered status it warrants. In the Dakotas, Royer and Marrone (1992d) and I agree it should have either threatened or endangered status, and based on the relatively few sites where we've found it in Iowa and Minnesota, combined with management concerns, I recommend a state status of some sort there also. The species also ranges marginally into Manitoba.

Ottoo Skipper. I do not have adequate data to address global status, but only in the Upper Midwest, where it is clearly rare in Illinois, Minnesota, Wisconsin, and much of Iowa (App. 20). Given the alarming trend of this species at Hole-in-the-Mountain, Minnesota (see "LITERATURE REVIEW - EFFECTS OF FIRE ON BUTTERFLIES" above), the species warrants careful status assessment and compatible management globally. The species has similarly declined about 99% since 1990 at Spring Green, Wisconsin--once a large population (App. 18). A massive management fire in spring 1992 burned our sample units 7a-c, where we used to find the majority of individuals. In five 1992-93 surveys postfire we found only one Ottoo at Spring Green--in 1993 in an area not managed with fire.

Leonard's Skipper. While a specialist, this species occurs in relatively many sites relative to effort (see "Population variability by habitat and geography" above). It appears able to reinvade areas recovered from human-caused degradation, so that it appears a relatively low priority for conservation action.

Pawnee Skipper. I do not have enough data to assess its status. It is not a high priority of any agency's or individual's status and monitoring work that I know of, consistent with my sense that the species is of relatively low concern.

Dakota Skipper. This species is extant in four of the five states comprising its historic range, for it was refound in Iowa in 1992 (McKown 1993), reversing the presumed extirpation there. In two states it already has the threatened/endangered status it warrants; in the Dakotas, Royer and Marrone (1992a) and I agree it should have threatened/endangered status (App. 20). The species also ranges marginally into Manitoba. Since the Dakota has or warrants threatened/endangered status in each state in its range, it warrants federal status also.

Arogos Skipper. Given the very few Arogos populations in our study (App. 7,8) and Royer and Marrone (1992c), I consider a careful review of its status a high priority (App. 20), especially since the eastern subspecies is a federal category 2 (candidate). This taxon may be the rarest prairie-specialist butterfly.

Regal Fritillary. Schweitzer (1992) produced a thorough status survey. The species is critically endangered east of prairie (Schweitzer 1992, Swengel 1993b). Within my study states, I have observed only one area--southwestern Missouri--with abundant Regals (App. 8) and public/private land use and management practices that, so long as they continue, justify a belief that Regals are stable and secure there. This species is also widespread in Minnesota (App. 6) but because of management concerns, I cannot assume long-term stability and security there. Only few and fragile populations are known in Illinois, Indiana, Wisconsin, and eastern Iowa, where management is also a concern; at some historical sites, I have yet to observe a Regal, indicating a declining trend (Tab. 5, App. 6). The preserves in northeastern Illinois are well surveyed and little prairie habitat exists off preserves (Panzer 1992 and pers. comm.); while fewer data are available from elsewhere in the state, even if multiple populations of any size still occur in Mason-Cass Counties or elsewhere, the species remains quite rare and threatened in Illinois. Given its rarity and regional declines, I continue to believe that federal threatened status is appropriate, as does P. Opler (pers. comm.) (App. 20).

Masters (1975) reported several small Regal populations in northwestern Wisconsin (Chippewa, Eau Claire, St. Croix Counties; none in Dunn or Polk; didn't search Burnett). He concluded the species could persist as very small populations

Table 5. Historical and current Regal sites in Illinois, Indiana, and Wisconsin. Our study sites (survey data in App. 6) are underlined. ¹R. Panzer (RP), pers. comm. 12/92, ² anonymous participants in classes/hikes led by A. Swengel, ³ S. Borkin in litt. 30 Sep 92, ⁴ R. Borth in litt. 10/93, ⁵ A. Williams in litt. 9/93

STATE	FIRST	LAST	LAST	
	FOUND	OBS.	SURVEY	NOTES ON REGAL ABUNDANCE/SITE
ILLINOIS				
Braidwood ¹	~1992			very scarce in 12 surveys/6 yrs, 400 ac sav.
<u>Byron</u>	1991	1993		1 specimen in nat ctr (3 Jul 91, C. Laurent, Chana, IL). We checked sev. times in 1993; as prairie is increasingly cleared each year, entire cleared prairie is annually burned.
Goose Lake ¹	1992			0 on 19 surveys 1992 (1500 ac dry-mesic and wet pr. and marsh); 1 in near powerline right-of-way
<u>Harlem Hill</u> ²	?	1993		We checked sev. times in 1993; 53 ac dry pr.
Iroquois ¹	1992?			most in 7-800 ac prairie; occ. 1 in 640 ac sav.
Mason-Cass Cos. ¹	?			1-2 difficult to find?--RP has no pers. exp.
<u>Nachusa</u> ¹	1993	1993		at most sev. doz. (R. Panzer); see App. 6, 17
INDIANA				
Cook ¹	~1989			40 ac site; not seen in 3-4 years
Prairie Chicken ¹	~1992			12-16 obs. in sev. hr; 640 ac sandy prairie
WISCONSIN				
Cedarburg Bog ³	1987	1987	?	strays found, no known population in area
<u>Crawford Co.</u>	1992	1993	1993	priv. 40 ac grazed prairie, best known WI pop.
Governor Dodge	1981?	?		habitat appears to be entirely old field
<u>Muralt</u>	1993	1993		about 40 ac dry prairie in larger preserve
<u>Oliver</u>	1993	1993		about 4 ac dry prairie, near Muralt
near Oliver ⁴	1984	1984		private grazing prairie
near Thomson ⁵	1993	1993	1993	private grazing prairie
<u>Pine Island</u> ³	1983	1983	1990, 93	"common" in 1983; degraded, some fire man.
<u>Spring Green</u>	1987?	1990-93		about 80 ac dry prairie in larger preserve
<u>Thomson/Thou.</u>	1990	1993	1993	see "Absolute levels in man. age classes" above

on very small (even <0.5 ac) remnants of original prairie vegetation. I suspect he may not have found all source populations for his observations. Our experience suggests that sporadic single individuals are better attributed to a population elsewhere in the vicinity, which might be in a degraded field discounted as "Regal habitat." We originally considered the fallow pasture at Greater Thomson too degraded to be worth surveying for Regals, yet that is where the population at the Thomson-Thousand's complex actually concentrates (see "Absolute levels in management age classes" above). Masters may also have been observing a suite of declining populations about to disappear, for I know of no records from this region since. Nevertheless, it would be valuable to resurvey his sites today, although we have found none in extensive surveys of central Wisconsin barrens (Swengel 1993a).

We independently prioritized the major threats to Regals in Wisconsin:

Scott Swengel:

1. fire management
2. inviability of unintensive farming
3. expiration of current CRP in 1995
4. rural housing for urban commuters (business development not major)

Ann Swengel:

- export of fire man. to private sector
- standard preserve management (fire)
- changing rural land use by farmers and for residences
- habitat fragmentation, isolation, reduction by fallow use

Gorgone Checkerspot. Its reputation for using degraded fields would indicate little cause for concern over its status, yet its rarity in our prairie and barrens (Swengel 1993a) surveys is disturbing. I recommend more attention to its status.

Site-specific recommendations

General. I recommend that management favorable for prairie biodiversity occur at all preserves (see rationale in "LITERATURE REVIEW - NATURAL MAINTENANCE OF GRASSLANDS" and "Management recommendations" below). Additional comments regarding specific study sites are in Swengel (1992a,b) and follow.

Illinois. Byron: In the hope Regals still live here, management should do no burns in 1994-95 and should implement a regime primarily of mechanical treatments, which should be unintensified in areas of high-quality prairie vegetation but aggressive in areas of dense exotics (e.g. sweet clover). Harlem Hills: For the sake of Ottoes and Regals, management here should be altered as at Byron. Nachusa: Since the small population here is the best known Regal occurrence in the state (Tab. 5 above), management should emphasize treatments beneficial to flora that are not harmful to Regals. Much of the site is quite amenable to mechanical management, so this should largely replace fire treatments--especially in the lowlands where Regals have concentrated lately. If fire continues at the site at all, part or all of places important to Regals should be designated never-burn units.

Iowa. Freda Haffner: No fire should occur here for 2+ years to allow recovery from too-intensive past fire management. Much of the site is amenable to mechanical management, while the steep areas will accumulate litter slowly (more slowly, if fire is stopped) so that frequent fire is unnecessary and spot-herbicide or spot-cutting can eliminate small areas of brush and weed invasion. Hayden: As at Haffner, discontinue all fire for 2+ years. For the first time, we observed a single Regal here on 10 Aug 93 (App. 6); although this does not show that a population lives here, it does indicate that one could become established here if management becomes compatible both for this butterfly and its habitat. Mechanical cutting should be restored here to reduce serious brush problems and favor native flora. Haying--the management used before Hayden was made a preserve, should be reinstated on a rotation frequent enough to get the brush back under control.

Minnesota. Bluestem and Bicentennial-Blazing Star: Do no fire for 2+ years to allow recovery from too-intensive past fire management. Mechanical management needs to be restored to these sites to correct major problems with sweet clover at all sites (see plates) and brush especially at Bluestem. Mechanical management can and should be the primary management at these sites. Hole-in-the-Mountain: Fire frequency and size of contiguous burned areas should be reduced considerably. Litter accumulation in the dry prairie is slow (although increased by fire). Light grazing should be restored, since this is how the site, with once high populations of specialist skippers, was managed pre-preservation. This may require some careful fencing or artful placement of drinking water to optimize effects in lowland areas. Spot mechanical and/or herbicidal treatments, as already occur here, should continue to address weed problems. Prairie Coteau: My unit 2 was not burned in 1993, as I requested (map of unit and recommendations in Swengel 1992b) although a large burn did occur in unit 1. Burns should be smaller and less frequent here for the sake of rare biodiversity; to the extent mechanical management is possible here, it should be used instead and if further management is necessary, restore grazing to the site. Staffanson: Haying/mowing management should be restored here, and fire de-emphasized or discontinued, for the sake of maintaining viable specialist populations.

Missouri. Continue to manage public prairies with a mix of haying, grazing, and burning that emphasizes haying and de-emphasizes burning, as this has proven very favorable for prairie flora and fauna.

Wisconsin. Dewey Heights and Spring Green: Burn units should be smaller with less frequent fire than in the past. At these sites, cutting has been more effective than fire at removing brush, so this should be the primary emphasis of future management. Litter accumulation at these sites is slow (but exacerbated by fire). Muralt-Oliver and Thousand's-Thomson complex: I am very pleased that managing agencies did no burning of areas occupied by Regals at these sites in 1993. No

fire should occur in 1994 either to continue to allow Regal numbers to build to safer and more wide-ranging levels. Mowing/other cutting, which occurred at both sites to beneficial effect in brush control in 1993, is widely feasible at both sites and should be the emphasis of future management. The possibility of restoring grazing at both sites, which have grazing histories, should also be explored.

LITERATURE REVIEW - NATURAL MAINTENANCE OF GRASSLANDS

Introduction

The fire paradigm. This hypothesis states that prairies are primarily herbaceous because frequent/intense fires, set either by lightning and/or Native Americans, reduce woody plants and favor native herbs. Fires less frequent than in prairie maintain the open canopy of savannas and barrens, with which prairie intergrades; fire should be least frequent in forest.

The questions. Given the widespread use and advocacy for frequent/intense fire management in tallgrass prairie and that the response of prairie butterflies to fire is contrary to the fire paradigm (see "RESPONSE TO MANAGEMENT" and "LITERATURE REVIEW - EFFECTS OF FIRE ON BUTTERFLIES" above), my questions are:

1. What is the evidence for prehistoric fire frequency in this biome?
2. What other process(es) were occurring simultaneously?
3. What conservation effects do fire and other processes have today?

Religion and science. Some have observed that discussions and interpretations of fire ecology border on the religious (Ackerman 1993:23). While I do not belittle religion (belief in things unproven/unprovable by science), scientifically based ecology and management require adherence to the scientific method: the interpretation of observable and measurable evidence and the study of testable hypotheses. Science distinguishes the rigor of evidence between (1) merely necessary and (2) also sufficient to (dis)prove a hypothesis. While a hypothesis may effectively be questioned or advanced merely with sufficient evidence, one can only (dis)prove a hypothesis when both necessary and sufficient (dis)proof obtain. Absence of proof may not disprove a hypothesis and vice versa, but hypotheses lacking strong substantiation cannot correctly be called scientifically established. Fervency of belief and adherence to orthodoxy (traditional/established beliefs) do not strengthen in the least any scientific substantiation, although they can be quite persuasive and/or stifling sociopolitically, often to the detriment of objective scientific inquiry. Conservationists may feel a need to act in the absence of adequate science, but should not state that science substantiates such actions and should proceed cautiously, open to alternative hypotheses and future review as more evidence accrues.

Respect. Although possibly disrespectful in sociopolitical and religious contexts, it is not disrespectful--indeed, it is crucial--to sound scientific advancement for researchers to communicate widely among themselves and review (i.e. test) each others' work. By pursuing a scientific endeavor, one implies consent to this aspect of the scientific method. It is disrespectful, both personally and to science, for established scientists to ignore legitimate counterevidence and methodological questions or to answer such challenges by questioning the motives, intelligence, and/or character of the challengers rather than addressing the substance of their challenges.

Evidence advanced for the fire paradigm

Pioneer diaries. These eyewitness accounts of horrifying blazes appear to corroborate the fire paradigm, but they are inherently anecdotal--an incomplete, unscientific, skewed sample. Myers and Peroni (1983) fairly conclude that this evidence is weak, also demonstrated by the fact that this same source is severely questioned regarding data on prairie megafauna (see "Precontact prairie fauna" below and editor's note following Edwards 1978). Even at face value, unanswerable questions are daunting: How much area actually burned vs. total area "sampled"

(i.e. observed) by the witness? What sort of rough point fire frequency over what time period results? By logic, if the fire paradigm is correct, prior to effective fire suppression at the turn of this century, most prairie settlers would have lost their property and lives in prairie fires. Given the rapidity and thoroughness of 19th century prairie settlement, this clearly did not happen.

Scientific interpretation of eyewitness accounts. This requires implementation of standard methods of historical interpretation, i.e. assessing the account in view of the eyewitness's accuracy, objectivity, and historical context. The only times I have seen this done (Russell 1983, Higgins 1986b), no evidence was found for frequent large fires set by natives. By contrast, Higgins (1986b) found evidence that prairie fires were infrequent and could harm the natives' prey base, causing human famine. Like these authors, I question these writers' credibility because of (1) possible exaggeration resulting from the life-threatening horror of the fire event and (2) intense white hostility and cross-cultural misunderstanding toward natives. Those who choose this source to (try to) corroborate the fire paradigm scientifically should (as I have yet to find) translate the accounts into quantifications, even if rough: how many fires burned how much land in what total land area "sampled" during what time period.

Historical context. By definition, a pioneer account occurred during settlement, which many today seemingly confuse with European contact, implying that early settlement occurred when prairie was nearly pristine (undamaged by whites). In fact European contact well preceded settlement, and contact alone dramatically affected both native societies and native ecosystems (App. 21). Prairie settlers were observing an already greatly perturbed ecosystem increasingly depauperate of its natural abundance and diversity of native fauna and native societies severely stressed by pandemics of European diseases, by a diminishing prey base, and by white aggression. These societies could not have been functioning as in precontact times--indeed, must have been disfunctional postcontact--and gained new motives for setting fires that were unnecessary before: flushing out now rare game and discouraging an overwhelming new enemy--whites. Thus, settlers' observations do not closely correspond to precontact conditions.

Native American accounts. While on rare occasion a native source may be quoted to describe prairie fire, I have never found a systematic pursuit of this source of evidence for ecological application. It is biased to discuss native activities citing only white sources and observations. Many of the tribes still exist and have a strong interest in preserving their cultural history.

Anthropology/archaeology. I am surprised conservation ecologists apparently have rarely consulted anthropologists and archaeologists who attempt to reconstruct native activities, although for different reasons. I think back to many college anthropology classes, recalling native use of fire, aside from domestic purposes, to drive game for hunting and in slash-and-burn agriculture, but not for habitat management per se on any scale. Native activities could have significant but local impacts on the environment, such as opener habitats near settlements (Myers and Peroni 1983); this could include locally frequent fire that does not imply the ecosystem as a whole experienced or adapted to it. An estimate of about 20,000 natives precontact in Wisconsin (Nesbit 1973, Current 1977), an area of 54,426 mi² (Johnson 1991), results in about 2.7 mi² for each man, woman, and child to manage pervasively and frequently--implausible for apparent lack of motive and technology to do so. Plains grasslands were very sparsely populated until the widespread availability of domesticated horses in the 18th century--a postcontact effect (Dix 1975, Higgins 1986b)--and some believe that white settlers caused more fires than natives (Costello 1969), plausible since the former certainly caused many fires (Weaver 1954). One way that natives surely reduced woody canopy was by cutting branches and trees for firewood and building materials--again, a local effect.

Another useful source of information on native pre-industrial practice would be a broadly cross-cultural survey of similar societies worldwide, many studied in

more benign sorts of contact with whites that would provide better information on what these societies do typically and why. Note that while Australian aboriginal fire regimes are a matter of speculation only, white farmers increased the rate of fire use over what aborigines had used (Smith 1977, Gill and Groves 1981).

Prairie and savanna as anthropogenic systems. This is implausible, for prairie and savanna have existed in North America for millions of years (Simpson 1961, Costello 1969, Kurten 1971, Webb 1977). Their origin and maintenance for 99% of their existence occurred in the absence of man. Prairie and savanna in about their current location arose in the last 8,000 or so years in response to the recession of the last glacier, which also coincided with the arrival of natives south of the ice sheet (Pielou 1991). It is another argument that anthropogenic fire over the last few millenia was so frequent and pervasive as to indelibly affect prairie and/or savanna--one for which I cannot find evidence (see preceding).

Lightning. Although ground strikes are obviously apparent each year, lightning ignitions that get any sort of fire started are rare. Modern fires mostly occur in dry seasons--e.g., Arizona, California, Illinois, Louisiana, Wisconsin, Australia, but during lightning season in the Black Hills, South Dakota (Hanes 1971, Gill and Groves 1981, data provided by U.S. Forest Service)--even in places where lightning is asserted to have caused frequent/widespread natural fires prehistorically. By definition, dry seasons are sparse or lacking in lightning. This indicates a preponderance of human-caused ignitions (not by natives but by moderns)--e.g. arson, cigarettes, campfires, downed powerlines, dragging mufflers--and implies that much of modern fire suppression is not unnatural but is actually compensating for unnatural man-caused damage. Even an abundance of naturally occurring, highly flammable material can burn only if a spark is provided, but apparently nature doesn't ignite things very often--modern man does. Contrary to the peculiar statement to me by an attendant at Ramsey Canyon, Arizona, "Smokey the Bear" (i.e. fire suppression) cannot prevent lightning from starting fires; it can only reduce the area subsequently burned. Thus, we should be able to get at least an order of magnitude estimate of historical lightning ignition rates (not area burned) by current observation.

Furthermore, most successful lightning ignitions burn small areas. E.g., Higgins (1984) found 88% of lightning fires burned <9 acres--surely many fires this small must have died out before any suppression could have been applied to them. This is analogous to volcanic eruptions, which have a negative exponential distribution relative to intensity: most eruptions are small, and the larger the eruption, the rarer the event (Wilson 1992). This does not deny that lightning can and does ignite fires--even large ones--on occasion, nearly always in trees, which can incubate the flame within the bark until surrounding fuels dry out. Consistent with this, Higgins (1984) found that pine-savanna had 4-15 times as many lightning fires/unit area as grasslands, although all areas had low ignition rates. This contradicts the paradigm that burns should be less frequent the more the trees. In conclusion, even when fire managers justify frequent fire in their ecosystem on the basis of lightning, they do not conduct prescribed burns during lightning season, but rather during the dry season. This not only questions the naturalness of such management but further implies that it's a lot easier for man to get fires going in the dry season than for lightning to ignite them during thunderstorm season.

Tree-ring fire scar studies. Given the treelessness of grasslands, this method is difficult to apply to prairies. Two Missouri savanna studies found a fire every 3.2 to 4.3 years somewhere in the study areas during times of peak fire frequency (Guyette and Cutter 1991, Guyette and McGinnes 1982). We calculate the actual fire return interval at a given spot at about every 29 years in each study because only an average of 11-15% of the sample trees in the study had a fire scar in years when any fire occurred. Historical context is relevant to the interpretation of tree-ring data for these studies examined times of hostile native-white contact (which also precipitated native-native strife), so that a

number of warfare (not management or natural) fires probably occurred. Thus, the precontact ("natural") point fire return could have been much less frequent.

Increased woody canopy in absence of fire. One origin of this concept was the observation (Bragg and Hulbert 1976) of a Kansas pasture brushing in, with the apparent conclusion that fire might (must) be responsible for the herbaceousness of prairie since they felt they had eliminated the possibility that megafauna herbivory could have done so. This single anecdote of cattle grazing in the farm economy (i.e. not conservation management, in which case it might have been done differently) is not a scientific test of the efficacy of cow grazing for brush control, nor can cow grazing be expected to replicate the herbivory effects of a suite of native megafauna (see "Precontact prairie fauna" below). Even if grazing were disproven (and it is not), this alone does not prove the fire hypothesis.

Nevertheless, I will examine the possibility that absence of fire increases woody canopy and presence of fire decreases/eliminates it. Fire is clearly not obligatory to keep trees out of all prairie sites over a long period of time, although usually another non-fire process is occurring at unburned unshrubby prairies, e.g. haying, herbivory by cows and prairie dogs (Bond 1945, Weaver 1968, Anderson 1982). While Hayden Prairie, Iowa had very little woody invasion upon preservation following 80 years of haying, after haying stopped and fire management began, aspen and maple cover increased dramatically (Christiansen 1972--the author blames haying for this, but I don't understand how). With frequent fire but no other management apparent, the aspen continues to increase at an alarming rate today (pers. obs., independently corroborated by prairie experts from two other states). We have found remarkably little research demonstrating the efficacy of fire at controlling brush--there is a little documentation for some species (Anderson 1982) but other shrubs increase dramatically (Anderson and Schwegman 1991). Some research we've found requires an awful lot of fire to get a little result--implying ineffectiveness. E.g., 13 consecutive years of annual or biennial spring fire reduced number of aspen suckers by only 20% more than no treatment, although aspen suckers were larger in unburned than burned (Svedarsky et al. 1986).

Like D. Schlicht (pers. comm.), I simply do not see management burns generally appearing to control brush (see plates), and although my observations are qualitative, they are numerous. Besides the 311 burn units out of 1413 units surveyed 1988-93 in this multi-state study and the 21 burn units of 241 surveyed in Wisconsin barrens 1988-93 (Swengel 1993a), I have observed additional prairie burns incidentally. Intense tree-topping fires (which is what prescribed burns in both prairies and savannas usually are not, being confined instead to the herb layer) can kill cedars and pines (Curtis 1959, Kucera et al. 1963), although the skeletons remain standing, but it is not clear that a prairie/savanna herb layer then automatically develops, as opposed to thickets and forest succession. Numerous other problem species--chiefly aspens, cherries, oaks, sumacs, willows--may topkill during fires but rarely rootkill, so that they vigorously resprout post-fire, usually with more stems than prefire (pers. obs.). Thus, fires I've observed not only don't reduce, but don't even contain (stabilize) extent of canopy.

The Draft Exotic Control Manual (DECM 1992) of the Wisconsin Department of Natural Resources, which discusses selected species both exotic and native, indicates that those woody species for which fire is considered an effective control also have other effective treatments available, and in the case of fire-killed cedars, the trunks must still be cut to remove canopy cover and cutting alone is an adequate control. Three woody species are recommended to be controlled only in ways other than fire, and single-fire treatments are ineffective for two species. Smith (1993) reports similarly spotty results for fire control of various problem woody species native and exotic; often when fire is deemed effective, it is only in frequent and intense doses (e.g. annually or biennially for 5+ years).

Fire managers often respond that growing-season fires must be more effective. A little research shows that warm-season fires may reduce a few species (Anderson

1982) but other research is inconclusive, e.g. two summer fires two years apart reduced aspen but a single summer fire quickly lost its effect (Svedarsky et al. 1986). While the results I've seen from non-management summer fires (e.g. Lyndon Station fire in plates in Swengel 1993a) certainly wouldn't encourage me to pursue this further, it seems to me that if there are "right" and "wrong" times to burn (and this should be shown scientifically before being applied widely), one should only burn at the "right" times. It has also been suggested that fires "set back" the brush (whatever that means) to an acceptable degree. If, within the time frame of the fire rotation, brush is not reduced, but held constant or is increasing--and this should be readily measurable--then the treatment is ineffective. If the rotation is very frequent yet only maintains an ongoing epic battle with brush about to release, this is also ineffective. While I will readily grant that in the absence of fire and other processes, brushing in is a likely outcome, I cannot find evidence that fire at credible natural frequencies maintains open habitats. Given that prairie fires would naturally happen, although not necessarily frequently, it appears likely to me that whatever role/effect they had, it was not brush control.

Response of prairie flora to fire. The extensive subsurface biomass and buds of prairie flora have been called adaptations not just to drought but also to fire (Anderson 1982, Henderson 1982), but these are just as explicable as adaptations to herbivory (Milchunas and Lauenroth 1993). While often claimed, fire-obligate plants (i.e. species that must experience fire to persist) are elusive. While Henderson (1982) states that fire may be needed to prevent senescence of prairie dropseed, the quadrat frequency of this prairie grass was 82.0% after 80 years of haying at Hayden Prairie, Iowa and 80.9% 20 years later when fire had largely supplanted haying (Christiansen 1972); thus, this species thrived for a very long time without fire. Furthermore, dropseed was eliminated from late spring burn plots but unchanged on unburned plots in a ten-year study (Henderson 1990). Gill and Groves (1981) observed that plant species claimed to be fire-dependent for reproduction are often stimulated to flower and seed by leaf removal (browsing) or ethylene injection (which is released upon injury of plant tissues). This (and the subsurface plant parts) may explain why similarly timed mowing and burning have many similar effects on prairie plants (Daubenmire 1968, Hover and Bragg 1981, Hulbert 1988), although burning and mowing now usually have different effects because they are done at different times. Anderson (1982) also reported striking similarities in floristic responses to burning and grazing. Thus, from these results we cannot distinguish which was the more "natural" treatment nor to which process these responses adapted. Most Australian seeds that open better with fire are not fire-obligate to be released, for death of the plant often also stimulates release; North American jack pine has fewer closed cones in areas of infrequent than frequent fire (Gill and Groves 1981). In my area very few jack pine cones are closed, but much recruitment occurs nonetheless.

Management (cool-season) fires favor dominant native warm-season grasses (Collins and Glenn 1988). Given that prairies also have native forbs (wildflowers) and cool-season grasses, this implies that cool-season fires reduce floristic diversity; in fact, Henderson (1990) found that species richness declined in fire treatments over ten years, with pronounced forb decreases in late spring burns. Diversity increases with time since fire (Gibson and Hulbert 1987) and burns, especially frequent ones, reduce forb diversity (Kucera and Koelling 1964, Henderson 1981, 1990, Abrams and Hulbert 1987, Gibson and Hulbert 1987, Evans 1988, Gibson 1988, Zimmerman 1992). Repeated fire can eliminate annuals (Vogl 1974), of which there are some native to prairie. Conversely, warm-season fires dramatically increase cool-season grasses (Ewing and Engle 1988), thus also skewing the flora toward a grass component. In heathlands, infrequent fires produce higher plant diversity than frequent fires (Main 1981).

Reduced diversity in favor of grasses might be an ecologically acceptable outcome except that (1) it is favoring already dominant species and (2) no grasses

are endemic to prairie but some forbs are (Wells 1970). Consistent with this, as of 23 August 1993, no prairie grasses were listed under the federal Endangered Species Act, but several forbs were, e.g. Mead's milkweed (Asclepias meadii), Prairie bush-clover (Lespedeza leptostachya), Running buffalo clover (Trifolium stoloniferum), and eastern (Platanthera leucophaea) and western (P. praeclara) prairie fringed orchids, although of itself this does not mean that these forbs are fire-decreasers nor that the endangered species list is necessarily complete.

Fire also increases vegetative biomass (Daubenmire 1968, Henderson 1982), sometimes referred to as "renewing the prairie" (flora only, not fauna), which is a result of stimulating dominant grasses. Again, of itself such evidence does not indicate ecological benefit. Having more rather than less seems like a conservation benefit, but not if it's more of dominants at the expense of diversity and rarities, which it appears to be. Repeated fire can even create plant monotypes in various habitats, such as grasslands and marshes already low in diversity because of extreme conditions (Vogl 1974). Managing an ecosystem to create uniformity, even age/height, and maximum production has usually led to lower diversity, precisely because dominants must be stimulated to accomplish this (Rosenzweig 1992).

Increased forb flowering (also "renewing the prairie") occurs short-term postfire, all the more apparent by the usual proximity of areas one or more years postfire, which can have dramatically fewer flowers (see Monarchs and Liatris in "Analysis of adjacent like units" above). But how many and which species show these dramatic blooms (dominant forbs vs. rarer ones? warm-season ones rather than spring flora?). That forbs decline in the long term implies the short-term burst of flowers is at the expense of flowers later, burned or not. This effect also has an aesthetic (non-scientific) aspect. But many Wisconsinites like pine plantations, yet these are much less natural and diverse than actual forests (Terborgh 1992). Thus, aesthetics do not necessarily correlate with ecological benefit. Justifying fire management with an aesthetic seems at cross-purposes to conservation, for this teaches the public that we should only conserve that which is pretty and that prettiness indicates successful conservation. Instead, we should cultivate an attitude that whatever is natively diverse and ecologically sound is also aesthetically pleasing, even if it must be an acquired taste--not that we shouldn't appreciate when aesthetic and conservation interests coincide, but the beauty of prairie butterflies does not seem to endear them to fire managers.

The botanical effects do not endorse the concept that fire is ecologically sound or necessary for the floristic biodiversity of prairie. Invoking current fire effects on flora as indicators of previous prevailing processes, though, implies that such an approach is admissible with other components of the ecosystem, and I cannot imagine how one could construct a plausible, parsimonious fire paradigm based on the response of prairie butterflies and grassland birds to fire (see "RESPONSE TO MANAGEMENT," "LITERATURE REVIEW - EFFECTS OF FIRE ON BUTTERFLIES," and "LITERATURE REVIEW - EFFECTS OF FIRE ON BIRDS" above).

Nutrient cycling. This is frequently cited as a fire benefit, but ash amounts that result from fire have not been demonstrated to affect prairie flora, although such attempts have occurred (Old 1969, Hulbert 1988). "Locking up" nutrients in accumulated biomass is not considered ecologically detrimental to other ecosystems (e.g. old-growth forest). Most nutrients vaporize in prairie fires rather than return to the soil (Boerner 1982)--there seems to be general agreement on this point, although apparently some dispute this, as in Ackerman (1993)--and much of what remains is leached away by precipitation (Boerner 1982). But even if a rapid return of nutrients were occurring, why is this good for biodiversity? Increasing the nutrient capital of European dry grasslands degrades them and greatly reduces floristic diversity by favoring a few aggressive plant species that outcompete the many species previously co-existing in the stressful conditions of dry sterility (Hopkins 1991). Hobbs and Hunneke (1992) consider fertilizing terrestrial communities akin to eutrophication in aquatic habitats.

