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Part 3: How does habitat management affect butterflies? by Ann B. Swengel

Summary. Management isn't studied compared to an "ideal" but instead in comparisons among existing examples, so it's important to examine what's being compared to what and establish objective methods of comparing results of different management approaches consistently. An important factor affecting how a butterfly species responds to management is whether the butterfly is in the vegetation being affected. Dispersal tendency can determine how quickly the species comes back into a treated area. Degree of specialization of the butterfly species affects not only how likely it is that there are survivors occurring in the surrounding landscape around the treated area but also how picky or not the butterfly is about the vegetation. The more flexible, the more likely the butterfly can make use both of long untreated as well as recently treated areas in the vicinity. This in turn makes it more likely that the butterfly population can persist in and around a managed site. Typically, butterflies with more than one generation per year recover more quickly, or have higher numbers sooner, after a fire than those with just one generation per year. How do the key plants for that butterfly respond to the management? If the plant is in a favorable and abundant condition after the fire, this is more favorable for the associated butterflies. Response to management does not appear to sort by ecosystem affiliation but rather by taxonomic affiliation, so that both species favored and disfavored by each management occur in each ecosystem type.

I've spent so much space describing scientific methods and statistics so that I can tell you general patterns in the scientific literature and my extensive personal observations in the context they were learned. So you'll hear about tendencies and comparisons. I'm using all research available to me, involving other insect and invertebrate groups and other parts of the world as a context, to understand butterflies and habitats in the Midwest. My approach is to look at the effects on insects broken into time periods: immediate (as the management is happening), short term (in the few weeks and months afterward), intermediate term (from several months to a year or two afterward), long term (the several years after that), and the very long term (after the management has been happening for decades). This involves both the direct effects on the animal and what is happening to the plants, which in turn affects the animals. This section will be a general overview on insects that then focuses on grassland and specialist butterflies in more detail. That's because my purpose here is conservation, which means taking care of the most vulnerable species.

BURNING AND INSECTS

A consistent pattern across many studies is that a single event of burning an area causes a greater reduction in insects than an equal sized single event of mowing. This reduction is both greater and lasts longer. While it may not be directly in view and obviously visible when the fire is happening, a lot of insects get combusted or exposed to lethal heat during a fire. While this can include adult insects with capacity to fly away from the flames, it especially affects less mobile immature life stages in the fuel. This reduction is due not just to the greater mortality from the actual treatment (for example, in comparison of burning to mowing) but due to the longer "shock" phase following the treatment when conditions are barer and harsher until the vegetation regrows to the condition it was in before. The post-fire environment is harsh due to extreme microclimate (from lack of vegetative shelter) and lack of food (both plant and animal, except there may be a brief initial flush or increase in carcasses). Because of this, fire has long been an agricultural pest reduction tool (burning the stubble after harvest).

However, a given species can be more vulnerable to mowing or another alternative to fire than to burning, or to a specifically timed mowing compared to a specifically timed burning, due to where the species is at the time the management occurs and what resources the species needs. For example, the leadplant moth (Schinia lucens) is resilient against both cool-season burning and season-long light to moderate cattle grazing because the cool season is when the moth is underground as a pupa (unaffected by the heat or the shock phase afterward) and the cattle avoid grazing on leadplant, the moth's caterpillar food plant. However, while I do not have formal analysis on this, I would expect a mid-summer mowing to remove the availability of the flower parts at the time the moth caterpillars need them, and thus, have an immediate negative effect on the population. A similar result would occur if the leadplants got burned in midsummer.

Insect species vary greatly in their response to fire once a few months of vegetative growth have developed. At this point, some species may typically stabilize already to pre-fire numbers, others remain lower, and others may actually be higher. This relates to how many individuals of the species are able to gain access to the burned area and how suitable the burned area is as habitat for them. The fresh vegetative growth and the reduced number of insects there (due to fire-caused mortality) can make for very attractive vegetation. Some flowers typically have spectacular

blooms in the first growing season after a burn, for example wild lupine and leadplant, and these are valuable nectar flowers, not to mention caterpillar food plants. For equal treatment, though, I need to mention that other flowers do not bloom strongly in this period. For example, in units where we know there's an abundance of both lupine and phlox, which have similar flowering times, we'll see the strong lupine bloom in that first spring after fire but have great difficulty even finding stems of the phlox. This is also both a great nectar flower and a lep (moth) caterpillar food plant.

Likewise, the longer-term consequences of burning, in the years after a given fire, vary greatly among insect species. The second growing season after a burn typically looks a lot different vegetatively. Some or a lot of litter (dead plant matter) has accumulated as a result of last year's growth. This provides more variety in microclimate and ameliorates dry periods, but also reduces new plant growth in this year. As a result, I expect to see fewer flowers of those species that flowered strongly last year, but more flowers of those that had little bloom last year. Insect species that had a boom from the flush of growth last year will probably be lower in number this year. Meanwhile, species that had much lower numbers last year than pre-fire, but are still present, are likely to continue rebuilding their numbers. However, this rebuilding doesn't necessarily go in a directly linear way (always in one direction). Plus, in all these patterns related to year(s) since fire, there is a separate factor of annual fluctuation. A "good" or "bad" year climate-wise can exert an opposite or magnifying influence on these population patterns due to management.

An important factor affecting how a butterfly responds to burning is whether the butterfly is in the fuel or not. When the burning happens, usually in the cool season, most of the butterflies present in the site are in an immature life stage. If they are above ground in the grassland layer, they are in the fuel most targeted to be burned. If they are up in a tree above the flames, they may not be affected directly by the flames. In the cool season, even those few species in the adult life stage are unlikely to be able to flee the flames if exposed to them. But in the warm season, even when many adult butterflies are active and evident, it's still true that many butterflies present in the site are in an immature stage unable to escape if exposed to fire. More moths than butterflies habitually occur underground as an immature, and if they are there, again, they are not directly affected by the fire. Many adult butterflies seen in a grassland in summer may not be in the grassland layer when it burned. They may not even be in the site itself.

Many other factors also affect how a butterfly species responds to burning. The dispersal tendency of the butterfly (how localized or wide-ranging its flights) can determine how quickly it comes back into the burned area. Degree of specialization of the butterfly species affects not only how likely it is that there are survivors occurring in the surrounding landscape around the burned area but also how picky or not the butterfly is about the vegetation. The more flexible, the more likely the butterfly can make use both of long unburned as well as recently burned areas in the vicinity. This in turn makes it more likely that the butterfly population can persist in and around a burned site. Typically, butterflies with more than one generation per year recover more quickly, or have higher numbers sooner, after a fire than those with just one generation per year. How do the key plants for that butterfly respond to fire? I've already mentioned above about the divergent responses we've seen between lupine and phlox, two species of great importance to our study species. If the plant is in a favorable and abundant condition after the fire, this is more favorable for the associated Lepidoptera.

