

SURVEY OF THE BUTTERFLIES OF THE WAH'KON-TAH PRAIRIE, MISSOURI

GARY NOEL ROSS¹

McGuire Center for Lepidoptera and Biodiversity,
Florida Museum of Natural History, University of Florida, Gainesville, Florida 32611, USA
e-mail: gnr-butterfly-evangelist@juno.com

ABSTRACT.— The Wah'Kon-Tah Prairie Preserve is located in southwestern Missouri and is a remnant of the once extensive Tallgrass Prairie Ecosystem. The preserve consists of 2,332 acres (944 hectares) within the Osage Plains-Flint Hills Ecoregion of Missouri. The preserve is owned by The Nature Conservancy (Missouri Office) but managed by both the Conservancy and the Missouri Department of Conservation, El Dorado Springs Division. Between May and October 1998, the author lived on the newly acquired Thoreson Ranch that linked the original Wah'Kon-Tah Prairie Preserve and Mo-Ko Prairie Preserve. Daily butterfly inventories were conducted and recorded weekly. The cumulative total of species observed was 74 (71 during this survey, 2 by others, and 1 by the author in 2002). Tallgrass Prairie management involving haying, burning, and tree removal as they affect butterflies in general and the regal fritillary (*Speyeria idalia* (Drury)) in particular are discussed. The possible role of micronutrients and/or phytochemicals procured through nectaring by regal fritillary butterflies is discussed. Selected photographs of habitat and the regal fritillary are included.

KEY WORDS: conservation, bison, burning, ecology, ecoregion, El Dorado Springs, fire, Flint Hills, grazing, haying, Great Plains, Konza Prairie Research Natural Area, maintenance, micronutrients, Midwest, Mo-Ko Prairie, Nearctic, North America, Osage Plains, phytochemicals, regal fritillary, *Speyeria*, Tallgrass Prairie, The Nature Conservancy, Thoreson Ranch.

"The nation behaves well if it treats the natural resources as assets which it must turn over to the next generation increased, and not impaired in value."

Theodore Roosevelt

The word prairie is a French word meaning "meadow" (Duncan, 1979). Technically, prairies constitute the Grassland Biome (Clements and Shelford, 1939; Kendeigh 1961). Within North America, the term "Northern Temperate Grassland" is often used to describe the distinct vegetation formation (Shelford, 1963). Prairies appear in the interior of large continental land masses such as Eurasia, Africa, Australia, and South America (see Clements and Shelford, 1939, Kendeigh, 1961, Sanderson, 1967, and Shelford, 1963 for excellent descriptions). Depending upon where they occur, various names are used to describe this distinctive land type: steppe, puszta, veld, pampas, prairie, plains (Kendigh, 1961). At one time grasslands covered 42 per cent of the earth's surface (Kendeigh, 1961).

Grasslands develop where rainfall is reduced to between 40 inches (100 cm) and 12 inches (30 cm) (Shelford, 1963) due to distance from oceans, especially where large mountain masses intercede to block moisture-laden winds (Sanderson, 1967). Grasslands everywhere possess marked similarities in climate, physiognomy, and animal mores (Kendeigh, 1961). In appearance, grasslands are characterized by a "predominance of grass and an absence of trees (except along rivers and streams), by gently rolling topography, and by periodic drought" (Reichman, 1987).

The Grassland Biome is the largest biome in North America (Shelford, 1963). This ecological unit ranges in three extensive belts (the "Prairie Belt"), running generally north and south from Edmonton, Alberta (Canada) almost to Mexico City, a distance of 2400 miles (3840 km), and from the Pacific Coast to western Indiana (Shelford, 1963). To quote from *Where the Sky Began: Land of the Tallgrass Prairie*, by Madson (1995):

"The first real grassland seen by travelers from the East was tallgrass prairie, with giant grasses up to twelve feet high in some places. Farther west, this merged into mixed prairie, which still wore tallgrasses on lower, well-watered elevations but which was composed of shorter midgrasses in greater frequency. As big bluestem grass was a character of the tall prairie, so little bluestem was characteristic of the mixed prairie. In turn, that mixed prairie melted off into shortgrass country the Great Plains, with their short wheat grasses and buffalo grasses."

Tallgrass prairies represent a relatively small portion of the grasslands that occur around the world. But because of relatively abundant rainfall, Tallgrass Prairie is the most intricate of the three kinds of prairies (Duncan, 1979; Larrabee and Altman, 2001). In North America, Tallgrass Prairie once included portions of 14-18 states, one Province of Canada (Manitoba), and spanned from 400,000 square miles (256 million acres; 1.04 million km²) (Duncan, 1979) to 221,875 square miles (142 million acres; 574,000 km²) (Madson, 1993, 1995; Reichman, 1987). The eastern beginnings occurred in northwestern Pennsylvania, where grassy openings (meadows) appeared in heavy deciduous forest (Madson, 1995). Moving westward, the trees dwindled and the grasslands proliferated in what has become known as the American Midwest. These "giants" then extended westward to the eastern borders of North and South Dakota, Nebraska, Kansas, Oklahoma, and Texas (a coastal variation of the system occurred along the Gulf of Mexico in southeastern Texas and southwestern Louisiana). Throughout the ecosystem the landscape was pastoral with a subtle beauty. Soaring grasses undulated across a treeless earth beneath a domed heaven; the horizon encircled but was always just beyond reach (see Covers). This unique land was derived from a timeless interplay between moderate amounts of rainfall, diversified deep-rooted grasses, large herbivorous mammals, and fires generated periodically by both lightning and native peoples. Although the landscape was dominated by vast expanses of grass, often "taller than a horse and rider" (Ladd, 1995), wildflowers frequently carpeted the deep, rich, black soil (Fig. 2-3).

1. Research associate. Mail address: 6095 Stratford Ave., Baton Rouge, LA 70808.



Fig. 2. Section of prairie that had been hayed the previous summer: A. Ashy sunflower (*Helianthus mollis*) (Asteraceae) is a common summer species. B. Same section of prairie two months prior (early June): pale purple coneflower (*Echinacea pallida*) (Asteraceae) and butterfly weed (*Asclepias tuberosa*) (Asclepiadaceae) often create spectacular displays.

In *Tallgrass Prairie Wildflowers*, Doug Ladd (1995, page 6) includes as a prologue a quote from Eliza Steele describing her 1840 impression of an Illinois prairie:

"A world of grass and flowers stretched around me, rising and falling in gentle undulations, as if an enchanter had struck the ocean swell, and it was at rest forever. . . . You will scarcely credit the profusion of flowers upon these prairies. We passed whole acres of blossoms all bearing one hue, as purple, perhaps, or masses of yellow or rose; and then again a carpet of every color intermixed, or narrow bands, as if a rainbow had fallen upon the verdant slopes. When the sun flooded this Mosaic floor with light, and the summer breeze stirred among their leaves the iridescent glow as beautiful and wondrous beyond anything I had ever conceived. . . ."

Duncan (1979) describes the original Tallgrass Prairie as a "teeming factory of life" that supported 80 species of mammals, 300 species of birds, and thousands of kinds of insects and other animal life.

But the biota were in constant flux. To quote from Collins *et al.* (1998, page 302):

"In contrast to many other systems where ecological processes are constrained by chronic limitations of a single resource,

organismic to ecosystem processes and dynamics in tallgrass prairie are products of spatial and temporal variability in three primary limiting resources: light, water, and N. Variability in and switching among these primary limiting resources are caused by both extant and historical regimes of fire, grazing, and climate. Moreover, responses to these factors are strongly dependent on topographic and landscape position. As a result of this complexity, tallgrass ecosystems exhibit distinctly nonequilibrium dynamics."

Modern man has exploited the Tallgrass Prairie ecosystem more than any other. Estimates vary, but today no more than 2-10 percent of original Tallgrass Prairie remains (Madson, 1993). By and large, the native grasses have been replaced with domesticated cousins such as corn, wheat, and milo (Fig. 4); native grazers such as American bison (buffalo), pronghorn, elk, and deer have been replaced by domesticated livestock. In essence, the Tallgrass Prairie is today the American Heartland, producing much of the world's foodstuffs. Whatever "natural" Tallgrass Prairie is left consists of relatively small parcels of fenced lands (Fig. 5). Because of the absence of grazing and browsing mammals as well as natural and man-caused fires, these lands are continually subjected to incursions by seeds from forest species brought in by settlers over the past two centuries.

Consequently, "natural" Tallgrass Prairie lands now must be artificially managed. Usually, a rotational regime involving selective grazing (usually cattle and goats), haying with large mowers, and controlled burns is employed on a cyclical basis in order to destroy shrubs and trees that otherwise would rapidly invade to establish a forest of shade and in time, completely obliterating the domain of the grass (Fig. 6B, D). (Those areas in which tree invasion is aggressive, actual tree cutting and applications of herbicide are often employed). Fire management usually occurs with an interval of 2-5 years. Haying usually occurs on an annual basis with usually only one-third to one-half of the site being hayed at any given time. Times for burning and haying are determined by weather conditions and availability of funds and labor. In general, haying occurs in mid summer and burning anywhere between mid summer and late fall (occasionally in winter and early spring, also). These rotational schemes create a checkerboard landscape. It is ironic that in the past, the U.S. government as well as local governmental agencies encouraged the planting of trees on prairie lands in order to generate valuable wood stores (Palmer, 2000). Today the Tallgrass Prairie as a natural ecosystem is extinct.

Within Missouri, approximately one-fourth of the entire state (12-15 million acres; 4.8-6.07 million hectares) was classified as Tallgrass Prairie prior to 1800 (Auckley, 1994). By the late 1960's, this had dwindled to 250,000 acres (101,000 hectares) (Anon., 1994). Today between 40,000 (16,000 hectares) and 80,000 acres (32,000 hectares) survive (Auckley, 1994; Schroeder, 1982), less than one-third of one percent of the original area. The majority of these remnants remain in private ownership. A little less than 18,000 acres (7280 hectares) remain protected in the public prairies system (Auckley, 1994). These are managed by one or more of the following: Missouri Department of Conservation, Missouri Department of Natural Resources, Missouri Prairie Foundation, The Nature Conservancy of Missouri, and the University of Missouri (Botany Department).

Modern conservationists now realize that although much of the original Tallgrass Prairie ecosystem is extinct, there remain fragmented parcels of prairie lands. Also, conservations now realize that the ecosystem approach to preserving Earth's imperiled plants and animals is more productive than concentrating efforts on individual species or units of land prescribed by political or other artificial boundaries (Stolzenberg, 1998). As such, taxonomic surveys based on distinct natural or ecological regions, termed "ecoregions," are taking on increased significance.