Litter removal. While excessive litter accumulations may appear to disfavor certain prairie plants, this does not mean that periodic complete elimination of cover by burning is beneficial. Indeed, litter is not only useful as cover but also as niches for animals; its elimination, even briefly, eradicates their habitat (Lamotte 1975). Given that fire stimulates dominant grasses, it only briefly alleviates litter buildup, for fire actually causes greater litter problems in the future by increasing production. It takes 4-6 years for litter to reach prefire or long-unburned duff levels in dry prairies, but only 1-3 years in mesic (Vogl 1974, Henderson 1982). In Missouri, postfire plots can actually have more litter after only 1 year postfire than unburned controls, and litter in unburned plots actually decreased over time while the duff in annually burned plots exceeded unburned by the end of each year (Kucera and Ehrenreich 1962). Brehm and Hulbert (1980) found that while 45% of prairie litter and standing dead plant matter decomposed from April to August, 55% did if the litter was trampled on 1 April, indicating that if trampling occurred continuously as in prehistoric prairies with native ungulates (see "Precontact prairie fauna" below), litter would decompose even more rapidly. Furthermore, even if heavy litter may reduce flower and/or biomass production, its accumulation over time post-fire apparently does not harm diversity, which also increases with time since fire (see "Response of prairie flora to fire" above).

Warming the ground. This results from fire but no one has explained why this is ecologically beneficial, especially since it is accompanied by greater diurnal temperature extremes because of lack of insulating litter (Samways 1990).

Weed control. The idea that fire should control exotic plants doesn't make sense to me for weeds ought to be well adapted to fire, since they are adapted to disturbance, especially human-caused (Curtis 1959), and humans cause a lot of fires (see "Lightning" above). My experience bears this out: e.g. sweet clovers and thistles proliferate postfire where few or none were evident prefire (see plates) but spot mechanical control (possibly combined with herbicides) have appeared more effective at containing and reducing these species. Numerous studies have documented that fire promotes invasive flora, both native and alien, not just in prairie but also in heaths and scrubs (Vogl 1974, Main 1981). Curtis and Partch (1948) and Dibold (1986) found that fire allowed more weedy invasion than no treatment and mowing, respectively. Ruderals, which take advantage of the opening in the canopy, invade even more after warm-season fires (Ewing and Engle 1988).

According to DECM (1992), burning is not particularly effective for weed control. Fire is claimed effective only for three species, but for one of these, only repeated treatments may be effective--disfavorable for biodiversity management. Fire of all types or fire alone is completely ineffective for several species, while for other species only certain types of fire (i.e. a narrow phenological window) are effective or have mixed effectiveness or are effective only combined with other treatments. While most exotics have recommended treatments other than fire, for many species an effective treatment that is cost-effective and relatively benign for non-target species (i.e. as broadcast fire is not) is elusive. Bluegrass, for which fire may be most touted, is only reduced somewhat or contained, not eliminated by fire. E.g., 13 consecutive years of annual or biennial spring fire reduced bluegrass cover by only 30-40% vs. no change in unburned (Svedarsky et al. 1986). Smith (1993) indicates the same species-specific, rather spotty efficacy of fire in weed control as in DECM (1992). In both manuals, fire can often only be considered effective if one is willing to achieve only reduction rather than elimination of the weed and/or one is tolerant of the need for frequent treatments, which I would find more acceptable if they were highly restricted as spot treatments to infested areas. These are rather lax standards for success not necessarily enjoyed when alternatives are evaluated (e.g. spot herbiciding).

Animal adaptations to fire. Contrary to claims in press releases, brochures, and articles in the popular press that animals, especially birds and mammals, are adapted to fire and suffer little mortality, examples of mass animal mortality in

both wild and management fires in prairie and other habitats include the Greater Prairie Chickens (Bent 1932), small prairie mammals (Costello 1969, Harty et al. 1991), tree squirrels (Wise 1986), and birds in Australia (Reilly 1991). Because of variability in fire behavior and ethological characteristics, animals' responses are not adequate to assure a high probability of surviving fire and its aftermath, and a vertebrate "shock phase" occurs postfire as with insects (see "LITERATURE REVIEW - EFFECTS OF FIRE ON INSECTS" above) (Main 1981, McClure 1981). Typically the generalist and invader animals benefit while specialists decrease postfire. E.g. omnivorous (generalist) African mammals recolonize burned areas faster than specialist and insectivorous mammals (research reviewed by de Van Booyesen and Tachton 1984); this is also true of Australian birds (McFarland 1988). In heath and scrub, animals feeding on a narrow spectrum of plants (i.e. specialists) are disfavored by fire (Main 1981). As for whether fire was beneficial for bison, while their forage (grasses) produced more biomass postfire (see "Effects on prairie flora of fire" above), Costello (1969) considered it "reasonable" to assume that prairie fires killed many bison outright and also caused them to starve if all above-ground grass was burned off over a large area.

Drought and fire. Although this is when natural fuels are most flammable, yet not necessarily most likely to receive a natural ignition from lightning, prescribed-burned prairie during droughts results in disproportionately greater decline in plant diversity (Henderson 1990) and bird abundance (Zimmerman 1992) than in unburned prairie. Soil moisture measurements in early spring can anticipate incipient droughts in time to avert these fires (Zimmerman 1992).

Fire is (more) natural. What is "natural"? "Natural" for its own appearance is a culturally biased, subjective aesthetic, although "natural" as measured in biodiversity is scientifically quantifiable. Fire management relies heavily on the use of advanced ("natural"?) machinery to imitate (how well?) what is believed (how accurately?) to have been natural fire, and requires unnatural landscape features (e.g. mowed, disked, or plowed firebreaks; uniform geometrically precise burns). Alternate treatments may also look highly unnatural--e.g. haying, spot-herbicideing--yet they may actually be mimicking a natural process at least as well as fire (see "Precontact prairie fauna" below) and appear more beneficial to biodiversity. Besides, prairies so fragmented and small that they can't support most of their common native megafauna by definition are unnatural. How can "natural" processes be made to occur there? Which is the more worthy "natural" value: natural processes or native biodiversity? I vote for biodiversity. It is faith--not science--when one believes that fire has its own magically natural and essential but as yet unidentified effect on the ecosystem beyond what science has established as the effects of particular treatments on biodiversity. This belief is no more or less valid than that of a butterfly researcher who may find magic in a prairie supporting rare butterflies (and conversely, a permanently de-flowered prairie if they are lacking). But none of these kinds of magic has a basis in science.

Summary of evidence advanced for fire. I conclude that convincing evidence, while avidly sought, has not yet been brought forward to substantiate that prairie fires either were frequent prehistorically or are beneficial today for conservation of biodiversity, yet a disturbingly large body of contrary evidence exists. I am not denying that prairies burned, but the frequency of fires occurring anywhere within a large area is quite different from frequency at an average given point, and I suggest that while fires somewhere within prairie may have occurred frequently (whatever that means), the scientific evidence for a prehistoric point fire frequency remotely close to that on many prairie preserves today does not exist. Given that, the continued assertion of universally very frequent presettlement prairie fire has the appearance of an after-the-fact explanation for why modern fires do not have the degree and kinds of effects desired (e.g.. brush and weed control). While I welcome fire managers to continue their science--so long as it entails (1) testable hypotheses that allow the possibility to confirm or refute the

fire paradigm and (2) scientific sampling on an experimental rather than wide scale, I also believe it would be more beneficial for biodiversity to seek other explanations for the processes causing wood- and weed-free, biodiverse prairies.

Precontact prairie fauna

The North American prairie has been called the 'American Serengeti', particularly prior to the extinction wave at the end of the last ice age (Wilson 1992), but also more recently, for what was lost in diversity was counterbalanced by sheer numbers--possibly the greatest biomass density of terrestrial vertebrates globally (Allen 1954)--until European contact. The diversity of native prairie mammals extirpated or seriously reduced since contact is amazing; precontact range maps of selected species (Maps 2-5) are a somewhat crude measure estimating their areal coverage but not regional abundance. Of primary relevance to tallgrass prairie are beaver, porcupine, elk, and bison; regionally relevant are Richardson's ground squirrel (northwestern Minnesota), mule deer (Minnesota), moose (west central and northwestern Minnesota), and antelope (westernmost Minnesota and Iowa).

Measures of abundance are extrapolations since scientific surveys did not occur prior to these species' indiscriminate reductions, but are based on an abundance of measurable and quantifiable evidence, e.g. fossils, skins and specimens, records of commerce (e.g. trapping), as well as eyewitness accounts. These accounts have apparently been much more rigorously questioned by the standard methods of historical (and scientific) interpretation than fire accounts (see "Evidence advanced for the fire paradigm" above), probably because much more independent evidence exists for animals than for fire. E.g., extrapolations of bison numbers from eyewitness accounts are rather universally rejected because they produce astronomical numbers, even though some of these accounts appear rather reliable. In fact, people who discounted reports of bison numbers produced even more astronomical estimates when they observed the herds themselves (Allen 1954, Roe 1970, McHugh 1972). Ironically, current estimates of bison--generally about 60,000,000, range 30,000,000-120,000,000, with most living in the prairies and plains (Hall and Kelson 1959, Morris 1965, Kibs and Wunschmann 1968, Nowak 1991)--are based on converting the biomass of the rangeland carrying capacity for cows into bison numbers, then sometimes subtracting a few million to allow for elk and pronghorn. Thus, zoologists assume that bison were limited by forage, i.e. they were eating up most of the primary production in prairie.

Wisconsin had "many thousands" of bison (Jackson 1961), elk were formerly abundant southward and westward (herds of 400 seen, Matthiessen 1959) but present throughout, and moose were abundant northwestward (DNR undated). Useful as this information is, it does not account for small- and even large-scale variability of animal density within their main range. But while one can quibble about the regional, even rangewide abundance of particular species, even on an order of magnitude, one cannot but conclude that the mammal fauna of the prairie ecosystem has been profoundly reduced in biomass and diversity since contact.

Vegetative effects of fauna. Although it is impossible for science to show how now extirpated animals would affect a site if they were present, they were clearly having significant effects, with ecological release of the flora resulting in their absence (App. 22). E.g., bison not only very heavily grazed ("over-grazed") the prairie in some years to the horror of white eyewitnesses, but also tore up trees and in high densities converted savannas into prairies (Larson 1940, Allen 1967, Edwards 1978, England and DeVos 1969, Moore 1988). Although bison are less selective in their diet than most herbivorous mammals, they nearly exclusively graze on grasses: >80% grasses and 96% a common finding in nearly all studies reviewed (Meagher 1986). While bison and cattle are generally considered rather similar in food habits (Jackson 1961, Collins 1987), bison eat twice as much warm-season and 50-75% as much cool-season grass biomass but fewer forbs and shrubs than domestic cattle (Peden et al. 1974, Schwartz and Ellis 1981).

This suggests the exceeding dominance of grasses in prairies today is at least in part an ecological release from bison grazing, corroborated by the finding that tallgrass prairie advanced westward after bison were eliminated (Larson 1940, Allen 1954) and the general tendency in grasslands, particularly those with a long evolutionary history of grazing, for grazing to decrease the abundance of the most dominant flora (Milchunas and Lauenroth 1993). Since bison may have helped prairies spread and persist eastward, e.g. in Tennessee, and not just by herbivory but also by rubbing trees (Seton 1929, Allen 1954), this suggests the ecological release from bison eastward allowed forest and savanna to expand westward. Cattle are also more sedentary (a benefit in the context of domesticity, where pronounced migratory habits are unfavorable) than bison, implying that while bison could apply intense herbivory pressure, it was not nearly as constant locally as we observe today in cow pastures. But since bison can climb hills so steep people cannot follow and reach places only mountain sheep roam among large animals (Roe 1970) and traverse extensive forests (Meagher 1986), no prairie site was inaccessible to them.

Browsers native to prairie eat ("set back," "control") most plants fire managers constantly battle (App. 22). E.g., beavers occurred in stupendous numbers precontact (Matthiessen 1959), lending credence to Jackson's (1961) statement that beavers created and maintained many low prairies in Wisconsin. Even reductions in tree squirrels, which occurred at immensely higher numbers presettlement than today (Wise 1986), must have resulted in an ecological release especially in recruitment of oaks, hazelnuts, and hickories, whose seeds these species prefer. White-tailed deer are apparently at about the same density in Wisconsin as around 1800 and are therefore not more abundant today than precontact (Jackson 1961). Their herbivory effects, which considerably open a shrubby understory, are quite apparent from exclosures, e.g. at Sandhill Wildlife Area (see plates in Swengel 1993a), but the areas both inside and outside such exclosures anywhere in Wisconsin are also exclosures of elk, moose, and bison. Thus, these extirpated species had herbivory effects additive to those now seen for deer, which conservationists tend to decry as damaging to the flora (e.g. Girard et al. 1993), even though deer are native and naturally abundant. What would conservationists think of even more ungulate herbivory, even though this was naturally occurring prehistorically?

Elsewhere, browsers in normal densities can control brush effectively. In Russian steppes slightly cooler than Wisconsin savannas, moose preferred oak savanna habitats and reduced oak biomass production by 50% while at a population density held artificially low because of the objectionable "damage" they caused (Zlotin and Khodashova 1980). In Alaska moose can cause the deciduous serot of forest succession to be skipped because of their tremendous species-specific herbivory ("damage") (Miquelle and Van Ballenberghe 1989). It may seem contradictory that browsers inhabited prairies if prairies were primarily herbaceous. Apart from the numerous records clearly documenting their presence, browsers would plausibly be on the prairie because (1) woody species occurred in riparian areas and even out in prairie more widely than commonly imagined (Higgins 1986a) and (2) if woody species were in a position to colonize prairie such that hypothetical fires were necessary to continually beat them back, why wouldn't browsers instead be utilizing this food source?

Northern pocket gophers, Richardson's ground squirrels, and prairie dogs are much maligned for their presumed damage to rangeland and forage competition with livestock because these rodents are found only in areas that are closely cropped from heavy grazing ("overgrazing"). However, these species follow, rather than cause, heavy grazing (Hall and Kelson 1959, Burt and Grossheider 1976). Given this, it follows that a constantly close-cropped prairie vegetation occurred widely in the historic ranges of these species, including westernmost Minnesota, which bison in fact maintained on millions of acres of the Plains (Costello 1969).

The whole suite of native prairie megafauna had interactive grazing effects not necessarily evident from the effects of each alone. E.g., prairie dogs and

cattle grazing together maintain brushfree, floristically diverse short- and mixed-grass prairie indefinitely, while neither species alone does (Bond 1945). This implies that bison and other ungulates in combination with pocket gophers and ground squirrels might have done the same in tallgrass prairie. Variability in the diversity and abundance of mammalian herbivores in different micro- and macro-regions of precontact tallgrass prairie would cause variable herbivory effects, marvelous conditions for the evolution of biodiversity but a challenge for its conservation now on fragmented, scattered preserves.

I freely admit I cannot present research on how some important but now extirpated species, e.g. elk, interacted in the prairie ecosystem because this can't be studied today, which is precisely the point. Their absence predisposes our ignoring their relevance to understanding how the prairie biome functioned precontact. We may never know well enough how the mammalian herbivores affected "pristine" precontact prairie, which was actually a hardworking rangeland maintaining a vast megafauna (Schumacher 1975). We can, however, proceed with an understanding that herbivory was pervasive precontact, with a logical result that canopy and fuel load were considerably reduced, leading to large natural firebreaks, and seek ways to "restore" these effects on preserves today in ways demonstrated to benefit what lives there now.

Faunistic nutrient cycling and niche creation. Those interested in nutrient cycling should consider the immense resource turnover occurring in prehistoric prairie via megafauna herbivory. In another ecosystem, moose, roe deer, and European hares facilitate much of nutrient cycling in Russian steppes (Zlotin and Khodashova 1980). The resulting fur and dung also created niches on which truly obligate invertebrates (in the strictest sense of the word) depend (Morris 1971).

Analogous grazing systems. Worldwide some grassland systems remain relatively intact. The Serengeti offers an approximate parallel to tallgrass prairie in length of growing season, large ungulate biomass, and plant productivity. There ungulates create a "grazing lawn" ("overgrazing" to our eyes?), yet their herbivory stimulates 80% greater plant production and increases floristic diversity (McNaughton 1983, 1985, also found in other grazing systems, e.g. Shrimal and Vyas 1975), and improves forage quality compared to experimental exclosures, with so little litter (fuel) remaining as to preclude nearly all fires while maintaining a very open landscape (McNaughton 1983, 1985). Some have proposed that prairie was also primarily a grazing system (Larson 1940, England and DeVos 1969, Moore 1988).

"Disturbance" and "damage" of herbivores. While perhaps a semantic finepoint, I believe these terms contribute to biased and inaccurate constructs of prairie ecology. I question the term "disturbance" to describe feeding by herbivorous megafauna, since this term usually does not apply (rather arbitrarily) to feeding by other herbivores--e.g. mice, birds, insects--nor is this or a comparable term used to describe other exchanges between trophic levels, e.g. carnivory, decomposition, soil converted to plant biomass. This term implies a discrete event; as other disturbances like lightning, fires, and windthrows are, and can also have a negative connotation by association with such unnatural human-caused disturbances as plowing, whereas herbivory by prairie fauna is a continuous phenomenon of varying degrees of intensity through time by species that very much ought to be there and ought to be doing what they are doing.

"Damage" (and "overgrazing") by normally behaving native herbivores at (sub)normal densities is another unobjective and objectionable concept that arbitrarily singles out one of many exchanges among trophic levels. Soil displacement and utilization by plants are not "damage" nor is carnivory nor decomposition. The concept of "damage" appears to derive from horticulture and forestry, in which both humans and other animals may be competing for plant yields. But prairie preserves are not in management to maximize harvest (biomass) but to maintain biodiversity; prairie biomass production could be increased fivefold by planting them in corn, but no conservationist (including us) would advocate this.

By the reasoning (adapt, leave, or die) that fire managers have used to assume that butterflies known to live in prairie must be adapted to fires assumed (I believe incorrectly) frequent (see "INTRODUCTION" above), the prairie flora must assuredly be assumed adapted to herbivory. Indeed, both Mack and Thompson (1982) in North America and McNaughton (1984) in Africa have found evidence for co-evolution of grassland floristic communities and large ungulates. Prairie grasses are especially adapted to grazing, for they grow from the base, not the tips, allowing them to continue production despite grazing (Costello 1969). Thus, the absence of this herbivory may in fact be more "damaging" to the flora than its presence. In fact, grazing promotes evenness in plant composition especially in grasslands with a strong evolutionary history of grazing (Milchunas and Lauenroth 1993).

Images of prehistoric prairie. How one conjures prehistoric prairie determines the image one seeks to reproduce in preserve management. Most apparently imagine the prehistoric prairie landscape as vast expanses of tall grasses, which settlers described after 90% of the bison were destroyed. This image appears to be a result of recent animal extinctions caused by white settlement. Although I gather most managers would be horrified to have anything approaching the "grazing lawn" occurring anywhere at any time in a prairie preserve, the evidence on megafauna indicates that herbivory pressure was immense in prehistoric prairie.

Analogy of grazing and haying. Unintensive haying (no more than once per year) has been beneficial for maintaining brushfree native prairie flora (Weaver 1968, Solecki and Toney 1986) and mowing can be effective as a "browsing" control of brush. E.g. mowing eliminated a recently developed brush problem at a wet prairie in Ontario and dramatically restored floristic diversity, particularly of regionally significant species (Dugan et al. 1990). The benefits of prairie haying are also evidenced by the fact that many prairie preserves deemed worthy of conservation were hay prairies for generations pre-preservation.

Since no one would assert that Natives were haying the prairie, one might dismiss this as a highly unnatural modern management of serendipitous efficacy, as I did until the butterfly data forced me to examine it more closely. The specialist butterflies are strikingly averse to fire (generally presumed the dominant prehistoric prairie process), but all species I've been able to compare fare much better in haying situations. Thus, they are better adapted to haying than fire. Meanwhile, some species show somewhat analogous responses to haying and grazing, in that they do better in both of these (e.g. Regals; Dakotas in North and South Dakota) than under fire management, even though grazing is almost always represented only by private cattle farming, a poor analogy for prairie preserve management. Specialist grassland birds show a similar aversion to fire and apparent adaptation to grazing and haying. The "grazing lawn" and heavy grazing (as bison at least sometimes did) sounds like a recently cut field to me.

Nevertheless, while mechanical and faunistic cutting actually do share many similarities, haying is a more discrete and uniform phenomenon, while grazing is a more constant, gradual process leading to higher local diversity of impact (Hopkins 1991). Note that while fire is clearly catastrophic for many insects, Morris (1975) also considered cutting catastrophic because of its discrete suddenness in comparison to grazing, a gradual process. Furthermore, haying removes more resources from prairie than grazing, e.g. 35 to 1 kg/ha/yr of nitrogen, 11 to trace kg/ha/yr of phosphorus, 3 to trace kg/ha/yr of potassium in haying and grazing respectively (Owensby and Anderson 1969). Of course, the mechanically cut vegetation can remain in place; although this would not alleviate litter accumulation as much as hay removal, the litter decomposes more rapidly than if it is left standing uncut and more of the nutrients would remain within the site.

Replication of natural processes. The claim of some fire managers that they are mainly concerned with restoring natural processes (as opposed, apparently, to the conservation of biota) would ring truer if they were equally zealous for all processes by including now reduced or absent megafauna herbivory in the management

equation. The small size of habitat patches may preclude reintroductions but not other methods of biotic or mechanical grazing at a site. Even when reintroduction in a prairie is actively pursued, I have never found conservationists proposing or actually reintroducing any megafauna either at a diversity (bison are just a start) or density that even approaches those prehistorically. While one may argue that herbivory pressure comparable to that precontact might be "damaging" (i.e. disfavorable to biodiversity) on today's fragmented preserves, it is disingenuous to assert that the ecosystem is not adapted to an herbivory process known to have prevailed precontact but at the same time to aspire to restore another process (fire) at precontact frequency, even though this is currently unknown even to an order of magnitude, could easily (I believe probably) be occurring on preserves at much greater than prehistoric frequencies, and seemingly regardless of the effects on extant animal populations such as specialist birds and butterflies.

A hypothetical example: Given that kangaroo rats severely reduce by up to 99% the prevalence of heavy-seeded native annuals in the Chihuahuan desert (Terborgh 1988), suppose that kangaroo rats were somehow extirpated from this ecosystem, resulting in ecological release of the annuals. Would managers be willing to restore these animals at all or in any numbers, or would this be considered too "damaging" to the flora, no matter how natural the rats might be?

Climate/soil

Abundant paleontological evidence indicates that on a geologic time scale, climate determines general vegetation characteristics and expansions/contractions of habitats (King 1981, Pielou 1991). Prairie occurs in areas with a certain range of precipitation-evapotranspiration ratios; the west-facing Mississippi River Bluff prairies surrounded by forest are explained by microclimatic variation within and outside of this range (Transeau 1935). Even on a small scale, the prairie-forest border moved back and forth in response to wet and dry periods, e.g. major tree diebacks in droughts of 1913-14 and the 1930s (Weaver 1954). Pielou (1991), although not discussing the frequency of fire, described how fossil and palynological data indicate that fire resets vegetational communities to the one appropriate for current climatic conditions, probably by opening bare ground to invading seeds. While ecological inertia slows the migration of plant communities in response to climate change, so that vegetation can locally persist centuries later than it "should" based on climate, a massive fire can quickly allow one community to replace another (Pielou 1991). Since Wisconsin has been wetter but not commensurately hotter in the past 12 years (Tab. 6), current climatic conditions have apparently become more favorable for forest vegetation, suggestive that management fires are accomplishing the opposite of intended by resetting the vegetation to that best adapted to current climate. This may explain why, although many assert that fire (ought to) eliminates woody seedlings, it often appears that fire enhances recruitment of woody seedlings by opening the herb canopy.

Table 6. Number of three-month running averages 1951-80 for temperature and precipitation from 1982-92 in two regions of Wisconsin that were above, near, and below normal (NOAA 1987, 1992, 1993).

	-----TEMPERATURE-----			---PRECIPITATION---		
	above	near	below	above	near	below
	<u>normal</u>	<u>normal</u>	<u>normal</u>	<u>normal</u>	<u>normal</u>	<u>normal</u>
Cluster 2. (West Central and Central Wisconsin reporting stations)						
1982-92	65	11	56	73	8	51
1993				(many)		
Cluster 4. (Southwest and South Central Wisconsin reporting stations)						
1982-92	53	5	74	74	3	55
1993				(9+)		

Applications to biodiversity/ecosystem conservation

This definition of biodiversity--"the full set of species, genetic variation within these species, the variety of ecosystems that contain the species, and the natural abundance in which these items occur" (Office of Technology Assessment 1987 as cited in Redford and Stearman 1993, emphasis mine) encompasses ecosystems and landscapes. It is impossible to fully achieve biodiversity conservation as defined above globally, for some species and ecosystems will be disproportionately under-represented relative to their occurrence prior to human civilization, while others will be relatively (not necessarily absolutely) overrepresented in relation to the previous occurrence. Thus, conservationists prioritize the rarest aspects of biodiversity by targeting rare species and rare ecosystems for conservation action, as these are the aspects of biodiversity most likely to be permanently lost.

Biodiversity in grasslands. While the prairie flora has the greatest biomass, it contains relatively little of this ecosystem's biodiversity. No grasses are endemic to prairie (Wells 1970) but some forbs and even more fauna are. The scale of this difference is evident by examples. A 15-acre Michigan old field (Evans 1975) had 153 flowering plants (7% of species) but ≥ 1997 animal species (93%); insects comprised 92% of the animal diversity--271 fauna species (14%) belonged to the Order Lepidoptera (butterflies and moths)--and 4% were vertebrates. Thus, 89% of the field's species diversity was invertebrate. Up to 1080 species of Lepidoptera have been recorded in a European dry grassland <10 hectares in size, and in Austrian dry grasslands 1041 of the insect species present were dependent on this habitat type--and 85% of these were red-list species (van Dijk 1991). Lepidoptera are a substantial portion of terrestrial animal biodiversity--they are exceeded only by beetles, with social insects (Order Hymenoptera) nearly as diverse--and animals are much more diverse than flora (Wilson 1992).

Despite this, managing ecosystems such as prairies for the benefit of insects may not appeal even to conservationists, much less the general public. Although some species have been found to be keystones whose decline or loss significantly alters the entire ecosystem (Wilson 1992), I have no evidence this is the case with any prairie insects and don't expect it to be the case either. I suspect that all the specialist butterflies could disappear (and have in some places) without detectable effects on the ecosystem--or even more than a few people noticing their absence. Insects serve a much more useful conservation role as fine-tuned ecological indicators that are numerous, therefore affording much potential for replication (confirmation) of results. Declines and extirpations of prairie-obligate insect species are in fact indicative of an already existing disintegration or perturbation of a site (Moffat and McPhillips 1993). Thus, whether one chooses to target insects for specific conservation action, the health of an ecosystem's insect community reflects the overall ecological quality of the site.

Fire and other processes in biodiversity conservation. From our results and literature review, I cannot find evidence that floristic or faunistic diversity of tallgrass prairie is adapted to fire as a dominant or prevailing ecological process, nor that they benefit from fire management today. I have no research to cite that demonstrates a benefit from fire for the prairie ecosystem (biodiversity, not biomass), although I have synthesized much research to show that fire typically favors generalists and invaders and disfavors habitat specialists, which runs counter to the conservation strategy of especially targeting rare and endemic species for action. This does not mean that fire has no place in the conservation of biodiversity. Fire combined with other management types is more beneficial than fire alone, and infrequent fire is more beneficial than frequent fire, so I admit the possibility that fire may have a limited role beneficial to biodiversity conservation, although I don't have any research to cite in favor of this. It is also possible that there are fire-dependent species of conservation concern, although I have no substantiation for this either. I remain baffled, however, by the pervasive, intensive use of fire as the dominant or sole approach for conservation

management especially but not only in tallgrass prairie, for highly experimental and weakly or not scientifically substantiated procedures should not be done on a grand scale, for this allows the possibility of huge mistakes. Furthermore, the efficacy of mechanical cutting and particular kinds of herbivory in maintaining weedfree, woodfree, floristically and faunistically diverse grasslands indicates a general adaptation of the ecosystem to some sort of prehistoric herbivory regime. Thus, this should have a primary role in modern prairie management.

Scientific discussion of this report. I have no doubt that many fire managers disagree with my literature review, although I encourage them to use the scientific method, rather than their fervent hopes and beliefs, to evaluate the role of fire in the ecosystem. By drawing on the data (not necessarily the opinions and conclusions) of the citation classics, I find considerable substantiation for my findings. BUT the extent to which we disagree on fire effects and roles only reinforces my point that the benefits and efficacy of fire management are by no means established. Therefore, this management should not be discussed as if it were efficacious, and should not be applied pervasively and constantly in prairie preserves, although it is. I enthusiastically invite response to this report and especially welcome additional relevant scientific papers. I will gladly receive scientific communication and refutation, but I reject emotional and personal attack as inappropriate. If, as some apparently contend, fire is obviously essential to ecosystems, then science should not have much difficulty substantiating it, and there is no need to invoke "religion" and emotion. If someone can scientifically demonstrate how biodiversity, including my study species, are adapted to fire and benefit from it, I will welcome the data.

CONCLUSIONS

Principles

Study what is most important to know, not what is easiest to measure. Most fire research addresses easily quantified things, e.g. rates of nutrient turnover, biomass, numbers of flowers, body counts of insects (identified only to order or family!). While this is valid information, it has no obvious application to conservation of biodiversity, which must relate fire to how rare and specialist populations respond, not to total biomass produced. It is more difficult to design such research and produce definitive answers, but it CAN be done. Likewise, it is much easier to tally number and extent of prescribed burns (e.g. TNC 1993), or account for dollars and man-hours expended. But this seems to value "the more, the better," rather than the ecological benefits accrued, if any. The more I hear only about how much time and how much press and how many acres and how much fun were associated with prescribed burns, the more I find myself unavoidably concluding that nothing better was found to say about these fires. Instead, tell me how rare flora and fauna are faring postfire, and whether fire management is demonstrably the best course of action on behalf of rare biodiversity.

Design research to make fair comparisons among management types. It is unfair to compare plots grazed or hayed to produce a nearly or completely constant "golf course" sod with burned plots treated no more frequently than once per year. To be fair, all treatments should be sampled at similar intensities. Either burn in a way to replicate the "golf course" as much as possible (with no application to conservation management I can think of) OR (preferably) graze/hay unintensively enough to be fairly compared with conservation fire management. Since fire managers do not feel bound to burn only the way farmers do, grazing and haying for prairie management need not conform to farm practices either. It's no great accomplishment for conservation fire to appear better ecologically than farm procedures done for profit with no attempt to conserve biodiversity, although I have cited instances in this report where farm practices can be more beneficial than conservation fire for birds and butterflies. The real test pits only conservation-type treatments of grazing, mowing/haying, and fire. An important

corollary is the fact that science CANNOT determine which management type (e.g. fire, haying, grazing) is better when only one is being studied (e.g. different age classes within a fire prairie).

Discard the idea that fire prairies are the baseline for prairie biota. This is circular. On the one hand, managers burn to learn how it will change a prairie (and hope it will--i.e. "enhance" or "renew" it), yet then use the species composition of fire prairies (preserves already in fire management) to define the prairie biota. But a considerable subset of the prairie community is fire decreasing, no matter what kinds of fires are done. If measurements are taken only after (many years of) fire, one's understanding of the prairie biota may be highly skewed to underrepresent fire decreasers. A related line of circular and self-fulfilling reasoning justifies prairie fire management. Because prairies burned a lot, they must be adapted to fire and because prairies are adapted to fire, they must have burned a lot. This does not allow the construction of scientifically testable hypotheses to confirm or refute the fire paradigm. Perhaps it does not occur to some that the fire paradigm needs to be tested, but that is the scientific method, and even the most seemingly self-evident truths must be verified. If something is so self-evidently true, science should easily substantiate it, but some "self-evident truths" have been found scientifically untenable.