Specialists tend to have one generation per year and lower dispersal, so how can specialization be an independent factor affecting response to fire? There is some ability to distinguish these variables from each other. For example, 'Karner' Melissa Blue and Mottled Duskywing are multivoltine (more than one generation per year). Regal Fritillary has a "grassland" relative, the Aphrodite Fritillary, and a generalist relative, the Great Spangled Fritillary, and all these fritillaries are univoltine (one generation per year). There is also a bit more distantly related immigrant multivoltine relative, the Variegated Fritillary. All of the univoltine fritillaries appear to have strong flight ability, covering more ground (even just when I am watching them) than many other specialists that we have also tracked at length. On the other hand, a number of other grassland species (e.g., Common Wood-Nymph) and generalists (e.g., Banded Hairstreak) are univoltine.

In our surveys, the first year after fire (year 0 in our parlance) is pretty consistently negative for the specialist and grassland butterfly categories. Generalist and immigrant species are often less pronounced and consistent in pattern but this category comprises relatively more kinds of species. Immigrants are most likely to be most fire positive in that first year. Other generalists may also peak in that first year after fire or they may not show that much difference from that first to the next year. In comparing among management types, specialist abundance typically is higher in comparable haved than burned prairie, although a few species were lower in haved than burned. However, in those few cases, if there was enough sample available to get statistical significance for another management type (e.g., having + light grazing, grazing alone, even long-term idling or non-management), the species almost always was significantly higher in some other management than burning. Thus, while burning was most likely to be negative for specialist and grassland butterflies, no one other management type was optimal for all of them either.

For butterflies that typically show marked reduction immediately after fire, there can be large variation in how that individual species, even an individual popula-

tion, responds to individual fires, particularly due to spatial scale (size of burn and size of nearby unburned occupied refuge) and to climate post-fire. For example, for Karners, the generation directly affected by the fire pretty consistently shows a sharp reduction compared to earlier and later generations. The next generation, though, can be a wildcard, even after taking account of variation between the spring and summer broods (the latter typically larger than the former) and dramatic annual fluctuations regionally. Usually it takes several more generations to rebuild to prefire expectations of population size, assuming typical rotational fire management. But when a protracted drought of several years followed that fire, we've seen the population may be retarded in ability to rebuild numbers for several more years. On the other hand, I am thinking of a Karner site where the burn unit itself is very large but most of it is not Karner blue habitat. The Karner habitat is in one corner of the unit, and while small (only a few acres), it can support a dense large Karner population. Additional Karner blue habitat adjoins up and down a roadway, some of which has not been fire-managed. When the unit got burned in the spring, sometimes by the second (summer) generation, numbers were within the range of pre-fire expectations (or higher). This appears to have been a confluence of excellent climate and immediately adjacent recolonizers. Mind you, I have not often seen this even when the spatial configuration of burn and refuge appeared similar. Unfavorable climatic fluctuation appeared to relate to some particularly slow recoveries but sometimes even that doesn't look like a contributing factor to some poor recoveries either.

Likewise, for Poweshiek Skipperling, we observed the same pattern of bifurcation. For this univoltine prairie specialist, the immediate effect was not particularly variable. The generation affected by the fire had very low numbers, if any, in the burned unit, and if present, biased toward the edge of the burn near an unburned occupied refuge. It's in the next generation(s) after the fire where the wildcard presents itself: Does the population recover or not? How many fire events does the Poweshiek population recover from before a fire event occurs they don't recover from? As a result, for some species there may be a split point of recovery/viability or not: does the population rebuild its numbers to prior expected levels (or even higher) or not? We have seen a few instances of good recovery after the first year following a fire, and this is especially memorable because of the wonderful spectacle of abundant Poweshieks. But more instances of inadequate or non-recovery have occurred in the 3-6 years before the next fire.

Situations where burning shows the most favorable results for specialist butterflies. (1) A relatively small portion of the habitat patch actually used by the butterfly in that site is burned, and in plots that are small in an absolute sense (number of acres), especially if that is the first fire done in that population. (2) The core area for that butterfly is not ever in fire management (a "permanent non-fire refu-

gium" or "perm" for short), and that core receives compatible management, if needed, to maintain the habitat as suitable. Sometimes this is a deliberate conservation plan (e.g., part of a reserve designated as a perm, with deliberate effort to prevent unplanned fire there) or it is serendipitous. For example, neighboring private farmland is lightly managed in a way compatible with maintaining prairie flora and butterflies without fire. (3) Entirely unburned patch(es) occupied by the butterfly occur within the perimeter of the burn. I don't mean incompletely burned fuel (e.g., where the fire passed so quickly that only the top of the fuel was scorched) but places skipped entirely by the burn.

Situations where burning shows the most unfavorable results for specialist butterflies. Most or all of the population of the butterfly is concentrated into a relatively small area, and all of that area has been in fire management. This is particularly unfavorable if that concentration area is all within one fire management unit so that all of it gets burned when any of it is burned. This situation is also risky due to wildfire hazard. An unplanned fire that combusts most or all of the core area can result in large decline/loss of that population. However, the entire population does not have to be burned at once for there to be high risk of protracted population decline/loss. If the core area is burned on a 2-6 year rotation (1/6 to 1/2 burned per year), this can also lead to population decline/loss. The area that has to serve as the unburned refuge (source for recolonization) may not have recovered much or at all since it last burned.

Nothing is always or never in insect mortality or survival. Even species thought to be entirely vulnerable (above ground in the grassland fuel unable to move away from the flames) do not necessarily show 100% mortality from a fire. In some cases this can be attributable to a small area within the burn perimeter skipped by the fire, or sheltered from the fire by a boulder or rocky outcrop. In other cases, it turns out that another previously unknown population occurred within dispersal distance, explaining how a population could continue to occur in what was thought to be an isolated site burned in its entirety. Or the species has an alternate caterpillar food plant found outside the bounds of the burn. But in other instances, it's hard to come up with such an explanation. Plus, there may be direct evidence of survival, for example with an enclosure placed over the ground that contains the adult insect after it emerges from the last immature stage. How else could the survival happen? We have reported observations of Karner caterpillars essentially underground, even though I had not dug them up. They had fallen or crawled down into the air space alongside the lupine stem and root below ground. I can imagine eggs falling off a surface and ending up down a hole or mixed into the dirt. But I need to caution that I have never found a Karner caterpillar in a spot recently burned (actually combusted; not a skip). So this is a hypothetical scenario, not a reliable way to count on survival.

I would caution that amazing insect survival stories

pop up in a variety of contexts and are not the same as probability of population survival. Schaus' Swallowtail survived the storm surge from Hurricane Andrew (barely) even though the entire vegetation was inundated and denuded. But the viability of the population was in doubt so that the population was subsequently augmented by captive releases. Regal Fritillaries occur at Buena Vista (the subject of another article published online by SWBA) but we haven't found any other analogous sites with reliable Regals in Wisconsin, and Buena is still depauperate in prairie specialist butterflies (especially skippers), however much its butterfly fauna does overachieve its old field vegetation. Jutta Arctic occurs in occasional detections in small isolated bogs, being more abundant and regular in larger bogs. In these small bogs, it must be occurring either as a low-density but resident population or as repeated dispersers in from elsewhere to achieve detection there again, this in bogs smaller and more isolated than most prairies. I favor the former explanation but either is amazing. The point isn't that any individuals survive at all; the point is whether the population persists viably over the long term.