Within Missouri, The Nature Conservancy has defined four ecoregions: Central Tallgrass, Flint Hills/Osage Plains, Ozarks, and Mississippi River Alluvia (Anon., 1998b; 2000). Although both tallgrass ecoregions (Central Tallgrass and Flint Hills/Osage Plains) are of special concern to conservationists, the Flint Hills/Osage Plains division located in western Missouri and extending into eastern Kansas and extreme northeastern Oklahoma is smaller and hence more vulnerable. Unlike the Central Tallgrass Ecoregion farther north, the Flint Hills/Osage Plains Ecoregion comprises the very last unplowed, though heavily grazed, Tallgrass Prairie of any size in North America (Duncan, 1979). And since the region was never glaciated (Reichman, 1987), in depth investigations there are crucial. Studies are now underway both in Missouri and Kansas to identify the region's biota. [The most celebrated and largest protected Tallgrass Prairie in the United States is Konza Prairie Research Natural Area (KPRNA), located south of Manhattan, Kansas. The preserve consists of 8,616 acres (3,487 hectares), originally a working cattle ranch, but now administered by the Division of Biology, Kansas State University (Knapp, *et al.*, 1998).]

This report on the Wah'Kon-Tah Prairie Preserve is the first published comprehensive survey of the butterfly fauna of a major



Fig. 3. Wah'Kon-Tah Prairie in spring and summer following a controlled burn the previous summer: A. Early spring (April): Bird's foot violet (*Viola pedata*) (Violaceae) and Indian paint brush (*Castilleja coccinea*) (Scrophulariaceae). B. Late spring (May): Wood betony or lousewort (*Pedicularis canadensis*) (Scrophulariaceae), shooting star (*Dodecatheon meadia*) (Primulaceae), and Indian paint brush (*Castilleja coccinea*) (Scrophulariaceae); inset is wild bergamot (*Monarda fistulosa*) (Lamiaceae), which begins to bloom in early summer. C. Mid summer (July): Colony of black-eyed Susan (*Rudbeckia hirta*) (Asteraceae).

sector of the Flint Hills/Osage Plains Ecoregion. While ecologists may decry the demise of the Tallgrass Prairie Ecosystem, we must not forget that the replacement of the region's native plants and animals with domesticated grains and forage crops has allowed America to profit greatly. In reality, the United States is the undisputed bread basket of the world and the only recognized "Super Power."



Fig. 4. The vast majority of America's heartland is now intensively cultivated, making the prairie provinces the bread basket for the world: A. Milo; the native sunflower, *Helianthus annuus* (Asteraceae) is a common field "weed;" B. Soybeans. C. Wheat. D. Corn and Mr. Mike Gurley, a fourth generation farmer/rancher in Appleton City, St. Clair County. Within present-day Missouri, less than one-third of one percent of original Tallgrass Prairie remains. And with only 2-10 percent remaining for the entire continent, the Tallgrass Prairie Ecosystem is the most endangered of all. (Photographs from St. Clair County.)

Fig. 5 (next page). Plants once abundant on the Tallgrass Prairie are currently found only as remnants along fencerows, on abandoned homesteads, and on a few preserves such as the Wah'Kon-Tah: A. Installing new fence marking new boundary of Wah'Kon-Tah Prairie Preserve (crop is commercial fescue grass grown for hay and seed). B. Fence with spring blooming native rose vervain (*Glandularia canadensis*) (Verbenaceae). C. The tall native summer sunflower (*Helianthus annuus*) on edge of man-made pond. D. Fence and early-summer butterfly weed (*Asclepias tuberosa*) (Asclepiadaceae) with orange sulphur butterfly (*Colias eurytheme*) (Pieridae); the white-flowering species is prairie beardtongue (*Pentstemon tubaeiflorus*) (Scrophulariaceae). E. Fence at an old homesite with non-native spring bearded iris (*Iris* sp.) (Iridaceae). F. Gate at an old homesite with non-native summer daylilies (*Heemerocallis* sp.) (Liliaceae). (Photographs from Cedar and St. Clair Counties.)







Fig. 6. Although farming is now the primary enterprise on prairie lands of the Midwest, cattle and goat ranching is also important (A and C). However, invasion by woody plants is an on-going problem. For prairie vegetation to be maintained, trees must be routinely killed by chemical sprays (B) or removed physically (D). Some land managers advocate the occasional pasturing of cattle and goats to control unwanted vegetation (see also Fig. 19). (Photographs from Cedar and St. Clair Counties.)



Fig. 7. The Flint Hills/Osage Plains Ecoregion of Missouri is named for the type of underlying rock (flint) and the indigenous Native American (Osage) culture that once dominated the region. Additionally, the Osage tribe lends its name to the osage-orange tree (*Maclura pomifera*) (Moraceae) also called Bois d'arc and "hedge bush." The tree is medium size and bears quantities of large green fruit (inset) containing a white pithy center relished by cattle. (Photograph from Dr. Bill Neale's homesite, El Dorado Springs.)

Location and History of the Wah'Kon-Tah Prairie

Wah'Kon-Tah Prairie Preserve is located at 37.52 N latitude and 94.01 W longitude, immediately east and northeast of the community of El Dorado Springs, population 3868, and approximately 22 miles (36 km) east of the community of Nevada, population 4000. The prairie is located in both Cedar and St. Clair Counties in southwest Missouri and is easily accessed by paved state highway 82, county highway H, and Lake Hills Road; state highway 82 bisects the preserve.

In addition, the prairie is boarded by several unpaved farm roads. Ecologically, the Wah'Kon-Tah lies within the Osage Plains Natural Region of Missouri (Heitzman and Heitzman, 1987 (1996)) and the Flint Hills/Osage Plains Ecoregion (Anon., 1998b; 2000). The word osage refers to the Osage Tribe, a midwestern group of Native Americans. The word also refers to a native tree, osage-orange (*Maclura pomifera*) (Moraceae), noted for its orange-colored wood, and which because of its durability is used in the manufacture of furniture and fence posts; the tree bears a conspicuous large green fruit relished by livestock (Fig. 7).

The Wah'Kon-Tah Prairie Preserve is owned by The Nature Conservancy (TNC) (Missouri Office) and maintained by both the conservancy and the Missouri Department of Conservation, El Dorado Springs District (MDC) (Toney, 1994). Until December 1997, the preserve consisted of three independent parcels of land: (1) Wah'Kon-Tah Conservation Area, 1,040 acres (421 hectares) in St. Clair County, purchased by TNC in 1973, 1976, 1981 and 1993

with funds by Miss Katherine Ordway); (2) the Mo-Ko Conservation Area, 420 acres (170 hectares) in Cedar County, purchased by TNC in 1974 and 1975 with funds by Miss Katherine Ordway (Anon., 1991; Toney, 1994); and (3) the Thoreson Ranch, 872 acres (353 hectares) in Cedar and St. Clair Counties, a two-generation family ranch and homesite owned by Ted and Sue Thoreson, bordering the Mo-Ko prairie (Fig. 1). With the acquisition of the Thoreson Ranch in December 1997, TNC was able to connect the Wah'Kon-Tah and Mo-Ko units to establish a single sanctuary of 2,332 acres (944 hectares) and bearing the common name Wah'Kon-Tah (Summerhof, 1998).

The names Wah'Kon-Tah and Mo-Ko reflect and honor the cultural legacy of the Osage Indians, former residents of the region (Anon., 1991; Schroeder, 1982). Wah'Kon-Tah translates as "Giant Spirit" or "Great Mystery," and Mo-Ko refers to "medicine" (Toney, 1994). The newly constituted Wah'Kon-Tah is Missouri's second largest tract of Tallgrass Prairie. [Prairie State Park with 3,462 acres (1,401 hectares) in Barton County and 15 miles (25 km) west of the small community of Lamar is the largest.] The Wah'Kon-Tah Prairie is open to the public and visitation is encouraged (Fig. 8). To date, no permanent trails exist. Off-road vehicles, pets and horses are not permitted. Scientific investigations require permission from The Nature Conservancy (Missouri Office) headquartered in St. Louis.

History of the Butterflies of the Wah'Kon-Tah Prairie

For years, *Butterflies and Moths of Missouri*, by J. Richard and

Joan E. Heitzman (1987/1996), has been the standard reference for Missouri's butterflies. The volume contains good text and colored photographs of virtually all of the state's 156 species (125 residents and colonists, 31 vagrants) (Robbins and Opler, 1995; Ross, 1995b). Unfortunately, citations for locales are very broad, referring only to general regions of the state.

Between 1993 and 1999, Ann and Scott Swengel, of Baraboo, Wisconsin, conducted annual, one-day butterfly counts on the original Wah'Kon-Tah and Mo-Ko units, but included the nearby Monegaw Conservation Area as well. The surveys were part of the official "Fourth of July Butterfly Count" program sponsored initially by the Xerces Society and later by the North American Butterfly Association (NABA). These reports (Opler and Swengel, 1994; Swengel and Opler, 1995-2000) report a cumulative total of 45 species. Additionally, the Swengels have reported separately on the results of some of their observations on the regal fritillary, *Speyeria idalia* (Drury) (Nymphalidae: Argynninae) and arogos skipper, *Atrytone arogos* (Boisduvall & Leconte) (Hesperiidae: Hesperinae) on the Wah'Kon-Tah and Mo-Ko prairies (Swengel, 1993, 1997; Swengel and Swengel, 1997). Hammond (1984), Hammond and McCorkle (1984), Hovanitz (1963), Stolzenburg (1992) and Williams (1999) have all contributed reviews on the status of the regal fritillary.

I was introduced to the prairies of southwest Missouri in September 1996 when I visited Prairie State Park and the Wah'Kon-Tah, Mo-Ko, and Monegaw Prairie Conservation Areas to observe regals. My objective was to compare the butterfly's behavior with that of the related *Speyeria diana* (Cramer), a species I was researching on Mt. Magazine in northwestern Arkansas (Ross, 1997, 1998a,c,d, 2001a,b, 2002, 2003b, 2004a,b; Ross and Henk, 2004). I returned to the area both in the early summer and fall of 1997. During 1996 and 1997 I documented my butterfly sightings in Prairie State Park and contributed these reports to personnel there.