Conservation of flora and fauna need not conflict. As Hopkins (1991) observed, management for both plants and animals has been traditionally viewed as incompatible but the two groups don't have to be at odds in grassland conservation. While prairie managers clearly give me the impression that management (i.e. fire) for prairie flora conflicts with that for animals (especially prairie insects, and flora should naturally be favored), I disagree. First, I do not see the benefits to flora of fire management that I also clearly see as damaging to animals, and I do see the benefits from conservation haying and grazing for both flora and fauna. Moreover, animals, especially specialist insects, require a healthy and diverse, native and natural flora to thrive. Finally, conservation of ecosystems by definition is a holistic approach. Somehow all these species co-existed, despite competition and predation, in the same ecosystem prehistorically, so it should be possible for most (with the exception of megafauna on small preserves) to co-exist favorably on preserves today. This should, at least, be our starting assumption. I recognize that rare species can and should cause us to differentially emphasize the management of particular species at particular sites and subsites. I suspect that much of the "conflict" is a human artifact, in that scientists from different fields may conflict in their particular interests and priorities and preferences.

Invertebrate conservation is not at odds with other conservation objectives. This study shows a correlation of numbers and response between prairie butterflies and grassland birds. Tiger beetle diversity correlates highly with other vertebrate and invertebrate taxa (Pearson and Cassola 1992). There's a certain logic in this tendency, for the same evolutionary opportunities and constraints apply to all biota, and species living in the same habitats must adapt to the same conditions and processes (although in different ways and to different niches).

Conserve ecosystems from the top down instead of bottom up. Animals in the higher trophic levels, such as prairie grouse, depend on healthy lower trophic levels, so that successful conservation of the higher levels requires success at the lower levels too. While I advocate paying attention to the conservation of all biodiversity, if one must choose, focus on the higher levels rather than the lowest (the flora). A focus on the flora hopes or presumes that if the flora looks the way we think it should be, the associated animals must agree with us, while a focus on higher trophic levels lets the animals speak for themselves. It is possible to have the flora without the associated fauna, but one cannot have the fauna to any healthy degree without a healthy flora. I and others have seen both sides of this equation with prairie-specialist butterflies. If conservation focuses on flora, that may be all we get but if we succeed at conserving the associated fauna, we

will necessarily succeed in conserving the flora too. E.g. southwestern Missouri devised its management combination of haying, grazing, and fire to conserve prairie chickens and grassland birds, but it has also been successful at maintaining or enhancing rare plants as well (Christisen 1985, Solecki and Toney 1986, T. Toney pers. comm.), not to mention specialist butterflies.

Maximizing plants may not benefit associated insects; it is management, not preservation status, that determines whether these insects persist. E.g., in England, removal of grazing after site preservation increased the abundance of wild thyme, larval food for the rare Large Blue (Maculinea arion), but directly caused the extinction of the butterfly by eliminating the habitat for ant species with which it had an obligatory mutualistic relationship (Warren 1992).

Management diversity favors biodiversity. A diversity of treatment types (not just different ways of applying one kind of management) is most likely to maintain the most prairie floristic biodiversity (Collins and Barber 1985, Collins 1987, Collins and Glenn 1988). Such approaches also lead to higher arthropod diversity (Usher and Jefferson 1990). A mosaic of fire and non-fire management areas is favorable to conservation of rare grassland gallinaceous birds and antelopes in South Africa (research review by de Van Boysen and Tachton 1984). I suspect that much resistance to diversifying conservation management of prairie away from primary/sole reliance on fire results from an antipathy toward farming, not from science. Farming destroyed most of prairie, but also was responsible for maintaining much of what was left (both what became preserves and remains in private property) and may hold the key to optimal prairie management today (i.e. grazing, haying).

Opt for diversity in management approach and appearance within and among sites rather than a single "best management approach" and appearance for prairie everywhere. "One-size-fits-all" management approaches do not take into account differences among sites and the benefits of diversity among sites. E.g. if a prairie site's land use history has significantly skewed its species composition toward grazing increasers, then a radical change in management, e.g. to fire, is not likely to favor biodiversity, for some of the grazing increasers will likely not be fire tolerant and some fire-tolerant grazing decreasers will likely no longer exist at the site. Thus, I recommend that managers accommodate the specific needs of particular rare species at a preserve, which will vary among sites; such accommodation may require varying management goals and approaches within a site (Hobbs and Huenneke 1992). Moreover, we will never be able to evaluate the long-term effects of different conservation strategies--and discover better techniques--if we don't do different things. Conformity is a human value; diversity is a natural value.

Emphasize results over fashion. Southwestern Missouri is the only place I know of where (some) tallgrass prairie preserves are managed primarily with haying rather than fire. The relative merits of this approach are readily apparent, but it was only by paying close attention to results, not abstract (untested) theories of the day, that such management must have persisted. Managers who apply fire as frequently and widely as possible today would do well to remember that "Smokey the Bear" was once as fashionable. Given that they feel fire suppression was applied too frequently and widely and simplistically, how can they be so certain that posterity will not also think the same about today's fancy with fire?

Apply "sustainable development" to prairie. It is delightful to see high-quality prairie vegetation with specialist butterflies, sometimes in amazing numbers, on private property in conservative haying and grazing regimes. In southwestern Missouri, hay prairies produce farm profit and prairie biodiversity (including fauna) at the same time (T. Toney pers. comm.), where a variation on a single midsummer hay cut is applied to both public and private prairies beneficially for conservation. Not only that, haying the preserves builds cooperation with local farmers, who do the cutting and take the hay, and helps pay for preserve management, as with grazing at Pine Butte, Montana (Cheater 1993).

Do not assume that floristic diversity and endemism reflect faunistic

diversity and endemism. Invertebrate surveys should be included in biodiversity assessments because their patterns of diversity cannot be assumed to follow those of vertebrates and plants. In some cases plant diversity positively correlates with that of invertebrates, but sometimes the correlation is inverse or non-existent (Oliver and Beattie 1993).

Invertebrate surveys are feasible. Conservation should not and need not be based on plants alone. First, invertebrate surveying has been clearly demonstrated feasible using brief training sessions of biotechnicians to identify species (as with tiger beetles, Pearson and Cassola 1992) or to sort samples into "recognizable taxonomic units" (Oliver and Beattie 1993). Furthermore, conservation agencies do not have to do this work themselves. E.g. our research is a volunteer labor; while we have sometimes received grants (for which we are very grateful), our time (including months of data analysis) have been entirely volunteer. We and other volunteer experts on invertebrates want to contribute, but I have experienced these (perhaps unwitting) barriers. (1) (Fire) management occurs before invertebrate surveyors even know the site exists, yet surveys should occur prefire (see below). (2) I have never been approached by any managers of my study sites in the Upper Midwest (i.e. they have never initiated communication with me) regarding future management or other conservation issues at these site(s), even though they clearly know about my research and what my concerns and expertise are (Swengel 1990a, 1991b, 1992a-b); I have nevertheless apparently had some small effects, for which I am grateful, but I initiated those discussions. This gives the impression, no matter how unintended, that my study species and my expertise are not valued.

Surveys are as important as management. If money and manpower exist to manage a site, then the site can (and should) be thoroughly surveyed for biodiversity first. A site simply cannot be effectively managed for biodiversity when managers do not know what's there. The effectiveness of management is best evaluated in comparison with pre-management measurements. If you don't have the time/money to survey, you don't have the time/money to manage either. Surveys should also be ongoing during management. How else can you know you're being successful?

Re-examine the benefits of single-species conservation. While conservation of ecosystems has an intuitively obvious appeal, with demonstrable benefits on a gross scale (e.g. large parks and wilderness areas), how individual rare species fare is the ultimate test of the efficacy of any conservation program. Rare species should remain an important focus of conservation, as they contribute disproportionately to landscape-scale diversity and are the most likely components to be lost globally.

Tallgrass prairie is a biodiversity conservation hotspot. Prairie once occurred over a huge expanse and has been mostly destroyed (see "Introduction"). I think that sociopolitical factors explain why the biodiversity of tallgrass prairie is not adequately recognized as a globally high conservation priority:

- prairie is perceived too far gone (decimated, uninteresting), in effect giving up on what's left; yet small sites can maintain high diversity for long periods;
- the "charismatic megafauna" are largely gone (even though they are a tiny minority of prairie biodiversity);
- the region has a relatively thin human population density but high human development effect--a rare occurrence; usually they correlate, so that the higher the development effect, generally the larger the scientific and conservation constituency and greater the dollars available to advance a conservation agenda;
- experts on prairie fauna (the predominant diversity of prairies) are thinly spread over taxonomic groups and space; this was a huge biome, with a fair amount of biogeographical variation.

Management recommendations

Comments on fire. In previous reports (Swengel 1991b, 1992a-b), I have discussed what my data substantiated about how NOT to burn, e.g. do not burn in a 1-4 year rotation. Some have misinterpreted this to endorse a five-year rotation,

which I never have and do not now, for I do not have data substantiating this as tenable for prairie-specialist populations. My data do strongly indicate that alternate management types are preferable. Frequent fire depresses specialist butterfly populations too much, but infrequent fire in the absence of other processes produces poorer habitat for these species than if alternate conservation management treatments were being applied. Even if fire were the main ecological process in prehistoric prairie, there are at least five important ways that modern fire management diverges from its prehistoric occurrence, which would have been patchier, more variable seasonally, of an unknown frequency (so that modern rotations could be much too frequent), in the context of vast unburned surrounding prairie habitat, and in combination with other processes (especially immense herbivory). If fire is applied to prairie preserves, it should be done in a way that much more closely approximates these precontact realities. I do not recommend that burning be banned, for I can admit the possibility that fire in some form and frequency might have some benefit to biodiversity, but I anxiously await and expect scientific confirmation of this and the use of fire only commensurate with scientific substantiation of its benefits for biodiversity.

Our highest-priority recommendations. My co-researcher and I listed the recommendations we most want to see applied as soon and widely as possible for the benefit of prairie biodiversity.

Scott Swengel:

1. Institute haying on large percentages of previously burned prairies.
2. Reduce fire dramatically: no 1994 fires at sites with any fire in 1993; $\leq 10\%$ area burned/year/site.
3. Graze hilly sites hard to hay.
4. Continue the management that maintained the prairie (light grazing, annual haying) before preservation.
5. Control brush with mowing and heavy brushing equipment: handcutting too labor-intensive.
6. Apply the same rules to management of private prairies. They should be preferentially grazed/hayed to be more cost-effective for owners.

Ann Swengel:

Minimize fire in the management regime to be the least used option.
Use mechanical treatments first to accomplish as many management goals as possible.

Set aside (even small) never-burn management areas for other treatments, especially mechanical cutting.
Diversify types of management treatments (i.e. not just fire).

Doing nothing is a viable alternative, especially until adequate surveying and monitoring have been established.

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ILLINOIS		J1	Ag	Jn	J1	Ag	Se	Jn	J1	Ag
<u>Prairie site</u>	<u>County</u>	<u>91</u>	<u>91</u>	<u>92</u>	<u>92</u>	<u>92</u>	<u>92</u>	<u>93</u>	<u>93</u>	<u>93</u>
Ayers	Carroll	31	27	30						30
Bicentennial	Ogle	31	27	30	15		1	29		
Byron	Ogle							29	21	24
Harlem Hills	Winnebago							29	21	24
Nachusa	Lee/Ogle	31	27	30	15	11	1	29		24
Thomson-Fulton	Whiteside	31	27	30						30

IOWA		Jn	Ag	Jl	Ag
<u>Prairie site</u>	<u>County</u>	<u>91</u>	<u>91</u>	<u>92</u>	<u>93</u>
Cayler	Dickinson				16
Crossman	Howard		21	1	10
Haffner	Dickinson				16
Hayden	Howard		21	1	10
Hoffman	Cerro Gordo				10
Kalsow	Pocahontas	28	21	22	10
Stinson	Kossuth	28	21		10

MINNESOTA		Jn	Jn	Jn	Jl	Jl	Au	Jl	Au	Jl	Au
<u>Prairie site</u>	<u>County</u>	<u>88</u>	<u>89</u>	<u>90</u>	<u>90</u>	<u>91</u>	<u>91</u>	<u>92</u>	<u>92</u>	<u>93</u>	<u>93</u>
Audubon	Clay			25	18	10	7, 8	9, 10	20	9	19
Bicentennial	Clay			26	19	11	8	9	19	8, 9	18
Bicentennial Hay	Clay							11	19	8, 9	18
Blazing Star	Clay			26	19	11	8	10	19	8	18
Bluestem	Clay			25	18	10	6	9	20	9	18, 19
Chippewa	Chippewa					8	5	7	18	6	17
Foxhome	Vilkin					10	7, 9	8	20	7	19
Frenchman's Bluff	Norman								19	8	18
Hole-in-the-Mountain	Lincoln	20	30	18	16	8	5	6, 7	17	5, 6	16
Kettledrummer	Vilkin					10		8	20		19
Lundblad	Murray							6	17	5	16
Ordway	Pope					17	9	6	8	18	7
Prairie Coteau	Pipestone							6, 7	17	5, 6	16
Prairie Marshes	Lyon							6	17	6	17
Seven Sisters	Douglas/Otter Tail			20	12	6	8	8	18	7	20
Staffanson	Douglas			17	9	6	8	8	18	10	17
Town Hall	Vilkin					10	7, 9	8	20	7	19
Twin Valley	Norman			26	19	11	8	10	19	8	18
Western North	Vilkin					10	7, 9	9	20	9	19
Western South	Vilkin						7			7	19
Zimmerman	Becker			19		8			19	8	18

MISSOURI		Jn	Jn
<u>Prairie site</u>	<u>County</u>	<u>92</u>	<u>93</u>
Bellamy Hay	Vernon	18	
Buffalo Vallow	Barton		18
Bushwacker	Vernon		14
Catlin	Barton	18	18
Clear Creek	Barton	18	
Comstock	Barton		14
Cook	Barton		15
Diamond Grove	Newton	17	
Dorris Creek	Barton	16	15
Dorsett Hill	Cass	19	18

Flight Lake	Vernon	15	
Gama Grass	Vernon	15	14
Gay Feather	Vernon	18	16
Golden	Barton	16	15
Hunkah	Barton	16	17
Indigo	Dade	17	
Little Osage	Vernon	15	14
Little Osage W Hay	Vernon		14
Mo-Ko	Cedar	18	16
Mo-Ko E Hay	Cedar	18	
Mo-Ko SE Hay	Cedar	18	
Mo-Ko SSE Hay	Cedar	18	
Monegaw	Cedar	18	16
Mo-Ho-I	Barton		17
Mon-Shon	Barton		17
Montevallo Hay	Vernon	18	
Mount Vernon	Lawrence	17	
Niwatthe	Dade	17	15
Osage	Vernon	15	14
Pawhuska	Barton		15
Penn-Sylvania	Dade		15
Penn-Sylvania W Hay	Dade	17	
Prairie State Park	Barton	16, 17	15, 17
Redwing	Barton		17
Ripgut	Bates	15	14
Risch	Barton	18	18
Sky	Cedar	19	16
Taberville	St. Clair	19	16
Treaty Line	Barton		15
Tzi-Sho	Barton	16	17
Vah-Kon-Tah	St. Clair	18	16
Vah-Sha-She	Jasper	16	17

[illegible]

Appendix 2. Nectar records of specialist species. Data from Dana (1991): V=very common (100's of visits), C=common (~35), F=frequent (11-25), O=occasional (5-10), R=rare (2-4), S=single.

OTTOE AND DAKOTA SKIPPERS	OT IL-VI 1990-93				OTT MINN 1990-93				DAK MINN 1990-93			
	mal	fem	uns	all	male	fem	uns	all	male	fem	uns	all
Yarrow <u>Achillea millefolium</u>												S
Prairie dandelion <u>Agoseris</u>									1 R			1
Leadplant <u>Amorpha canescens</u>	1	1		2								
Showy milkweed <u>Asclepias speciosa</u>									1		1	2
Butterfly weed <u>A. tuberosa</u>	2			2								
Whorled milkweed <u>A. verticillata</u>												S
Green milkweed <u>A. viridiflora</u>					O	R						S
Ground plum <u>Astragalus</u>					S				18 C	7 F	5	30
Aster, upland white <u>A. ptarmic.</u>	1			1								
<u>Calylophus serrulatus</u>									R	R		
Thistle, Hill's <u>Cirsium hillii</u>	1			1								
Thistle <u>Carduus</u>			1	1							S	3
Golden aster <u>Chrysopsis</u>									1			1
Canada thistle <u>Cirsium arvense</u>									S			
Thistle <u>Cirsium</u>					O	O					S	
Coreopsis <u>Coreopsis</u>	9			9								
Pale purple coneflower <u>E. angus.</u>					12 V	V			12 15 V	8 V		23
Fleabane <u>Erigeron</u>	1	1		2					3 R	R		3
Mustard <u>Erysimum inconspicuum</u>											S	
Blanketflower <u>Gaillardia aristata</u>									30	19	11	60
Bedstraw <u>Galium</u>									2		1	3
Wild licorice <u>Glycyrrhiza lepidota</u>										1		1
Blue lettuce <u>Lactuca</u>					R	R			S			
Blazingstar, dwarf <u>L. cylindracea</u>	9	5	2	16								
Blazingstar, dotted <u>L. punctata</u>					R	R						
Yellow flax <u>Linum sulcatum</u>									S			
Alfalfa <u>Medicago sativa</u>									1		2	3
Yellow sweet clover <u>M. officinalis</u>										R		
Wild bergamot <u>Monarda fistulosa</u>	31	18	2	51	R							
Sundrops <u>Oenothera</u>									2			2
Locoweed <u>Oxytropis</u>					S				1 F	R		1
Slender penstemon <u>Penstemon</u>									1			1
Prairie-clover, purple <u>Petalost.</u>	6	2		8	S	S						
Prairie-clover, white <u>P. candidum</u>						S						
Phlox <u>Phlox</u>					3				3	S		
Coneflower, gray-headed <u>R. pinnata</u>	1			1								
Black-eyed Susan <u>Rudbeckia hirta</u>	3	1		4					4	1		5
Groundsel <u>Senecio</u>										S		
Rosinweed <u>Silphium integrifolium</u>	2			2								
Rigid goldenrod <u>Solidago rigida</u>	1	3		4								
Goat's rue <u>Tephrosia virginiana</u>	1			1								
Goat's beard <u>Tragopogon pratensis</u>										S		
Alsike clover <u>Trifolium hybridum</u>									1 R	R		1
Red clover <u>Trifolium pratense</u>									1			1
Vervain <u>Verbena</u>	1			1	F	O			O	F		
Death camas <u>Zigadenus</u>									1			1
TOTAL	68	33	5	106	15				15	83	36	142

Appendix 2. continued.

POYESHNIK & AROGOS SKIPPERS	POV MN 1990-93	ARO MN 1990-93				ARO MD 1992-93			
	all	mal	few	uns	all	mal	few	uns	all
Prairie dandelion (<u>Agoseris</u>)	2								
Ground plum (<u>Astragalus</u>)	4								
Nodding thistle (<u>Carduus</u>)			1	5	6				
Golden aster (<u>Chrysopsis</u>)	1								
Thistle (<u>Cirsium</u>)			1		1				
Coreopsis (<u>Coreopsis</u>)	32		1		1	1			1 2
Pale purple coneflower (<u>E. angust.</u>)	34		1	3	26	30			
Purple coneflower (<u>E. pallida</u>)									73 73
Flaebane (<u>Erigeron</u>)	1								
Ox eye (<u>Helioopsis helianthoides</u>)	65								
Pale spike lobelia (<u>Lobelia</u>)	8								
Sundrops-wilted (<u>Oenothera</u>)	1								
Locoweed (<u>Oxytropis</u>)	1								
Purple prairie clover (<u>Petalostemum</u>)			1		1				
Sainfoin (<u>Psoralea onobrychis</u>)									1 1
Black-eyed susan (<u>Rudbeckia hirta</u>)	5								
Vervain (<u>Verbena</u>)			1		1				
TOTAL	154	1	8	31	40	1			76 77

LEONARD'S/PAVLEE SKIPPERS

LEONARD'S/PAVLEE SKIPPEES	ILL-VIS 1992-1993				MINNESOTA 1992-93			
	mal	fem	uns.	all	mal	fem	uns.	all
Wild onion (<u>Allium</u>)					4	1	3	8
Purple aster (<u>Aster</u>)					2			2
Golden aster (<u>Chrysopsis</u>)					1			1
Rough blazingstar (<u>Liatris aspera</u>)	3	2	24	29	1			1
Dotted blazingstar (<u>L. punctata</u>)					13	2	5	20
Purple prairie clover (<u>Petalostemum</u>)						1		1
Upright coneflower (<u>R. columnifera</u>)					1		1	2
Gray goldenrod (<u>S. nemoralis</u>)						1		1
Rigid goldenrod (<u>Solidago rigida</u>)					1			1
TOTAL	3	2	24	29	21	5	8	34

REGAL FRITILLARY

[illegible]

Appendix 2. continued.

[illegible]

REGAL FRITILLARY

REGAL FRITILLARY	mal	few	uns	all	mal	few	uns	all	all
MISSOURI	15-19	Jun	92	1992	14-18	Jun	93	1993	1992-93
Yarrow (<u>Achilles millefolium</u>)	1	1		2					2
Indian hemp (<u>Apocynum cannabinum</u>)	6		1	7	2			2	9
Sullivant's milkweed (<u>A. sullivanti</u>)	3		1	4					4
Common milkweed (<u>Asclepias syriaca</u>)	15	1		16					16
Butterfly weed (<u>Asclepias tuberosa</u>)	11			11	11			11	22
Ceanothus (<u>Ceanothus</u>)					10			10	10
Coreopsis (<u>Coreopsis</u>)	53	9	4	66	83		1	84	150
Deftford pink (<u>Pianthus armeria</u>)	4			4	1			1	5
Pale purple coneflower (<u>R. pallida</u>)	358	31	58	447	168		1	169	616
Fleabane (<u>Erigeron</u>)					3			3	3
Shrub honeysuckle (<u>Lonicera</u>)	6			6					6
Wild bergamot (<u>Monarda fistulosa</u>)	65	7	2	74	2			2	76
Wild quinine (<u>Parthenium integrifolium</u>)	4			4					4
Beardtongue (<u>Penstemon digitalis</u>)					1			1	1
False dragonhead (<u>Physostegia virginiana</u>)	3			3					3
Smooth sumac (<u>Rhus glabra</u>)	3			3					3
Black-eyed Susan (<u>Rudbeckia hirta</u>)					4			4	4
Sensitive briar (<u>Schrankia uncinata</u>)	1	2	2	5	1			1	6
Red clover (<u>Trifolium pratense</u>)					4			4	4
Total	533	51	68	652	290		2	292	944

Appendix 3. Results of analysis of variable effects (Mann-Whitney analysis) for specialist species. Mean rates (per hour) lacking similar letters after they are significantly different ($P < 0.05$ two-tailed). Near significant values ($0.05 < P < 0.06$) are underlined--e.g. B means the value was nearly significantly different from A but since it was not significant, it is treated as an A). Boldfaced letters were significant at $P < 0.01$. (A)=not tested because sample 6. The largest subsample possible for recently burned vs. unburned is presented, with additional subsamples if large enough for statistical testing. Flight period is in phenologically adjusted Julian date unless otherwise noted.

species:	Poweshiek	Poweshiek		Ottos	Ottos			
flight:	170-182			187-216				
geography:	Minnesota			7 sites in WI & IL having species				
	N	mean		N	mean			
	<u>units</u>	<u>rate±sd</u>		<u>units</u>	<u>rate±sd</u>			
A. weather:								
poor	55	8.45± 31.53 A		18	10.97± 19.12 A			
mediocre	63	12.88± 36.03 AB		42	6.88± 11.62 A			
good	72	14.44± 32.88 B		87	9.92± 20.83 A			
B. add to select:	nothing							
year:								
1990	-			41	12.82± 21.71 A			
1991	-			17	13.60± 17.36 A			
1992	86	17.73± 39.57 A		36	9.93± 21.62 AB→ 1993 than			
1993	101	5.29± 5.29 B		51	4.47± 12.05 B 1990-91			
C. add to select:	1992	1993		1990-1991	1992-1993			
prairie type:								
wet	22	4.60± 10.10 A	23	0.40± 1.09 A	-			
mesic	17	3.13± 6.59 AB	21	3.20± 10.13 A	-			
dry	47	29.15± 50.37 B	57	8.03± 26.43 A	57	13.28± 20.49	83	7.06± 17.13
veg. quality:								
degraded	6	2.22± 5.44 A	5	0.00± 0.00 (A)	9	0.35± 1.05 A	13	1.83± 3.24 A
semi-deg.	24	5.34± 9.15 A	25	2.94± 9.68 A	10	14.98± 22.11 B	19	4.47± 9.11 A
high qu.	56	24.70± 47.32 A	71	6.49± 23.80 A	38	15.89± 21.63 B	51	9.35± 20.83 A
diversity:								
uniform	25	3.46± 7.71 A	37	2.07± 7.71 A	57	13.28± 20.49	83	7.06± 17.13
diverse	61	17.74± 45.55 A	64	7.15± 25.05 A	-		-	
size:								
small	26	17.69± 31.19 A	35	12.58± 33.10 A	37	14.34± 17.05 A	62	8.88± 19.20 A
large	60	17.74± 42.93 A	66	1.42± 5.79 A	21	10.77± 25.55 A	25	1.41± 5.61 B
D. recent burn status:								
1. add to select:	dry	nothing		not degraded	small sites			
burned	8	0.42± 1.25 A	22	0.22± 0.72 A	6	1.51± 1.74 A	5	6.50± 10.12 (A)
unburned	38	35.96± 53.90 B	79	6.70± 23.08 A	42	17.73± 22.26 B	54	9.59± 20.28 A
2. add to select:	wet & mesic							
burned	7	0.00± 0.00 A						
unburned	32	4.83± 4.83 A						

Appendix 3. continued.

species:	Lennard's	Pawnee	Pawnee	Dakota
flight:	Aug 20+	Aug 10+		171-179
geography:	9 sites in Illinois	4 sites in Minnesota	4 sites in Minnesota having species	Minnesota
				Minnesota having species
	N mean	N mean	N mean	N mean
	units rated	units rated	units rated	units rated
A. weather:				
poor	-	3 18.94± 15.61 (A)		55 4.95± 10.85 A
mediocre	-	3 4.20± 3.67 (A)		63 2.53± 5.61 A
good	31 12.91± 22.80	27 28.11± 42.69 A		69 4.33± 12.74 A
B. add to select:	nothing			
year:				
1990	(0 individuals)	-		-
1991	(5 individuals)	-		-
1992	(0 individuals)	16 42.61± 50.33 A		86 2.78± 6.88 A
1993	31 12.91± 22.80	17 8.63± 11.32 B		101 4.87± 12.37 A
C. add to select:	1993	1992	1993	1992-1993
prairie type:				
wet	-	1 0.00± 0.00 (A)	1 0.00± 0.00 (A)	45 0.17± 1.15 A
mesic	-	-	-	38 1.41± 3.32 A
dry	31 12.91± 22.80	15 45.45± 50.75 A	16 9.17± 11.47 A	104 6.44± 13.05 B
veg. quality:				
degraded	2 0.00± 0.00 (A)	-	-	11 0.00± 0.00 A
semi-deg.	13 13.39± 21.63 A	5 43.89± 33.99 (A)	6 3.76± 7.79 A	49 1.10± 2.97 A
high qu.	16 14.13± 25.33 A	11 42.03± 57.76 A	11 11.29± 12.36 A	127 5.33± 12.05 A
diversity:				
uniform	31 12.91± 22.80	4 10.26± 16.33 (A)	5 0.00± 0.00 (A)	62 1.14± 4.66 A
diverse	-	12 53.40± 53.61 A	12 12.22± 11.77 A	125 5.28± 11.88 B
size:				
small	10 19.15± 28.08 A	6 26.66± 28.44 A	7 3.22± 7.25 A	61 0.83± 4.49 A
large	21 9.94± 19.91 A	10 52.19± 59.17 A	10 12.42± 12.42 A	126 5.40± 11.92 B
D. recent burn status:				
1. add to select:	nothing	nothing	nothing	diverse, dry units in large prairies
burned	5 0.00± 0.00 (A)	7 15.04± 15.54 A	3 6.25± 10.83 (A)	19 6.35± 12.73 A
unburned	26 15.39± 24.17 A	9 64.06± 58.19 B	14 9.14± 11.75 A	55 9.20± 15.10 A
2. add to select:				wet & mesic uniform units, large
burned				10 0.00± 0.00 A
unburned				20 1.02± 2.68 A

Appendix 3. continued.

species:	Regal	Regal	Regals/mile	Gorgone
flight:	191-239	-	-	-
geography:	V. Upper Midwest	Missouri	Missouri	Upper Midwest- only units that had any Gorgones
	N mean units rate±sd	N mean units rate±sd	N mean units rate±sd	N individuals units /total time
A. weather:				
poor	72 11.52± 18.74 A	9 35.19± 43.51 A	9 22.01± 25.50 A	
mediocre	73 26.93± 28.16 B	39 33.24± 52.02 A	39 27.75± 47.90 A	
good	212 22.80± 26.17 B	92 41.46± 58.94 A	92 42.11± 66.52 A	
B. add to select:	not poor	nothing	nothing	
year:				
1990	45 25.92± 29.54 A	-	-	
1991	76 23.53± 26.65 A	-	-	
1992	73 23.07± 25.68 A	43 30.95± 35.19 A	43 35.76± 52.49 A	
1993	91 23.75± 28.77 A	97 42.23± 62.94 A	97 37.29± 63.49 A	
C. add to select:	nothing	nothing		
prairie type:				
wet	79 18.80± 20.72 A	10 13.76± 23.51 A	10 15.73± 26.25 A	
mesic	73 11.93± 18.79 B	12 13.61± 23.42 A	12 11.13± 20.63 A	
dry	133 33.42± 31.43 C	117 43.81± 59.22 B	117 41.57± 63.96 B	
veg. quality:				
degraded	20 16.98± 17.14 A	5 4.80± 10.73(A)	5 2.00± 4.47(A)	
semi-deg.	85 25.18± 28.43 A	5 11.83± 17.76(A)	5 8.00± 12.61(A)	
high qu.	180 24.00± 27.90 A	130 41.11± 57.35 A	130 39.27± 61.70 A	
diversity:				
uniform	117 10.92± 15.87 A	22 14.08± 21.05 A	22 13.52± 23.15 A	
diverse	168 32.87± 30.12 B	118 43.37± 59.26 B	118 41.16± 63.88 B	
size:				
small	120 17.80± 18.99 A	63 28.88± 42.46 A	63 25.35± 37.43 A	
large	165 28.27± 31.56 B	77 46.85± 64.19 A	77 46.20± 72.63 A	
D. recent burn status:				
1. add to select:	dry	dry, diverse	dry, diverse	prairies
	diverse, large			
burned	19 16.58± 16.72 A	14 4.06± 7.46 A	14 2.24± 3.78 A	4 4/1.47=2.73/hr
unburned	56 48.31± 39.14 B	96 52.04± 62.26 B	96 49.82± 67.84 B	10 28/6.22=4.50/hr
2. add to select:	mesic,			barrens
	uniform, large			
burned	11 4.56± 4.56 A			0
unburned	16 14.87± 13.72 B			16 118/7.11=15.84/hr
3. add to select:	wet,			
	uniform, large			
burned	13 2.80± 5.94 A			
unburned	21 20.93± 18.07 B			
4. add to select:	dry,			
	diverse, small			
burned	6 17.33± 21.95 A			
unburned	44 29.62± 15.72 A			
5. add to select:	mesic,			
	uniform, small			
burned	6 0.14± 0.35 A			
unburned	17 1.59± 5.36 A			

Appendix 4. Same type of table as Appendix 3 for selected non-specialist species.