What does fire do to plants? It burns (kills) some seeds and seedlings, not just brush but also herbaceous plants. It removes litter, which creates a warmer exposed microclimate. It creates a simplified (short and uniform) above ground regrowth of vegetation. It may or may not topkill woody plants, depending on how high up flames went. The stems remain standing regardless. Most brush resprouts from the roots. It exposes soil for seeds to establish afterward-native prairie as well as weeds, brush and trees too. If adventive plants (native or exotic) are in the seed bed or nearby, this can lead to proliferations of them. It shifts to taller thicker grass growth. Unless a drought, vigorous regrowth results in a tall dense structure and heavy litter accumulation during the first growing season after fire. If a drought, then less plant growth may occur than if not burned because the drought is exacerbated by the warmer exposed microclimate after a fire.

Dominant grasses like bluestem are favored and uncommon flowers tend to be disfavored, with a shift to proportionately more and taller grass and fewer wildflowers over time. In the first growing season after fire, the flowering can be quite pretty compared to unburned years both prior and following. However, with the shift to grass, the flower display, although still pretty, can become reduced in a burned year compared to the blooms in previous burn years.

Was the fire stand-replacing or not? This is more of an issue where there are many trees, which can be referred to as a "stand." But this can be understood for the brush and trees in a prairie too. Were the woody plants (the stand) killed above ground, so that they have to be replaced by a new generation of tree growth from the roots up? Or did the above-ground growth of the woody plants survive (rise above) the lethal extent of the fire? A stand-replacing fire (top-killing trees and brush in the burned area) means that any new woody canopy has to arise from the ground up. Even if none of the woody plants actually die, this "reset" requires them to resprout from the roots. For a few months, or even a few years, the actual area of canopy coverage by woody plants is likely to be reduced, even if the number of stems stays the same or even increases. This can increase area of uncanopied habitat. However, if not killed, at some point the woody plants grow taller than the turf and/or expand laterally farther than before, especially if more stems resprout from the roots than existed prior. Plus, I've seen many management fires that in whole or in part are not stand replacing (the woody plants are not top-killed). In that case, the woody plants are not reduced, even temporarily, and expand unchecked.

Stand replacement has a more dramatic effect the more woody plants there are, and the more tall and overshadowing the canopy is per woody stem. If tall shading trees are top-killed, there is more relative reduction in canopy. By contrast, topkill of a short dense thicket of shrubs (assuming enough fuel to carry the fire through and upward in the thicket) will result in little and brief canopy reduction, before resprouting and new seedlings replace and perhaps even increase canopy. Another variable is the kind of woody plants. Aspens, oaks, and willows densely regrow from topkill. Red cedars and jack pines primarily respond to topkill by seedling recruitment from the seedbed.

Wildfires are more likely to be stand-replacing than management fires. That's because stand-replacing (crown) fires are riskier and harder to ensure that they remain under control. As a result, crown fires do not occur as much in management burning. This can result in relatively minor impact of management fires on existing canopy.

Where substantial woody canopy occurs, "mineral" firebreaks are more likely to be used to ensure fire containment. Mineral firebreaks have exposed soil made by disking or lightly plowing strips around the perimeter of the area to be burned. This has the side effect of providing conditions in the firebreak adjoining the burned area that are relatively more favorable for weedy plants (native and alien) and less favorable for more sensitive native plants.

While it is often said that fire controls brush and weeds, our literature search has turned up studies with minor reductions even with a lot of burning, or no change or even increases in weeds and brush similar between burned and control plots. Our observations of many burned sites agree with this literature. The harsh environment following fire favors adventive and dominant plant species (both native and alien, grassy and broadleaved, herbaceous and woody), because they are able to compete in a wider range of soil and climate conditions in that region. This is true for other leveling treatments (heavy grazing, clear-cutting) which also result in dramatic change of the microclimate and provide bare ground to colonize. These conditions also allow the expansion of brush and

weeds if they had a toehold in the site or neighborhood. Exotic plant management guides frequently recommend burning the affected area even five or more years in a row to start getting some control. This advice agrees with my observations that an individual fire produces relatively little weed reduction. As for coniferous brush, I see relatively little outright kill even though they are highly flammable and usually die if completely top-killed. Deciduous woody plants, whether top-killed or not, remain alive to grow and expand between fires.

In the longer term, in both our readings and our observations, Scott and I see a "reset" of the vegetation, with the landscape context a key variable that contributes to the variation in result in burned prairies. What's underneath (in the ground as seeds and roots) and in neighboring patches supplies sources of plants that weren't necessarily evident in the prairie pre-fire. That's why we think in terms of "resetting." In the fossil record, relict vegetation (no longer appropriate for the climate in an area) may persist until a fire or other ground-baring event (e.g., tree-throw) occurs, allowing the vegetation prevalent in the surrounding landscape more opportunity to colonize the site. We see fire operating similarly in sites today, allowing opportunities within the prairie preserve for the brush and weeds prevalent in our region and thriving outside preserves. A reset concept helps explain the wide range of outcomes in sites that are in fire management, both among sites and even in the same site in different fires. Sometimes beautiful prairie vegetation regrows after a fire and sometimes weeds proliferate. The context of what lurks unseen in the ground as a seed bed and what occurs in nearby plots appears to contribute to this.

Timing of fire matters as does climatic context. Burning in the cool season occurs when many plants are dormant. Growing season fires can disfavor those plants actively invested in above ground growth at that time while those that are not active (already senesced or not yet growing) may be unaffected. Climate can also be a factor. Drought exacerbates the harsh microclimate after a fire. Abundant rains can result in lush regrowth. Which plants are favored by which condition will be prominent and is not predictable ahead of time.

Some stated goals of conservation management, often promoted as benefits of burning, do not necessarily appear desirable for butterfly conservation. One is removing most or all dead plant litter. Litter is cover for insects and moderates the microclimate near ground level. This can be a useful resource for many animals. Second is a dramatic "renewal of the vegetation" due to clearing out the above ground live and dead plant matter. Some fresh growth can be valuable, and may be preferred for egg-laying and caterpillar forage, but other butterfly immatures may prefer less vigorous, even weak growth. Third is stimulating tall grass growth (three or more feet tall), which appears to me to be an unfavorable structure for many specialist butterflies. Fourth is restoring processes and letting nature take its course. Nature extirpates as well as fosters biodiversity. Random events, even natural ones, can have permanent negative consequences for animal populations occurring in isolated habitat patches.

The compounded consequences of burning, after burning has been the management for many years, vary greatly among butterfly species. As illustrations of the range of outcomes, here are better outcomes than average in our survey results. A better outcome (for a time) occurred at Oliver Prairie since it still had enough Ottoe Skippers to qualify as an actual population at the start of our surveys in the late 1980s, even though this small site had been preserved and fire-managed for several decades prior. A similar outcome occurred at Dewey Height Prairie for the same skipper, up until the last few years. Regal Fritillaries continued to be seen sporadically at Oliver in the 1990s and this decade, even though it is tiny and usually burned in its entirety, and the nearest known population is at Muralt Bluff, about a mile away, and it is fragile and not all that large there either. Bluestem Prairie had Poweshiek Skippers in decent numbers in the 1990s despite large burn units burned for some years. Crex Meadows (the subject of another article published online by SWBA) continues to have an excellent array of specialist species, even though large burns occur there. But the butterfly species most averse to fire that I know of in range (Cobweb Skipper) has not appeared at all in our surveys here (so far, anyway), although we have found it in a similar-looking area elsewhere farther north in the county. Otherwise, the most sensitive species do not occur at Crex because they are apparently out of range here (Frosted Elfin; Poweshiek, Ottoe, Arogos Skippers). All prairie and savanna specialists we've found at Crex also occur in adjacent areas of Burnett County Forest that are not in fire management. Furthermore, non-fire-managed patches (as of this writing) occupied by specialists living at Crex are scattered around the site, usually as roadside rights-of-way.