Having become enamored with the prairie and the role of The Nature Conservancy in protecting and managing prairie sites throughout Missouri, in 1998 I accepted a contract from the conservancy to become their "Lepidopterist in Residence." Between May 2 and October 4, 1998 I resided in the recently vacated home of Ted and Sue Thoreson on their homesite, the conservancy's new-

ly acquired property known as the Thoreson Ranch (Fig. 1, 9-10). My responsibilities included research on the life history of the regal fritillary butterfly (*Speyeria idalia*), a survey of Wah'Kon-Tah's butterflies, detailed photography of the region, and to serve as liaison person between the conservancy and the community of El Dorado Springs (Ross, 2003a,b, 2004a,b; Ross and Henk, 2004; Ross and Nickle, in prep.).

During my 1998 residency, I also visited the following nearby public prairies for comparisons: Bushwhacker Lake Conservation Area, Gay Feather Prairie Conservation Area, Golden Prairie, Little Osage Prairie Conservation Area, Osage Prairie Conservation Area, Prairie State Park, Ripgut Prairie Natural Area, Sheldon L. Cook Memorial Meadow, Schell-Osage Conservation Area, Schwartz Prairie, Sky Prairie Conservation Area, and Taberville Prairie Conservation Area. In August 2002 I was able to revisit the Wah'Kon-Tah to conduct a one-day survey as part of a "NABA Butterfly Count" (Swengel and Swengel, 2003). The butterfly data from my 1998 residency constitute the basis of this paper.

Description of the Site

According to Auckley (1994),

"The prairies of northern and western Missouri did not have the limitless reaches of those farther west. Timber was never far away. Settlers here could live among the trees and have lumber for homes and rail fences while using the prairie. They did not hitch teams to the special plow designed for cutting sod used in building prairie sod houses."

These "comfortable" conditions were a result of the region's relatively high amount of rainfall. The National Climatic Data Center (NCDC, Asheville, NC) furnished the following climatic data for El Dorado Springs, the nearest weather station to the Wah'Kon-Tah Prairie:

Temperatures: June: average high, 84.7°F (29°C); average low, 61.8°F (12°C); average norm, 73.3°F (22°C). December: average high, 44.0°F (7°C); average low, 21.3°F (-6°C); average norm, 32.7°F (1°C). Year: average high, 67.1°F (20°C); average low, 42.3°F (6°C); average norm, 54.7°F (12°C).

Precipitation: June: average, 5.37 inches (136mm). December: 2.30 inches (58mm). Year: average, 42.59 inches (1082mm).



Fig. 8. Today the Wah'Kon-Tah Prairie Preserve serves as an outdoor classroom. Common non-consumptive educational activities include plant identification (A), photography (B), hiking, and bird and butterfly watching. The Wah'Kon-Tah welcomes the public free of charge. Dr. Bill Neale (A), a retired dentist and county coroner who lives near the Wah'Kon-Tah, often uses his photographs to campaign for prairie stewardship.



Fig. 9. The silos on the old Thoreson Ranch homesite are distinctive, even on a foggy morning. The structures — the tallest in the region — were originally used for storing cattle feed. After purchasing the ranch, TNC decided to retain the silos as a landmark.

The Wah'Kon-Tah prairie is classified as an Upland Ozark border prairie (Toney, 1994); although the preserve is technically within the Osage Plains Natural Region, it borders the more eastern Ozark Border Natural Region (Heitzman and Heitzman, 1987 (1996)). The Wah'Kon-Tah is also known as a mesic prairie because it occurs on sites that are relatively well drained and that receive relatively high moisture through most of the growing season (Ladd, 1995). Mesic prairies are the most luxuriant of all North American prairies and have been exploited the most for agriculture.

Within the Wah'Kon-Tah, soils are cherty silt loam, derived from cherty limestone and sandstone (Toney, 1994). Topography is rolling with elevations between 850 and 950 feet (253 and 289 m). Because the topography is relatively rocky, the sod was never broken by the original settlers, though the original Wah'Kon-Tah and Mo-Ko units were disturbed during private ownership. For example, in the early 1900s a portion of the Wah'Kon-Tah was used as a golf course (several artificial ponds remain). Later, the land was seeded with commercial fescue grass, a cold season variety touted as superior to native species for cattle production. The land was periodically grazed, hayed, and harvested for seed (fescue grass). Also, the Thoreson Ranch (the 1997 annexation) (Fig. 1) was a working ranch consisting of grazing cattle and goats, and agriculture crops including fescue grass and corn. Another 20 acres had been severely altered by the construction of ponds, holding pens for livestock, rearing sheds for dogs, silos, a spacious residential house, and accessory buildings to store machinery and supplies (Fig. 9-10).

Today all three units of the Wah'Kon-Tah Prairie Preserve exhibit evidence of past shrub and tree invasion. Indeed, one never is out of sight of trees: on adjacent lands, along fencerows, in drainage gullies, or simply standing alone as silent vanguards from the East. In the mid 1970's much of the Mo-Ko had actually degenerated to woodland (Anon., 1991) dominated by black cherry (*Prunus serotina*) (Rosaceae), persimmon (*Diospyros virginiana*) (Ebenaceae), roughleaf dogwood (*Cornus drummondii*) (Cornaceae), winged sumac (*Rhus copallinum*) (Anacardiaceae), and smooth sumac (*Rhus glabra*) (Anacardiaceae). Many of the draws dissecting the land and fencerows today remain lined with shrubs and trees, especially American elm (*Ulmus americana*) (Ulmaceae), buttonbush (*Cephalanthus occidentalis*) (Rubiaceae), elderberry (*Sambucus canadensis*) (Caprifoliaceae) and osage-orange (*Maclura pomifera*) (Moraceae), also called Bois d'arc and "hedge bush" (Fig. 7).

Management of open habitats, including tallgrass sanctuaries, is extremely difficult (Swengel, 2001). Stewards have learned that large scale financing and labor, and continual assessment of vegetation and animal responses are constant concerns. To further complicate matters, different species respond differently to specific managerial formats. For example, prairie butterflies are usually dependent upon specific forbs for both host and nectar. Since these plant species thrive best with annual burnings, management favoring fire would seem ideal for butterflies. But there is a downside. If fires are widespread and occur during egg laying and larval development, butterfly populations are impacted negatively (see



Fig. 10. When purchased by TNC, the Thoreson Ranch homesite contained a variety of lands and buildings: warm-weather pastures for cattle and goats, pastures of fescue grass for winter livestock feed, ponds for watering livestock, a sizable family home, silos, kennels for dogs, and storage sheds and hangers for hay and equipment: A. Homesite during spring bloom; dominant flowering species is pale purple coneflower (*Echinacea pallida*) (Asteraceae). B (next page). Same site in early autumn with rough blazing star (*Liatris aspera*) (Asteraceae).

Swengel, 1996 and Swengel and Swengel, 1997 for further discussion). On the other hand, prairie chickens require a management regime that does not include annual fires, but rather small-scale haying or grazing late in the year. Obviously, there can be no standard formula for managing all tallgrass preserves. Each parcel must be evaluated independently, often generating considerable professional and public controversy, which in turn often leads to poor management.

The Wah'Kon-Tah was originally leased to MDC for management, which undertook the work themselves or subcontracted it out to independent individuals. Profits were used to finance MDC projects. Management practices concentrated on controlling encroachment of woody species. Since 1999 TNC has been assuming an ever-increasing role in determining the Wah'Kon-Tah's future. For example, in 2000, TNC staffed the old Thoreson house with an official land steward with the task to develop a comprehensive program for long-term management of all forms of indigenous wildlife, including butterfly species. Initially, TNC was hoping to eventually reintroduce a small herd of American bison, the icon of the American prairies, to the property as had been successfully accomplished in Prairie State Park farther south (Larson, 1988) and Konza Prairie Research Natural Area in Kansas (Reichman, 1987). This plan was ultimately abandoned due to the high costs of adequate fencing.

Plant diversity on the Wah'Kon-Tah is high, with over 220 species recorded (Anon., 1991). One species, Mead's milkweed (*Asclepias meadii*), is federally endangered (Anon., 1998a). The

following are common (see Ladd, 1995, for a more comprehensive listing and description of Missouri's Tallgrass Prairie species):

Grasses (Poaceae)

- Big bluestem (*Andropogon gerardii*)
- Canada wild rye (*Elymus canadensis*)
- Gama grass (*Tripsacum dactyloides*)
- Indian grass (*Sorghastrum nutans*)
- Little bluestem (*Schizachyrium scoparium*)
- Panic grass (*Panicum oligosanthes*)
- Prairie cord grass (*Spartina pectinata*)
- Prairie dropseed (*Sporobolus heterolepis*)
- Switch grass (*Panicum virgatum*)

Forbs

- Acanthaceae
 - Hairy wild petunia (*Ruellia humilis*)
- Apiaceae
 - Cowbane (*Oxypolis rigidior*)
 - Rattlesnake master (*Eryngium yuccifolium*)
- Apocynaceae
 - Prairie dogbane (*Apocynum cannabinum*)
- Asclepiadaceae
 - Butterfly weed (*Asclepias tuberosa*)
 - Common milkweed (*Asclepias syriaca*)
 - Green milkweed (*Asclepias viridiflora*)
 - Spider milkweed (*Asclepias viridis*)
 - Whorled milkweed (*Asclepias verticillata*)



Asteraceae

Ashy sunflower (*Helianthus mollis*)
 Black-eyed Susan (*Rudbeckia hirta*)
 Boneset (*Eupatorium* spp.)
 Compass plant (*Silphium laciniatum*)
 Coreopsis (*Coreopsis* spp.)
 Goldenrod (*Solidago* spp.)
 Grey-headed coneflower (*Ratibida pinnata*)
 Ironweed (*Vernonia* spp.)
 New England aster (*Aster novae-angliae*)
 Pale purple coneflower (*Echinacea pallida*)
 Pasture thistle (*Cirsium discolor* and *C. altissimum*)
 Prairie blazing star (*Liatris pycnostachya*)
 Rough blazing star (*Liatris aspera*)
 Scaly blazing star (*Liatris squarrosa*)
 Sky blue aster (*Aster oolentangiensis*)
 Sunflower (*Helianthus annuus*)

Boraginaceae

Hoary puccoon (*Lithospermum canescens*)

Commelinaceae

Common spiderwort (*Tradescantia ohiensis*)

Euphorbiaceae

Flowering spurge (*Euphorbia corollata*)

Fabaceae

Cream wild indigo (*Baptisia bracteata*)
 Goat's rue (*Tephrosia virginiana*)
 Lead plant (*Amorpha canescens*)
 Prairie clover (*Dalea* spp.)
 Sensitive briar (*Mimosa quadrivalvis*)

Lamiaceae

Obedient plant (*Physostegia virginiana*)

Mountain mint (*Pycnanthemum tenuifolium*)
 Wild bergamot (*Monarda fistulosa*)