species:	Great Spangled	Great Spangled	Aphrodite	Aphrodite
flight:	166-224	-	166-194	166-194
geography:	Upper Midwest	Missouri	E. Upper Midwest (longitude 94°)	E. Upper Midwest
	Y	Y	Y	Y
	mean	mean	mean	mean
	rate	rate	rate	rate
A. weather:	units	units	units	units
poor	169 1.24± 7.02 A	9 0.26± 0.77 A	56 3.23± 11.07 A	
medicore	238 1.79± 5.53 A	39 0.75± 2.55 A	8.40± 16.81 B	
good	546 2.26± 6.59 A	92 0.49± 1.97 A	126 6.09± 16.66 AB	
B. add to select:	nothing	nothing	weather not poor	weather not poor
year:				
1990	134 1.01± 2.83 A		23 7.42± 12.07 A	
1991	81 4.05± 13.07 A			
1992	363 2.18± 5.87 A	43 1.01± 2.91 A	95 2.32± 5.85 B	
1993	371 1.49± 5.52 A	97 0.34± 1.57 A	66 13.37± 25.00 A	
C. add to select:	nothing	nothing	1990, 1993	1992
prairie type:				
wet	159 5.36± 11.86 A	10 0.63± 1.33 A	6 16.45± 16.47 A	6 1.01± 1.71 A
mesic	117 2.26± 5.92 B	12 0.00± 0.00 A	1 0.00± 0.00(A)	1 10.00± 0.00(A)
dry	661 1.06± 3.83 B	117 0.60± 2.25 A	82 11.64± 22.89 A	86 2.36± 6.06 A
veg. quality:				
degraded	149 0.75± 2.53 A	5 0.00± 0.00 A	25 16.97± 22.37 A	24 1.97± 4.89 A
seal-deg.	240 1.96± 6.31 A	5 0.00± 0.00 A	19 4.55± 5.94 A	16 0.76± 2.14 A
high qu.	555 2.22± 7.06 A	130 0.59± 2.16 A	45 12.06± 26.16 A	53 3.04± 6.96 A
diversity:				
uniform	482 2.82± 8.22 A	22 1.20± 3.26 A	67 9.76± 22.87 A	66 2.44± 6.34 A
diverse	462 1.01± 3.32 B	118 0.43± 1.79 A	22 16.11± 20.41 B	27 2.21± 4.76 A
size:				
small	605 1.60± 5.71 A	63 0.54± 2.05 A	65 9.09± 23.19 A	66 2.44± 6.34 A
large	344 2.57± 7.51 A	77 0.55± 2.13 A	24 16.85± 19.99 A	29 2.06± 4.64 A
D. recent burn status:				
1. add to select:	wet, uniform	nothing	uniform	nothing
burned	31 6.86± 10.32 A	18 0.35± 1.02 A	0 0.65± 2.08 A	33 1.44± 4.06 A
unburned	70 7.53± 15.40 A	122 0.58± 2.21 A	61 10.65± 23.80 A	62 2.79± 6.59 A
2. add to select:	not wet, uniform			
burned	75 1.24± 3.59 A			
unburned	306 1.71± 5.54 A			
3. add to select:	not wet, diverse			
burned	94 0.42± 1.43 A			
unburned	303 1.01± 3.27 A			

Appendix 4. continued.

species:	Aphrodite	Aphrodite	Konarch	Konarch
flight:	161-224	161-224	-	-
geography:	V. Upper Midwest (longitude 94°)	V. Upper Midwest (longitude 94°)	Missouri	Missouri
	Y	Y	Y	Y
	mean	mean	mean	mean
	rate	rate	rate	rate
A. weather:	units	units	units	units
poor	42 6.31± 12.27 A		9 1.31± 2.32 A	
medicore	64 10.89± 16.53 AB		39 4.56± 8.30 A	
good	188 13.29± 20.47 B		92 7.04± 11.27 A	
B. add to select:	weather not poor	weather not poor	nothing	nothing
year:				
1990	45 9.04± 11.32 AB			
1991	43 12.77± 15.39 A			
1992	73 7.33± 12.95 B	43 11.55± 13.56 A		
1993	91 18.44± 26.39 A	97 3.51± 7.17 B		
C. add to select:	1990-91, 1993	1992	1992	1993
prairie type:				
wet	47 24.51± 25.76 A	19 14.04± 19.35 A	5 21.25± 14.35(A)	6 5.43± 5.52 A
mesic	42 7.73± 11.59 B	20 2.54± 6.98 B	4 7.87± 4.45(A)	8 2.17± 3.13 A
dry	90 13.17± 20.68 B	34 6.06± 9.35 A	34 10.56± 13.80 A	83 3.50± 7.56 A
veg. quality:				
degraded	17 24.86± 26.32 A	3 0.00± 0.00(A)	1 5.45± 0.00(A)	4 0.00± 0.00(A)
seal-deg.	46 16.70± 24.21 AB	24 9.89± 15.31 A	1 7.00± 0.00(A)	4 2.50± 5.00(A)
high qu.	114 12.01± 18.76 B	46 6.47± 11.66 A	41 11.81± 13.84 A	89 3.72± 7.39 A
diversity:				
uniform	63 18.20± 25.56 A	31 10.22± 16.88 A	9 16.45± 14.60 A	13 3.23± 4.92 A
diverse	116 13.06± 18.48 A	42 5.19± 8.66 A	34 10.25± 13.20 A	84 3.56± 7.48 A
size:				
small	76 19.41± 25.79 A	31 6.58± 13.15 A	22 9.37± 12.05 A	41 3.49± 7.17 A
large	103 11.52± 16.64 B	42 6.40± 12.88 A	21 13.63± 14.94 A	56 3.53± 7.24 A
D. recent burn status:				
1. add to select:	wet, not degraded, large	not mesic	nothing	nothing
burned	10 7.02± 7.09 A	10 1.52± 2.68 A	7 6.54± 13.77 A	11 6.42± 11.65 A
unburned	13 22.20± 17.56 B	43 10.91± 15.22 B	36 12.14± 13.64 A	66 3.14± 6.35 A
2. add to select:	not wet, not degraded, large			
burned	22 4.10± 4.80 A			
unburned	51 11.23± 16.25 A			
3. add to select:	not wet, not degraded, small			
burned	8 2.40± 3.78 A			
unburned	44 16.46± 23.19 A			

Appendix 4. continued.

species:	Monarch	Monarch	Monarch	Monarch
flight:	early (<215)	early (<215)	early (<215)	early (<215)
geography:	E. Upper Midwest (longitude>94°)	E. Upper Midwest (longitude>94°)	V. Upper Midwest (longitude>94°)	V. Upper Midwest (longitude>94°)
	N mean units ratesd	N mean units ratesd	N mean units ratesd	N mean units ratesd
A. weather:				
poor	67 7.40± 20.80 A		71 5.24± 10.69 A	
mediocre	99 12.20± 17.78 B		92 5.46± 8.26 A	
good	215 9.24± 14.74 B		151 6.46± 9.09 B	
B. add to select:	weather not bad	weather not bad	weather good	weather good
year:				
1990	49 11.75± 14.68 A		53 8.08± 7.93 A	
1991	22 8.24± 7.97 A		28 11.89± 11.73 A	
1992	146 13.71± 17.34 A		38 5.32± 9.23 B	
1993	93 4.42± 13.58 B		31 0.33± 1.42 C	
C. add to select:	1990-1992	1993	1990-1991	1992
prairie type:				
wet	8 30.84± 30.61 A	8 1.89± 2.68 A	23 8.32± 7.42 A	13 8.37± 13.70 A
mesic	2 51.54± 44.60(A)	1 12.00± 0.00(A)	23 11.27± 13.44 A	10 4.05± 5.71 A
dry	201 11.83± 14.26 A	83 4.58± 14.32 A	35 8.86± 7.57 A	15 3.52± 5.47 A
veg. quality:				
degraded	48 19.57± 22.49 A	23 10.51± 25.11 A	9 19.98± 16.51 A	4 10.00± 20.00(A)
semi-deg.	49 12.49± 15.17 AB	15 4.65± 9.46 A	19 6.52± 7.08 B	11 5.69± 11.05 A
high qu.	117 10.09± 12.29 B	55 1.81± 3.41 A	53 8.63± 7.55 B	23 4.33± 5.30 A
diversity:				
uniform	155 8.83± 11.41 A	51 1.99± 3.84 A	31 7.40± 7.28 A	18 6.07± 8.93 A
diverse	59 23.09± 21.45 B	42 7.38± 19.49 A	50 10.63± 10.56 A	20 4.64± 9.66 A
size:				
small	205 7.32± 10.62 A	64 4.77± 15.72 A	22 11.13± 13.87 A	18 4.83± 8.84 A
large	105 15.90± 21.76 B	29 3.64± 7.05 A	59 8.74± 7.33 A	20 5.76± 9.77 A
D. recent burn status:				
1. add to select:	not degraded, nothing	nothing	not degraded	nothing added
uniform, small				
burned	31 13.75± 16.43 A	7 5.68± 13.30 A	17 9.09± 6.00 A	6 0.74± 1.81 A
unburned	98 7.27± 8.76 A	86 4.32± 13.68 A	55 7.75± 7.86 A	32 6.18± 9.81 A

Appendix 4. continued.

species:	Monarch	Monarch	Monarch	Monarch
flight:	early (<215)	late (>214)	late (>214)	late (>214)
geography:	V. Upper Midwest (longitude>94°)	E. Upper Midwest (longitude>94°)	V. Upper Midwest (longitude>94°)	V. Upper Midwest (longitude>94°)
	N mean units ratesd	N mean units ratesd	N mean units ratesd	N mean units ratesd
A. weather:				
poor		33 20.46± 36.65 A	57 393.85±1476.9 A	
mediocre		42 26.50± 26.08 B	48 42.37± 64.61 A	
good		244 17.82± 24.91 C	137 237.64±1378.7 A	
B. add to select:	weather good	weather good	nothing	nothing
year:				
1990		25 10.54± 14.55 A	-	
1991		89 13.47± 20.59 A	66 696.41±2380.0 A	
1992		29 32.14± 30.63 B	87 100.61±515.06 AB	
1993		101 19.35± 27.02 C	105 57.07±205.55 B	
C. add to select:	1993	1990, 1991, 1993	1991	1992-1993
prairie type:				
wet	23 0.11± 0.53 A	15 9.08± 12.69 A	26 291.96±662.99 A	50 204.05±725.15 A
mesic	21 0.73± 2.29 A	1 70.59± 0.00(A)	15 2532.2±4559.0 A	43 46.34± 83.32 B
dry	57 0.58± 2.20 A	195 16.35± 23.92 A	25 20.83± 34.13 B	99 25.77± 36.93 C
veg. quality:				
degraded	5 0.00± 0.00(A)	49 19.87± 24.11 A	6 50.81± 55.84 A	9 14.13± 22.59 A
semi-deg.	25 0.00± 0.00(A)	65 12.72± 23.24 A	22 403.18±814.98 A	53 74.92±284.56 B
high qu.	71 0.71± 2.32 A	97 16.44± 23.52 A	38 971.58±3062.2 A	130 81.91±422.67 B
diversity:				
uniform	37 0.48± 1.78 A	142 13.54± 23.65 A	34 1330.7±3210.3 A	73 157.34±505.25 A
diverse	64 0.52± 2.08 A	69 21.34± 22.80 B	32 26.65± 39.31 B	119 27.40± 36.83 B
size:				
small	35 0.29± 1.36 A	140 13.04± 22.57 A	29 326.49±727.65 A	83 106.05±525.73 A
large	66 0.61± 2.22 A	75 21.21± 24.31 B	37 989.91±3101.1 A	109 54.53±204.36 A
D. recent burn status:				
1. add to select:	nothing	uniform, small	not dry, uniform	not degraded, wet, uniform
burned	22 0.78± 3.10 A	25 20.30± 28.37 A	15 2931.1±4402.0 A	9 372.68±640.54 A
unburned	79 0.42 1.53 A	111 11.68± 21.19 A	19 67.12± 57.57 B	26 239.15±931.14 B
2. add to select:		diverse, large	dry, diverse	not degraded, mesic, uniform
burned		10 15.90± 14.91 A	7 29.77± 40.30 A	6 94.75±175.95 A
unburned		59 22.26± 23.66 A	18 17.35± 32.03 A	23 52.73± 69.41 A
3. add to select:				not degraded, dry, diverse
burned				17 19.41± 21.26 A
unburned				73 28.62± 39.13 A

Appendix 5. Ranking of sites in the Upper Midwest by maximum single-day survey totals of Poweshiek and Dakota Skippers. I have never seen these species in Illinois and Wisconsin. All tabulated surveys occurred during the species' flights.

STATE SITE	---POWESHIEK---			----DAKOTA----			--YEARS VISITED--						
	MAX.	YEAR	YEAR	MAX.	YEAR	YEAR							
	OBS.	OBS.	OBS.	OBS.	OBS.	OBS.	88	89	90	91	92	93	
Iowa													
Stinson	24	1989	1989	-	-	-		X		X			
Freda Haffner	9	1989	1989	-	-	-		X					
Cayler	7	1989	1989	-	-	-		X					
Crossman	1	1989	1989	-	-	-		X			X		
Hayden	1	1989	1989	-	-	-		X			X		
Kalsow	0	-	-	-	-	-				X	X		
Minnesota													
Hole-in-the-Mountain	246	1989	1993	11	1989	1993	X	X	X	X	X	X	
Prairie Coteau	196	1992	1993	11	1992	1993					X	X	
Staffanson	115	1992	1993	0	-	-			X	X	X	X	
Bluestem	37	1992	1993	12	1992	1992	X		X	X	X	X	
Ordway	35	1992	1993	0	-	-			X	X	X	X	
Blazing Star	24	1988	1988	6	1988	1993	X		X	X	X	X	
Clinton	22	1988	1988	0	-	-	X						
Prairie Marshes	18	1992	1992	1	1989	1989		X			X	X	
Chippewa	15	1988	1992	1	1992, 93	1993	X			X	X	X	
Bicentennial	13	1988	1992	56	1993	1993	X		X	X	X	X	
Lundblad	4	1989	1989	0	-	-		X					
Pembina Trail	3	1988	1988	0	-	-	X						
Audubon	2	1992	1992	0	-	-			X	X	X	X	
Twin Valley	4	1992	1993	2	1993	1993			X	X	X	X	
Western North	2	1992	1993	1	1993	1993				X	X	X	
Swift County'	1	1988	1988	0	-	-	X						
Bicentennial Hay	0	-	-	30	1992	1993					X	X	
Frenchman's Bluff	0	-	-	18	1993	1993						X	
Anna Gronseth	0	-	-	0	-	-	X						
Blue Mound SP	0	-	-	0	-	-	X	X					
Buffalo River SP	0	-	-	0	-	-	X						
Expandere WMA	0	-	-	0	-	-		X					
Foxhome	0	-	-	0	-	-				X	X	X	
Kettledrummer	0	-	-	0	-	-				X	X		
Malmberg	0	-	-	0	-	-	X						
Pankratz	0	-	-	0	-	-	X						
Pipestone NM	0	-	-	0	-	-		X					
Red Rock	0	-	-	0	-	-		X					
Seven Sisters	0	-	-	0	-	-			X	X	X	X	
Town Hall	0	-	-	0	-	-	X			X	X	X	
Western South	0	-	-	0	-	-						X	
Zimmerman	0	-	-	0	-	-			X	X		X	

'Nature Conservancy property west of Appleton, preserve name unknown.

Appendix 6. Ranking of sites in the Upper Midwest by maximum single-day survey total of Ottoe Skippers and Regal Fritillaries. All tabulated surveys occurred during the species' flights; R=visit during Regal but not Ottoe flight; * = bad weather.

STATE SITE	-----OTTOE-----			-----REGAL-----			--YEARS VISITED--						
	MAX.	MAX.	YEAR	MAX.	MAX.	YEAR	88	89	90	91	92	93	
	OBS.	OBS.	LAST	OBS.	OBS.	OBS.							
Illinois													
Wachusa	0	-	-	26	1993	1993	X			X	X	X	X
Harlem Hill	1	1993	1993	0	-	-							X
Ayers	0	-	-	0	-	-	X	R		X	X		
Bicentennial	0	-	-	0	-	-	X	R		X	X	X	X
Byron Forest Pres.	0	-	-	0	-	-							X
Thomson-Fulton	0	-	-	0	-	-	X			X	X		
Iowa													
Freda Haffner	2	1989	1989	25	1989	1989	X						R
Stinson	0	-	-	17	1991,93	1993	X			X			X
Kalsow	0	-	-	16	1991	1993				X	X	X	
Cayler	0	-	-	13	1993	1993	X						R
Hayden	0	-	-	1	1993	1993	X			X	X	X	X
Crossman	0	-	-	0	-	-	X			X	X	X	
Hoffman	0	-	-	0	-	-							X
Turin Loess Hills	0	-	-	0	-	-				X			
Minnesota													
Hole-in-the-Mountain	13	1989	1992	418	1990	1993	X	X	X	X	X	X	R
Chippewa	0	-	-	190	1991	1993	X			R	X	X	R
Bicentennial	0	-	-	157	1991	1993	X			X	X	X	R
Staffanson	0	-	-	104	1991	1993				X	X	X	R
Prairie Coteau	0	-	-	104	1993	1993						X	R
Bicentennial Hay	0	-	-	93	1993	1993					R	X	R
Prairie Marshes	0	-	-	77	1992	1993		X				X	R
Ordway	0	-	-	74	1990	1993				X	X	X	R
Bluestem	0	-	-	62	1990	1993	X			X	X	X	R
Blazing Star	0	-	-	51	1991	1993	X			X	X	X	R
Town Hall	0	-	-	43	1992	1993	X				X	X	R
Foxhome	0	-	-	42	1992	1992					X	X	R
Seven Sisters	0	-	-	35	1991	1993				X	X	X	R
Audubon	0	-	-	31	1991	1993				X	X	X	R
Western South	0	-	-	26	1991	1993					R		R
Twin Valley	0	-	-	24	1991	1993				X	X	X	R
Western North	0	-	-	16	1992	1993					X	X	R
Blue Mound SP	0	-	-	15	1988	1989	X	X					
Frenchman's Bluff	0	-	-	5	1992	1992						R	R
Pipestone NM	0	-	-	2	1989	1989		X					
Swift County	0	-	-	2	1988	1988	X						
Kettledrummer	0	-	-	1	1992	1992					X	X	R
Lundblad	0	-	-	1	1993	1993		X				R	R

*Nature Conservancy property west of Appleton, preserve name unknown.

Appendix 6. continued.

STATE SITE	-----OTTOE-----			-----REGAL-----			--YEARS VISITED--						
	MAX.	MAX.	YEAR LAST	MAX.	MAX.	YEAR LAST							
	OBS.	OBS.	OBS.	OBS.	OBS.	OBS.	88	89	90	91	92	93	
Minnesota (continued)													
Anna Gronseth	0	-	-	0	-	-						X	
Buffalo River SP	0	-	-	0	-	-						X	
Clinton	0	-	-	0	-	-						X	
Expandere	0*	-	-	0*	-	-						X	
Malmberg	0*	-	-	0*	-	-						X	
Pankratz	0*	-	-	0*	-	-						X	
Pembina Trail	0*	-	-	0*	-	-						X	
Red Rock	0	-	-	0	-	-						X	
Zimmerman	0	-	-	0	-	-						X	
Wisconsin													
Crawford County	1	1992,93	1993	60	1993	1993						X	X
Muralt	51	1990	1993	38	1990	1992	X	X	X	X	X	X	X
Thomson-Greater	0	-	-	21	1992	1993						X	X
Oliver	14	1990	1992	4	1991	1993						X	X
Spring Green	80	1990	1993	0	-	-			X	X	X	X	X
Dewey	36	1992	1993	0	-	-			X	X	R	X	X
Rush Creek	13	1991,93	1993	0	-	-						X	X
Black Earth	0	-	-	1	1989	1989	X	X	X	X	X	X	X
Thomson	0	-	-	1	1990,92,93	1993					X	X	X
Thousand's II	0	-	-	1	1992,93	1993	X	X	X	X	X	X	X
Blue River	0	-	-	0	-	-				R		X	X
Dike 17	0	-	-	0	-	-			X	X	X	X	X
Gasser	0	-	-	0	-	-			X	X			
Highway X	0	-	-	0	-	-					X	X	X
Pine Island	0	-	-	0	-	-							X
Schluckebier	0	-	-	0	-	-			X	X		X	X
Spring Green Vest	0	-	-	0	-	-							X
Thousand's I	0	-	-	0	-	-			X		X	X	R
Vale	0	-	-	0	-	-							X

Appendix 7. Ranking of sites in the Upper Midwest by maximum single-day survey total of Arogos Skippers. I have never seen this species in Illinois, Iowa, or Wisconsin. All tabulated surveys occurred during the species' flight.

STATE SITE	YEAR		ARO. LAST	--YEARS VISITED--						
	MAX.	OBS.	OBSERVED	88	89	90	91	92	93	
Minnesota										
Hole-in-the-Mtn new	32	1990	1992			X	X	X		
Hole-in-the-Mtn old	5	1991, 1992	1992	X	X	X	X	X		
Ordway	2	1990, 1991	1992			X	X	X		
Prairie Coteau	2	1993	1993					X	(X)	
Staffanson	2	1991	1992			X	X	X		
Bicentennial	1	1990, 1991	1990	X		X	X	X		
Chippewa	1	1991, 1992	1992	X			X	X		
Bicentennial Hay	0	-	-					X		
Blazing Star	0	-	-	X		X	X	X		
Bluestem	0	-	-	X		X	X	X		
Clinton	0	-	-	X						
Anna Gronseth	0	-	-	X						
Audubon	0	-	-			X	X	X		
Blue Mound State Park	0	-	-	X	X					
Buffalo River SP	0	-	-	X						
Expandere VMA	0	-	-		X					
Foxhome	0	-	-				X	X		
Kettledrummer	0	-	-				X	X		
Lundblad	0	-	-		X					
Malmberg	0	-	-	X						
Pankratz	0	-	-	X						
Pembina Trail	0	-	-	X						
Pipestone NM	0	-	-		X					
Prairie Marshes	0	-	-		X			X		
Red Rock	0	-	-		X					
Seven Sisters	0	-	-			X	X	X		
Swift County ¹	0	-	-	X						
Town Hall	0	-	-	X			X	X		
Twin Valley	0	-	-			X	X	X		
Western North	0	-	-				X	X		
Western South	0	-	-							
Zimmerman	0	-	-			X	X			

¹Nature Conservancy property west of Appleton, preserve name unknown.

Appendix 8. Ranking of sites in Missouri by maximum single-day survey totals of Arogos Skippers and Regal Fritillaries.

STATE SITE	YEAR		ARO. LAST	YEAR		ARO. LAST	--YEARS VISITED--						
	MAX.	OBS.	OBS.	MAX.	OBS.	OBS.	88	89	90	91	92	93	
Missouri - public prairies													
Mo-Ko	0	-	-	283	1993	1993					X	X	
Taberville	2	1992	1993	180	1993	1993					X	X	
Little Osage	2	1992, 93	1993	137	1992	1993					X	X	
Vah-Kon-Tah	5	1993	1993	118	1993	1993					X	X	
Monegaw	1	1992	1992	102	1993	1993					X	X	
Tzi-Sho	4	1992	1992	78	1993	1993					X	X	
Clear Creek	20	1992	1992	66	1992	1992					X		
Osage	2	1993	1993	66	1993	1993					X	X	
Red Wing	0	-	-	66	1993	1993					X		
Gay Feather	7	1992	1992	64	1992	1993					X	X	
Ripgut	0	-	-	52	1992	1992					X	X	
Gama Grass	0	-	-	49	1992	1993					X	X	
Catlin	0	-	-	45	1992	1993					X	X	
Buffalo Vallow	0	-	-	39	1993	1993					X		
Prairie State Park	12	1992	1992	38	1992	1993					X	X	
Risch	10	1992	1992	16	1992	1993					X	X	
Mon-Shon	0	-	-	12	1993	1993					X		
Niawatha	2	1992	1993	12	1993	1993					X	X	
Treaty Line	0	-	-	12	1993	1993					X		
Sky	0	-	-	10	1993	1993					X	X	
Mo-No-I	0	-	-	9	1993	1993					X		
Hunkah	0	-	-	6	1992	1993					X	X	
Pawhuska	0	-	-	5	1993	1993					X		
Bushwhacker	0	-	-	4	1993	1993					X	X	
Dorsett Hill	0	-	-	4	1992	1993					X	X	
Vah-Sha-She	0	-	-	4	1992	1993					X	X	
Comstock	0	-	-	3	1993	1993					X		
Golden	0	-	-	3	1993	1993					X	X	
Penn-Sylvania	0	-	-	2	1993	1993					X		
Diamond Grove	1	1992	1992	1	1992	1992					X		
Dorris Creek	0	-	-	1	1992	1992					X	X	
Cook	0	-	-	0	-	-					X		
Flight Lake	0	-	-	0	-	-					X	X	
Indigo	0	-	-	0	-	-					X		
Mount Vernon	4	1992	1992	0	-	-					X		
Missouri - point scans of private hay prairies													
Little Osage V Hay				15	1993	1993						X	
Mo-Ko E Hay				6	1992	1992					X		
Penn-Sylvania Hay				5	1992	1992					X		
Bellamy Hay				3	1992	1992					X		
Montevallo Hay				2	1992	1992					X		
Mo-Ko SSE Hay				2	1992	1992					X		
Mo-Ko SE Hay				2	1992	1992					X		

Appendix 9. Results of Mann-Whitney U test for effects of recent fire in the Upper Midwest, presented as number of tests in that category of significance out of the total number of tests for that species. A non-significant ($P \geq 0.05$, two-tailed test) change is defined as a two-fold difference between means in recently burned and unburned units. Sig=significant ($P < 0.05$), Ns=non-significant, dec=decrease, inc=increase.

1990-92 DATA Species	Total individuals	Sig dec	Ns dec	No change	Ns inc	Sig inc
specialists:						
Poweshiek Skipper (<i>Oarisma poweshiek</i>)	902	1/1				
Regal Fritillary (<i>Speyeria idalia</i>)	2,595	3/3				
Ottoe Skipper (<i>Hesperia ottoe</i>)	344	1/2	1/2			
Arogos Skipper (<i>Atrytone arogos</i>)	67	2/2				
grasslands:						
Aphrodite Fritillary (<i>Speyeria aphrodite</i>)	1,168	1/5	3/5	1/5		
Common Wood Nymph (<i>Cercyonis pegala</i>)	10,932	3/5		2/5		
Meadow Fritillary (<i>Glossiana bellona</i>)	827	3/3				
Silver-bordered Frit. (<i>Glossiana selene</i>)	261	1/1				
Black Swallowtail (<i>Papilio polyxenes</i>)	253	1/3	2/3			
Melissa Blue (<i>Lycaeides melissa melissa</i>)	321	1/2	1/2			
Common Ringlet (<i>Coenonympha inornata</i>)	212	1/2	1/2			
Delaware Skipper (<i>Atrytone delaware</i>)	81	1/2	1/2			
Tawny-edged Skipper (<i>Polites themistocles</i>)	96	2/4	1/4	1/4		
Crossline Skipper (<i>Polites origenes</i>)	81	2/2				
Eastern Tailed Blue (<i>Everes comyntas</i>)	228	1/1				
American Copper (<i>Lycaena phlaeas</i>)	195					1/1
generalists:						
Coral Hairstreak (<i>Harkenclenus titus</i>)	165	1/3	2/3			
Great Spangled Frit. (<i>Speyeria cybele</i>)	431	1/2	1/2			
Clouded Sulphur dates 165-197 (<i>C. philodice</i>)	817	1/2	1/2			1/2
Northern Broken Dash (<i>Vallengrenia sgeremet</i>)	141	2/4		2/4		
Cabbage White (<i>Artogeia rapae</i>)	885	1/3	1/3			1/3
Clouded Sulphur dates 198-253 (<i>C. philodice</i>)	5,864		2/3			1/3
Orange Sulphur (<i>Colias eurytheme</i>)	3,154		4/6	1/6	1/6	
Pearl Crescent (<i>Phyciodes tharos</i>)	83		1/1			
American Lady (<i>Vanessa virginiensis</i>)	26		1/1			
immigrants/migrants:						
Variegated Fritillary (<i>Euptoieta claudia</i>)	78		1/1			
Monarch dates 165-214 (<i>Danaus plexippus</i>)	1,305		2/2			
Painted Lady (<i>Vanessa cardui</i>)	620		1/2			1/2
Monarch dates 215-254 (<i>Danaus plexippus</i>)	23,815		2/5	1/5	2/5	

1990-93 DATA Species	Sig dec	Ns dec	No change	Ns inc	Sig inc
Poweshiek Skipper	1/3	2/3			
Ottoe Skipper	1/2	1/2			
Dakota Skipper	1/2	1/2			
Pawnee Skipper	1/2	1/2			
Regal Fritillary	3/5	1/5	1/5		
Leonard's Skipper	1/1				
Arogos Skipper	1/1				
Aphrodite Fr.-V. Upper Midwest	2/4	2/2			
Aphrodite Fr.-E. Upper Midwest	1/2	1/2			
Great Spangled Frit.	1/3	2/3			
Monarch-early-V. Upper Midwest	1/3	2/3			
Monarch-early-E. Upper Midwest		2/2			
Monarch-late-E. Upper Midwest		2/2			
Monarch-late-V. Upper Midwest		3/5		2/5	

Appendix 10. Results of Mann-Whitney U test for effects of recent fire in Missouri, presented as number of tests in that category of significance out of the total number of tests for that species. A non-significant ($P \geq 0.05$, two-tailed test) change is defined as a two-fold difference between means in recently burned and unburned units. Sig=significant ($P < 0.05$), Ns=non-significant, dec=decrease, inc=increase.

1992 DATA Species	Total individuals	Sig dec	Ns dec	No change	Ns inc	Sig inc
specialists:						
Regal Fritillary	931	1/1				
Arogos Skipper	71		1/1			
grasslands:						
Crossline Skipper	29		1/2	1/2		
Delaware Skipper	95			1/1		
Black Swallowtail	83			1/1		
Eastern Tailed Blue	69			1/1		
Tawny-edged Skipper	158				1/1	
generalists:						
Northern Broken Dash	16		1/1			
Coral Hairstreak	7		1/1			
American Lady	189		1/1			
Clouded Sulphur	21			1/1		
Orange Sulphur	270			1/1		
Great Spangled Fritillary	25			1/1		
Pearl Crescent	320			2/2		
immigrants/migrants:						
Painted Lady	220			1/1		
Monarch	327			1/1		
Variegated Fritillary	142			1/2	1/2	

1992-93 DATA Species	Sig dec	Ns dec	No change	Ns inc	Sig inc
specialists:					
Regal Fritillary	1/1				
Arogos Skipper		2/2			
generalists:					
Great Spangled Frit.			1/1		
immigrants/migrants:					
Monarch			1/1		

Appendix 11. Summary of species response in pair analysis by category of management history. C=M pairs of units consistent with overall category trend, T=M pairs statistically tested with Chi-square goodness of fit test, S=M pairs in sample. Consistency is defined as an individual-pair trend following to any degree (not necessarily significantly) the direction of a significant category trend. For a random (non-significant) category trend, consistency is individual-pair non-significance. A response index >1 decreases with more recent fire (increases with longer time since fire); <1 increases with more recent fire.

Category:	N pairs		Total		Total		P	Response	Mean	Liatrie	
	C/T	S	obs	exp	obs	exp				abundance	burn
			burned	unburned	burned	unburned	value	index			unburn
			recently	2+ years							
specialists:											
Poweshiek Skipper	2/2	2	1	83.86	286	203.14	0.0000	118.07			
Dakota Skipper	0/0	2	5	12.51	15	7.49	0.0012	5.01			
Pawnee Skipper	1/1	1	6	25.72	31	11.28	0.0000	11.78			
Arogos Skipper	0/0	0									
Regal Fritillary	7/8	14	65	139.09	251	176.91	0.0000	3.04			
grasslands:											
Tawny-edged Skipper	0/0	0									
Eastern Tailed Blue	0/0	3	8	4.92	3	6.08					
Melissa Blue	0/0	4	9	6.40	2	4.60					
Aphrodite Frit.	5/5	12	27	71.10	148	103.90	0.0000	3.75			
Silver-bordered Fr.	5/5	8	11	95.17	261	176.84	0.0000	12.77			
Meadow Fritillary	2/2	7	4	17.20	73	59.80	0.0005	5.25			
Common Ringlet	0/0	1	1	0.66	0	0.34					
Common Wood Nymph	6/9	17	249	369.70	700	579.30	0.0000	1.79			
generalists:											
Clouded Sulphur	1/1	5	41	46.17	54	48.83	0.3382	1.25			
Orange Sulphur	2/2	14	90	74.63	60	75.37	0.0152	0.66			
Cabbage White	0/0	7	10	7.56	5	7.44	0.3154	0.51			
Great Spangled Fr.	1/1	12	26	20.42	28	33.58	0.1542	0.65			
Pearl Crescent	1/1	2	15	11.10	9	12.90	0.1644	0.52			
immigrants/migrants:											
Variegated Frit.	1/1	5	23	13.15	4	13.85	0.0003	0.17			
Painted Lady	1/1	6	22	10.43	1	12.57	0.0000	0.04			
Monarch-early	2/2	5	34	31.01	29	31.99	0.5310	0.83			
Monarch-late	8/8	10	1165	361.7	352	1155.3	0.0000	0.09	1264.0	326.0	

Appendix 11. continued.