On the other hand, here are worse than average outcomes in fire-managed sites. Spring Green saw rapid decline in Regal Fritillary and Ottoe Skipper even though fire management had not occurred there for all that long, burning occurred rotationally (not the entire site), and not all of the site was in fire management. I remain astounded that we have yet to find a Frosted Elfin in the relatively small part of Bauer-Brockway Barrens managed with a single fire, even though we have surveyed there a lot for many years (including areas where we found them prior to the management fire), they occur very nearby in the not-fire-managed area, and the entire site is within the perimeter of a wildfire in the late 1970s. Bicentennial, Blazingstar, and Prairie Coteau prairies in Minnesota had declines in their Poweshiek Skipper numbers rather rapidly (over the course of about 15-20 years) given that the fire management occurred rotationally in units (not entire site at a time). Subdetecta-

bility occurred in the 1990s at the first two sites (which are near each other) and in the past decade for the third. After Regal Fritillaries became undetectable in one patch at Pine Island Wildlife Area after it was burned in its entirety, we have not seen Regal Fritillaries there since, even though we have surveyed annually for over a decade and another population, although fragile, occurs about a mile away.

Butterflies tend to perform better in wildfire than fire management. The wildfires that have produced better results for butterfly species richness and abundance are less frequent than management fires, once per decades compared to every year or two, are stand-replacing (creating substantial increase in open habitat), and occurring in a context of nearby suitable areas longer unburned and also occupied by the butterflies. The wildfire results in a change in habitat from more closed (usually supporting fewer kinds of butterflies) to more open (usually supporting more kinds of butterflies), rather than maintaining an already existing habitat as is.

But some biases may contribute to wildfire appearing more favorable than management fires. Most wildfire observations are "retrospective." When a neat site gets found with a neat fauna discovered there, the site history is investigated and it's discovered that a wildfire had occurred there. This selects only for the "good" wildfire sites, and "bad" ones (where the regrowth was unsuitable vegetation or localized butterflies were extirpated and did not recolonize) aren't documented. Meanwhile, more "before" and "after" information is available from preserves in fire management, even if the earlier period isn't a true "before" (before any fire management at all). In those few cases where "before" is available for wildfires, some apparent extirpations of localized butterflies are being reported. So the bifurcation (split point) described above is also apparent for wildfire-either a very negative outcome (extirpation) or some kind of survival/persistence. As more attention is focused on butterfly surveying and fire research, I expect more "before" and "after" data to become available on wildfires.

Let me infer a very long-term result of burning. In Great Britain, traditional agricultural practices include burning, and these practices continue in agricultural contexts and reserves today. These include burning hillsides because of excessive growth of gorse (a prickly shrub), winter burns to remove the higher parts of the grass overstory (so to speak) and allow more light lower to the ground for more growth, and burning heaths. For butterfly conservation, these burns are not as large and frequent as I typically see in the Midwest, and a variety of other managements are also used (mowing, trampling, grazing, tree-cutting, etc.). Nonetheless, many British reserves are remarkably heavily managed (from my point of view), including with fire. With extensive butterfly monitoring data, the butterfly conservationists are leading the charge for such active management. Is this a continental-scale paradox? Is their situation so different from ours as to have no application here? Let me instead suggest that centuries of these practices have resulted in a fauna that can only contain species resilient to these practices. Consider this. Britain is thought naturally to have been primarily forest, but has had several millennia of extensive human impacts on the landscape. It is jarring for me to attend "woodland" conservation presentations there because the focus is not on mature forest-interior or old growth habitat, but instead on early successional habitat (recent cuts, savannas, and the like). Astonishingly enough, this once primarily forested island is now so depauperate in mature forest species of plants, butterflies, and birds that this habitat is of little conservation value, since so few species benefit and many species of conservation need on a national and continental scale still exist there that require earlier successional habitats with a mix of open and wooded habitat. So I would caution that our British colleagues are remarkably more knowledgeable of the habitat requirements and populations limitations of their Lepidoptera, but are dealing with incomplete faunas-the faunas that have, over the very longterm, been able to survive in a highly human-altered and deforested landscape.

I do not want to hasten the arrival of the day here when all that we have is a human-tolerant fauna. I want also to keep the species that are not compatible with highly human-altered landscapes. Instead of only having those species that accommodate me, I want to try to accommodate them all. Research from extensive Brazilian rainforests (the opposite of England in many ways!) underlines this. Some butterfly species there are very averse to human alteration of the landscape, and occur only in the most pristine locations. Despite huge human effects in the midwestern landscape, some populations of these most sensitive species most averse to habitat degradation still exist and most need conservation consideration.

GRAZING AND INSECTS

Heavy grazing has the immediate effect of resulting in ecological "simplification": a relatively homogenous short plant structure with a more extreme microclimate, with reduced numbers and abundance of many kinds of insects. When heavy grazing first gets started, I'm not able to parse how much of the insect reduction is due to direct mortality and how much is due to unsuitable plant conditions. However, the insects die from a combination of being eaten, trampled, starved, or unable to survive the microclimatic condition. Once heavy grazing has been in place for a while, the harsh conditions preclude successful reestablishment of most insect species, perpetuating the depauperate insect fauna. Even unpalatable plants may be affected, though not necessarily by being eaten but by being trampled. However, heavy grazing can also be an opportunity for these plants to increase, due to reduced competition from palatable plants and increased opportunities for establishment in bare ground. Nonetheless, a few insects prefer short turf and bare ground, and so are more abundant with

heavy than lighter grazing. These species, such as some grasshoppers, might be relatively abundant given suitable climate, even if the overall insect fauna is poor in number of species.

Moderate grazing has the immediate effect of resulting in a heterogeneous vegetation. Moderate grazing is distinctly noticeable by reducing height of some plants. The turf is heterogeneous, with some areas noticeably grazed but others not so much. Relative palatability of plants is quite evident, with some species obviously preferred (and more reduced in stature and occurrence) and others avoided altogether. Some direct mortality to insects can occur due to being eaten, trampled, or starved because the required resource has been removed. But the primary negative impacts are likely to be due to reduced vegetative resources that encourages emigration or limits breeding success. Again, some insects prefer or are suited to the growth habit in a moderately grazed system. Even some prairie specialists, such as Regal Fritillary and Dakota Skipper, have shown evidence of being persistent, even abundant, in this land use.