Liliaceae

Wild hyacinth (*Camassia scilloides*)

Onagraceae

Large-flowered gaura (*Gaura longiflora*)

Oxalidaceae

Violet wood sorrel (*Oxalis violacea*)

Polemoniaceae

Prairie phlox (*Phlox pilosa*)

Primulaceae

Shooting star (*Dodecatheon meadia*)

Rhamnaceae

New Jersey tea (*Ceanothus americanus*)

Rosaceae

Pasture rose (*Rosa carolina*)

Rubiaceae

Stiff bedstraw (*Galium tinctorium*)

Scrophulariaceae

Indian paintbrush (*Castilleja coccinea*)

Prairie beardtongue (*Penstemon tubaeiflorus*)

Wood betony (lousewort) (*Pedicularis canadensis*)

Verbenaceae

Blue vervain (*Verbena hastata*)

Rose vervain (*Glandularia canadensis*)

Violaceae

Arrow-leaved violet (*Viola sagittata*)

Bird's foot violet (*Viola pedata*)

The Wah'Kon-Tah is bucolic and dominated by warm-season grasses, green throughout spring and summer but which take on a



Fig. 11. Wah'Kon-Tah landscape in autumn. The flaming red leaves of winged sumac (*Rhus copallinum*) (Anacardiaceae) produce a color-dot matrix on the autumn prairie. Although invasive, this woody species provides excellent shelter during inclement weather and night for prairie wildlife, including many species of butterflies. Yellow forb is goldenrod (*Solidago* sp.) (Asteraceae); white flowering species is stiff bedstraw (*Galium tinctorium*) (Rubaceae)

patina of bronze during the fall (inside Front Cover). Although the key players such as big bluestem, Indian grass, switch grass, and prairie cordgrass do not attain legendary heights, they nonetheless are the most expansive and most majestic of all the prairie plants, the "redwoods of the prairie" (Duncan, 1979). Beginning in early spring and continuing until frost, there are seasonal massive explosions of multicolored wildflowers that create a fantasy-like tableau. Spring dominants are: bird's foot violet, hoary puccoon, Indian paintbrush, shooting star, wild hyacinth, and wood betony. Summer dominants are: butterfly weed, black-eyed Susan, compass plant, coreopsis, lead plant, pale purple coneflower, prairie blazing star, sunflowers (especially ashy sunflower), and wild bergamot (Fig. 2-3). Fall dominants are: asters, ironweeds, rough blazing star and sunflowers; winged sumac, an invasive shrub, adds crimson foliage to autumn's profusion of color (Fig. 11). During some years, seeds of native species are harvested for reseeding parcels of land being reclaimed and/or for sale to commercial companies (Fig. 12).

Animals of interest on the Wah'Kon-Tah include: Henslow's sparrow (*Ammodramus henslowii*) (Emberizidae), greater prairie chicken (*Tympanuchus cupido*) (Phasianidae), scissor-tailed flycatcher (*Tyrannus forficatus*) (Tyrannidae), upland sandpiper (*Bartramia longicauda*) (Scolopacidae), coyote (*Canis latrans*) (Canidae), prairie mole cricket (*Gryllotalpa major*) (Orthoptera: Gryllotalpidae) (Anon., 1991, 1998a), and the "pink katydid" (*Amblycorypha parvipennis*) (Orthoptera: Tettigoniidae (Atkinson, 1998; Ross, 2003a; Ross and Nickle, in prep.). Wild turkey

(*Meleagris gallopavo*) (Phasianidae) and Virginia white-tailed deer (*Odocoileus virginianus*) (Cervidae) are fairly common and hunted as game with special permit. American bison or American buffalo (*Bos bison*) (Bovidae), American elk (*Cervus canadensis*) (Cervidae) and the gray wolf (*Canis lupus*) (Canidae) were common in historical times, but are now extinct within the wild.



Fig. 12. Mr. Mervin Wallace, founder and owner of Missouri Wildflowers Nursery, Jefferson City, employing his personally designed lightweight harvester for collecting seeds of native prairie wildflowers. Processed seeds are marketed to anyone wishing to restore native prairie. Seed harvest can provide supplemental cash for prairie landowners. The Nature Conservancy occasionally contracts with Mr. Wallace.

Ticks and chiggers are common during much of the summer and fall; Lyme Disease is rare.

Methods of Survey

Because of the multifaceted duties associated with my position with The Nature Conservancy of Missouri, I conducted my surveys for butterflies whenever circumstances permitted: always once but usually three to five times per week. The data were recorded at the end of each week. During my previous research in the region (1996 and 1997), I had learned that butterfly populations on the prairie exhibit pronounced clumped or aggregated distributions, i. e., individuals occur in irregular, non-random patterns (see Odom, 1971). My previous observations indicated that the vast majority of butterfly species were spending most of their time in close proximity to their host or nectar plants. Of course, this is a tendency for butterflies regardless of ecosystem. Within the prairie environment, however, butterflies seem to exhibit particularly strong sedentary behaviors. This probably results from at least two pronounced characteristics of the prairie ecosystem. First, the habitat consists of great expanses of assorted grasses. Flowering forbs, major sources of nectar and host plants for the vast majority of prairie species, usually are found as localized colonies (sometimes extensive), scattered throughout the grass (Fig. 2-3). As such, food and host plants tend to be concentrated and butterflies have little need to wander far. Second, wind is virtually a daily occurrence throughout the prairie landscape. This, of course, discourages flight.

These peculiar circumstances coupled with the conclusion of Shapiro (1975) that the quantification of the abundance of all species in a small region is "virtually futile," convinced me not to conduct my inventories based on a typical transect method or mark-recapture method commonly employed for quantitative analyses of butterflies (Jolly, 1965; Seber, 1965; Pollard, 1977; Pollard and Yates, 1993) (also see Comments on *Speyeria idalia*, below). Instead, I focused my attention on areas with obvious concentrations of butterflies, e.g., colonies of butterfly-friendly wildflowers, roadsides and fencerows with wildflowers, and areas with damp soils for butterfly species prone to puddling (Boggs, 1998; Ross, 1998b) (Fig. 13). By spending extended periods of time in these areas, I was able to empirically document, reasonably well, both species and density levels. Special attention was given to *Speyeria idalia*.

In order to reduce the risks of missing very specialized species and ecotones, once a week I undertook walks across other sections of the prairie. These walks followed loosely laid out transects 30 feet (10m) apart and included not only typical grassy regions, but also transitional areas (ecotones) that exhibited marked diversity in topography and vegetation, e.g., crests, ponds, gullies and other drainage channels, and wooded prairie margins. Traversing the various sections of the Wah'Kon-Tah was usually not difficult. Regularly scheduled haying and burning keep vegetation relatively low; vehicular traffic associated with prairie management creates paths that ease foot tracking. I was in the field as often as weather and extraneous commitments permitted. Fieldwork averaged five days per week; results were recorded at week's end. A typical workday began at approximately 0830 CDST and continued to approximately 1730 -1800 CDST. Since mid summer sun on the prairie can be unforgiving, on particularly hot days I returned to my base to rest between noon and approximately 1500 CDST.

Species' abundances were qualified as follows:

Abundant = commonly observed in large numbers, 20 or more individuals;

Common = commonly observed, but not in large numbers, 4-19 individuals;

Uncommon = seldom observed, 2-3 individuals;

Rare = unlikely, but not out of normal range, 1 individual;

Stray = out of normal range, 1-2 individuals.

Butterfly identifications were made by sight, often with the aid of a pair of binoculars: Celestron Regal, 8 X 42. Individuals of small species, particularly, hesperiids, were frequently netted for closer observation and for comparisons with field guides; butterflies were later released. Determinations are based on Glassberg (1999), Heitzman and Heitzman (1987/1996), Opler and Krizek, Opler and Malikul (1992), and Pyle (1981). Taxonomy follows Anon. (1995) and Miller and Brown (1981).

Plant determinations are based on Fernald (1950) and Ladd (1995). Bird taxonomy follows Anon. (1998c). Mammal taxonomy follows Schwartz, and Schwartz (1986).

Results of Survey

The table (p.18) lists butterfly species, dates observed, and status.

General Comments

Even though the Wah'Kon-Tah Prairie Preserve consists of only 2,332 acres, its butterfly fauna is decidedly rich for a temperate fauna. During this survey, I recorded 71 species of butterflies. Additional surveys in 1993 (Opler and Swengel, 1994), 1999 (Swengel and Opler, 2000), and 2002 (Swengel and Swengel, 2003) increase the total to 74. This is approximately one-half of the 156 species known to occur in the entire state. I theorize that the actual number is considerably greater because all surveys concentrated on summer and fall months whereas a number of butterfly species, e.g., Pieridae (whites), Lycaenidae (hairstreaks), Riodinidae (metalmarks) and Hesperidae (skippers), are univoltine (a single generation each year) with adults on the wing only for a brief time in spring. During this study, only one "spring" butterfly, the pierid *Anthocharis midea* (Hübner), was observed (two occasions in early May) (Ross, 1995a, 1996). Also, many small butterflies, particularly hesperiids, often occur in small numbers and can easily be overlooked. Another factor that probably will affect the diversity of butterflies on the Wah'Kon-Tah will be the restoration of much of the original Thoreson Ranch to prairie status. TNC anticipates that within the next five years, most of those 872 acres will provide excellent prairie habitat for native butterfly (and other animal) species. Therefore, I estimate that the actual number of butterfly species that eventually will be recorded from the preserve will be 85-90.

Upon my arrival at the Wah'Kon-Tah on May 2, 1998 most tree species were just beginning to leaf, although dogwood and red bud trees were ending their flower cycle. Garden daffodils had peaked, peonies were in full bloom, and irises were in bud. On the prairie, the grasses were just beginning to emerge, but on sections of land that had been burned the previous year, violets, wood betony, and Indian paintbrush were ablaze, creating a picturesque color-dot matrix superimposed on a canvas of black. Butterfly populations were very low. The eclosion of early spring univoltine species had past, and not until the last week in May, when nighttime temperatures remained above 60°F (16°C), was there a noticeable increase in numbers of species or individuals. But by late May and early June, butterfly weed and pale coneflower burst into bloom and butterfly flight season was well on its way.

The weeks with the fewest number of species (25) were May 3-9 and September 27-October 3). The weeks with the greatest number of species (57-65) were between June 14-20 and August 16-20 with the maximum (65) occurring August 9-15.