Category:			burned		burned		burn		burn	
			recently		last year				1 yr	
specialists:										
Poweshiek Skipper	1/1	1	1	6.55	11	5.45	0.0034	13.20		
Dakota Skipper	2/2	3	26	27.16	60	58.84	0.8782	1.07		
Pawnee Skipper	0/0	1	5	3.42	6	7.58				
Arogos Skipper	0/0	2	3	1.94	1	2.06				
Regal Fritillary	2/2	7	86	122.55	165	128.45	0.0000	1.83		
grasslands:										
Tawny-edged Skipper	0/0	1	4	2.73	1	2.27				
Eastern Tailed Blue	0/0	3	0	4.03	8	8.97				
Melissa Blue	1/1	7	25	47.42	66	43.58	0.0000	2.87		
Aphrodite Frit.	3/3	5	19	24.29	36	30.71	0.1930	1.50		
Silver-bordered Fr.										
Meadow Fritillary										
Common Ringlet	1/1	3	13	10.52	6	8.48	0.3620	0.57		
Common Wood Nymph	3/5	9	232	263.20	355	324.80	0.0121	1.24		
generalists:										
Clouded Sulphur	1/2	6	65	48.86	27	43.14	0.0011	0.47		
Orange Sulphur	2/3	10	52	60.17	70	61.83	0.1647	1.31		
Cabbage White	1/1	2	9	11.34	25	22.66	0.5034	1.39		
Great Spangled Fr.	0/0	5	4	5.01	5	3.99				
Pearl Crescent										
immigrants/migrants:										
Variegated Frit.	0/0	4	4	2.44	1	2.56				
Painted Lady										
Monarch-early	1/1	7	36	31.14	28	32.86	0.2759	0.74		
Monarch-late	1/1	3	155	124.31	24	54.69	0.0000	0.35	2040.0	360.0

Appendix 11. continued.

Category:	burned last year				unburned 2+ years				burn 1 yr	unburn
specialists:										
Poweshiek Skipper	1/1	6	69	63.71	66	72.29	0.3641	0.84		
Dakota Skipper	0/0	5	6	4.74	5	6.26				
Pawnee Skipper	0/0	0								
Arogos Skipper	0/0	2	3	1.45	0	1.55				
Regal Fritillary	4/4	10	58	84.54	121	94.46	0.0000	1.87		
grasslands:										
Tawny-edged Skipper	0/0	0								
Eastern Tailed Blue	0/0	1	1	0.49	0	0.51				
Melissa Blue	0/0	4	8	7.10	7	7.90	0.8370	0.79		
Aphrodite Frit.	2/2	5	13	22.34	32	22.66	0.0084	2.43		
Silver-bordered Fr.	1/1	6	6	11.77	26	20.23	0.0532	2.52		
Meadow Fritillary	0/0	2	0	3.12	10	6.88				
Common Ringlet	0/0	1	0	0.88	2	1.12				
Common Wood Nymph	4/6	11	196	192.56	318	321.44	0.7885	0.97		
generalists:										
Clouded Sulphur	0/1	6	16	10.88	11	16.14	0.0685	0.46		
Orange Sulphur	2/5	11	127	88.26	101	139.74	0.0000	0.50		
Cabbage White	1/1	4	22	18.65	14	17.35	0.3410	0.68		
Great Spangled Fr.	0/0	4	12	8.78	8	11.22	0.2197	0.52		
Pearl Crescent	0/0	1	0	0.49	1	0.51				
immigrants/migrants:										
Variegated Frit.	0/0	2	4	1.88	1	3.12				
Painted Lady	0/0	2	1	1.07	2	1.93				
Monarch-early	1/1	6	14	11.74	17	19.26	0.5148	0.74		
Monarch-late	3/3	6	52	104.19	186	133.81	0.0000	2.79	60.0	173.3

Appendix 11. continued.

Category:	unburned 2+ years				unburned 2+ years				unburn	unburn
specialists:										
Poweshiek Skipper	1/2	4	87	77.67	88	97.33	0.1793	0.81		
Dakota Skipper	0/0	3	6	4.59	2	3.41				
Pawnee Skipper										
Regal Fritillary	4/4	7	80	72.90	87	94.10	0.3034	0.84		
grasslands:										
Tawny-edged Skipper	0/0	1	0	0.55	1	0.45				
Eastern Tailed Blue	0/0	1	2	1.66	1	1.34				
Melissa Blue	0/0	8	3	9.76	16	9.24	0.0040	5.63		
Aphrodite Frit.	0/0	5	7	10.15	15	11.85	0.2574	1.84		
Silver-bordered Fr.	0/0	2	2	2.21	1	0.79				
Meadow Fritillary										
Common Ringlet	0/0	3	2	3.32	4	2.68				
Common Wood Nymph	2/3	8	82	68.67	93	106.33	0.0469	0.73		
generalists:										
Clouded Sulphur	0/0	4	3	2.61	5	5.39				
Orange Sulphur	0/1	10	25	23.61	36	37.39	0.8143	0.91		
Cabbage White	0/0	3	4	6.77	14	11.23	0.2686	2.11		
Great Spangled Fr.	0/0	3	4	3.29	2	2.71				
Pearl Crescent										
immigrants/migrants:										
Variegated Frit.										
Painted Lady	0/0	1	1	0.29	0	0.71				
Monarch-early	0/0	4	8	5.81	5	7.19	0.3458	6.08		
Monarch-late	1/2	5	48	60.97	89	76.03	0.0321	1.49	264.0	450.0

Appendix 12. Percentage each study species in the Upper Midwest deviated from a random (expected) distribution equal to proportion of time spent in that burn age class of units 1988-92. Tabulation is limited to flight period and geography selections described in "Methods." Total time is measured in hours.

Species	to- tal time	N in- divi- duals	N units	Years since last fire	Volti- sm
				0 1 2 3+	
Specialists:					
Poweshiek Skipper	15.6	242	51	- 97.3 - 5.0 +109.5 +111.1	1
Ottoe Skipper	27.1	91	196	- 80.1 + 34.2 + 52.9 - 12.6	1
Arogos Skipper	22.3	55	87	- 75.9 - 67.2 - 60.1 +225.2	1
Regal Fritillary	46.7	1,096	137	- 47.4 + 28.3 + 29.3 +118.3	1
Grasslands:					
Silver-bordered Fritillary	30.5	171	105	- 87.5 - 80.1 +348.2 -100.0	2
Meadow Fritillary	125.8	528	453	- 71.0 +215.9 - 64.2 - 72.2	2
Common Ringlet	14.2	117	47	- 65.2 - 78.7 -100.0 +313.7	1
Melissa Blue	43.3	256	150	- 59.0 - 28.7 - 60.7 +432.4	2-3
Crossline Skipper	68.3	76	274	- 56.9 - 7.1 +223.8 - 26.1	1-2
Delaware Skipper	67.5	70	204	- 56.7 - 32.1 +136.6 + 36.5	1
Aphrodite Fritillary	117.6	539	421	- 50.4 + 5.1 +111.5 + 16.5	1
Black Swallowtail	81.4	129	282	- 29.4 - 27.9 + 69.9 + 30.1	2-3
Common Wood Nymph	130.0	5,332	460	- 16.5 + 44.8 + 34.7 - 34.3	1
Tawny-edged Skipper	112.5	71	394	0.0 - 8.5 + 52.9 - 26.8	1-2
Eastern Tailed Blue	147.6	150	546	+ 44.0 - 69.5 - 36.0 + 12.4	3+
American Copper	14.5	193	48	+ 67.6 - 85.5 + 27.7 - 29.5	2-3
Generalists:					
Great Spangled Fritillary	112.9	235	367	- 34.3 + 93.4 + 55.5 - 70.5	1
Pearl Crescent	147.6	58	546	- 31.2 - 26.8 + 6.1 + 71.7	3+
Northern Broken Dash	84.5	129	260	- 29.4 - 27.9 + 69.9 + 30.1	1
American Lady	91.7	19	297	- 21.9 - 31.9 - 54.3 + 19.7	2-4
Clouded S. flight:198-253	93.9	5,207	358	- 3.6 0.0 + 74.5 - 24.0	3+
Cabbage White	147.6	674	546	+ 19.6 - 19.2 + 31.6 - 27.3	3+
Clouded S. flight:165-197	53.1	523	183	+ 30.0 - 1.7 - 40.6 - 39.9	3+
Orange Sulphur	133.2	2,177	482	+ 43.6 - 13.6 - 37.4 - 35.9	3+
Coral Hairstreak	94.0	96	301	+ 80.1 - 36.5 - 47.1 - 58.3	1
Immigrants/Migrants:					
Variegated Fritillary	67.0	20	202	+ 12.5 0.0 - 76.5 + 20.9	3+
Monarch 165-214	94.8	903	302	+ 29.7 - 17.5 - 4.3 - 26.6	3+
Monarch 215-254	52.8	22,364	244	+ 55.5 - 94.4 - 90.0 - 96.5	3+
Painted Lady	147.6	170	546	+ 91.8 - 62.6 - 64.0 - 59.7	3+
Total individuals	147.6	45,997	546	+ 64.8 - 38.1 - 28.1 - 54.2	

Appendix 13. Percentage each study species in Missouri deviated from a random (expected) distribution equal to proportion of time spent in that management age class of units 1992-93. Total time is measured in hours.

Species	to- tal time	N in- divi- duals	N units	Years since last fire	
				0 1	
FIRE PRAIRIES					
Specialists:					
Arogos Skipper	10.2	9	28	- 82.7 +146.9	
Regal Fritillary	10.2	94	28	- 75.0 +133.3	
Grasslands:					
Crossline Skipper	9.2	8	27	- 58.4 + 88.0	
Delaware Skipper	9.2	17	27	- 41.3 + 62.2	
Black Swallowtail	9.2	19	27	- 21.1 + 31.8	
Common Wood Nymph		0			
Tawny-edged Skipper	9.2	45	27	- 4.0 + 5.8	
Eastern Tailed Blue	10.2	20	28	+ 32.8 - 58.3	
Generalists:					
Great Spangled Fritillary	10.2	2	28	+ 56.3 -100.0	
Pearl Crescent	10.2	71	28	- 18.6 + 33.1	
Northern Broken Dash	9.2	2	27	- 16.8 + 25.3	
American Lady	9.2	12	27	- 24.8 - 37.3	
Clouded Sulphur	10.2	9	28	+ 4.2 - 7.5	
Cabbage White		0			
Orange Sulphur	10.2	136	28	- 6.9 + 12.2	
Coral Hairstreak		2			
Immigrants/Migrants:					
Variegated Fritillary	10.2	56	28	- 2.3 + 4.2	
Monarch	10.2	95	28	- 13.5 + 37.5	
Painted Lady	9.2	43	27	+ 12.1 - 18.3	
HAY PRAIRIES					
Specialists:					
Arogos Skipper	20.8	32	70	- 42.7 + 28.0	
Regal Fritillary	20.8	1,591	70	+ 6.1 - 11.6	
Grasslands:					
Crossline Skipper	20.8	42	70	- 1.8 + 3.5	
Delaware Skipper	20.8	23	70	+ 6.3 - 11.9	
Black Swallowtail	20.8	94	70	+ 15.3 - 29.0	
Common Wood Nymph		0			
Tawny-edged Skipper	20.8	85	70	+ 7.8 - 14.8	
Eastern Tailed Blue	20.8	12	70	+ 52.7 -100.0	
Generalists:					
Great Spangled Fritillary	20.8	10	70	+ 6.9 - 13.0	
Pearl Crescent	20.8	63	70	- 36.9 + 70.1	
Northern Broken Dash	20.8	13	70	- 29.5 + 55.9	
American Lady	20.8	61	70	+ 47.6 - 90.4	
Clouded Sulphur	20.8	31	70	+ 23.1 - 43.8	
Cabbage White		2			
Orange Sulphur	20.8	189	70	+ 22.0 - 41.7	
Coral Hairstreak		2			
Immigrants/Migrants:					
Variegated Fritillary	20.8	39	70	+ 25.3 - 48.1	
Monarch	20.8	175	70	+ 40.4 - 76.8	
Painted Lady	20.8	99	70	+ 15.7 - 29.9	

Appendix 14. Kruskal-Wallis one-way analysis of variance of deviation from random distribution in each burn age class by species groups (habitat niche breadth, voltinism, family) and within species groups among burn age classes. Rank is positively correlated with overrepresentation (i.e. low rank=low numbers). Spec=specialist, grass=grassland, gen=generalist, imm/mig=immigrant/migrant. HES=Hesperiidae, PAP=Papilionidae, PIE=Pieridae, LYC=Lycanidae, NYM=Nymphalidae, SAT=Satyridae, DAN=Danaidae.

UPPER MIDWEST								P	Chi
niche breadth:	mean	mean	mean	mean	mean	mean	mean	value	Square
	rank	rank	rank	rank	rank	rank	rank		
	(N=4)	(N=12)	(N=9)	(N=4)	(N=4)	(N=4)	(N=4)		
year 0	4.75	12.46	18.83	24.25				0.0038	13.4139
year 1	19.25	13.63	16.44	11.63				0.5328	2.1980
year 2	16.88	17.33	15.17	5.75				0.1207	5.8221
year 3	23.50	15.46	12.83	10.00				0.1124	5.9845
voltinism:	1.0	1.5	2.0	2.5	3.0				
	(N=11)	(N=2)	(N=2)	(N=3)	(N=11)				
year 0	10.50	13.50	3.50	16.17	21.55			0.0097	13.3427
year 1	17.23	18.50	16.00	8.50	13.73			0.5392	3.1138
year 2	17.45	23.75	16.50	14.50	10.82			0.2185	5.7547
year 3	18.50	13.00	2.00	20.17	12.82			0.0762	8.4600
univoltine species									
niche breadth:	spec	grass	gen						
	(N=4)	(N=4)	(N=3)						
year 0	3.25	6.25	9.33					0.0549	5.8030
year 1	6.25	5.50	6.33					0.9306	0.1439
year 2	5.25	6.75	6.00					0.8150	0.4091
year 3	7.75	6.50	3.00					0.1605	3.6591
family:	HES	PAP	PIE	LYC	NYM	SAT	DAN		
	(N=7)	(N=1)	(N=4)	(N=4)	(N=9)	(N=2)	(N=2)		
year 0	8.36	14.50	21.50	21.75	13.11	11.50	24.00	0.0593	12.1272
year 1	15.79	12.50	18.88	6.50	18.00	15.50	8.50	0.2947	7.2954
year 2	21.21	22.50	15.50	10.50	14.00	9.50	7.50	0.2276	8.1498
year 3	19.79	21.50	10.25	15.50	13.33	18.50	7.50	0.3918	6.2887
year after burn:	0	1	2	3	N	maximum			
					species	rank			
specialists	3.0	8.0	10.0	13.0	4	16		0.0249	9.35294
grasslands	19.3	21.3	30.5	26.9	12	48		0.1822	4.86145
generalists	21.2	18.8	18.8	15.2	9	36		0.6859	1.48448
immigrants	14.3	7.0	5.5	7.3	4	16		0.0441	8.09559

MISSOURI								P	Chi
niche breadth:	mean	mean	mean	mean	mean	mean	mean	value	Square
	rank	rank	rank	rank	rank	rank	rank		
	(N=2)	(N=5)	(N=6)	(N=3)					
Burn									
year 0	1.50	7.40	10.67	10.67				0.1091	
Hay									
year 0	3.00	8.60	8.33	12.33				0.2839	

Appendix 15. Spearman rank correlation of species groups with deviation from random distribution in each burn age class (see App. 12,13). Rank correlates positively with underrepresentation (i.e. low numbers-high rank). Coding for habitat niche breadth: 1=specialist, 2=grassland, 3=generalist, 4=immigrant/migrant. Ns=not significant.

grouping:	niche breadth		voltinism		univoltine niche breadth	
	coeffi- cient	P value	coeffi- cient	P value	coeffi- cient	P value
Upper Midwest - burn						
year 0	-0.68700	<0.01	-0.58459	<0.01	-0.76088	<0.01
year 1	0.11927	ns	0.21099	ns	0.00482	ns
year 2	0.35064	<0.06	0.36832	<0.05	-0.11558	ns
year 3	0.42532	<0.05	0.26553	ns	0.57307	ns
Missouri - burn						
year 0	-0.57138	<0.05				
Missouri - hay						
year 0	-0.45587	ns				
correlation with:			year since burn			
Upper Midwest - burn						
specialists			0.77611	<0.01	N=16	
grasslands			0.25759	ns	N=45	
generalists			-0.19372	ns	N=36	
migrants/immigrants			-0.54571	<0.05	N=16	

Appendix 16. Absolute levels in management age classes: mean observation rates (per hour) of specialist and selected other species in burn and hay age classes, using the same Mann-Whitney subsample selection to describe both burn and hay samples (if such a comparison is possible), with the added restriction that data from the Upper Midwest was restricted to Minnesota (the only state in this region where hay prairies were sampled).

species:	Pawnee			Pawnee			Dakota			Arogos		
	<u>N</u>	<u>mean</u>		<u>N</u>	<u>mean</u>		<u>N</u>	<u>mean</u>		<u>N</u>	<u>mean</u>	
	<u>units</u>	<u>rate±sd</u>		<u>units</u>	<u>rate±sd</u>		<u>units</u>	<u>rate±sd</u>		<u>units</u>	<u>rate±sd</u>	
Minnesota												
year:	1992			1993			1992-1993			1990-1992		
burned												
year 0	0	15.04± 15.54		3	6.25± 10.83		19	6.35± 12.73		22	0.59± 1.89	
year 1				4	14.22± 11.97		17	11.41± 17.75		13	0.95± 2.05	
year 2							4	1.14± 2.29		10	0.31± 0.96	
year 3							4	2.37± 4.74		1	5.33± 0.00	
year 4							2	1.30± 1.84		-		
year 5+							-			9	6.53± 6.75	
hayed												
year 0	2	149.74± 58.22		2	20.43± 20.61		1	18.00± 0.00		1	0.00± 0.00	
year 1							2	51.96± 0.76				
Missouri												
year:										1992		
burned												
year 0										4	0.24± 0.48	
year 1										4	4.44± 3.78	
hayed												
year 0										7	3.01± 5.18	
year 1										4	7.64± 10.25	
species:	Arogos			Regal			Poweshiek			Poweshiek		
	<u>N</u>	<u>mean</u>		<u>N</u>	<u>mean</u>		<u>N</u>	<u>mean</u>		<u>N</u>	<u>mean</u>	
	<u>units</u>	<u>rate±sd</u>		<u>units</u>	<u>rate±sd</u>		<u>units</u>	<u>rate±sd</u>		<u>units</u>	<u>rate±sd</u>	
Minnesota												
year:				1990-1993			1992			1993		
burned												
year 0				19	16.58± 16.72		9	0.42± 1.25		22	0.22± 0.72	
year 1				11	19.44± 22.74		8	21.27± 37.53		20	0.23± 1.03	
year 2				5	44.84± 25.07		7	36.43± 44.77		12	26.59± 47.62	
year 3				2	48.28± 25.18		2	33.85± 31.32		13	11.05± 27.92	
year 4				1	42.16± 0.00					2	3.91± 5.53	
year 5+				8	55.53± 40.18							
hayed												
year 0				4	29.79± 21.72							
year 1				2	125.00± 7.07							
Missouri												
year:												
burned												
year 0	9	0.00± 0.00		13	2.52± 4.97							
year 1	3	0.00± 0.00		7	15.91± 15.85							
hayed												
year 0	32	0.50± 1.42		39	71.68± 75.11							
year 1	19	0.87± 2.10		23	66.53± 60.17							
hayed - private (annually hayed)												
year 0				7	48.39± 48.59							

Appendix 16. continued.

species:	Ottoe Wisconsin-Illinois	Leonard's Wisconsin-Illinois	Gorgone Upper Midwest
	N mean units rate±sd	N mean units rate±sd	N mean units rate±sd
year:	1990-1991	1993	prairies-1990-1993
burned			
year 0	6 1.51± 1.74	5 0.00± 0.00	4 4/1.47= 2.73/hr
year 1	12 18.98± 19.23	4 10.00± 20.00	5 7/0.70=10.00/hr
year 2	11 14.40± 18.96	4 0.00± 0.00	1 1/0.18= 5.58/hr
year 3	4 18.42± 16.36	2 36.00± 50.91	2 2/0.41= 4.85/hr
year 4	-	2 18.09± 10.15	-
year 5+	10 18.90± 35.05	6 10.35± 24.34	4 7/2.19= 3.20/hr
year:	1992-1993		barrens-1990-1993
burned			
year 0	5 6.50± 10.12		-
year 1	12 3.63± 6.75		1 1/0.34= 2.94/hr
year 2	16 17.05± 29.53		1 1/0.26= 3.85/hr
year 3	8 21.53± 24.78		-
year 4	5 5.09± 7.48		-
year 5+	12 0.32± 0.86		3 7/0.88= 7.95/hr
year 15+			12 110/6.24=17.63/hr

species:	Great Spangled	Aphrodite	Aphrodite
	N mean units rate±sd	N mean units rate±sd	N mean units rate±sd
Minnesota	1990-1993	1990, 1991, 1993	1992
burned			
year 0	52 0.54± 1.33	22 4.19± 4.80	10 1.52± 2.88
year 1	42 0.81± 2.09	12 7.02± 8.51	7 2.99± 3.09
year 2	25 1.96± 3.17	5 10.78± 16.97	9 15.30± 21.72
year 3	19 1.37± 3.52	1 3.48± 0.00	1 7.62± 0.00
year 4	3 0.00± 0.00	1 6.49± 0.00	-
year 5	7 1.07± 1.91	7 12.62± 14.83	3 1.82± 3.15
hayed			
year 0	7 0.00± 0.00	1 4.62± 0.00	3 1.82± 3.15
year 1	9 0.00± 0.00	2 66.16± 1.64	
Missouri	1992-1993		
burned			
year 0	18 0.35± 1.02		
year 1	10 0.00± 0.00		
hayed			
year 0	44 0.38± 1.84		
year 1	26 0.55± 1.55		

Appendix 16. continued.

species:	Monarch - early	Monarch - early	Monarch - early
	N mean units rate±sd	N mean units rate±sd	N mean units rate±sd
Minnesota	1990-1991	1992	1993
burned			
year 0	17 9.09± 6.00	6 0.74± 1.81	22 0.78± 3.10
year 1	5 13.28± 9.49	9 8.55± 11.13	20 0.84± 2.25
year 2	1 19.32± 0.00	8 8.02± 13.32	12 0.65± 2.23
year 3	-	1 8.00± 0.00	13 0.00± 0.00
year 4	-	-	2 0.00± 0.00
year 5	-	-	2 0.00± 0.00
hayed			
year 0	-	-	-
year 1	-	-	2 0.00± 0.00
Missouri	1992	1993	
burned			
year 0	7 8.54± 13.77	11 6.42± 11.85	
year 1	6 13.95± 13.16	4 12.32± 13.37	
hayed			
year 0	7 19.60± 18.90	37 3.16± 5.22	
year 1	4 4.01± 6.35	22 0.48± 1.39	
species:	Monarch - late	Monarch - late	
	N mean units rate±sd	N mean units rate±sd	
Minnesota	1991	1992-1993	
burned			
year 0	7 29.77± 40.30	17 19.41± 21.28	
year 1	5 2.12± 4.75	12 18.11± 20.66	
year 2	1 3.38± 0.00	11 53.00± 61.68	
year 3	-	8 28.47± 39.19	
year 4	-	1 16.23± 0.00	
year 5	2 0.00± 0.00	-	
hayed			
year 0	-	4 64.36± 76.57	
year 1	-	4 48.89± 61.62	

Appendix 17. Observations of Regal Fritillaries at selected sites 1988-93. The maximum/unit summed takes into account the sex (if known) for all observations. E.g., on 15 Jul 92, the 8 individuals observed in 3S (out) were all males, while on the return, 6 males and 1 female were observed in 3S, so that a total of 9 different individuals (8 males and 1 female) were observed in this unit that day. Muralt burned units: 2 in 1988, 1 in 1989, 3S & 4 1991, 3N return & 2 1992. Units are mapped in Swengel (1992a,b).

Site	Unit	07-				30-				29- 11-				24-			
		28 19	02 08	30	04 23	08	03 20	31 20	27	30 15	21 11	25 01	30 13	18 21	11 25		
		Jn J1	Ag Ag	Ag	J1 J1	Ag	J1 J1	Ag	Ag	Jn J1	J1 Ag	Ag Sp	Jn J1	J1 Ag	Ag		
Muralt	1	88 88	89 89	89	90 90	90	91 91	91 91	91	92 92	92 92	92	93 93	93 93	93		
	2	9 1	0		2 0	4	0 0	1	0	0 0	0	0	0 0	0	0	0	1
	3N	0 0	0		0 0	0	0 0	0	0	0 0	0	0	0 0	0	0	0	0
	3S	0 0	0		0 0	0	0 0	0	0	0 0	0	0	0 0	0	0	0	0
	4	0 0	0		0 0	0	0 0	0	0	0 0	0	0	0 0	0	0	0	0
	4	0 0	0		0 0	0	0 0	0	0	0 0	0	0	0 0	0	0	0	0
	3S	0 0	0		0 0	0	0 0	0	0	0 0	0	0	0 0	0	0	0	0
	3N	0 0	0		0 0	0	0 0	0	0	0 0	0	0	0 0	0	0	0	0
	2	0 0	0		0 0	0	0 0	0	0	0 0	0	0	0 0	0	0	0	0
	1	0 0	0		0 0	0	0 0	0	0	0 0	0	0	0 0	0	0	0	0
Total Contacts		19 33	48	24	8	2	1	2	17	3	3	0	7	33	2	2	
Maximum/unit summed		13 29	38	15	7	2	1	2	11	2	3	0	7	24	2	2	
Oliver		0	0	0	4	1	0	0	0	0	0	1	0	0	0	0	
Machusa	1	0	0		6	3	8	3	0	3	13	0					
	2	0	2		0	0	0	0	0	1	0	0					
	3						0	0	0	0	0	0					
	2		1		1	0	0	0	0	0	2	0					
	1		0		0	0	1	1	2	0	8	0					
	4						0	0	0	0	3	0					
	5						0	0	0	0	0	0					
	6						0										
Total contacts		0	3		7	3	9	4	2	4	26	0					
Thomson	1		1	0		0	0	0	0	0	0	0					
	2		0	1		0	0	0	0	0	0	0					
	3					0	0	0	0	1	0	0					
	4					0	0	0	0	0	0	0					
	3					0	0	0	0	0	0	0					
	2					0	0	0	0	0	0	0					
	1					0	0	0	0	0	0	0					
Total contacts		1	1		0	0	0	0	1	0	0	1					
Thomson	3					1	3	0	0	0	0	0					
(Greater)	4					0	2	3	0	1	2	0					
	8					0	1	0	0	0	0	0					
	5					3	4	0	0	0	1	0					
	8					0	2	0	0	0	0	0					
	6					6	8	10	0	2	12	8					
	7					2	1	0	0	0	0	0					
Total contacts						12	21	13	0	3	12	11					
Thousand's	1	0			0	0	0	0	0	0	0	0					
Thousand's	11	0			0	0	0	0	0	0	0	0					
	2	0			0	0	0	0	0	0	0	1					
	2	0			0	0	0	0	0	0	0	1					
	1	0			0	0	0	0	0	0	0	1					
Total contacts		0			0	0	0	0	0	0	0	3					

Appendix 18. Observations of Ottoo Skippers at selected sites 1988-93. * = "very many." Units are mapped in Swengel (1992a,b).

Site	Unit	28-				07-				30-				29- 11-				20-			
		29 19	03 15	25 02	07	04 23	08	03 20	31	01 15	21 03	12	30 13	18 21	11						
		Jn J1	J1 J1	J1 Ag	Ag	J1 J1	Ag	J1 J1	Ag	J1 J1	Ag	Ag	Jn J1	J1 Ag	Ag						
Dewey	1	88 88	89 89	89 89	89	90 90	90	91 91	91	92 92	92	92	93 93	93	93						
	2	0 0	0	0	0	0	0	0	0	0	0	0	0	0	0						
	3	0 0	0	0	0	0	0	0	0	0	0	0	0	0	0						
	4	0 0	0	0	0	0	0	0	0	0	0	0	0	0	0						
	3	0 0	0	0	0	0	0	0	0	0	0	0	0	0	0						
	2	0 0	0	0	0	0	0	0	0	0	0	0	0	0	0						
	1	0 0	0	0	0	0	0	0	0	0	0	0	0	0	0						
Maximum/unit sum		6	6		1		9	0	36	3		26	0								
Muralt	1	5	32			1	20	3	20	0	0	2	9	0	0	6	2				
	2					1	0	0	1	0	0	0	0	0	0	0	0				
	3N					0	12	3	1	0	0	0	0	0	0	0	0				
	3S					0	0	0	0	0	0	1	0	0	0	0	0				
	4					2	0	5	0	0	0	0	0	0	0	0	1				
	4					0	0	0	0	0	0	0	0	0	0	0	1				
	3S					0	11	5	1	0	0	0	2	0	0	1	0				
	3N					5	1	0	0	5	0	0	5	0	0	3	0				
	2					0	3	2	5	0	0	0	0	0	0	0	1				
	1					0	0	0	2	0	0	0	5	0	0	0	0				
Total Cont		5	32		*	4	51	18	35	1	0	3	21	0		11	4				
Oliver		0				0	14	2	1	0	1	0	2	0		0	0				
Rush Creek							13	10	2							13					
Spring	1					0	1	0		0	0	0	0	0		0					
Green	6					2	1	1		0	0	0	0	0		0					
	8					0	2	0		0	0	0	0	0		0					
	9					0	0	8		0	0	0	0	0		0					
	7a					0	5	2		0	0	0	0	0		0					
	7b	3				3	57	1		0	0	0	0	0		0					
	7c					0	14	0		0	0	0	0	0		0					
	7d					0	0	0		0	0	0	0	0		0					
	3/2					0	0	0		0	0	0	0	0		0					
	5					0	0	0		0	0	0	0	0		0					
Total cont		3				5	80	12		0	0	0	0	0		1					

Appendix 19. Prioritization of study sites within each state by maximum single-day survey total (Appendices 5-8), diversity, and rarity of specialist species present: High priority, Medium priority, Other priority (not necessarily low priority, since a low maximum single-day survey total may reflect survey conditions rather than low population size or potential): If three orders of magnitude were observed for a species' survey totals, H=100, M=10, O=1; if only two orders of magnitude observed, H=10, O=1-9. Underlining indicates the highest priority sites, based on how many sites we've found them at and my review of their status and trends in other data.