Light grazing shows only a little impact on the vegetation compared to non-grazing. Light grazing may not be obviously noticeable in the plant growth and structure, except maybe right by a water or supplemental food source. As you might expect, direct impacts (mortality) for insects are mild, since the grazing is so light. Light grazing can still be useful since it can introduce local variation in resources and microclimates and reduce vegetative height, so that required resources are not overshadowed.

Within grazing systems where grazing occurs in each year, higher insect species richness and abundance tend to associate with less intensive grazing. Relatively more species peak in abundance in light grazing but a few peak in intermediate. When studies include an ungrazed treatment, these may have even more species richness and abundance, with this caution. If a site was formerly in a long-term grazing system, but still compatible with maintaining rich native flora, then long-term idling can result in reduction of plant richness, and in correspondence with that, insect richness and abundance also decline. Thus, a recently rested treatment has more insect richness and abundance than a long idled plot.

Remarkably enough, some insect groups, generally speaking, do not show sensitivity to grazing intensity. Ants may not show sensitivity to grazing intensity. Grasshoppers are variable on this point, in some studies showing some negative effects and in others not. Grasshoppers may have similar species occurrence between light and heavy grazing, but after several decades, abundance may be higher in light than heavy, but the literature is variable on this point.

How does grazing compare to mowing? Both affect insects by resource removal (plant structures being eliminated, even if temporarily) and by resulting in a more ex-

treme microclimate. When these particular factors affect the immature life stage, results can be pronounced. Mowing is more unselective and uniform (assuming the grazing is moderate to light). There is variability among studies and regions and insect groups whether mowing or grazing appears preferred. It is also possible to figure out ways to make the less preferred treatment more like the preferred one. For example, mowing can achieve heterogeneity by leaving unmowed strips between mown ones. As a result, the management choice can depend both on the target species and on the historical context—how has the site been managed in the past?

Effects of rotational grazing; i.e., having rest year(s) with no grazing between years with moderate to heavy grazing. In rest year(s) there is no direct insect mortality since grazers are not present. Plants grow taller, with more plant resources in more kinds of climatic conditions. Those insect species that like short turf may still have access to some of that but species that like taller turf start to have more of the conditions they require. The heavier the grazing before, the more the release from grazing will register an increase in abundance and richness of insects. However, insects that preferred the habitat in the currently grazed system will register decline. The heavier the grazing, the more dependent the site is on neighboring sites to replenish the insect fauna in rest years. The lighter the grazing pressure, the more in situ survival occurred and the quicker these species can increase in numbers when grazing is reduced or removed. However, the lighter the grazing, the less distinction there is between the grazing and no grazing. I've run across relatively less research on insects in rotational grazing rotated over years (one year with grazing followed by one or more years not grazed at all). I've found much more grazing research that compares insects in different intensities, seasons, durations, and types of stock for annual grazing, either among themselves or compared to no grazing at all.

In those sites where I've seen grazing and then grazing was removed, I've been surprised at how much brush increase occurred after grazing removal. In other words, the cattle were reducing brush more than I realized, even if brush was still present or even slowing increasing over the years the cattle were present. In those cases, along with the insect "bloom" comes a brush and weed release when the grazing ends. Although grazing can lead to weed development in a site due to conditions more suitable for weed establishment compared to other plants, when the cows are removed, those weeds can expand. So once again, the cows were containing the weeds also, at least the palatable ones.

Since heavy season-long grazing is unfavorable for maintaining native prairie plant diversity, it is also unfavorable for prairie insects. This broadcast intensive treatment is unsuitable for many prairie plants, but is suitable for a limited number of adventive native and non-native species.

When a site is released from such heavy grazing, it is typical for the site to remain impoverished of native plant diversity and be dominated by this limited number of plants that survive heavy grazing. However, if the site already has that plant composition, heavy grazing for a year or two focused on the problem areas can be useful for reducing brush. This is particularly effective if the brush is treated with mowing (or burning) to top-kill the branches first because the resprouting brush is more palatable.

Brief heavy grazing may be an option in sites with more prairie plant diversity but needs to be used with care. This approach may be called "once over" (for a single bout of heavy grazing for just a few days). It can also be repeated in 3-8 weeks, for a "twice over" or "thrice over" management. But I would caution that this is likely to be suitable only for sites that are already grazing-selected (depauperate) in flora and fauna. The concept is that the stock have to graze not only on preferred plants but also on everything else, such as brush, and trample undesirable unpalatable plants, such as thistles. Since the defoliation is brief, native plants (especially grasses) are more likely to survive the treatment. As a result, there may be less selective pressure against the most palatable native flora, since all forage gets brief if acute equal treatment. However, I do not have research at hand on how such management affects insects. My guess is that it falls between moderate and heavy seasonlong grazing. In such cases, it may be less risky to mow the site, especially just a portion of it, than to graze it heavily. Alternatively, this grazing can be focused on the portion of the site most needing brush control and containing herbaceous flora most resilient to grazing.

Very long-term effects of grazing. If insect survival within the grazed area is inadequate, so that recolonization is the only way for the insect population to survive, and that doesn't happen either, then grazing-sensitive insects are eliminated even if grazing pressure becomes reduced or removed subsequently. If grazing is too intense and too long, grazing sensitive plants are eliminated too. Some flora is very sensitive to grazing, so that it may not take that much grazing or that long a period of grazing to reduce floristic diversity long-term. This may not have much impact on butterflies because they are usually not dependent on rare plants, but other insect species may be dependent on that flora. On the other hand, light continuous grazing or moderate rotational grazing may maintain a more favorable diversity and structure of grassland flora than long-term nonmanagement. I suspect that some long-term negative impacts of grazing evident in flora and fauna missing in grazed sites today result from economic pressure in an adverse year. For example, in extreme droughts, severe overgrazing may have occurred in an agricultural context to try to get more stock to survive longer. I would expect conservation grazing to be more consistently attuned to forage carrying capacity because that grazing isn't about farm economic survival.

Scott and I have observed grazing systems in several midwestern states. Most of our prairie study sites are firemanaged, as might be expected since preserves offer the most sites most easily accessible to the public and most of these are fire managed. Our next largest sample of prairie sites comes from haying, since some Missouri preserves were hayed in the 1990s when we surveyed them. That leaves grazing with the short end of the stick so to speak and the biggest question marks for me, even though grazing seemingly offers the widest range of possible implementations (intensity, length, species of stock, etc.). We have augmented our formal surveys with some point counts peering over the fence at private property.

As might be expected, our results from surveys in grazing systems are highly variable, just as the grazing histories and regimes are highly variable. In Wisconsin (Hogback) in annual light-moderate cattle grazing, we found high specialist butterfly richness, with some individual species significantly higher than in burning or idling in the same state. Moderate rangeland grazing in eastern North Dakota (Sheyenne National Grassland) had relatively unfavorable results for many specialists compared to having or burning in the same region (counting western Minnesota). But a few specialists had the opposite of the general pattern (i.e., they were low in the Wisconsin grazing or high in the Sheyenne grazing). Many other lepidopterists have reported that sites in heavy or intensified grazing lost or lacked specialists, but in a few instances, less intensively grazed sites had abundant specialists of some species, especially Regal Fritillary and Dakota Skipper.