The most common butterfly species, i.e., species recorded as being either "abundant" or "common" during the entire study period, were *Colias eurytheme* (Pieridae), and *Phyciodes tharos*, *Polygona interrogationis*, and *Danaus plexippus* (Nymphalidae) (see Table for author names of species). The second most common, i. e., species



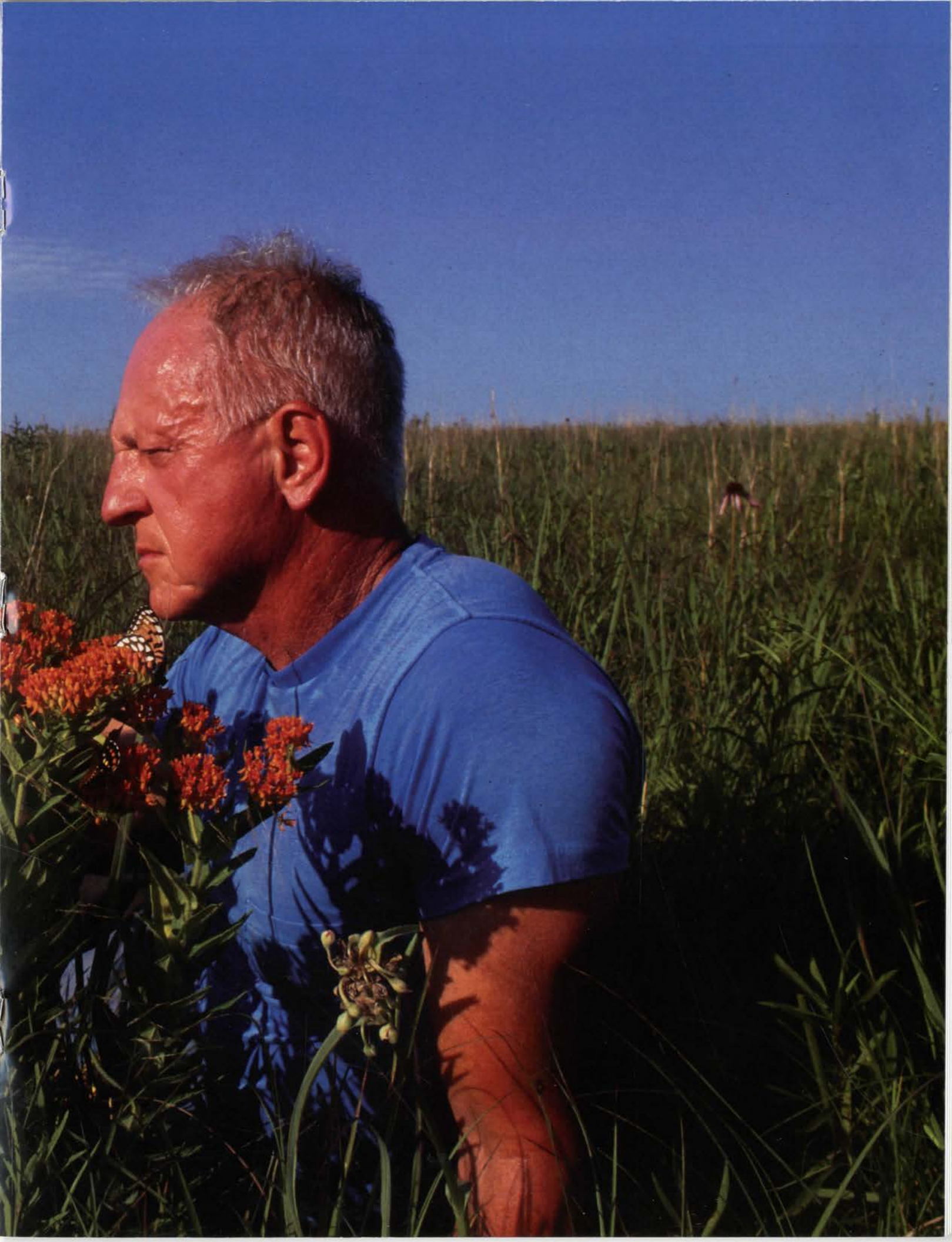




Fig. 13. In mid summer, common milkweed (*Asclepias syriaca*) is a virtual magnet for many species of butterflies. This social gathering consists of monarch (*Danaus plexippus*), great spangled fritillary (*Speyeria cybele*), regal fritillary (*S. idalia*) (all Nymphalidae) and orange sulphur (*Colias eurytheme*) (Pieridae). On the Wah'Kon-Tah, common milkweed is the primary summer host plant for the monarch.

recorded as common or abundant on every inventory except one, were *Pieris rapae* (Pieridae), *Vanessa virginiensis* (Nymphalidae), and *Everes comyntas* (Lycaenidae). Of these, only *P. interrogationis* and *P. rapae* were not widespread, being restricted basically to fencerows, roadsides, and disturbed areas surrounding the Thoreson homesite. *Danaus plexippus* was by far, the most conspicuous species throughout the survey and throughout habitats. One additional species, *Speyeria idalia*, was abundant and conspicuous during mid summer and early fall in those regions dominated by healthy prairie vegetation.

As mentioned earlier, the vast majority of butterfly species on the Wah'Kon-Tah preserve were most easily observed in areas with high concentrations of flowering plants. The most productive flowers were: roughleaf dogwood and winged sumac (late spring); butterfly weed and pale coneflower (early summer); common milkweed, prairie and rough blazing star, mountain mint and wild bergamot (mid summer); ironweed and pasture thistles (late summer, early fall) (Fig. 13, 14A, 15, 20, and Centerfold).

Several butterfly species were commonly encountered at mud puddles (roadside and damp areas boarding ponds are gullies): *Pterourus glaucus* (Papilionidae), *Colias eurytheme* and *C. philodice* (Pieridae), *Libytheana carinenta* (Libytheidae), *Phyciodes tharos* (Nymphalidae), and *Celastrina ladon* and *Everes comyntas* (Lycaenidae). *Phyciodes tharos* and *Everes comyntas* were attracted to damp earth in areas with fresh ash from a recent prairie burn.

The following species (all Nymphalidae) were attracted to coyote and fox scat: *Speyeria idalia* (Fig. 14C), *Nymphalis antiopa*,

Vanessa virginiensis, *Anaea andria*, and *Asterocampa celtis*. Male *S. idalia* were attracted to soil impregnated with human urine. *Nymphalis antiopa* and *Enodia anhedon* fed on dead fish along a creek side. *Polygonia interrogationis* (Nymphalidae) and *Lycaena hyllus* (Lycaenidae) were most common along roadside ditches bordered by American elm and dock (*Rumex* spp.).

The following species were most commonly encountered in disturbed areas around the Thoreson homesite: *Pieris rapae*, *Pontia protodice*, and *Nathalis iole* (Pieridae), and *Charidryas gorgone* and *Junonia coenia* (Nymphalidae).

During late August and throughout September, large numbers of *Danaus plexippus* (Nymphalidae) and *Phoebis sennae* (Pieridae) were observed moving in a south-southwesterly direction.

One species, *Agraulis vanillae* (Nymphalidae), was recorded in 2002 as a stray during my North American Butterfly Association (NABA) "Fourth of July Butterfly Count" (Swengel and Swengel, 2002).

The following species of butterflies were observed reproducing: *Pieris rapae* (Pieridae), eggs on stinkweed (*Thlaspi arvense*, Brassicaceae) in abandoned pastures on Thoreson Ranch); *Speyeria cybele* (Nymphalidae), in grass thatch near wooded area on original Wah'Kon-Tah Conservation Area;

Speyeria idalia (Nymphalidae), eggs in grass thatch in all sections of prairie;

Charadryas gorgone (Nymphalidae), eggs and larvae on sunflower (*Helianthus annuus*) bordering holding lagoons on Thoreson Ranch;



Fig. 14. Regal fritillary butterflies (*Speyeria idalia*): A. Female feeding on a favorite nectar plant, butterfly weed (*Asclepias tuberosa*). B. Male asleep on a grass stem in early morning. C. Group of males feeding on coyote scat (males were observed to feed on fox scat and human urine, too).

Polygonia interrogationis (Nymphalidae), eggs on American elm (*Ulmus americana*) along unpaved road fronting Thoreson homesite;

Junonia coenia (Nymphalidae), eggs and larvae on common plantain (*Plantago major*, Plantaganaceae) in lawn of Thoreson homesite;

Asterocampa celtis (Nymphalidae), eggs on hackberry (*Celtis* sp.) in fence row of original Wah'Kon-Tah Conservation Area;

Danaus plexippus (Nymphalidae), eggs, larvae and pupae on milkweeds (*Asclepias* spp.) and prairie dogbane (*Apocynum cannabinum*) throughout all sections of prairie.