State, site name	POV	OTT	LEO	PAV	DAK	BBA	RBG	GOR
Illinois								
Ayers Sand Barren								
Bicentennial								
Harlem Hill								
Macbush								
Iowa								
Cavlet								
Crossman								
Frede Haften								
Hayden								
Kaleov								
Stinson								
Minnesota								
Andubon								
Bicentennial								
Bicentennial May								
Blazing Star								
Blue Mound SP								
Bluestem								
Chilpewa								
Clinton								
Pokhom								
Frenchman's Bluff								
Hole-in-the-Mountain								
Kettledrummer								
Lundblad								
Ordway								
Pembina Trail								
Pipestone NM								
Prairie Coteau								
Prairie Marshes								
Seven Sisters								
Staffanson								
Swift County								
Town Hall								
Twid Valley								
Western North								
Western South								

Native Conservancy property west of Appleton, preserves name unknown.

Appendix 19. continued.

State, site name	POV	OTT	LEO	PAV	DAK	BBA	RBG	GOR
Missouri								
Missouri								
Buffalo Vallow								
Bushwhacker								
Cattin								
Clear Creek								
Comstock								
Diamond Grove								
Dorrie Creek								
Dorsett Hill								
Gama Grass								
Gay Feather								
Golden								
Hunkah								
Little Oeage								
Ko-Ko								
Konekay								
Ko-Ko-1								
Kon-Shon								
Mount Vernon								
Miamthe								
Oeage								
Pabushka								
Penn-Sylvania								
Prairie SP								
Red Wing								
Ripgut								
Risch								
Sky								
Taberville								
Treaty Line								
Tzi-Sho								
Vab-Kon-Tah								
Vab-Sha-She								
Vicconeta								
Black Barth								
Blue River Barren								
Crawford County								
Dewey								
Dike 17								
Kutale								
Oliver								
Rueb Creek								
Schuckebier								
Spring Green								
Spring Green West								
Thomson-Crester								
Thomson								
Thousand's II								

Appendix 20. Heritage inventory ranks and federal and state statuses (known to me) and my proposed rankings and statuses for selected prairie-specialist butterflies. Underlining indicates which part of a double rank the species' status is closer to.

CUR/CURR=current; PR/PROP=proposed

Heritage ranks:

G1=Critically imperiled globally because of extreme rarity (5 or fewer occurrences or very few remaining individuals or acres) or because of some factor(s) making it especially vulnerable to extinction.

G2=Imperiled globally because of rarity (6 to 20 occurrences or few remaining individuals or acres) or because of some factor(s) making it very vulnerable to extinction throughout its range.

G3=Very rare and local throughout range or found locally (even abundantly at some of its locations) in a restricted range (e.g., a single western state, a physiographic region in the East) or because of other factors making it vulnerable to extinction throughout its range; in terms of occurrences, in the range of 21 to 100.

S1=Critically imperiled in state because of extreme rarity (5 or fewer occurrences or very few remaining individuals or acres) or because of some factor(s) making it especially vulnerable to extirpation from the state.

S2=Imperiled in state because of rarity (6 to 20 occurrences or few remaining individuals or acres) or because of some factor(s) making it very vulnerable to extirpation from the state.

S3=Rare or uncommon in state (on the order of 21 to 100 occurrences).

SH=Of historical occurrence in the state, perhaps having not been verified in the past 20 years, and suspected to be still extant.

SR=Reported for state without persuasive documentation to accept or reject the report
(usually either very recent or old obscure reports).

SX=Apparently extirpated from state.

0 =No status designated

Statuses:

A =needs to be assessed

C2=category 2 (federal candidate species)

E =endangered

SC=special concern (watch or candidate species at state level)

T = threatened

---POWESHIEK--- ---OTTOE--- ---DAKOTA--- ---AROGOS--- ---REGAL---

RANK	STATUS	RANK	STATUS	RANK	STATUS	RANK	STATUS	RANK	STATUS
STATE CURR PROP	CUR PR	CURR PROP	CUR PR	CURR PROP	CUR PR	CURR PROP	CUR PR	CURR PROP	CUR PR

Range G2G3 G2G3 0 T/E G3? ? 0 A G2 C2 ? G2G3? 0 C2 G3 C2 T

[illegible]

Appendix 21. History of contact between Native Americans and Whites (Europeans) in Wisconsin, based on Jackson (1961), Nesbit (1973), Smith (1973), Current (1977), and Spencer et al. (1977).

about

1600 before and at beginning of direct contact, about 20,000 Natives in Wisconsin:

1. Long-standing residents (Menominee, Winnebago)
2. Displaced/immigrating tribes from Northeast and Southeast: (Chippewa [Ojibwa], Fox and Sauk, Kickapoo, Oneida, Potawatomi, Stockbridge, and others, at least temporarily)
3. Santee-Dakota: sometimes ranged into western Wisconsin

Warfare among tribes ensured

1634 Nicolet probably canoed from Lake Michigan into Wisconsin territory

1673 Jolliet and Marquette traversed Wisconsin by boat via the Fox-Wisconsin

French voyageurs trapped, establishing trading posts in garrisons.

British agents controlled trade.

Missionaries arrived.

Natives established economic relationships with French and British.

Natives cooperated and conflicted among themselves and Europeans.

1763 Treaty of Paris: Wisconsin transferred from French to British

1783 Treaty of Paris: Wisconsin transferred from British to Americans (on paper)

1815 Treaty of Ghent: Wisconsin transferred from British to Americans (in fact)

1815 American forts start being established in Wisconsin

Most white residents in Wisconsin were men engaged in fur trade

1816 White settlement began

Program of Native removal to reservations west of Mississippi River

Chippewa and Menominee succeeded in getting reservations in the state

Natives resisted, were forcibly removed, and some stragglers returned

1825 Probable year of extirpation of beaver from southern third of state

1832 Black Hawk War (Sauk and Fox resistance)

1832 White settlement accelerated

1832 Extirpation of bison in Wisconsin

1836 Wisconsin became a territory

1848 Wisconsin became a state

1860 Near extirpation of white-tailed deer from southern quarter of state

1870 Probable year of extirpation of porcupine from southern half of state

1875 Probable year of extirpation of elk in Wisconsin

1890 Probable year of extirpation of beaver from central third of state

1900 Near extirpation of beaver in Wisconsin

1921 Extirpation of moose in Wisconsin

Appendix 22. Food and economic and habitat impacts of selected prairie fauna, based on Hall and Kelson (1959), Jackson (1961), and Burt and Grossenheider (1976).

Richardson's Ground Squirrel (Spermophilus richardsonii)

Food: green vegetation, also meat

Economic impacts: may damage green crops; destroys many insects

Habitat impacts:

Thirteen-lined Ground Squirrel (Spermophilus tridecemlineatus)

Food: seeds, insects, occasionally meat; omnivorous

Economic impacts: follows clearing of land for agriculture; may damage crops, eats weed seeds and harmful insects; digs up newly planted or sprouted corn; damages vegetables

Habitat impacts:

Franklin's Ground Squirrel (Spermophilus franklinii)

Food: green vegetation, seeds, insects, meat, bird eggs; 30% diet is animal matter; seeds, foliage, grasses, grains

Economic impacts: destroys some grain and eggs of ground-nesting birds, also destroys many insects; particularly fond of eating newly planted corn and other grains--also when grains are ripe; eats vegetables; burrows a nuisance but not a danger to stock

Habitat impacts:

Northern Pocket Gopher (Thomomys talpoides)

Food:

Economic impacts: overgrazed range indicated, not caused, by, this species; considered harmful in cultivated areas (consume foliage and roots; mounds hinder harvesting)

Habitat impacts: in most uncultivated areas, they are distinctly beneficial to soil formation and vegetational productivity over the years; soil-forming agents (water conservation, aeration)

Plains Pocket Gopher (Geomys bursarius)

Food: roots, tubers, green herbage and leaves around burrow

Economic impacts: considered harmful in cultivated areas (consume foliage and roots; mounds hinder harvesting); usually inhabit waste areas in VI, so does not have major bad impacts

Habitat impacts: soil-forming, (water conservation, aeration)

Beaver (Castor canadensis)

Food: bark, cambium, twigs (by felling plants up to trees 1+ ft in diameter) of willows, alders, birches, aspens, also maple; also grasses & herbs near/in water, roots of aquatic plants

Economic impacts: timber destroyed but usually low-grade; important fur animal; occasionally cause floods; meat edible; said to harm trout streams

Habitat impacts: dammed streams eventually form ponds, which in turn form montane meadows (out west); water conservation; brush clearing; maintains open habitat of low prairie

Porcupine (Erethizon dorsatum)

Food: cambium layer of certain trees (various conifers, willow, beech, maple, aspen, birch), buds, forbs, twigs, leaves, young evergreen needles; usually lives in timbered areas but also in chaparral (i.e. scrub, savanna, barrens); may be well away from forest if suitable food, e.g. willow, available; in summer, also roots, leaves, stems, nuts, fruits

Economic impacts: undoubtedly damage, even kill trees on occasion; damages buildings, communication lines, trees; meat edible; neutral in VI; may locally damage forest plantings; negligible crop damage; nuisance of damaging various objects, buildings

Habitat impacts: may damage trees

Elk (Wapiti) (Cervus canadensis)

Food: grasses, herbs, twigs, bark; grasses, sedges, herbs, many browse woody plants; grazes and browses on seasonal basis (primarily browsing in winter; mainly grazes in spring; both in summer and fall)

Economic impacts: considerable damage to vegetables, pastures, grainfields, haystacks; prize game animal

Habitat impacts:

Black-tailed (Mule) Deer (Odocoileus hemionus)

Food: mainly browse on shrubs and twigs, also graze on grasses and forbs

Economic impacts: major big game animal; considerable damage to crops, range, forest land

Habitat impacts:

White-tailed Deer (Odocoileus virginianus)

Food: browses twigs, shrubs, acorns; fungi, grass & herbs in season; primarily a browser; occasionally grazes

Economic impacts: major big game animal; considerable damage to young orchards, vegetable and grain crops

Habitat impacts: (frequently cited as damaging native plants)

Moose (Alces alces)

Food: browse conifers, leaves of deciduous trees/shrubs, often bark, also aquatic plants, grasses and sedges; browses in winter on many woody shrubs (twigs, bark, saplings); mainly aquatic vegetation in summer; primarily a browser (willow, maple, mountain ash, birch, cherry, hazelnut, balsam fir)

Economic impacts: game animal

Habitat impacts:

Caribou (Reindeer) (Rangifer tarandus)

Food: lichens; also herbs, mosses, willows, grasses; occasionally browses

Economic impacts: important game animal

Habitat impacts:

Pronghorn (Antilocapra americana)

Food: browse on brush, also graze some on grass (weeds, some grass)

Economic impacts: slight competition for rangeland; mostly feeds on forage that domestic stock don't eat; big game

Habitat impacts:

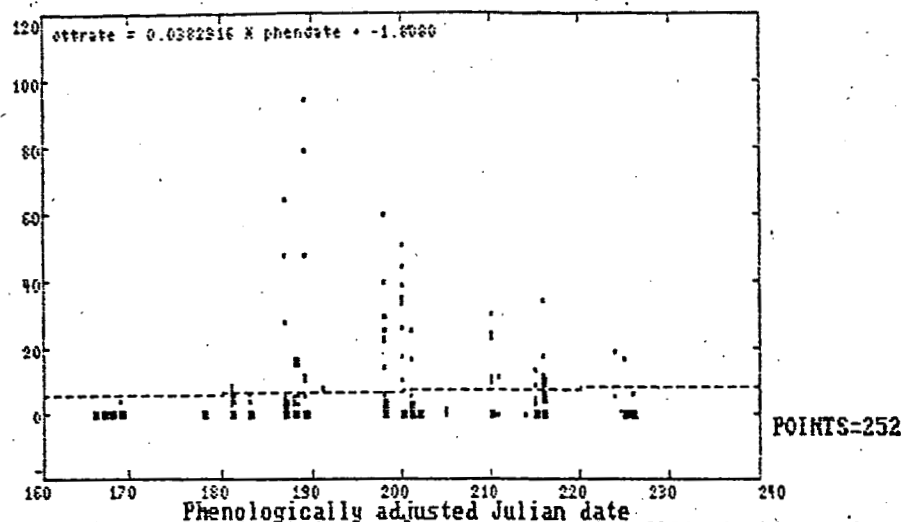
Bison (Buffalo) (Bison bison)

Food: graze on grass; occasionally browses on brush (e.g. sagebrush)

Economic impacts:

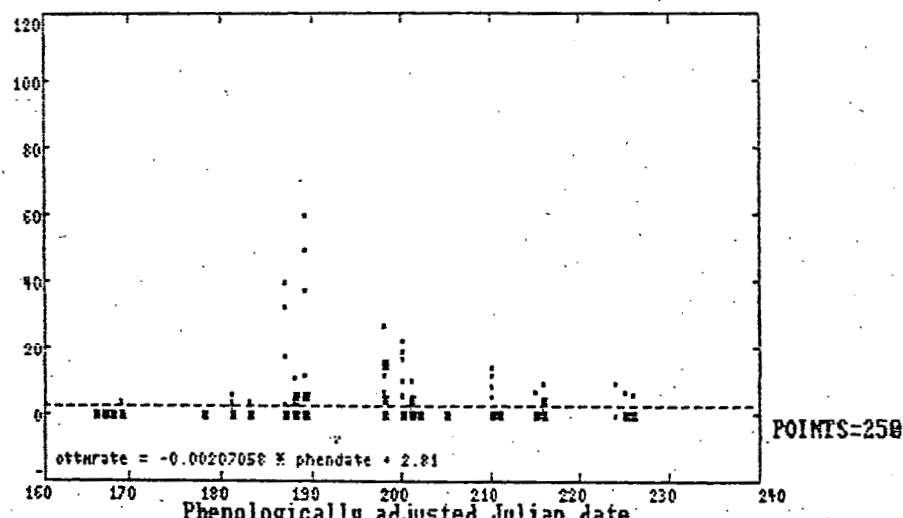
Habitat impacts: wallows

Ottoes/hour



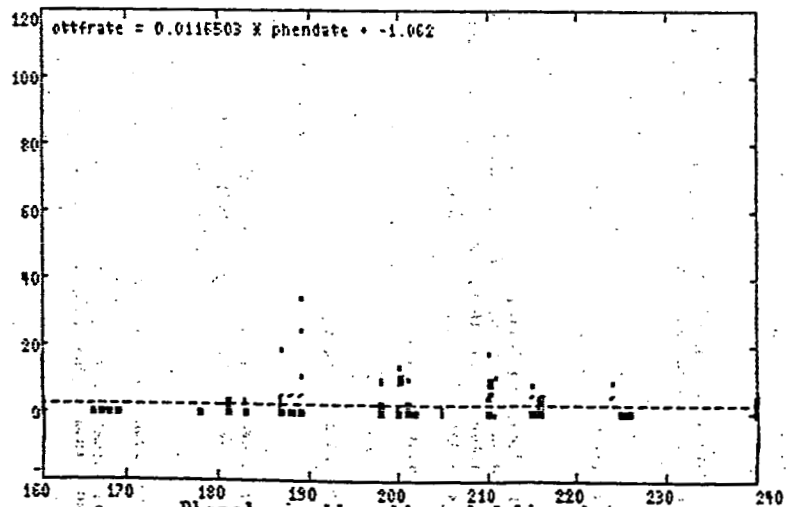
A1. Observation rates of all Ottoes per hour per unit, Illinois-Wisconsin

Male Ottoes/hour



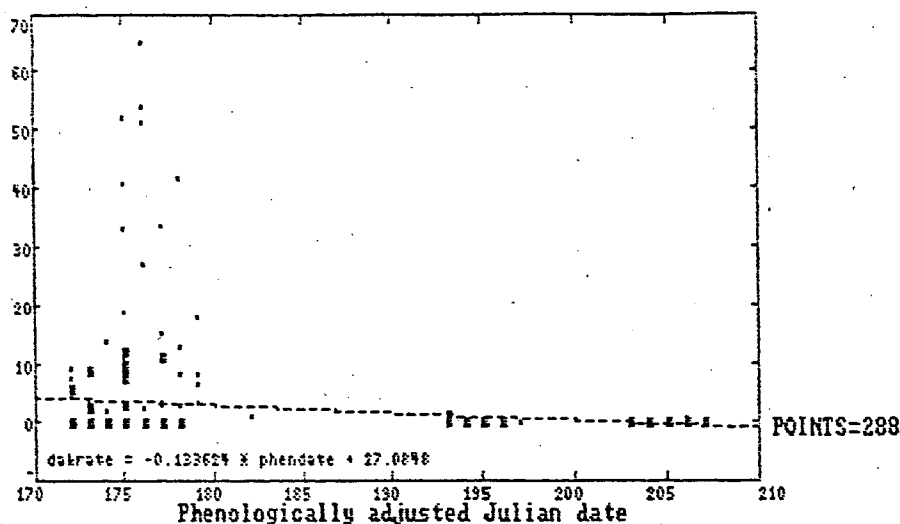
A2. Observation rates of male Ottoes per hour per unit, Illinois-Wisconsin

Female Ottoes/hour



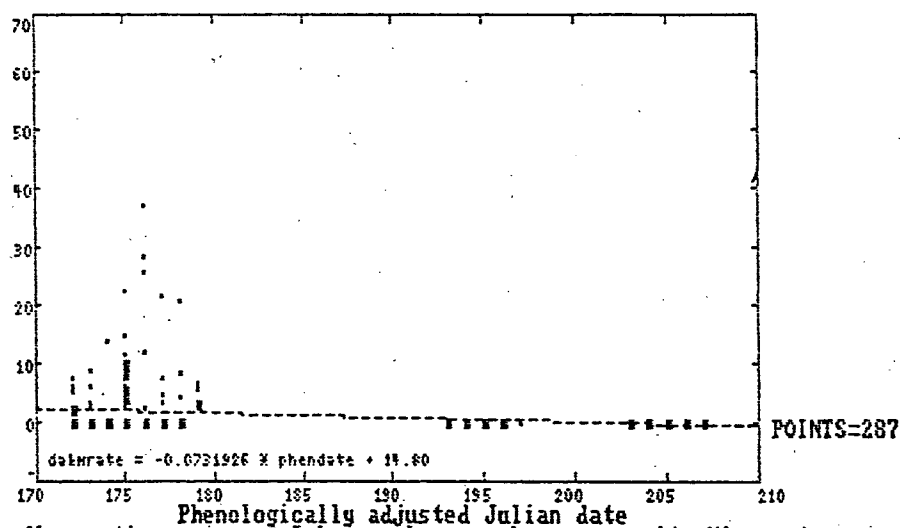
A3. Observation rates of female Ottoes per hour per unit, Illinois-Wisconsin

Dakotas/hour



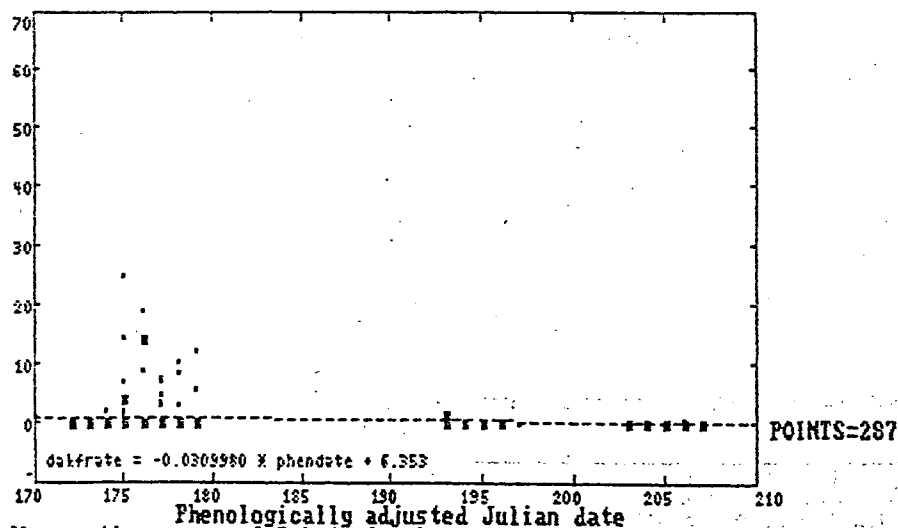
B1. Observation rates of all Dakotas per hour per unit, Minnesota

Male Dakotas/hour



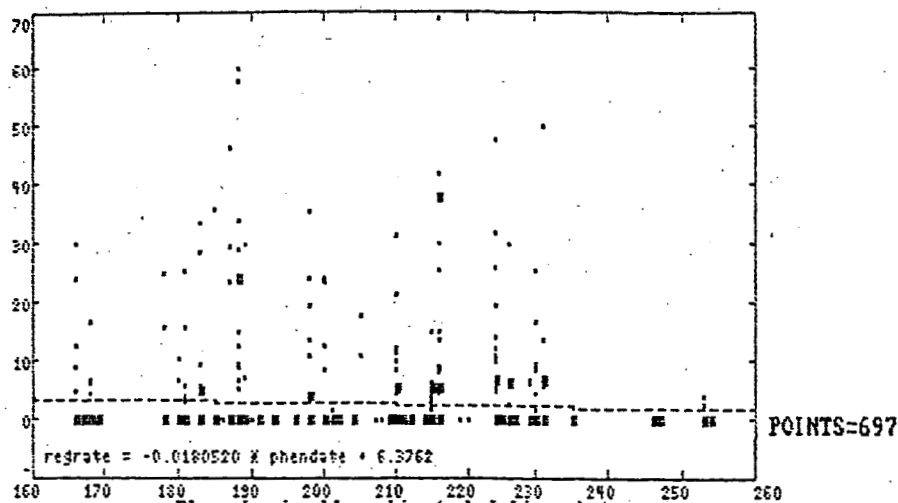
B2. Observation rates of Dakota males per hour per unit, Minnesota

Female Dakotas/hour



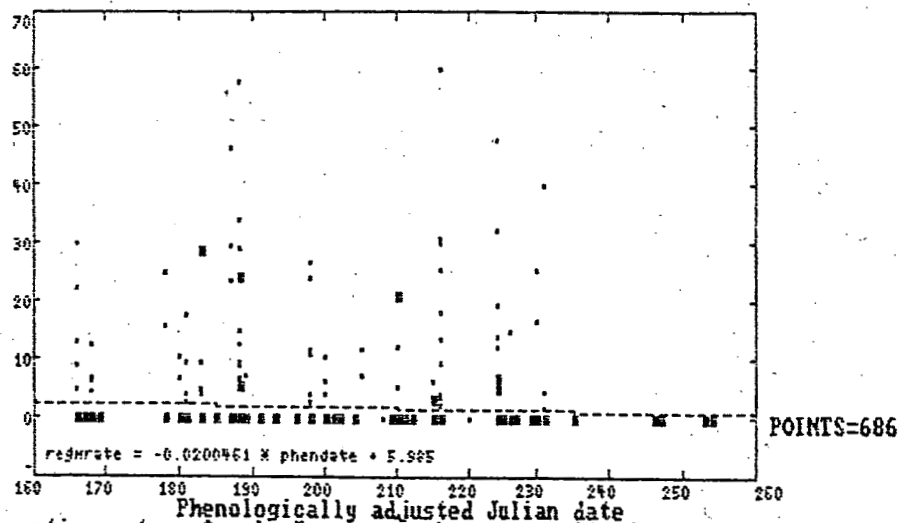
B3. Observation rates of Dakota females per hour per unit, Minnesota

Regals/hour



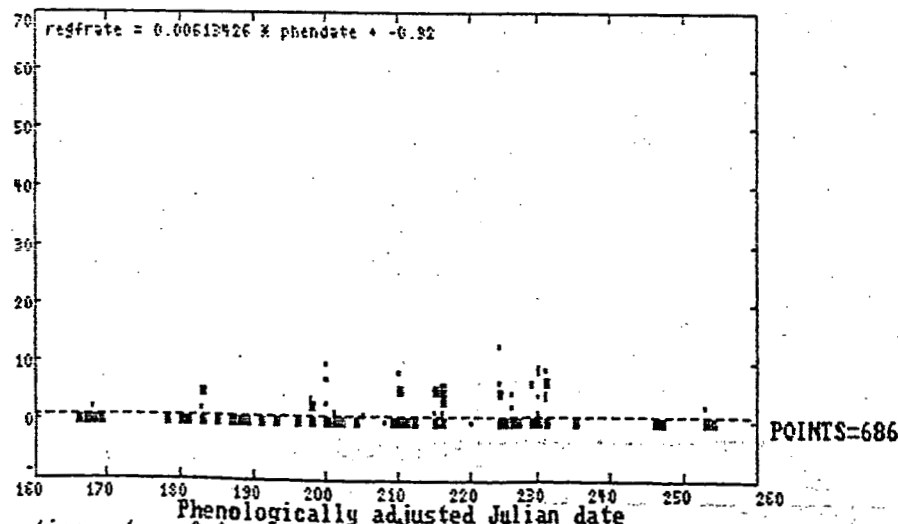
C1. Observation rates of all Regals per hour per unit, Eastern Upper Midwest

Male Regals/hour



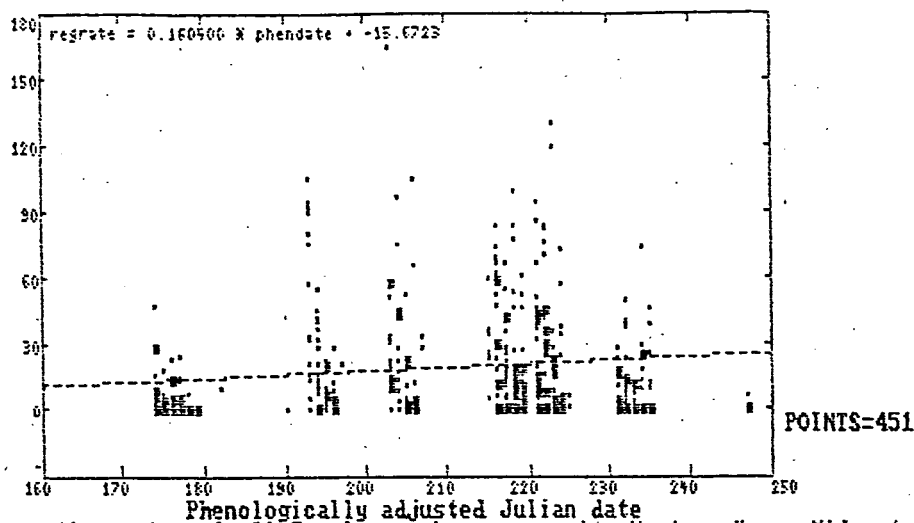
C2. Observation rates of male Regals per hour per unit, Eastern Upper Midwest

Female Regals/hour



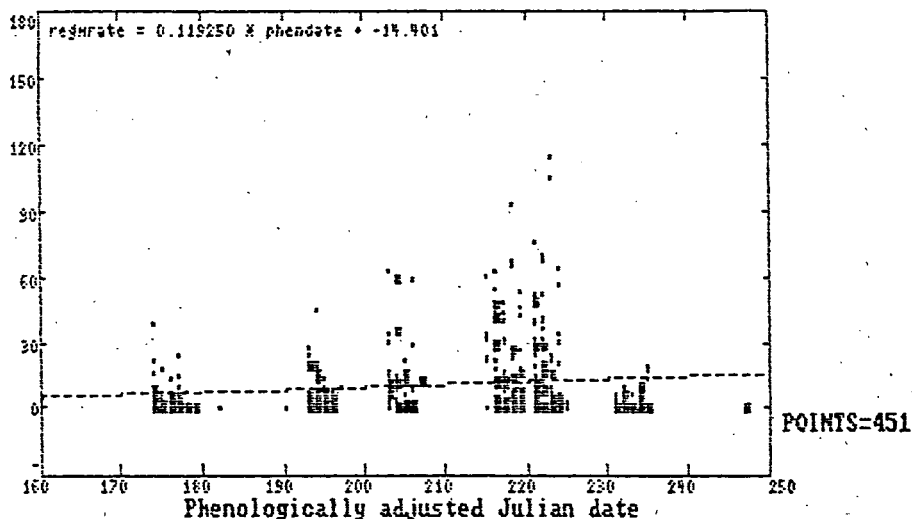
C3. Observation rates of female Regals per hour per unit, Eastern Upper Midwest

Regals/hour



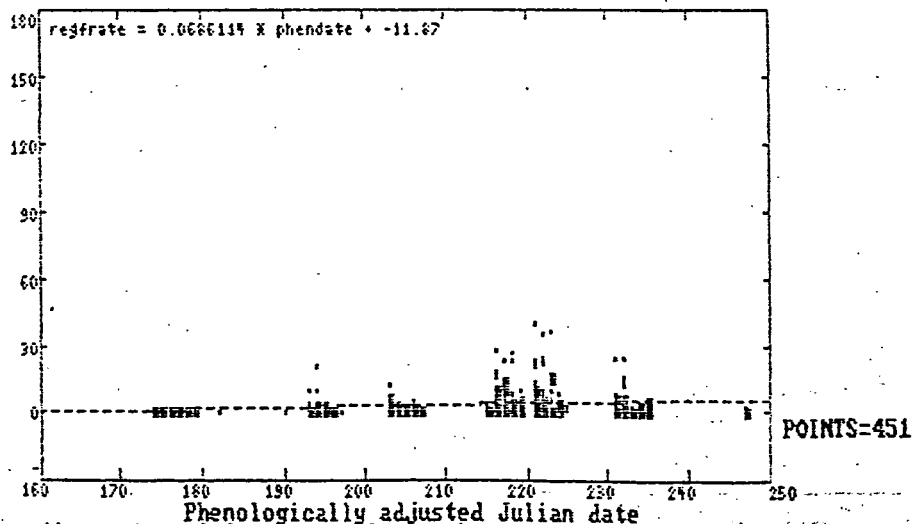
D1. Observation rates of all Regals per hour per unit, Western Upper Midwest

Male Regals/hour



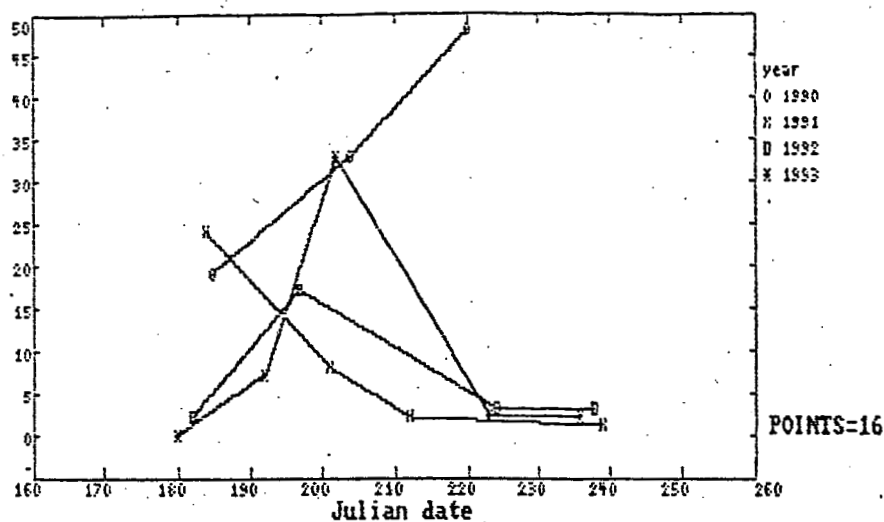
D2. Observation rates of male Regals per hour per unit, Western Upper Midwest

Female Regals/hour



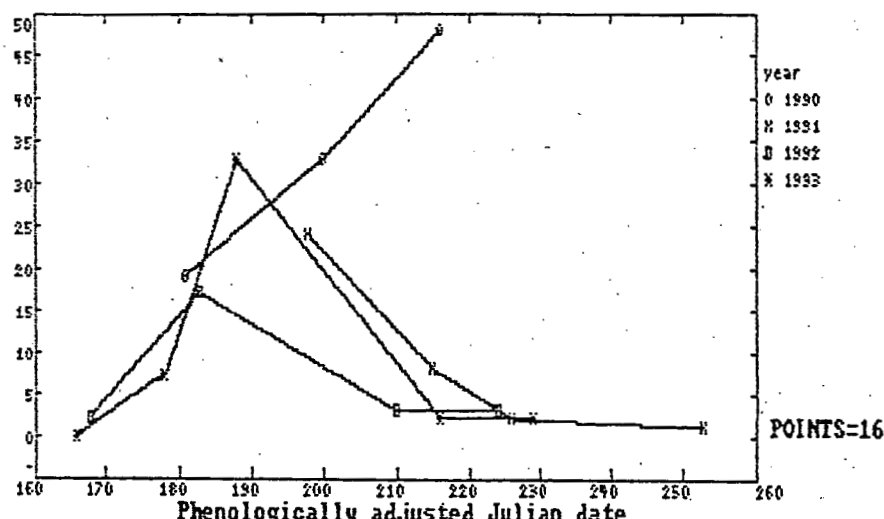
D3. Observation rates of female Regals per hour per unit, Western Upper Midwest