Buena Vista Grassland (Wisconsin) is where we've seen the most effective brush control by grazing. This is a large site primarily composed of old field vegetation. The unit may be cut/burned first if brushy, followed by one or two summers of heavy season-long grazing followed by rest years. Repeated browsing by the cows of the resprouting brush evidently occurs and the season-long duration of this stress root-kills much brush. In this case, the grazing is analogous to stand replacement (resetting or reducing woody plants) and for some years afterward the vegetation is substantially altered toward a more grassland structure, increasing area of that habitat. We've seen a "release" of butterfly abundance primarily in the second year following grazing. For example at both Hogback and Buena Vista, a sharp uptick in abundance of Regal and Aphrodite Fritillaries occurs then. However, this grazing intensity is unsuitable for undegraded prairie flora. Plus, if the above-ground growth of the woody plants survive (rise above) the grazing impact, then brush will expand unchecked.

At Sheyenne National Grassland (North Dakota), I couldn't tell how much of the semi-degraded vegetative condition at the time we surveyed was due to its dustbowl heritage and how much due to current grazing. Likewise for formerly grazed sites in southern Wisconsin, I can't tell how much the semi-degraded vegetation is due to grazing observed right before preservation and how much due to prior grazing. However, I expect grazing to lead to greater weediness, due to at least three factors: the baring of the soil surface by the animals (walking, wallowing), unpalatable weeds being avoided by the animals (such as thistles), and use of supplemental hay feed for the stock. On the other hand, many preserves were in an economic grazing use prior to conservation and yet their flora and fauna were still deemed worth conserving. This indicates the possibility that sometimes some weediness may be the price for also having a superior fauna of specialist butterflies.

I'd like to apply the same factors to grazing as described earlier for effects of burning on butterflies. This is more complicated to pull off, given how much more variable grazing is in practice. Where are the butterflies when the grazing happens? Survival in the grassland layer of the site depends on the grazing intensity (the lighter the grazing, the greater the survival). If survival is low, but after the grazing, the vegetation is suitable, then (as with burning), the dispersal tendency of the butterfly and number of generations per year can determine how quickly it comes back into the grazed area. Degree of specialization of the butterfly species affects not only how likely it is that there are survivors occurring in the surrounding landscape around a grazed area but also how picky or not the butterfly is about the vegetation. The more flexible, the more likely the butterfly can make use both of long ungrazed as well as recently grazed areas in the vicinity. This in turn makes it more likely that the butterfly population can persist in a grazed site. How do the key plants for that butterfly respond to grazing? In light to moderate grazing, for example, short flora such as violets (caterpillar food for fritillaries) may benefit from removal of some overtopping grass. However, butterfly species requiring resources that are preferred grazing forage will experience reduction.

MOWING/HAYING AND INSECTS

Throughout this series on management, when I discuss conservation applications of mowing (mechanical cutting that leaves the cut vegetation to lie in place) and haying (mowing with removal of the cut vegetation), I mean a single cut per year in an area of native herbaceous vegetation, not the entire patch and not more often than that.

The immediate effect of mowing and haying on insects includes some mortality. While adults leave unless immobile at the time of cutting, immatures are negatively affected, especially ones higher in the grass. Via an indirect means, it is evident that some adults and immatures do survive the immediate effect of mowing, since hay is a way that insects are transported from one site to another. Even adults can survive this, as we found out in an analogous situation when a Hackberry Emperor survived being rolled up in our tent and stowed in the trunk all day! Fortunately, the next night we were also camping, and in a place in range with hackberry trees.

However, most of the negative impact may come afterward in the short term. This is a "shock phase" due to the removal of resources. Adult butterflies leave the site (if the mowing occurred in the growing season). Immatures that are actively feeding may starve due to lost resources or die in an unsuitable microclimate that is harsher than before. However, other immatures may show little effect if not active while the vegetation is cropped short, as we have observed with 'Karner' Melissa Blues. Even in the short-term, while the vegetation is shorter than pre-cut, some butterflies return. The first are the most mobile and adventive. However, I have also observed specialists such as Regal Fritillary in recently cut areas. Plus, this reduction in insect species richness and abundance is less in amount and duration than in a comparable area burned. I think this is because both the direct mortality is less and the shock phase is not as pronounced (substantially more vegetation still exists after a mowing) nor lasts as long. However, an individual species can be very vulnerable to negative impacts of mowing/having, or a particularly timed instance of such cutting.

Cool-season cuts show less effect than growing season cuts in direct negative impacts. This is probably because insects are dormant then, and so are not deprived of required resources. This suggests that more of the mortality is due to the short term "shock phase" than to direct mortality from the experience of being in vegetation being cut. When the insects come out of dormancy, the plants mowed in the cool season are also regrowing and so there is relatively little disruption for the insects.

In the intermediate term (after the vegetation has mostly regrown through one year after the cut), insect species richness and abundance can be similar to precut levels. Some insect species are still recovering, with others peaking compared to earlier and later in the rotation. When treatment plots are small (30-50 x 30-50 m) or narrow strips embedded in untreated vegetation, little difference in insect richness may occur in the intermediate term between treatments and controls. An African study looked at grasshopper richness and abundance in relatively small plots and found both measures higher in burn than mow. But all burn plots were 1.5 years or more since last fire while all mowed plots were 0-8 months since cutting. Some species only occurred in the longest unburned (3 years prior) and some only in plots cut more than once per year. When plots are small these surprising results can occur that are against general patterns evident in larger treatment areas. The most negative short-term impacts occur when an entire patch is cut at once during the growing season; the least when only a portion is cut per year, especially if that cutting is spread out in staggered timings.

Most of our surveys in the first year following mow/hay occur in this time frame (weeks or months after the cut). In Missouri, where we had enough of a sample for more substantive analysis, abundance of each category of

butterflies (grouped as specialist, grassland, generalist, immigrant) was higher in the year following a summer haying than in the next year afterward. This difference was least for specialists and the decline greatest for immigrants. I would caution that vegetative productivity in Missouri is phenomenal; what long hot humid summers they have! This may contribute to the rapid positive response to mowing. With a more limited sample to analyze in Minnesota and eastern North Dakota, it appeared there was an increase from that first year to the second for specialists (Regal Fritillary, Dakota Skipper), and (with even less sample) anecdotally for Poweshiek Skipper.

Long term effects of mowing/having (in the sense of later years in rotational management). Short rotations (1-3 years) are often done in mowing and having regimes. Most of the information on longer time frames come from sites where mowing/haying has been abandoned. For example, in a European alpine meadow, there was a direct relationship between declining herbaceous flora (number of species) and more years since last hay cut. Butterfly diversity correlated with this, with more butterfly species in richer flora, except that "recently abandoned" fields (which had just changed from annual having to the first year no longer haved) had higher butterfly diversity than currently annually hayed fields. This study has the limitation that the fauna is presumably limited to those species that can survive in a landscape with annual having for decades. However, even for such a fauna, a rest year was still favorable. This suggests the overriding value of not cutting the entire patch at once. But it also suggests that recovery from cutting happens relatively quickly, so that the floristic effects (rather than direct impacts of insect mortality) were more important in driving the insect results.