TABLE

BUTTERFLY TAXA

	DATE: (1998)	5:3-9	5:10-16	5:17-23	5:24-30	5:31-6:6	6:7-13	6:14-20	6:21-27	6:28-7:4	7:5-11	7:12-18
FAMILY PAPILIONIDAE (Swallowtails)												
1. <i>Battus philenor</i> (Linnaeus): Pipevine Swallowtail	-	U	U	C	U	U	C	C	C	C	C	C
2. <i>Euryides marcellus</i> (Cramer): Zebra Swallowtail	U	-	U	U	U	U	U	U	U	U	U	-
3. <i>Papilio polyxenes</i> Fabricius: Black Swallowtail	C	C	C	C	U	C	C	C	C	A	A	A
4. <i>Papilio corydon</i> (Cramer): Giant Swallowtail	-	U	C	C	C	C	C	C	C	C	C	C
5. <i>Pierourus glaucus</i> (Linnaeus): Eastern Tiger Swallowtail	-	U	U	C	U	U	U	U	U	C	C	C
6. <i>Pierourus troilus</i> (Linnaeus): Spicebush Swallowtail	-	U	C	C	U	U	C	C	C	C	C	C
FAMILY PIERIDAE (Whites and Sulphurs)												
7. <i>Pontia protodice</i> (Boisduval and Leconte): Checkered White	-	-	-	-	-	U	U	U	A	A	A	A
8. <i>Pieris rapae</i> (Linnaeus): Cabbage White	C	C	C	A	C	C	C	A	A	A	A	A
9. <i>Anthocharis midea</i> (Hübner): Falcat Orange-tip	U	U	U	-	-	-	-	-	-	-	-	-
10. <i>Colias philodice</i> Godart: Clouded Sulphur	U	U	U	U	U	C	C	C	A	A	A	A
11. <i>Colias eurytheme</i> Boisduval: Orange Sulphur	A	A	A	A	A	U	U	A	A	A	A	A
12. <i>Zerene cesonia</i> (Stoll): Southern Dogface	-	-	-	-	-	U	U	U	U	U	U	U
13. <i>Phoebastria senoae</i> (Linnaeus): Cloudless Sulphur	U	U	U	U	U	U	U	U	U	U	U	U
14. <i>Eurema lisa</i> (Boisduval and Leconte): Little Yellow	-	-	-	-	-	U	U	C	C	C	C	C
15. <i>Eurema nicippe</i> (Cramer): Sleepy Orange	-	-	-	-	-	U	U	U	U	U	U	U
16. <i>Nathalis iole</i> Boisduval: Dainty Sulphur	-	-	-	-	-	-	-	-	-	-	-	-
FAMILY LYCAENIDAE (Gossamer-wing Butterflies)												
17. <i>Lycæna phlaeas americana</i> Harris: American Copper	-	-	-	-	U	U	U	U	U	U	U	U
18. <i>Lycæna zanthoides diene</i> (Scudder): Diene Copper	-	-	-	-	-	-	-	-	U	U	U	U
19. <i>Lycæna hylas</i> (Cramer): Bronze Copper	-	-	-	-	-	-	-	-	C	U	U	U
20. <i>Harkerianus titus</i> (Fabricius): Coral Hairstreak	-	-	-	-	-	-	-	U	U	U	U	U
21. <i>Strymon calanus</i> (Hübner): Banded Hairstreak	-	-	-	-	-	U	U	U	U	U	U	U
22. <i>Calycopis cecrops</i> (Fabricius): Red-banded Hairstreak	-	U	U	U	U	U	U	C	C	C	C	C
23. <i>Strymon melinus</i> Hübner: Gray Hairstreak	-	-	-	-	-	-	-	-	-	-	-	-
24. <i>Leptotes marina</i> (Reakirt): Marine Blue	-	-	-	-	-	-	-	-	-	U	U	U
25. <i>Hemiargus isola</i> (Reakirt): Reakirt's Blue	-	-	-	-	-	U	A	A	A	A	A	A
26. <i>Everes comyntas</i> (Godart): Eastern Tailed-Blue	A	A	A	A	A	C	C	U	C	C	C	C
27. <i>Celastrina ladon</i> (Cramer): Spring Azure	C	C	A	A	A	C	C	U	C	C	C	C
FAMILY NYMPHALIDAE (Brush-footed Butterflies)												
SUBFAMILY LIBYTHEINAE (Snouts)												
28. <i>Libythea carisenta</i> (Cramer): American Snout	-	U	U	U	U	C	A	C	U	U	U	U
SUBFAMILY HELICONINAE (Heliconians and Fritillaries)												
29. <i>Agraulis vanillae</i> (Linnaeus): Gulf Fritillary	-	-	-	-	-	-	-	-	-	-	-	-
30. <i>Euploetes claudia</i> (Cramer): Variegated Fritillary	U	U	U	U	U	C	C	C	C	C	C	C
31. <i>Speyeria cybele</i> (Fabricius): Great Spangled Fritillary	-	-	C	A	A	A	A	A	A	A	A	A
32. <i>Speyeria idalia</i> (Drury): Regal Fritillary	-	-	-	-	-	U	A	A	A	A	A	A
SUBFAMILY NYMPHALINAE (True Brush-foots)												
33. <i>Charidryas gorgone</i> (Hübner): Gorgone Checkerspot	-	-	-	-	-	-	-	-	-	-	C	C
34. <i>Charidryas sylvia</i> (Doubleday and Hewitson): Silvery Checkerspot	-	-	U	U	U	C	C	U	U	U	U	U
35. <i>Phyciodes tharos</i> (Drury): Pearl Crescent	A	A	A	A	A	U	A	A	A	C	C	C
36. <i>Polytonia interrogatoria</i> (Fabricius): Question Mark	A	A	A	A	A	A	A	C	C	C	C	C
37. <i>Polytonia comma</i> (Harris): Eastern Comma	U	U	U	U	U	C	C	U	U	U	U	U
38. <i>Nymphalis antiopa</i> (Linnaeus): Mourning Cloak	U	U	U	U	U	U	U	U	U	U	U	U
39. <i>Vanessa virginica</i> (Drury): American Lady	U	A	A	A	A	C	A	U	A	C	C	C
40. <i>Vanessa cardui</i> (Linnaeus): Painted Lady	U	U	U	U	U	-	-	U	U	-	-	U
41. <i>Vanessa atalanta</i> (Linnaeus): Red Admiral	U	U	U	U	U	U	U	C	C	C	C	C
42. <i>Junonia coenia</i> Hübner: Common Buckeye	U	U	U	U	U	U	C	C	C	C	C	C
43. <i>Limenitis arthemis aryanax</i> (Fabricius): Red-spotted Purple	U	U	C	C	A	A	C	C	C	C	C	C
44. <i>Limenitis archippus</i> (Cramer): Viceroys	-	U	U	U	U	U	U	U	C	C	C	C
SUBFAMILY CHARAXINAE (Leafwings)												
45. <i>Anax andria</i> Scudder: Goatweed Leafwing	C	C	C	C	C	C	U	U	U	U	U	U
SUBFAMILY APATURINAE (Emperors)												
46. <i>Asterocampa celis</i> (Boisduval and Leconte): Hackberry Emperor	-	C	C	C	C	A	A	A	C	C	U	U
47. <i>Asterocampa clyton</i> (Boisduval and Leconte): Tawny Emperor	-	-	-	-	-	-	-	-	-	U	U	U
SUBFAMILY SATYRINAE (Satyrs)												
48. <i>Enodia anthedon</i> A.H. Clark: Northern Pearly-eye	-	-	-	-	-	U	U	U	U	U	U	U
49. <i>Megisto cymela</i> (Cramer): Little Wood-Satyr	-	-	-	U	U	U	U	U	U	U	U	U
50. <i>Cercyonis pegala</i> (Fabricius): Common Wood-Nymph	-	-	-	-	-	-	-	U	C	A	A	A
SUBFAMILY DANAINAE (Monarchs)												
51. <i>Danaus plexippus</i> (Linnaeus): Monarch	C	C	C	C	C	A	A	A	C	C	C	C
FAMILY HESPERIIDAE (Skippers)												
SUBFAMILY PYRGINAE (Spread-wing Skippers)												
52. <i>Epargyrus clarus</i> (Cramer): Silver-spotted Skipper	-	-	U	U	U	U	C	U	U	C	U	C
53. <i>Achalarus lyciades</i> (Geyer): Hoary Edge	U	C	C	C	C	C	C	C	U	U	U	U
54. <i>Thorybes bathyllus</i> (J.E. Smith): Southern Cloudwing	U	C	C	C	C	C	C	U	U	U	U	U
55. <i>Thorybes pylades</i> (Scudder): Northern Cloudwing	C	C	C	C	C	C	C	-	-	-	-	-
56. <i>Staphylus hayhurstii</i> (W.H. Edwards): Hayhurst's Scallopwing	-	-	-	-	-	-	-	-	-	-	-	-
57. <i>Erynnis juvenalis</i> (Fabricius): Juvenal's Duskywing	-	-	C	U	-	-	-	-	-	-	-	-
58. <i>Erynnis horatius</i> (Scudder and Burgess): Horace's Duskywing	-	U	U	U	C	C	C	U	C	U	U	U
59. <i>Erynnis martialis</i> (Scudder): Mottled Duskywing	-	-	-	-	-	-	-	-	U	U	U	C
60. <i>Pyrgus communis</i> (Grote): Common Checkered Skipper	U	U	U	U	U	U	U	C	A	A	A	A
61. <i>Pholisora catullus</i> (Fabricius): Common Sootywing	U	U	C	C	C	C	C	C	A	A	A	A
SUBFAMILY HESPERIINAE (Grass Skippers)												
62. <i>Ancyloxypha numitor</i> (Fabricius): Least Skipper	-	-	-	-	-	-	-	-	-	U	U	-
63. <i>Hesperia attalus</i> (W.H. Edwards): Dotted Skipper	-	-	-	-	-	U	U	U	U	U	U	C
64. <i>Polites peckus</i> (W. Kirby): Peck's Skipper	-	-	U	U	U	C	A	C	U	U	U	C
65. <i>Polites themistocles</i> (Latreille): Tawny-edged Skipper	-	-	-	U	U	C	A	C	U	U	U	U
66. <i>Polites argenes</i> (Fabricius): Crossline Skipper	-	-	-	-	-	-	-	U	U	-	-	-
67. <i>Wallengrenia egeremet</i> (Scudder): Northern Broken-Dash	-	-	-	-	-	-	-	-	-	-	-	-
68. <i>Atalopedes campestris</i> (Boisduval): Sachem	-	-	-	-	-	-	-	-	-	-	-	-
69. <i>Atrytone arogois</i> (Boisduval and Leconte): Arogois Skipper	-	-	-	-	-	U	C	A	U	U	U	U
70. <i>Atrytone logan</i> (W.H. Edwards): Delaware Skipper	-	-	-	-	-	-	-	U	C	U	U	U
71. <i>Problema byssus</i> (W.H. Edwards): Byssus Skipper	-	-	-	-	-	-	-	-	C	C	C	C
72. <i>Poanes zabulon</i> (Boisduval and Leconte): Zabulon Skipper	-	U	U	U	U	U	U	U	U	U	U	U
73. <i>Euphyes ruficola</i> (Boisduval) = <i>vestris</i> (Boisduval): Dun Skipper	-	-	U	U	U	C	C	C	U	U	U	U
74. <i>Amblyscirtes vialis</i> (W.H. Edwards): Common Roadside-Skipper	-	-	-	-	U	U	U	U	U	U	U	U
TOTALS: 74 species (cumulative)		25	37	44	47	50	56	59	59	60	62	60

LEGEND:

Abundant (A)=commonly observed in large numbers, 20 or more individuals
 Common (C)=commonly observed, but not in large numbers, 4-19 individuals
 Uncommon (U)=seldom observed, 2-3 individuals
 Rare (R)=unlikely, but not out of normal range, 1 individual
 Stray (S)=out of normal range, 1-2 individuals
 Absent (-)=not observed

1998 (5:3-9-9:27-10:3)=this study
 1993 (6:16)=reported by A. B. Swengel in Opler and Swengel (1994)
 1999 (6:14)=reported by A. B. and S. Swengel in Swengel and Opler (2000)
 2002 (8:27)=reported by G. N. Ross in Swengel and Swengel (2003)