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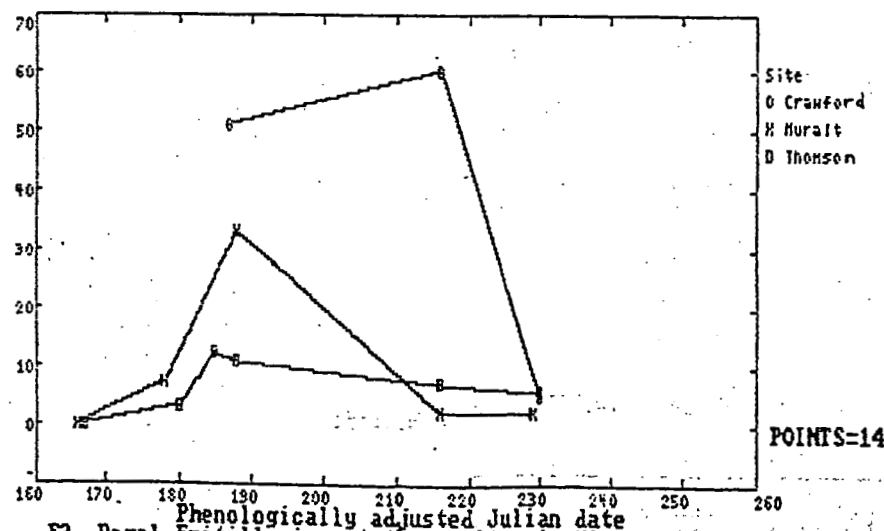
E1. Regal Fritillaries observed at Muralt Bluff, Wisconsin

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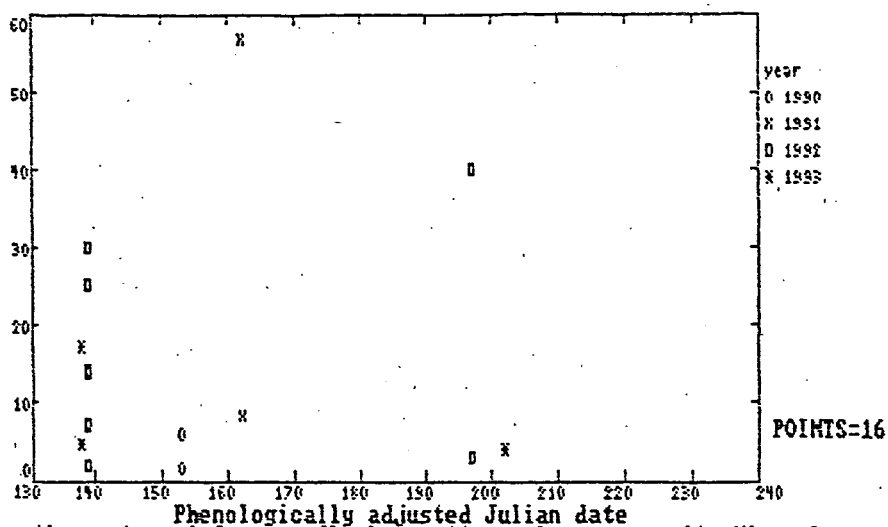
E2. Regal Fritillaries observed at Muralt Bluff, Wisconsin

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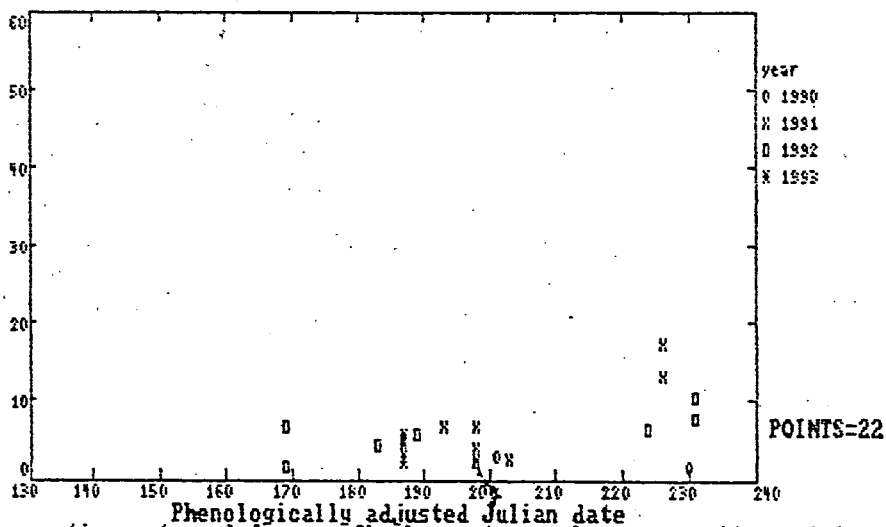
E3. Regal Fritillaries at three sites in Wisconsin 1993

Gorgones/hour

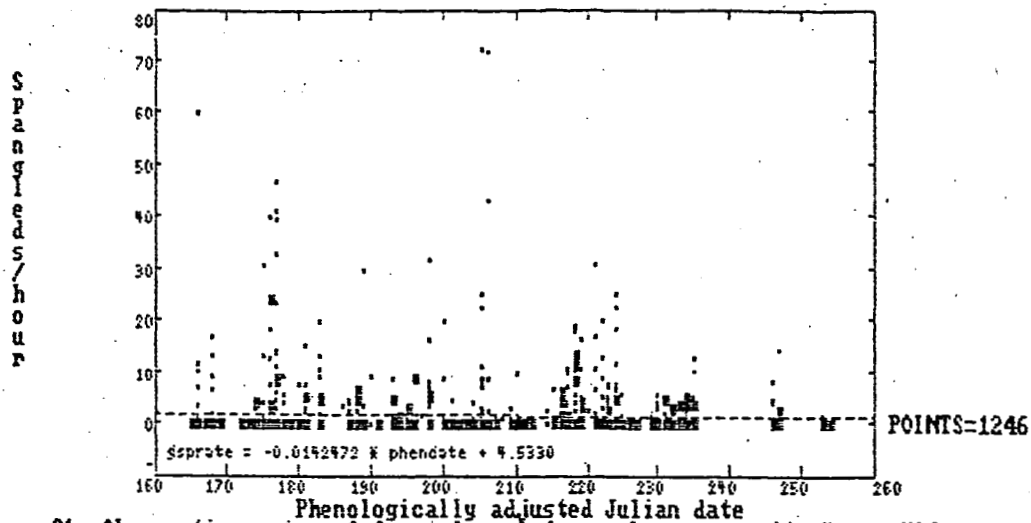


F1. Observation rates of Gorgone Checkerspots per hour per unit, Wisc. barrens

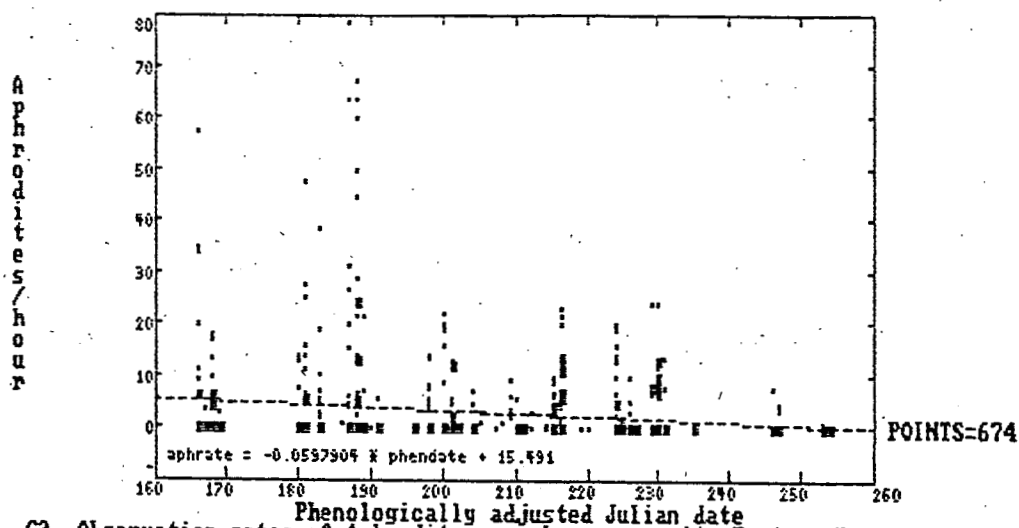
Gorgones/hour



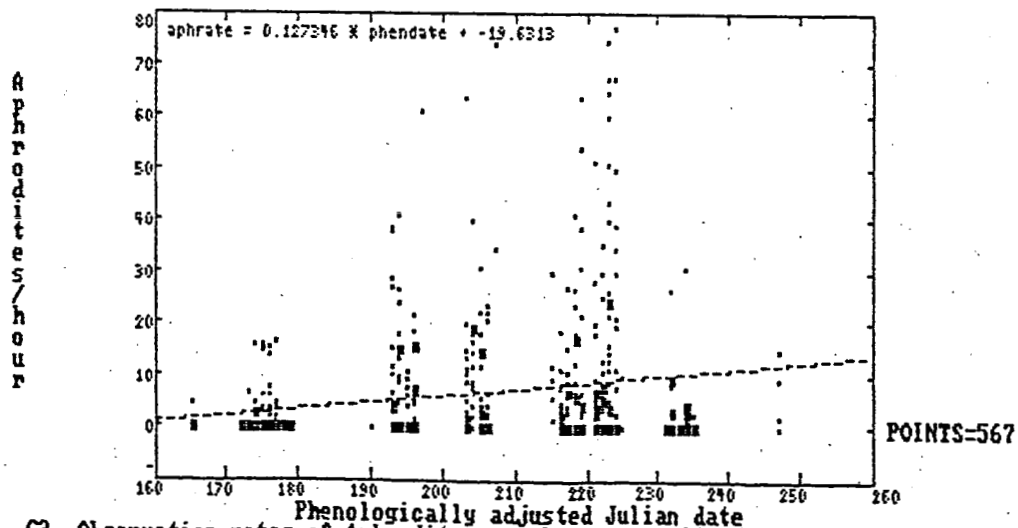
F2. Observation rates of Gorgone Checkerspots per hour per unit, prairies



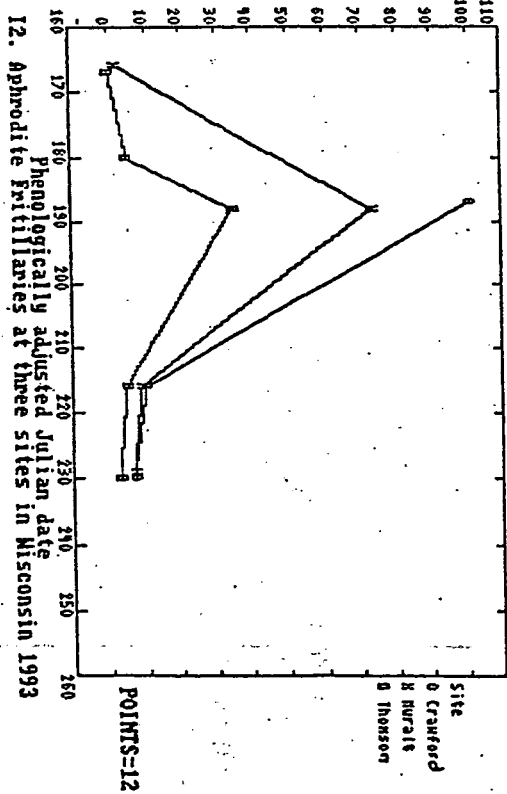
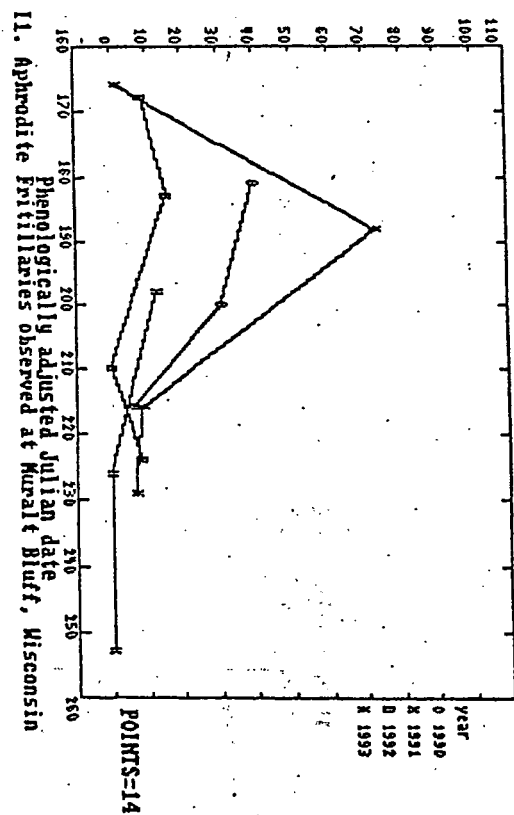
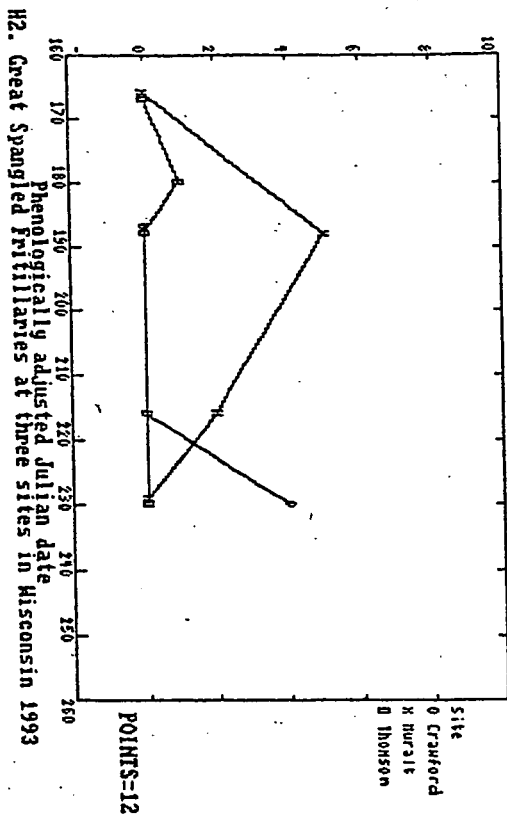
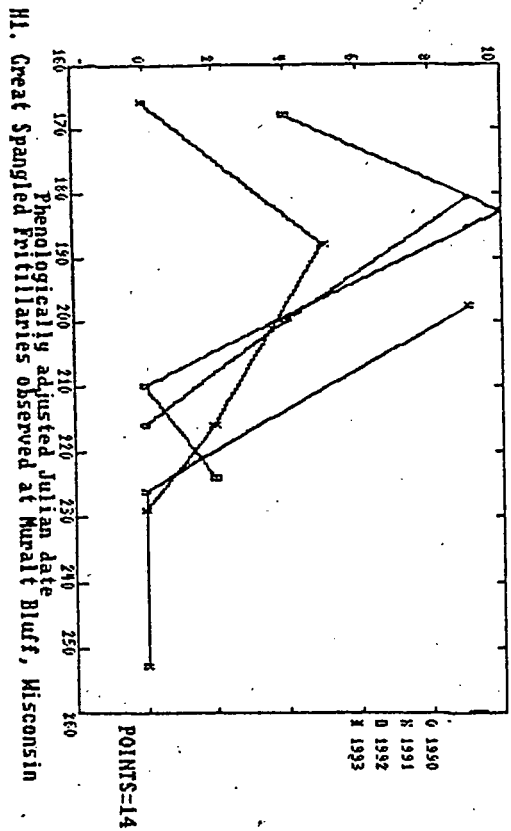
G1. Observation rates of Great Spangleds per hour per unit, Upper Midwest

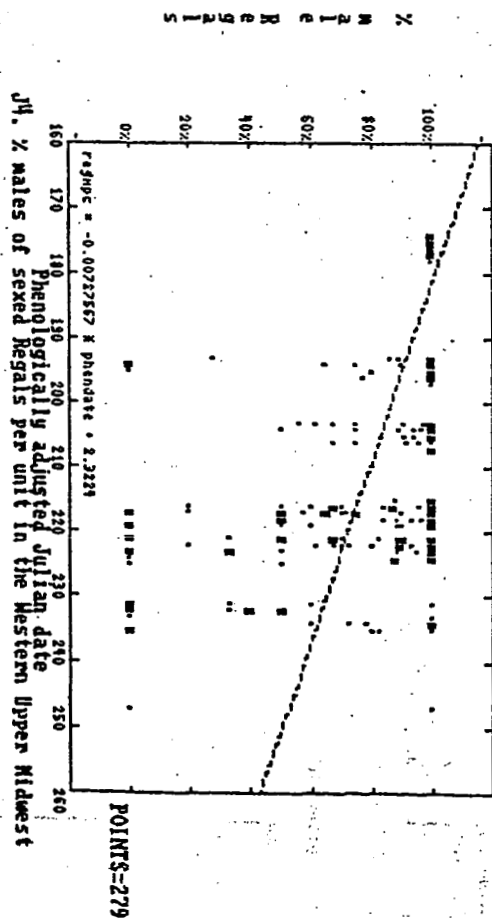
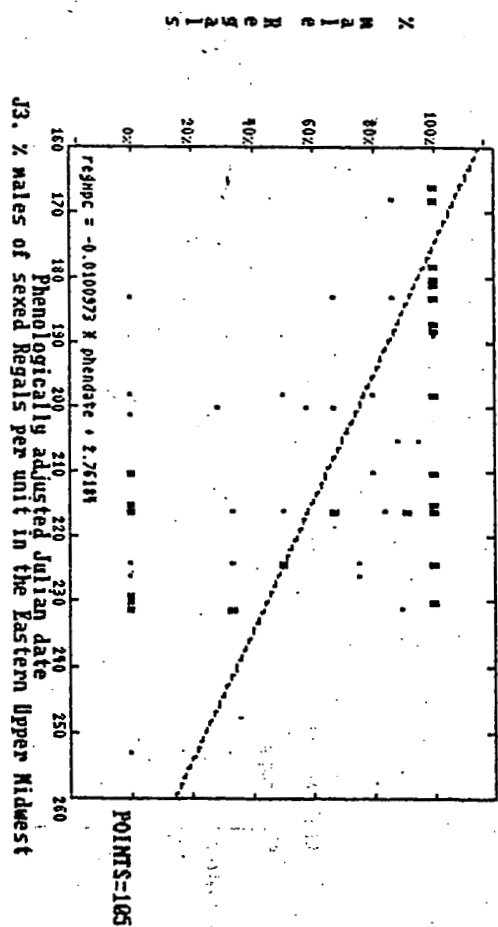
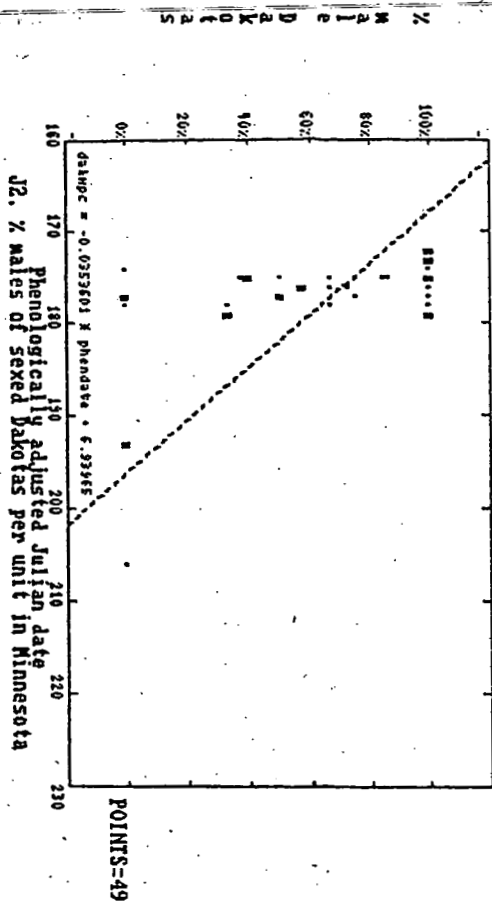
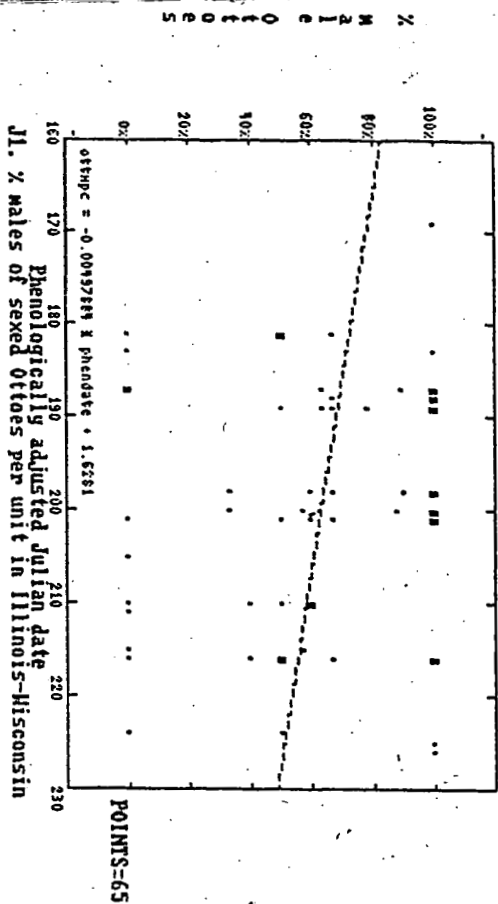


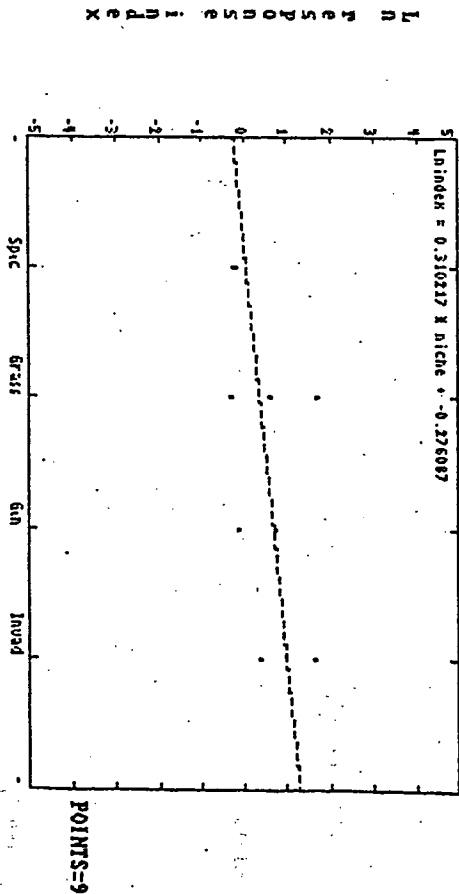
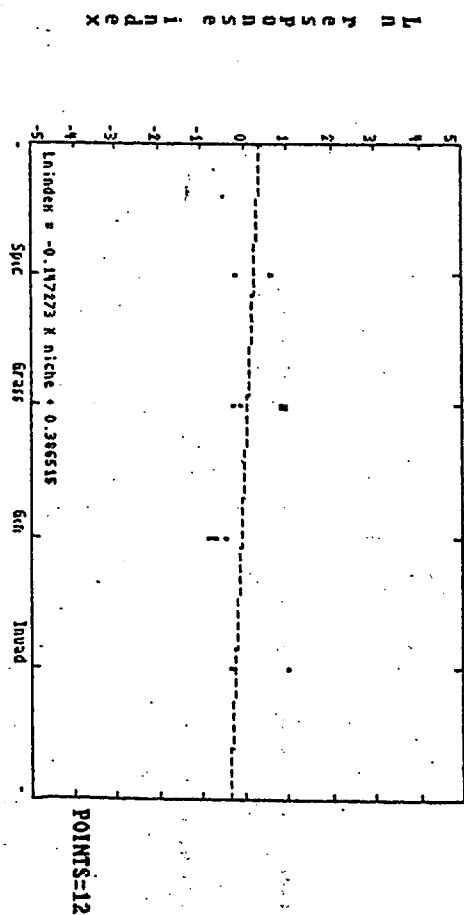
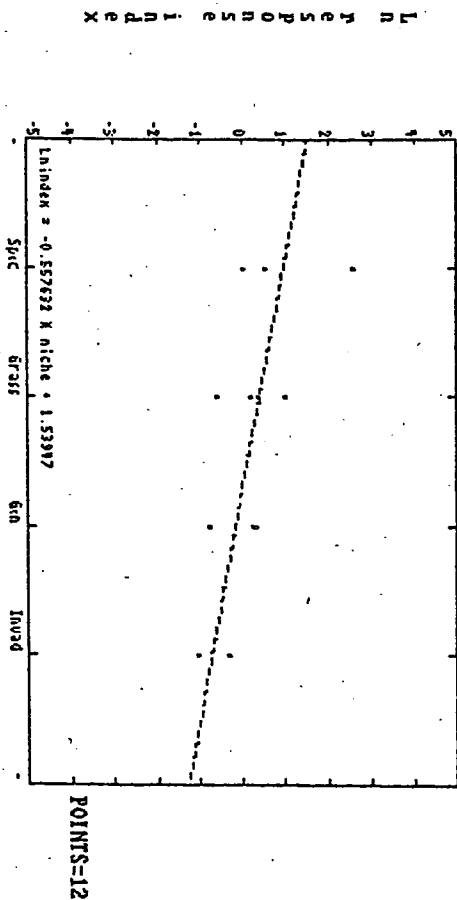
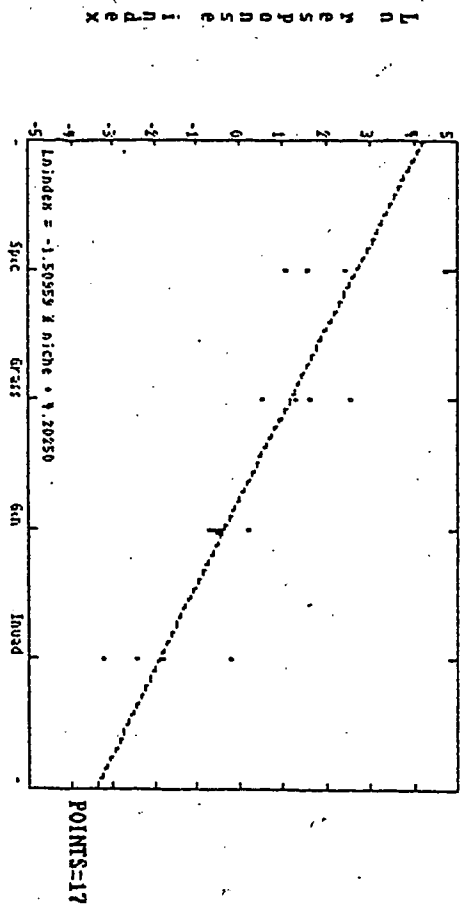
G2. Observation rates of Aphrodites per hour per unit, Eastern Upper Midwest



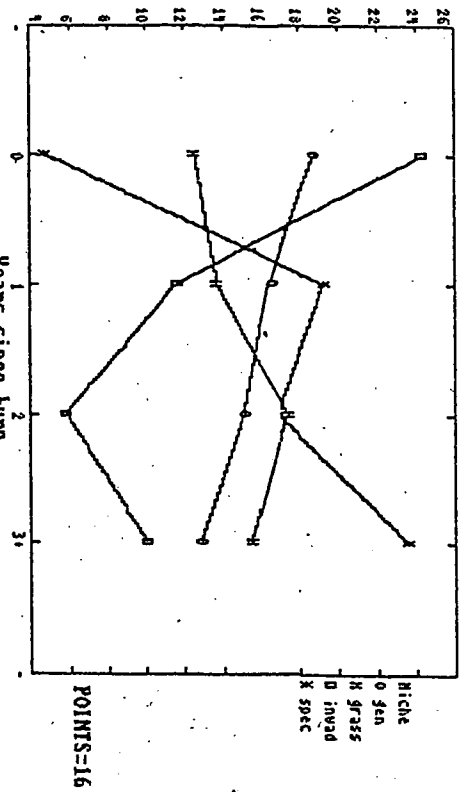
G3. Observation rates of Aphrodites per hour per unit, Western Upper Midwest



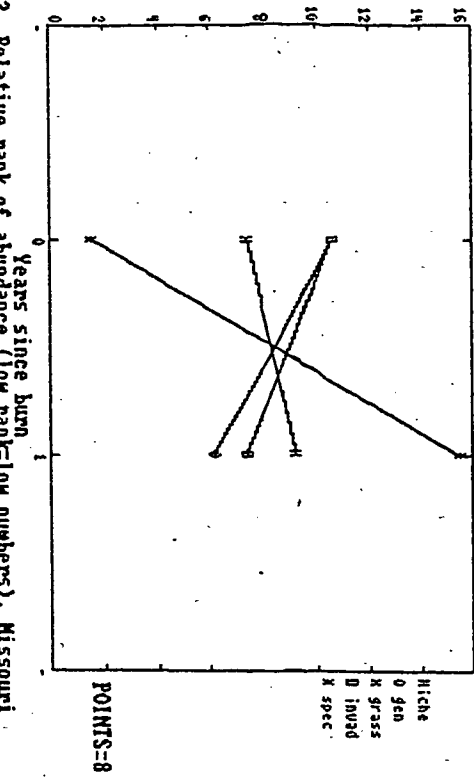




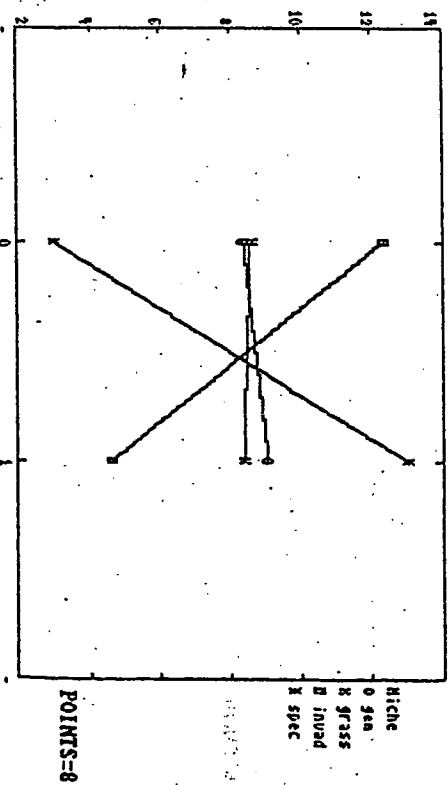
11. Relative rank of abundance (low rank=low numbers), Upper Midwest



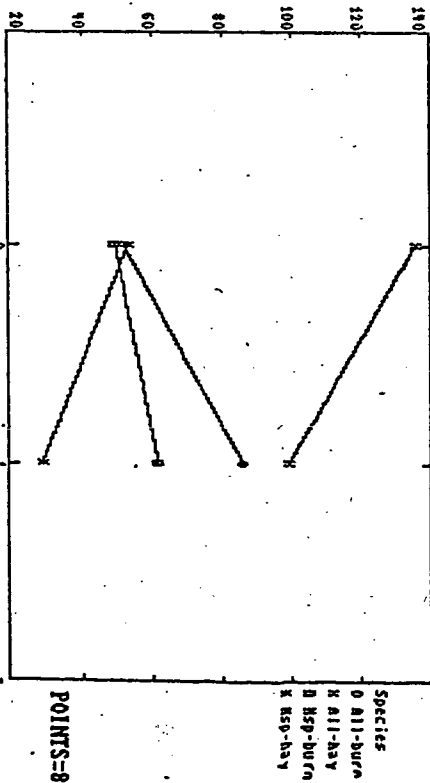
12. Relative rank of abundance (low rank=low numbers), Missouri