Very long term effects of mowing/having occur after decades. In our surveys, in both western Minnesota and western Missouri, all butterfly groups were significantly more abundant in rotationally haved than rotationally burned prairies. Counts of species totals produced significant results only in Missouri, with all butterfly groups significantly richer in hayed than burned prairies. I caution again, though, that some particular species, including a few specialists, were significantly lower in abundance in haved than burned, but still significantly higher in something else than burned. Haying, or certain haying regimes, are not optimal for all grassland and specialist butterfly species. Furthermore, in barrens mowing was not significantly different from burning for richness or abundance of any butterfly group. This mowing occurred primarily in rights-of-way instead of for conservation, so this is not a final conclusive answer for that management in a conservation context. However, our results in barrens, for management type and years since last treatment, suggest that it is the landscape context (less fragmentation) that associates with this more tolerant result, rather than that this fauna is more resilient to more drastic management. In other words, reinforcement from the surrounding landscape enabled the butterflies to have more favorable, less sensitive responses to management. Still, at the individual species level, most specialists showed a preference for a management type other than fire. It's just that they did not all prefer the same management. Nonetheless, Regal and Aphrodite Fritillaries, Dakota, Pawnee, and Arogos skippers were significantly more abundant in haying than burning; in barrens, Persius Duskywing was significantly more abundant in mowing than burning.

I'm not able to distinguish between mowing and haying as it affects butterflies because I've not run across any studies comparing the two, and while I've studied both, I've never studied both in sufficient amount in the same vegetation type and region. Most research on mowing and haying tend to occur in places where that was the traditional management—for example, marsh hay or mowed rights-of-way. The management may be continued in a conservation context, but again, arising out of seeing the traditional management already occurring. As a result, most of my mowing experience is in barrens and all my haying experience in prairies and old fields.

I'd like to apply the same factors to mowing/haying as described earlier for butterfly response to fire. Are the butterflies in turf or not? If they are above ground in the grassland layer, they are most directly affected by cutting. The number of generations per year and dispersal tendency of the species (how localized or wide-ranging its flights) can determine how quickly it comes back into the cut area. Degree of specialization of the butterfly species affects not only how likely it is that there are survivors occurring in the surrounding landscape around the cut area but also how picky or not the butterfly is about the vegetation. The more flexible, the more likely the butterfly can make use both of long uncut as well as recently cut areas in the vicinity. This in turn makes it more likely that the butterfly population can persist in a site that's mowed or haved. How do the key plants for that butterfly respond to cutting? Plants of short stature, such as violets, may thrive. Furthermore, does the cutting remove a key resource (e.g., flowers that are caterpillar food) when the butterfly species needs them, especially as immatures?

One key difference between burning and mowing/haying is that the latter removes the above-ground canopy of woody plants while fire does not. Mowing is always stand-replacing (although occasionally a shrub may bend under the machine and remain uncut). Sites managed with conservation-compatible mowing/haying usually have a strikingly herbaceous vegetative composition. In both burning and cutting, woody plants resprout from the roots. However, in rotationally mowed/hayed sites, the cutting is relatively more tolerated by insects than burning, so that cutting can be done relatively more frequently. Furthermore, cutting allows for the possibility of being a spot treatment (not broadcast), so that brushier areas can be treated more frequently than less brushy areas. Effects of mowing/haying on plants. This management can lead to flower-rich grasslands and spectacular flower displays in the first growing season after a cut. This "refreshes" growth (much as gardeners "dead-head" flowers) that can attract butterflies to come back in and use (for nectaring and egg-laying, for example). This management can also shift the structure to shorter dense turf and growth structure. Anecdotally, I've noted the possibility that doing the haying in fall leads to a dense sod with relatively more grass while a mid- to late summer cut is particularly flower rich (not as grass dominated).

IDLING (DOING NOTHING) AND SPOT (LOCA-LIZED) TREATMENTS

Doing nothing may be inadvertent, due to an oversight or lack of resources, but it can be a deliberate choice. It is not usually studied directly, but results of this strategy are obtained when it is used as a control for the active intervention being studied. This management type is also implied in studies of large wild places, by definition "idled" (not managed). Sometimes the term "idle" is applied to a site not being actively managed that year. That definition is not appropriate in my context here. Since fire regimes are often done in rotations of about 2-6 years, I think the same time frame should apply to other managements here too. If it was haved three years ago, that's a having rotation, not a combination of having and then idling. When I read others' studies, I try to re-label those in my mind as rotational management, rather than a change in management from active to idling.

For my purposes here, I define "idling" as at least 8-10 years since last management. I pick that because a previously burned unit made a permanent non-fire refugium started functioning as a "perm" at about 6-8 years since the last burn. If idling is a deliberate management choice, then I think of that as the plan for some years into the future, or until an obvious deleterious change in the habitat is evident. In that case, a broadcast management (burning, grazing, mowing/haying) may occur. Or a spot treatment (bush-hogging, mowing, herbiciding) may occur in the problem area, leaving large areas still idled.

Because of the difficulty in identifying how long a unit has been idle, and in getting the unit untreated long enough for my purposes here, I am limited in what I can say here. Idling is rarely an optimal strategy but sometimes it is more favorable for specialist butterflies than intensive management, such as large and/or frequent burning. Idling is especially favorable when the vegetation is relatively stable in structure and composition from year to year, rather than deteriorating in brush and weeds without active intervention. I need to caution that even when the vegetation appears stable to us humans, it can still change in a subtle way that can mean a big change (positive or negative) for a butterfly population if the change affects a key resource. I think of idling not usually as an indefinite strategy but as an appropriate interim while surveys and monitoring occur, while management is being studied, and the site history learned.

Vegetatively, idling offers resources useful for animals. Relative consistency in vegetation occurs year to year. Accumulated litter is a resource. Brush invasion is a concern, but some plots are relatively unbrushy, and if so, and if the sod and litter are dense, then brush may be slow to get established and expand. Some plants useful to butterflies (such as docks) are weedy and these plants may fare better in actively managed sites (where bare or lightly covered spots allow regeneration).

TIMBER HARVEST AND INSECTS

Timber harvest (tree cutting) is most likely to be relevant to savannas that have overgrown with trees. In that case, either selective or large scale (clear) cutting might be an option. I've found relatively little research to address butterfly conservation applications of timber harvest. Some research compares clear-cutting to wildfire, but the latter is not an active management and so this is not directly comparing two active management interventions. It also usually does not have pre-treatment (pre-wildfire) measurements. Another compared burning or not burning cut areas but the sampling occurred when cutting was a year old but the burning only a day old. This is not comparing similar time frames between the cut-only and the cut+burn. Others compare the first few years after thin+burn treatments to no treatment (forest). Butterflies, including canopy associated species of conservation interest such as Diana Fritillary, can be more abundant in these treatment areas, including the first growing season after treatment, than in controls.