7:19-25	7:26-8:1	8:2-8	8:9-15	8:16-22	8:23-29	8:30-9:5	9:6-12	9:13-19	9:20-26	9:27-10:3	(1993) 6:16	(1999) 6:14	(2002) 8:27	FREQUENCY (Max.:22)	SPECIES ID. NUMBER
C	C	C	U	U	C	C	C	U	U	U				20	1
-	-	-	U	-	-	-	-	-	-	-				11	2
A	C	C	C	C	C	U	U	U	U	U				22	3
C	C	C	C	C	U	U	U	U	U	-				20	4
C	C	C	C	C	U	U	U	U	U	-				20	5
C	C	C	C	C	C	U	U	U	-	-				19	6
A	A	A	A	C	C	U	U	U	U	U				17	7
A	C	C	C	C	C	U	C	U	U	U				22	8
-	-	-	-	-	-	-	-	-	-	-				2	9
A	A	A	A	A	C	C	C	A	C	C				22	10
A	A	A	A	A	C	C	C	C	U	U				22	11
U	U	C	A	A	C	U	U	-	-	-				14	12
U	C	A	A	A	A	A	A	A	A	A				22	13
C	C	A	A	A	A	A	C	C	C	C				19	14
U	-	C	C	C	C	C	U	U	U	U				16	15
-	-	U	U	C	C	C	C	C	U	U				9	16
U	U	U	U	U	-	-	-	-	-	-				12	17
-	U	U	U	U	-	-	-	-	-	-				9	18
U	U	U	U	U	-	-	-	-	-	-				6	19
-	U	-	-	-	-	-	-	-	-	-				8	20
C	C	C	U	C	U	U	U	U	-	-				5	21
C	C	C	C	C	C	C	U	U	U	-				19	22
-	-	-	C	C	C	C	U	U	U	-				20	23
C	C	U	U	U	-	-	-	-	-	-				1	24
C	C	C	C	C	A	A	C	C	C	C				4	25
C	C	U	U	U	-	-	-	-	-	-				22	26
														16	27
U	U	C	C	C	U	U	U	-	-	-				18	28
-	-	-	-	-	-	-	-	-	-	-				1	29
C	C	C	C	C	C	U	U	U	U	-				21	30
C	C	C	C	C	C	U	U	U	-	-				18	31
A	A	A	A	C	C	C	C	C	U	U				18	32
C	C	A	A	A	C	C	U	U	-	-				11	33
U	C	A	A	A	C	C	A	C	C	C				18	34
C	C	C	C	C	A	A	C	C	U	U				22	35
C	C	C	C	C	C	U	U	-	-	-				22	36
U	-	C	U	U	U	U	-	-	-	-				18	37
-	-	-	U	U	-	-	-	-	-	-				10	38
C	C	C	C	C	C	C	U	U	U	U				22	39
U	U	C	C	U	U	U	U	U	-	-				15	40
C	U	C	C	U	C	U	U	U	U	U				22	41
A	C	A	A	A	A	A	C	C	C	U				22	42
C	C	C	C	C	C	U	U	U	U	U				22	43
														20	44
U	C	U	U	C	U	U	-	-	-	-				18	45
U	U	U	U	C	C	C	U	U	-	-				19	46
U	U	U	U	U	U	-	-	U	-	-				10	47
U	U	U	U	U	U	-	U	-	-	-				14	48
C	C	C	U	U	C	C	U	C	U	U				15	49
														16	50
C	C	C	A	A	A	A	A	A	A	A				22	51
C	C	C	C	C	C	U	U	-	-	-				17	52
U	U	U	U	U	U	U	U	-	U	-				14	53
-	-	-	U	U	U	-	-	-	-	-				19	54
-	-	-	-	-	-	-	-	-	-	-				14	55
-	-	-	-	-	-	-	-	-	-	-				1	56
U	U	-	-	-	-	-	-	-	-	-				4	57
C	U	C	U	U	U	U	U	U	-	-				19	58
C	A	A	A	U	C	C	U	U	-	-				11	59
A	A	A	A	C	C	C	U	U	U	U				22	60
														22	61
-	-	U	U	U	-	-	-	-	-	-				5	62
C	C	C	U	U	U	U	U	U	-	-				1	63
C	C	C	C	C	U	C	U	U	U	U				20	64
U	C	C	C	C	C	U	U	-	-	-				20	65
-	-	-	-	-	-	-	-	-	-	-				15	66
A	A	C	C	A	C	A	C	C	C	U				2	67
U	C	C	C	C	U	U	U	-	-	-				13	68
U	U	-	U	U	U	-	-	-	-	-				14	69
C	C	C	C	C	C	U	U	-	-	-				12	70
U	U	-	U	U	U	U	U	-	U	-				13	71
U	U	U	U	U	U	U	-	-	-	-				14	72
-	-	U	U	U	U	U	-	-	-	-				18	73
														13	74
58	58	59	65	61	56	50	48	42	32	25					

U

S

R

Comments on *Speyeria idalia*

Although I will report in detail on the life history of the regal fritillary, *S. idalia*, later, I think it relevant to comment here on the species. In the past, the distribution of this species included a swath across central and eastern United States and a small part of extreme southeastern Canada (Allen, 1997, Clark and Clark, 1951; Ehrlich and Ehrlich, 1961; Glassberg, 1993; 1999a, 2001; Harris, 1972; Howe, 1975; Klotz, 1951; Opler and Krizek, 1984; Opler, 1992; Paulissen, 1975; Pyle, 1981; Tilden and Smith, 1986; Woodbury, 1994.). The species was even common within the city limits of Washington, D.C. (Clark, 1932). Recently, all populations in the East seem to have been extirpated except for two remnant colonies in Pennsylvania (Glassberg, 1993, 1998a,b,c, 1999b; Schweitzer, 1993; Williams, 1999). Currently, most populations occur west of the Mississippi River in the nation's heartland, the Midwest (Debanski and Kelly, 1998; Heitzman and Heitzman, 1996; Kelly and Debanski, 1998; Kopper, 1997; Kopper *et al.*, 2001; Nagel *et al.*, 1991; Opler and Swengel, 1993, 1994; Ross, 2001b, 2002, 2003b, 2004a,b; Ross and Henk, 2004; Stolzenburg, 1992; Swengel, 1993; 2002; Swengel and Opler, 1995, 1996, 1997, 1998, 1999, 2000, 2001; Swengel and Swengel, 2003; Williams, 1999).

Regals can appear to be numerous during the summer months on prairie lands that are routinely managed (Centerfold and Fig. 14). During Ann and Scott Swengel's one-day surveys between 1993 and 1999 (Opler and Swengel, 1994; Swengel and Opler, 1995, 1996, 1997, 1998, 1999, 2000, 2001) conducted as part of the North American Butterfly Association's "Butterfly Counts" program, *S. idalia* proved invariably to be the most commonly encountered species on the Wah'Kon-Tah prairie. Numbers ranged from a low of 413 (1999) to 1289 (1996) (average = 678). During the Swengels' seven years of conducting one-day counts on the Wah'Kon-Tah, the preserve has generated on four occasions the highest numbers of *S. idalia* recorded for any North American inventory. (The Wah'Kon-Tah numbers have been surpassed only by the following prairie sites: Sedalia, MO-653 (1993); Northern Loess Hills, IA-1292 (1995); Crane Meadows, NE-1422 (1996).

My observations on the Wah'Kon-Tah did not produce numbers as high as those recorded by the Swengels. My independent count (8 hrs) on June 16, 1998, the same day that the Swengels conducted their survey (3.57 hrs), chronicled only 364 individuals, not 731 as reported by the Swengels. In fact, on no occasion during my 1996, 1997, 1998, or 2002 (Swengel and Swengel, 2003) butterfly inventories on the Missouri prairies did I ever observe more than 400 individuals of *S. idalia*, and then only after nine field-hours. As possible explanation for the discrepancy in population estimates, I suggest the following. The Swengels' population estimates are based on a transect method (Pollard and Yates, 1993) in which they "walked at a slow pace on parallel routes 5-10m apart . . . and counted all adult butterflies observed ahead and to the sides, to the limit at which an individual could be identified, possibly with the aid of binoculars after detection, and tracked" (Swengel, 1997).

My field experience with regals indicates that most, particularly males — the predominant sex in June — tend to crisscross areas during morning hours as they patrol for emerging females. Later in the day, males tend to spend a good part of their time nectaring in localized areas rich in their preferred food plants. As such, if a surveyor is walking random transects counting every sighting, the resulting tally is likely to include numerous repeat individuals,

Fig. 15. A. An aged and tattered female regal fritillary (*Speyeria idalia*) (Nymphalidae) in late September. Females fly from late June/early July until the frosts of autumn, late September/early October. The final nectar source for female regals is pasture thistle (*Cirsium discolor* and *C. altissimum*) (Asteraceae). B. Pair (female above) of regals nectaring on a favorite late summer plant, rough blazing star (*Liatris aspera*) (Asteraceae).



A



B

skewing the data. Furthermore, Nagel *et al.* (1991) have employed both the transect method and a sophisticated "mark-recapture" strategy using the Jolly-Seber method (Jolly, 1965; Seber, 1965) for quantifying regal populations on Rowe prairie in Nebraska. In comparing their data derived from both transect and Jolly-Seber methods, the authors concluded "agreement between the two methods is not good; as great as 2.34X difference was found at one sample date." Murphy (1988) suggests that mark-recapture methods can be detrimental to individual butterflies and that the information on population densities always can be ascertained through simple observation and use of a low impact "sampling" technique such as that of Pollard (1977). Additionally, Murphy presents a plea "to government agencies, environmental consultants, and field biologists to restrict mark-recapture studies to non-endangered species, or to endangered species proven hardy enough to withstand human handling."

Because of differing opinions regarding the reliability of sampling methods, and not wishing to damage individual butterflies, I opted to employ direct observation for my assessments of regal population density (see Methods of Survey, above). By spending hours during an entire day in prime areas for regals and by making a concerted effort to avoid recounting individuals, I think my approach tends to minimize error. But regardless of the accuracy of either survey method, a population consisting of only several hundreds of individuals is not sufficiently high enough to guarantee long-term survival of the species.