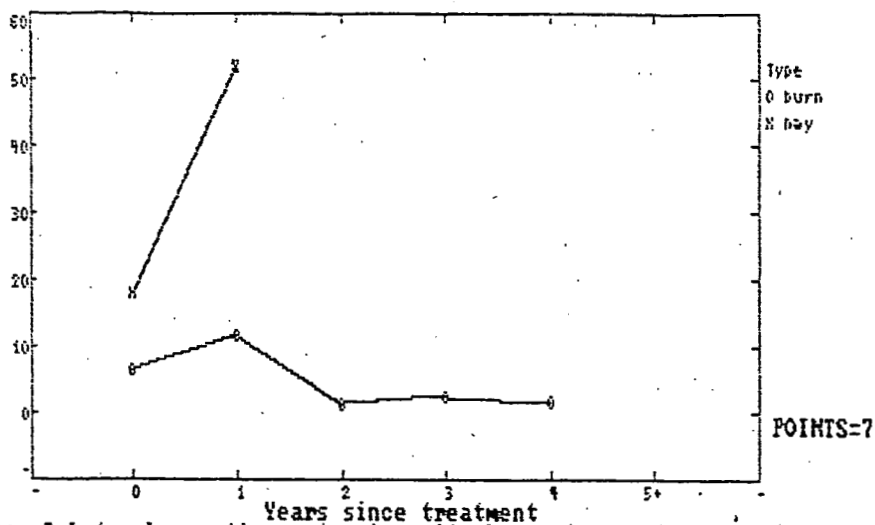
13. Relative rank of abundance (low rank=low numbers), Missouri



14. All & non-spec. (nsp) study species in burn & hay prairies (Missouri)

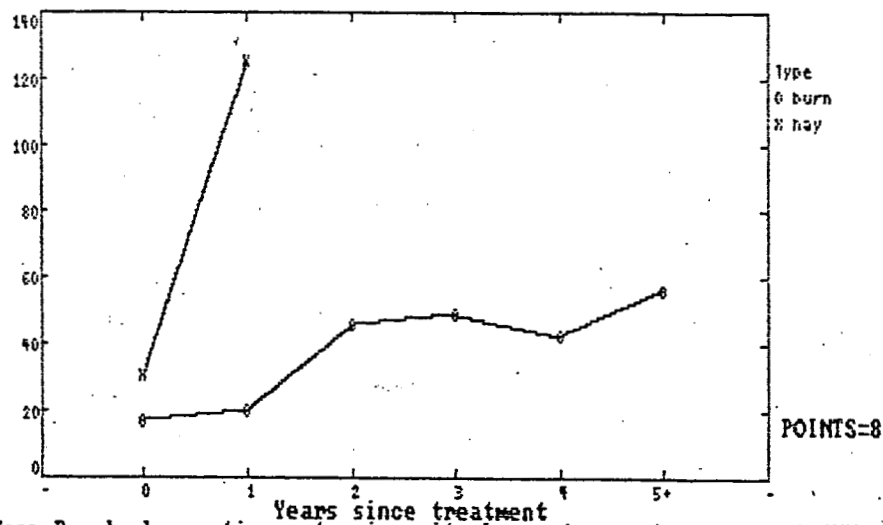


Dakotas/hour

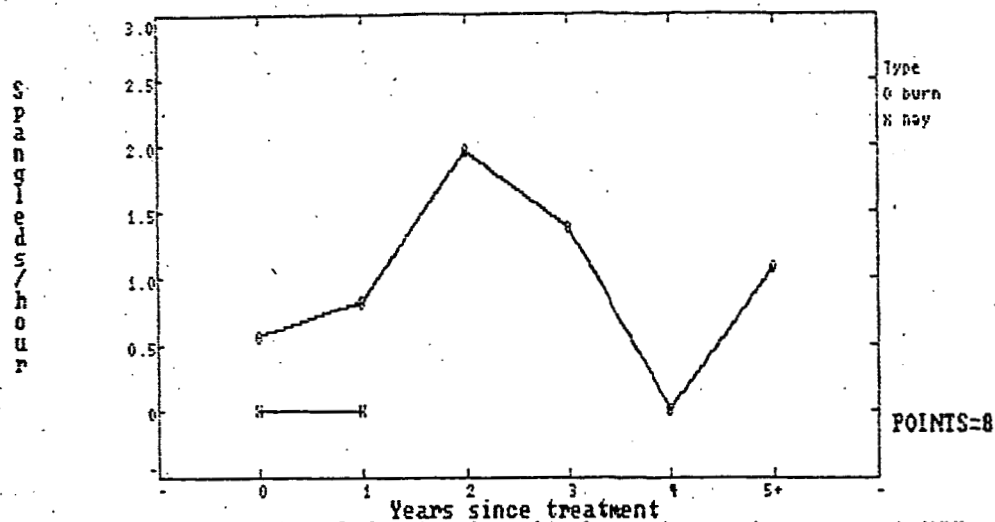


M1. Mean Dakota observation rates in units by most recent management (MN)

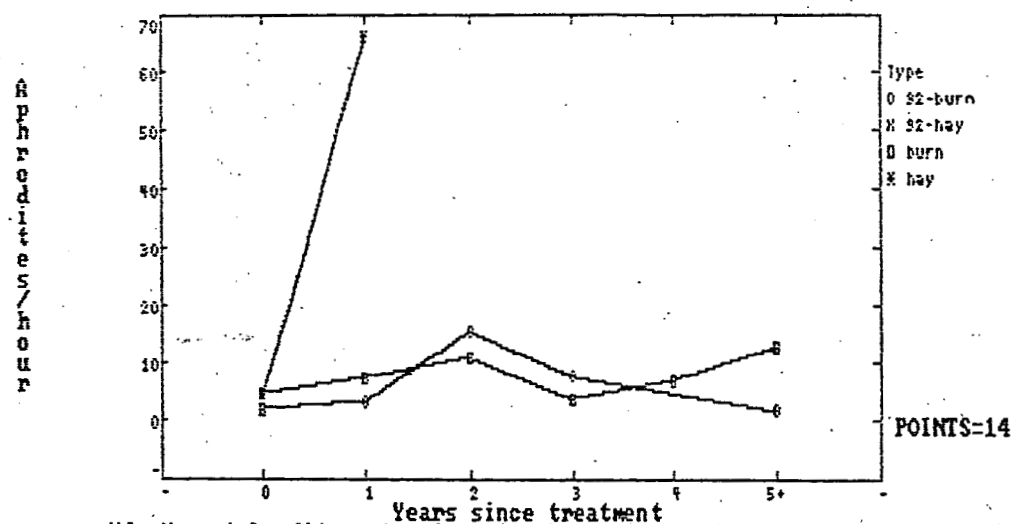
Regals/hour



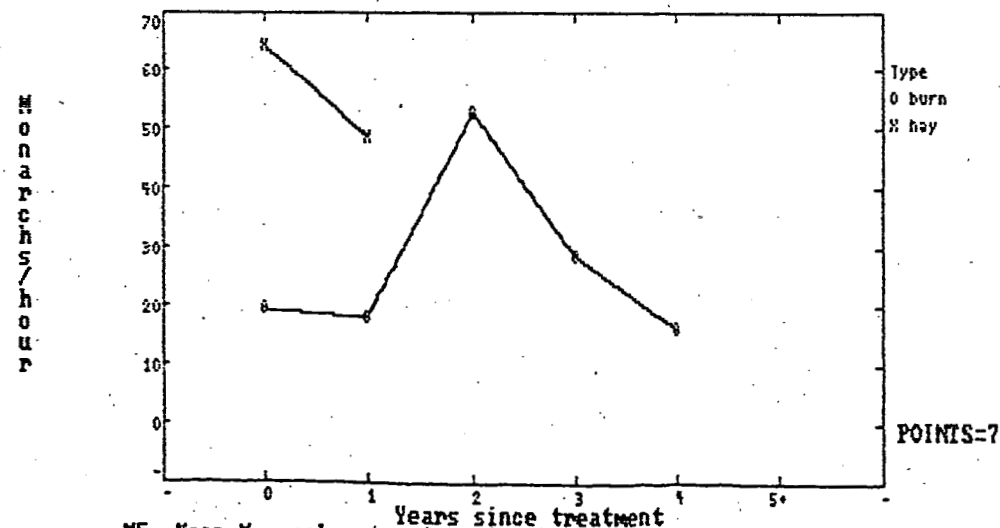
M2. Mean Regal observation rates in units by most recent management (MN)



M3. Mean Great Spangled rates in units by most recent management (MN)

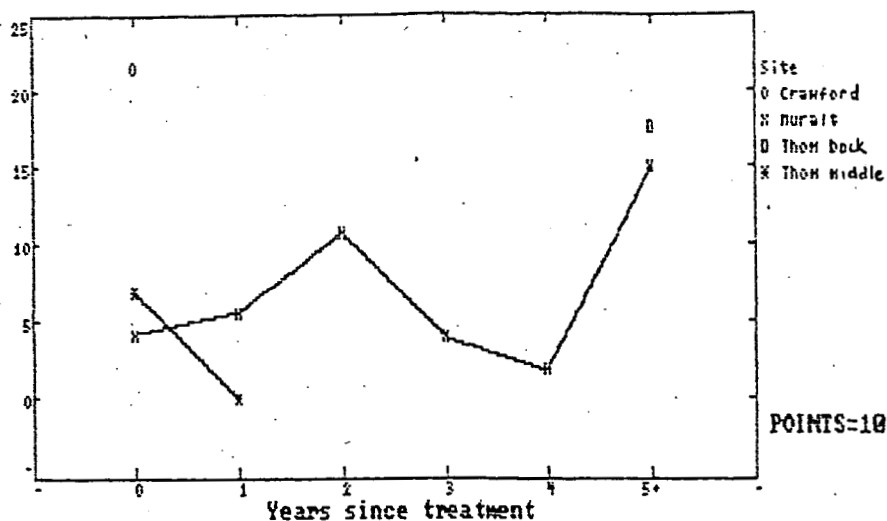


M4. Mean Aphrodite rates in units by most recent management (MN)



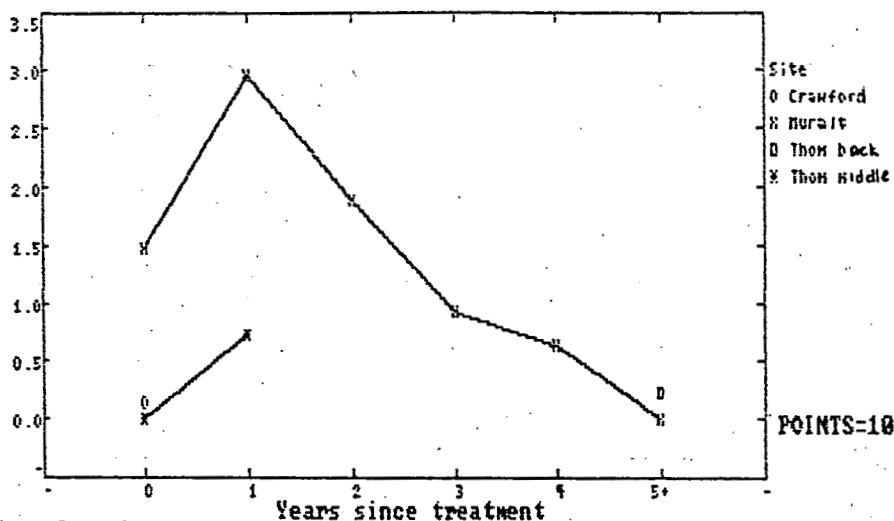
M5. Mean Monarch rates in units by most recent management (MN)

Regals/hour



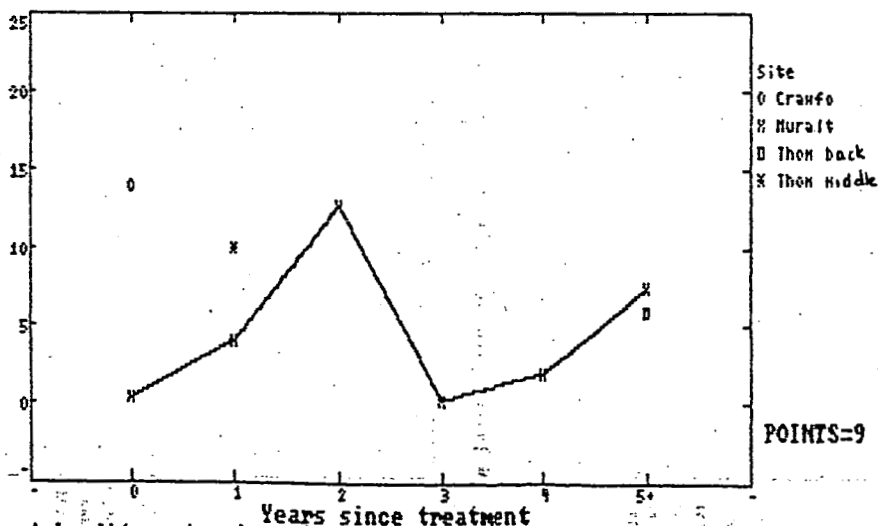
01. Mean Regal rates in units grouped by site and last management (WI)

Spangleds/hour



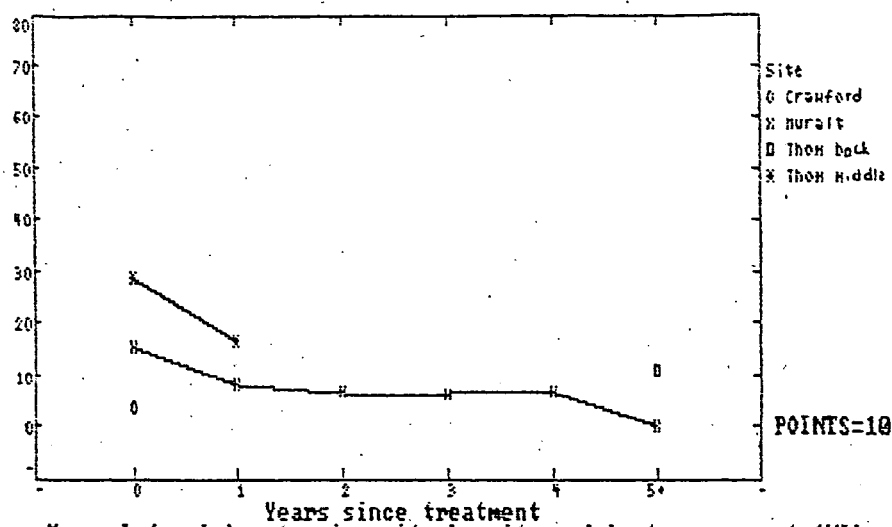
02. Mean Spangled rates in units grouped by site and last management (WI)

Aphrodites/hour



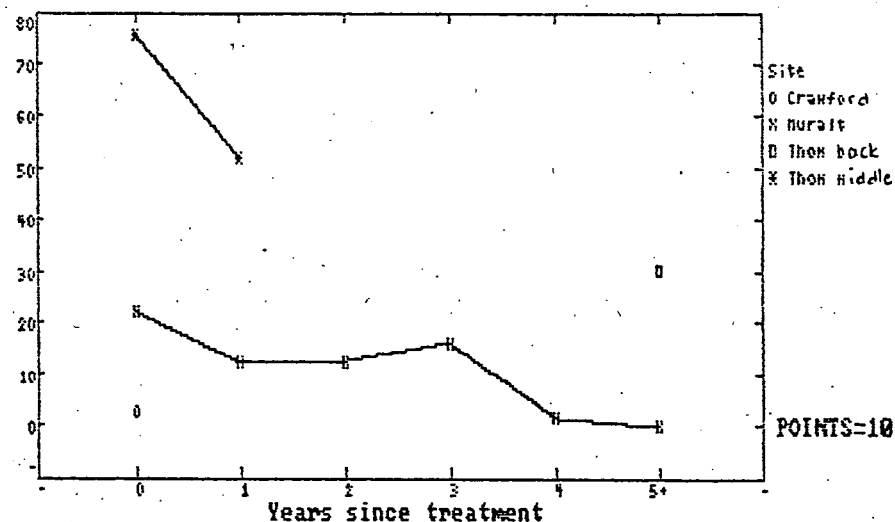
03. Mean Aphrodite rates in units grouped by site and last management (WI)

Monarchs/hour

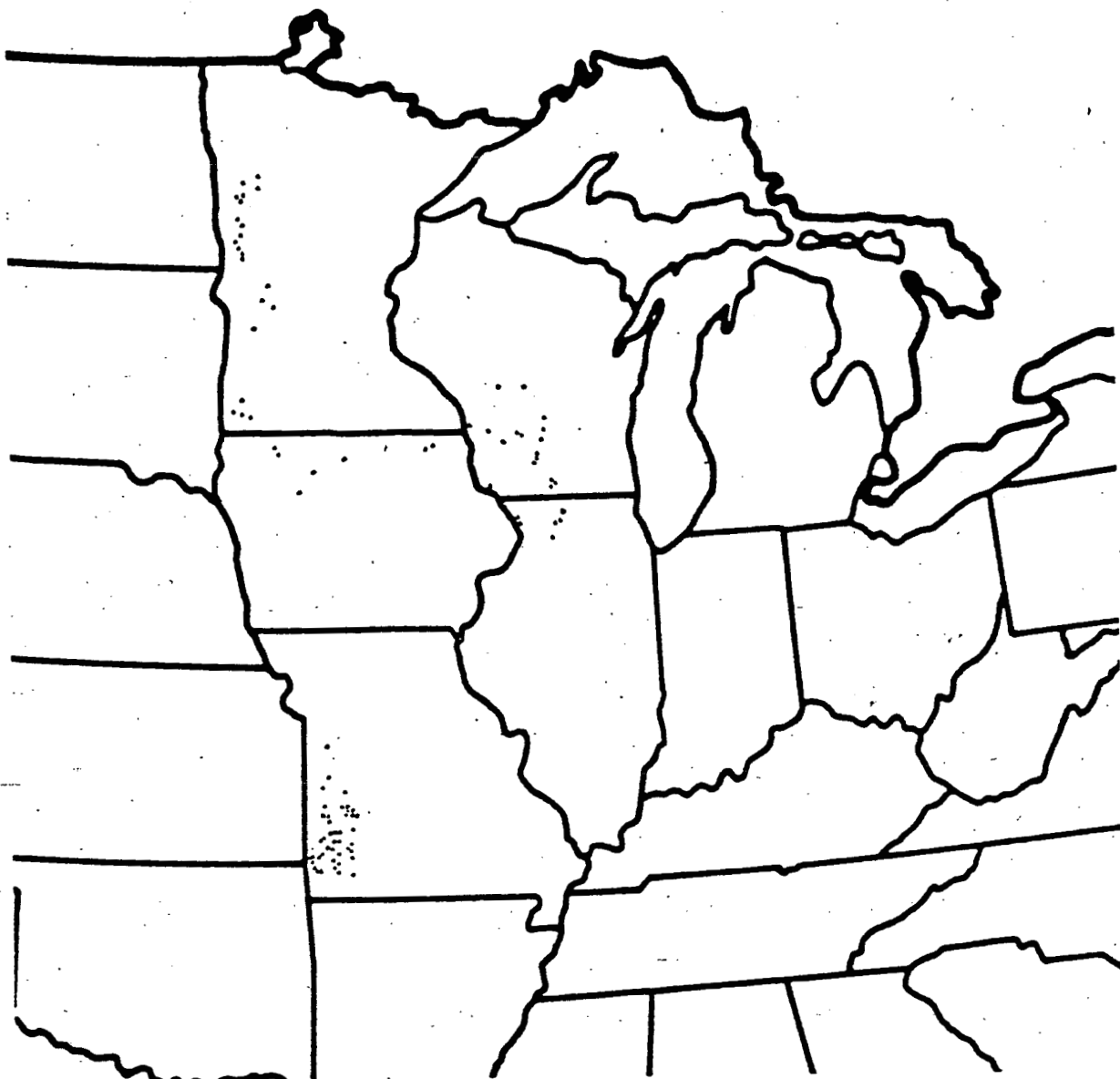


04. Mean Monarch (early) rates in units by site and last management (WI)

Monarchs/hour

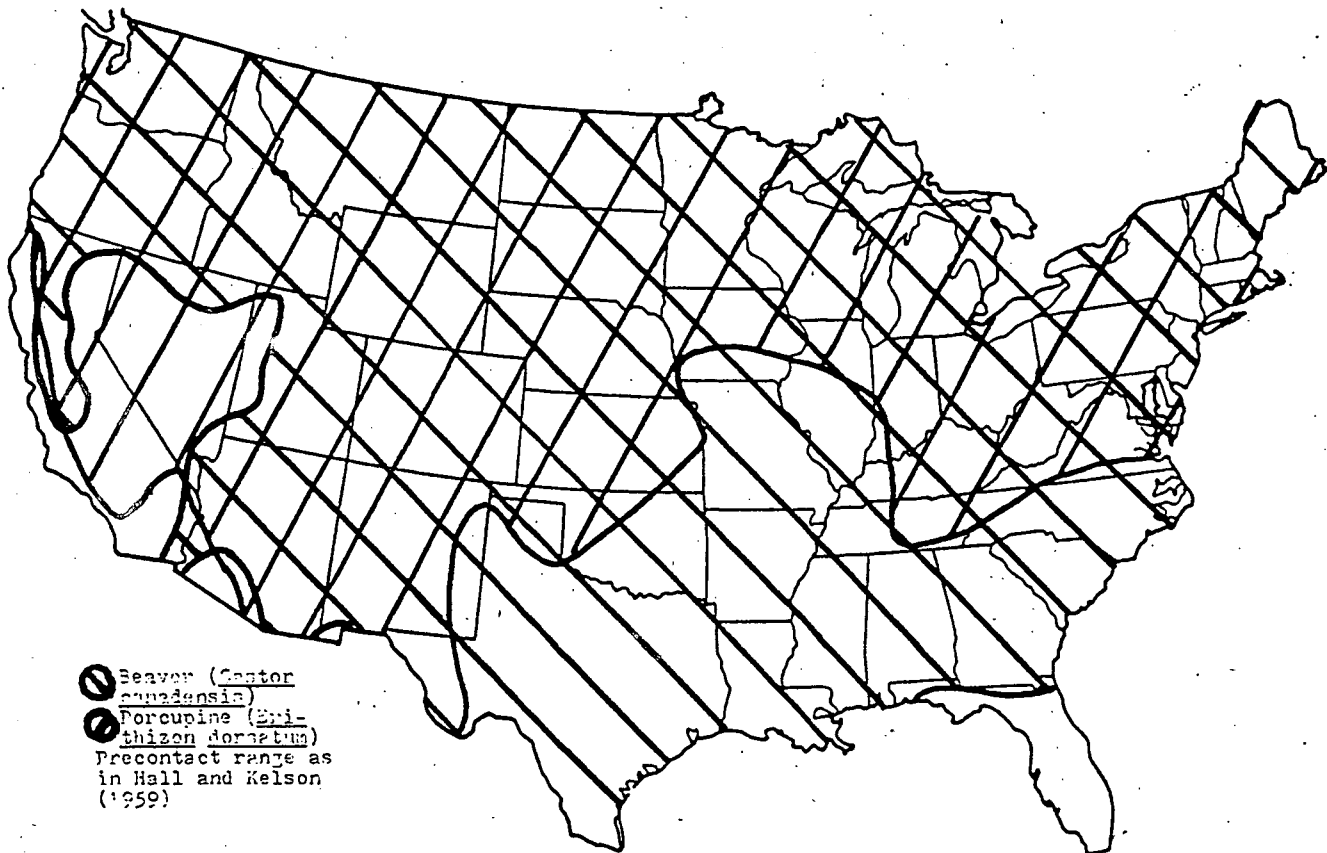


05. Mean Monarch (late) rates in units by site and last management (WI)



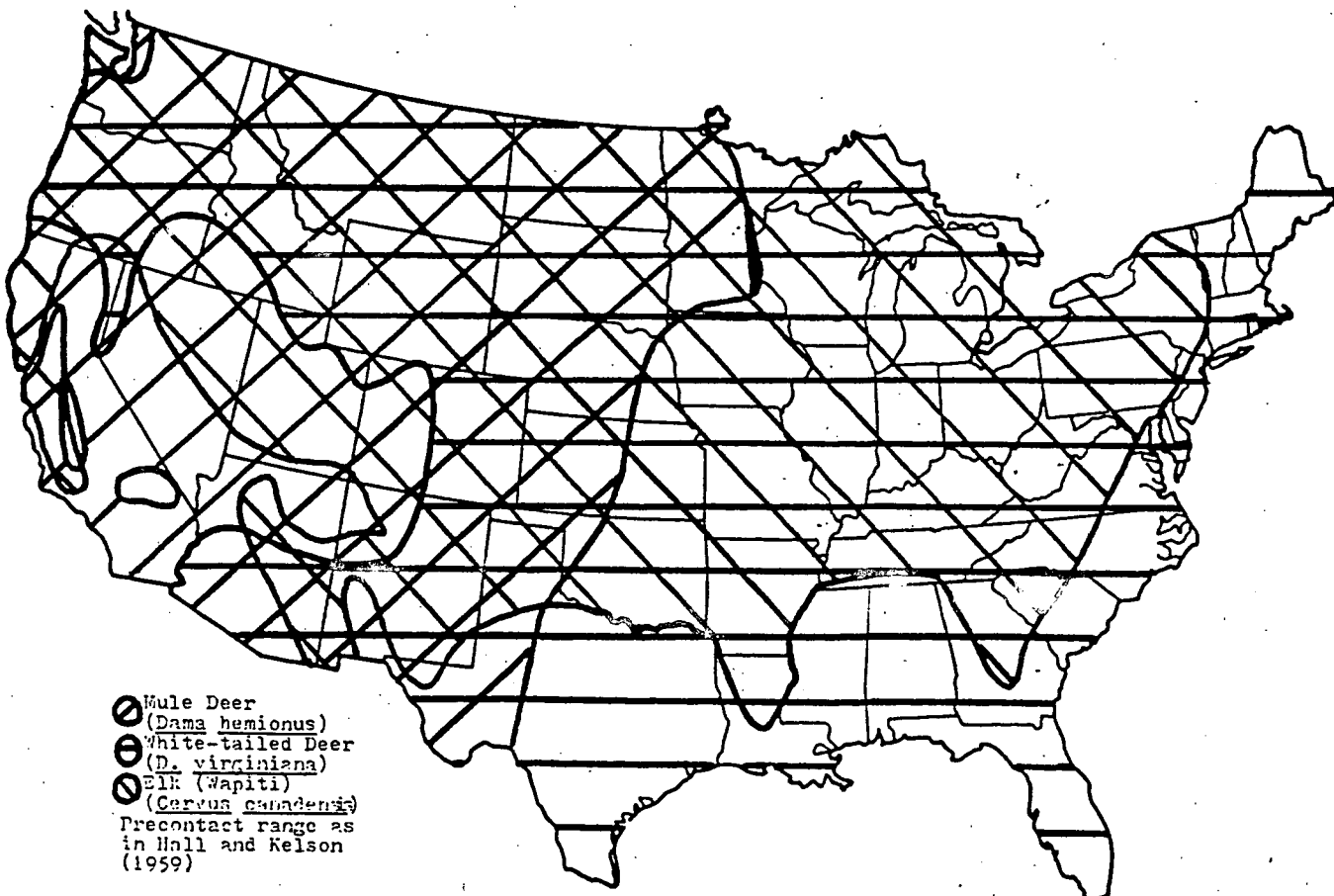
Map 1. Study sites 1990-93.

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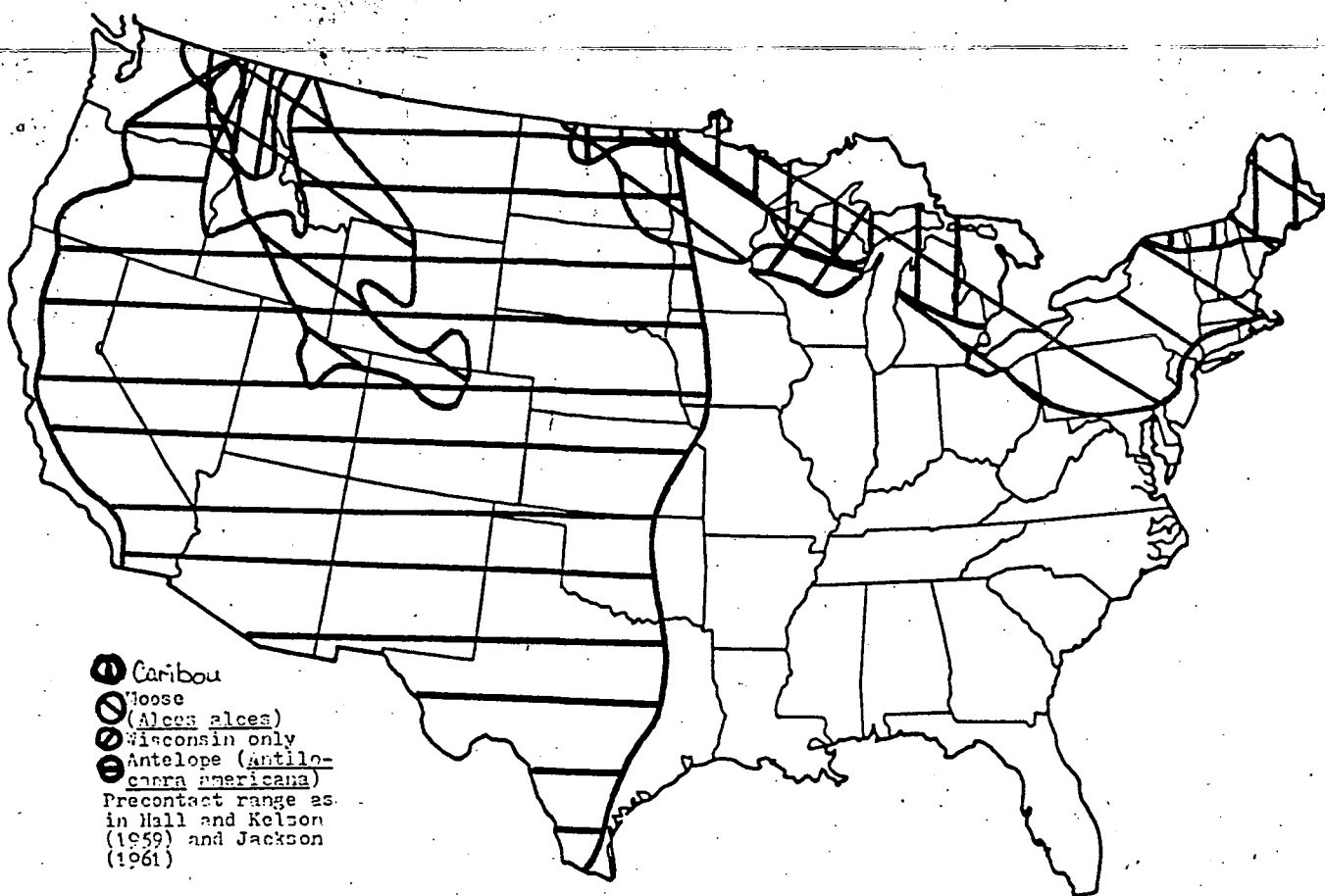
- ① Beaver (*Castor canadensis*)
 - ② Porcupine (*Erethizon dorsatum*)
- Precontact range as in Hall and Kelson (1959)

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- ① Mule Deer (*Dama hemionus*)
 - ② White-tailed Deer (*D. virginiana*)
 - ③ Elk (Wapiti) (*Cervus canadensis*)
- Precontact range as in Hall and Kelson (1959)

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