Incomplete as these scenarios are, here are some initial observations. Cutting alone can stimulate flowering via canopy reduction, but cutting plus burning can lead to even more of a flush in nectar and reduction of canopy. After all, this is a double treatment of clearing the above-ground vegetative layer, compared to a single treatment (cut only). The relatively favorable response of plants and butterflies fits the wildfire model discussed above (relative infrequency of treatment and context of longer untreated but occupied landscape). Let me raise the same caution voiced for wildfire: lack of pre-treatment surveys in and near the treatment plots. Furthermore, even many forest butterfly species are attracted to sunny areas and their nectar, while nonetheless needing more canopied areas for breeding. I would expect widely distributed butterflies (even in thin numbers) to cope with this cyclical management better than specialist butterflies localized either to open or canopied habitat. My concluding caution comes from the prairie experience. A management can look safe, even beneficial, when part of the habitat patch is managed that way, but not so when the entire patch has been. Some of these harvest studies may be occurring in landscapes that have not had the full cycle occur yet in all of the landscape.

ISSUES IN MANAGEMENT COMPARISONS

Management isn't studied compared to an "ideal" but instead in comparisons among existing examples. There is no BOOT (biological oracle of truth) that tells us the ideal fauna for a habitat or the best possible natural occurrence and abundance for species. In other words, all grading is on a curve. Something will come out better even when none did very well in an absolute sense. So it's always important to examine what's being compared to what? In an absolute sense, how many got found? Butterfliers have a sense of what's a lot or not: "better" may still mean hardly any found.

While there are lots of ways to rig science, in my experience I think this is not usually deliberate. Mostly I think this is unintentional, even unavoidable. Here's an example from my work. Alternatives to burning such as haying and grazing usually are not available to study in highquality native prairie vegetation, because most prairie preserves are in fire management and I assume that with all the preserves out there, by and large the highest quality sites were targeted for preservation first. However, most of these high-quality preserves were haved or grazed, often for decades, prior to preservation. In many regions, the only way to get a large independent sample of sites in having or grazing means going to private property. But these managements are being done for farm purposes, not conservation, and so may not be done in ways that are meant to be beneficial for conservation. As a result, this can underplay the potential benefits of these managements for conservation. In the one state in our study (Missouri) where having was widely used as a conservation management, we obtained the strongest positive results for that management.

Other inadvertent consequences results from starting to study a site just after conservation. This can be entirely innocent. It's a new site, interesting and exciting, plus a goal is to learn what all is there. But this fits the pattern of studying a site while it is still under the influence of past (pre-preservation) management but also experiencing new management too. I've also sometimes been amazed at sites missing from status surveys and research programs whole square miles of prairie refuges long preserved and in the same region. Instead, the study occurs where it's still possible to find prairie specialist butterflies in either private or conserved land. But both groups of sites are important for understanding what's happening with the study species.

My favorite way to test the effectiveness of a study method or validity of a line of logic is to reverse the treatment type. In the context of fire studies, at every mention of fire, I change the word "fire" in my mind to "cattle grazing," because attitudes about these two managements are about opposite for many conservationists. Or I make it about an entirely different field, such as human medicine. Would that logic convince me that the treatment works?

For example, many studies sample only burned prairies to see what's there only after fire management has started. Relatively few well established baselines exist for the insect faunas in sites prior to preservation. This requires extensive surveying for at least several years. Relatively many studies of fire management only document the fauna after fire management has been in existence, sometimes with all parts of the habitat patch burned prior to any faunistic surveys. Many of our flagship prairie preserves were grazed for a long time prior to conservation. Would you use the same setup to determine whether grazing is fine for all prairie species? I sure wouldn't. What about species that didn't survive the grazing at all, and only survived prior to preservation in haved prairies? Studying only the survivors of a management is analogous to studying only smokers who are still alive now, and seeing whether one pack a day makes a difference vs. three a day, or whether a reported history of smoking for ten years shows a difference in health from 30 years. Any smokers who have already died are not in the study at all. The data themselves are fine. X individuals of y species were surveyed in a specific location on certain dates with certain vegetative and management characteristics. It's what we think these observations teach us that needs careful thought.

It's my job here to try to establish fair standards and apply them to all managements, for example in evaluating "recovery." When number of species and individuals of butterflies increase in the 1-2 years after reduction or removal of haying or grazing, this is usually taken to mean that the management was harming the butterflies. But when this happens following burning, this is usually taken to mean that the "normal" cycle of fire is occurring. Instead, I think we should define "harm" and "recovery" the same way for all management types.

If it sounds compelling that if any specialists have survived in prairies burned for many years, burning isn't responsible for any paucity or absence of other specialists appropriate to the habitat, then let's turn that around and look at grazing for many years. We surveyed Sheyenne National Grassland in the 1990s, and even after decades of moderate to heavy annual grazing, we found widespread Regal Fritillaries and 'Pawnee' Leonard's Skipper, as well as Poweshiek and 'Assiniboia' Common Branded Skipper. In fairness, this site is a dustbowl reversion from prior attempts at cultivation, so some problems with the flora and fauna may be attributable to that and not subsequent management. However, we found only one each of Poweshiek and Assiniboia, and no Dakotas, even though they had been recorded here previously. Furthermore, we found Poweshiek in good numbers in a nearby rested hay prairie and an Arogos in an annually haved prairie. Thus, both the absences and the presences are important pieces of evidence.

Likewise, some forestry lands have a lot of great Lepidoptera in them but I do not assume that what's there now proves that what's going on there now will continue to result in great Lepidoptera. That's because of lag res-

Butterfly Conservation Management in Midwestern Open Habitats

¹² Part 3: How does habitat management affect butterflies? by Ann B. Swengel

ponses of Lepidoptera to changes in landscape context and variation in management practices. What lives there now relates a great deal to past management. Current management may take years or decades to show its full impact. If there are any positive results in any kind of forestry, this does not mean that all forestry activities of any kind must be OK; likewise for ranch grazing and farm haying. I need some outgroups of similar habitat type but different management type to provide context, or I need long-term data from within the sites to establish trend.

CONCLUSION

Response to management does not appear to sort by ecosystem affiliation but rather by taxonomic affiliation. That is, life history traits such as pupation underground are characteristics of certain groups of insects (certain genera or families). But different species in a given group occur in different kinds of habitats. There does not appear to be a concentration of species (regardless of taxonomy) with more defenses against fire in those ecosystems thought to burn more or to be fire-dependent.

A study in rural Sweden suggests the very long-term effects of management. Historical land use going back 200 years did a better job of explaining which plant species lived in the grasslands now than current land use did. Best was a consistent use, e.g., grazing or having, throughout the entire period. While long-term grazing produced the best floristic results now, a consistent use of having throughout the entire period was better than a switch from having to grazing, even decades ago. So conservation is better served when it is retrospective to before conservation in embracing site stability, rather than starting the "best" management now, only looking forward after conservation. Attempting to turn the clock back before any degradation can do more harm than embracing the semi-natural history and condition of the site now. To the extent that plant composition is a driver of the composition of a site's insect fauna (along with direct mortality to insects), this suggests the essentially permanent effects (at least on the scale of human lifetimes) of management choices that disfavor some of the flora in a site.

The positive responses of midwestern specialist butterflies to mowing/haying and light grazing can be understood two ways. (1) These hark back to the more diverse and abundant grazing and browsing fauna of prairie, savanna, and barrens back before European exploration and colonization. (2) That's how most sites had been managed for decades, even centuries, after European settlement, and so the fauna that has successfully persisted and found refuge there is a fauna tolerant of those managements.

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