Male regal fritillaries habitually appear only after the sun has warmed their grassy domain. They then bask with wings outstretched before taking to the air, usually between 1000 and 1100 CDST. Earlier, individuals easily flush when disturbed, as for example, when an observer walks across the prairie. At night, regals secure perches on stems of plants (grasses and ashy sunflower are favored) usually within a foot or two (0.5m) of the ground (Fig. 14B). Flight usually is just above vegetation level or within 10 feet (3 m) of the ground and because of a soaring component, resembles to some degree, that of monarchs. By mid afternoon, males usually begin to associate with patches of their favorite nectar plants. A male will then alight atop a flower head and begin to feed. If the air temperature is high and sunlight intense, the butterflies keep their wings tightly closed in a vertical position. The distinctive ventral silver patches probably act as solar reflectors, preventing over heating. In less severe conditions, wings are spread horizontally, a posture for maximizing surface area in order to capture solar radiation for increasing body temperature. Males will often visit scat from carnivores such as coyotes and foxes (Fig. 14C).

Female regals usually do not eclose until early July or even early August. Initially, they do not take to the wing from their secluded haunts until midday, oftentimes much later. They then move directly to flower heads to feed and bask. After a brief hour or so, they return to shaded perches, often within clumps of brush such as smooth sumac and roughleaf dogwood, where they remain until the next sunny day. When a patrolling male locates a female, the two usually spiral upward for distances as great as 100 feet (33m). If the female is receptive, the two will pair and rest in a shaded location for 2-3 hours. As the season progresses, females spend increasingly more hours nectaring on their favorite flowers (see below), although usually not vacating their night perches before 1100 CDST or noon. On particular autumn days, when morning temperatures are chilly and skies cloudy, females may not take to the wing at all, remaining on their secluded perches. But on those sunny days when temperatures are warm, both sexes will spend many hours perched atop flower heads, often feeding well into early evening (approximately 1845 CDST). While the silvery patches on the ventral wing surfaces probably function as solar reflectors, the over-all mottling of the

underwings creates a disruptive appearance, rendering the butterflies cryptic to potential predators. (I observed no bird predation although I did find two female regals trapped within spider webs.) By early fall, male regals are extremely tattered; females remain in good condition until the first killing frosts (Fig. 15A).

Regal fritillaries are partial to specific flowering plants for food sources (Centerfold and Fig. 14A, 15, and 20). Actually, the butterfly's temporal distribution is synchronous with the flowering of preferred sources of nectar. For example, male regals emerge almost precisely with the May-June blossoming of *Asclepias tuberosa* and *Echinacea pallida* (Centerfold, and Fig. 2B and 10A). Females emerge at the height of the summer blooming period for *Pycnanthemum tenuifolium* and *Liatris pycnostachya* (Fig. 10B and 15B) although *A. tuberosa* and *E. pallida* usually are still in evidence (Fig. 20). As summer fades into fall, *L. aspera* (Fig. 10B), *Monarda fistulosa* (Fig. 3B) and *Vernonia* spp. are favored. Last in the sequence are *Cirsium discolor* and *C. altissimum*, which continue blooming to the first killing frosts (Fig. 15A). Although there usually is an abundance of many other species of flowering plants, regals routinely show little interest in them. While Nagel *et al.* (1991) mention that only 5.2% of the regals caught during their surveys on Rowe Sanctuary in Nebraska were feeding on flowers, those species utilized included *Asclepias speciosa*, dogbane, yellow spined thistle, swamp milkweed and ironweed.

Regals often congregate on single plants and even single flower heads in what can best be described as "social feeding" (Ross, 1998c, 2001b, 2002, 2003b, 2004a,b) (Centerfold and Fig. 15B). On occasion I have counted as many as 10 individual regals (often accompanied by other species) on a single plant of *A. tuberosa*. Individual butterflies will often jostle for a particular flower or position on a flower and as mentioned earlier, regals (predominantly males) are attracted to scat and urine. "Feeding frenzies" provided me great opportunities for in depth observations and photography. The flight season for males is typically June through July; that for females, July through September (see Table for exact data).

Comments on *Speyeria idalia* and Prairie Management

1. Haying (Mowing)

Having spent more than six months over a six-year period observing butterflies and prairie management in southwest Missouri, I can state unequivocally that our attempts to recreate Tallgrass Prairie consistent with historical accounts have proven, at best, only marginally successful. For excellent reviews of grassland dynamics, refer to Knapp *et al.* (1998) and Murphy *et al.* (1990).

Today, the "ecosystem approach" to conservation (Grumbine, 1994), which emphasizes the reproduction of natural ecological and evolutionary processes to manage ecosystems, is often advocated as "our best opportunity to describe, understand, and to fit in with nature." However, this method seems to have definite drawbacks when it comes to managing open habitats such as prairies (see Swengel, 2001 for review). For example, the rotational cycles of haying (mowing) and burning to manage prairie lands certainly do retard advances by invasive woody plants and certainly do encourage selected species of grass and wildflower (Fig. 16-17). Conversely, the continual removal of vegetation removes valuable nutrients from soils. Now even the most luxuriant mesic prairies do not produce grass equal in stature to that experienced during the country's pioneer era. One might assume that the application of artificial fertilizers to re-enrich soils would compensate for losses due to haying and burnings. Then again, prairie managers have learned that artificial supplements encourage the germination of seeds of non-native species over those of natives; therefore, artificial soil enhancement is not currently employed. In the past, the coaction between native herbivores and grass-eating insects produced massive

amounts of organic material in the form of feces, urine, and dead bodies, all of which served to fertilize the prairie soils. Weighty ungulates also trampled and churned the ground with their hoofs, inadvertently aerating and enhancing soils (Shelford, 1963) (see Grazing and Browsing, below). Likewise, large-scale mowing exposes relatively sizable land areas to intense solar heating. Auckley (1994) reports that soil temperatures differ drastically between hayed and non-hayed areas. Higher temperatures, of course, alter plant germination, flowering, and reproduction, and these in turn affect animals.

2. Fire (Burning)

Fires and prairies are synonymous. Madson (1995), Collins and Wallace (1990), and Collins and Steinauer (1998) have good discussions of the role of fire in prairie management (Fig. 3 and 18). For indication, Madson mentions that some of the Native Americans inhabiting southern Michigan called fire *sce-tay*, the same term used by them for "prairie." Fires had two causes: lightning sparked and man torched (the latter, for at least 5000 years of history). Both were common. But prairie grasses are highly fire-tolerant, just as they are to periodic grazing, and so prairie fires never result in a biological holocaust. Because the grass dies back each winter, a considerable amount of mulch and thatch tends to accumulate from year to year. This dense mat shades and insulates the prairie soil, preserving winter chill well into the beginning of the normal growing season.

By removing this biotic clutter, fires serve several purposes. First, more light, warmth, and moisture can reach the soil, stimulating grasses and forbs in early spring (Knapp *et al.*, 1998) (Fig. 3A and 18B). Second, the actual black ash surface resulting from burning acts as a heat-trapping blanket, increasing ground temperature to jumpstart spring germination. Third, fire kills, those plants that are non-fire tolerant, suppressing shrubs and trees that continually try to encroach upon prairie lands from the East. Finally, fire unlocks the treasure-trove of minerals held within vegetation, thus returning valuable nutrients to the earth for recycling. In effect, fires provide natural fertilizers for the upcoming season of growth. But on the downside, "high light levels at the soil surface in burned prairie increase evapotranspiration, and result in warm, relatively dry conditions" (Collins and Steinauer, 1998).

Today most fires occur during "controlled burns," but even these are often suppressed on most prairie lands. First, fires can easily get out of hand and endanger surrounding property. Second, because of the extreme precautions that must be honored, every controlled burn is inordinately expensive. As such, prairie management with fire is always questionable. Therefore, when a "controlled burn" is instituted managers are prone to burn as great an area as possible, at a time most convenient for them, and when weather conditions (such as wind and relative humidity) do not favor run-away-fires (usually mid summer). Unfortunately, these "controlled burns" often occur during prime reproductive activities of animals and plants. Needless to say, results can be catastrophic for both short and long term.

My observations on Missouri's prairies lead me to conclude that most prescribed burns include too great a percentage of the total preserve. In the past, when the prairie was "endless," the amount of land burned by either lightning or Indian ignited fires was relatively unimportant. Threatened animals could move into safe zones. And in those venues where fires ravaged thousands of acres, the surrounding unburned prairie would serve as a reservoir for the eventual repopulation of the seared lands. But today all of that has changed. There are no nearby havens. Fences, roads, farms, ranches, townships, and even adjacent mowed prairie impede nearby relocations. With no options, many animals simply get trapped and

perish. In a sense, today's preserves exist in a vacuum; they are virtual islands surrounded by inhospitable waters. And of course, annual fires can be extremely devastating to both plants and animals. Research by Collins and Steinauer (1998) on Konza Prairie indicates that "annually burned sites are less variable from year to year than infrequently burned treatments."

All fritillary butterflies within the genus *Speyeria* are among the most sensitive organisms in native ecosystems, and are among the first to be exterminated as a result of widespread human disturbance (Hammond and McCorkle, 1984). Because the Tallgrass Prairie ecosystem is now virtually totally manipulated by man, *Speyeria idalia* is in a particularly precarious position. (For an example of complex species-environmental interactions involving another univoltine butterfly, see Ross, 1995a, 1996.) Like all single-brooded and single-host butterflies, *S. idalia* each year has one and only one chance for successful reproduction, and hence, species survival. Unfortunately, *S. idalia* has a life cycle that exposes for long periods of time all stages of its development stages to habitat disturbances.

In summary, on the Wah'Kon-Tah, *S. idalia* females deposit hundreds to even thousands of eggs on grass thatch on the ground during a six to eight week period in late summer. (Wagner (1995) recorded 2450 eggs over a period of 12 weeks for a female in captivity.) After 30-36 days, tiny larvae emerge, crawl to the dark underside of their perch and become quiescent. They remain in this non-feeding, suspended condition (diapause) concealed within ground litter through fall, winter, and spring. Then, with the early growth of violets, (arrow-leaved violet, *Viola sagittata* is the preferred host although Kopper (1997) and Kopper *et al.* (2001) state that *V. pedatifida* and *V. pratincola* are used in Kansas), the larvae begin feeding. Larvae feed mainly during the night, spending daylight hours hidden within dried thatch. Larvae mature in mid May, pupate, and then emerge as adults throughout the summer (males in late May through mid June, females in July and August).

Theoretically, mowing or burning a prairie hosting *S. idalia* anytime between late summer of one year and early summer of the following devastates large numbers of regal immature stages that are living in ground litter and feeding on low growing hosts. Swengel (1996, 1997; Stolzenburg 1992;) and Williams (1999) suggest that *S. idalia* is a prairie specialist that is affected more by habitat burning than by mowing, and that burnings in mid summer when winged regals could fly clear of the flames would be most desirable. This study supports this supposition. For example, I found that haying adversely affects prairie violets, regals' hosts. The increased exposure to sunlight and heat often kills plants. Fires also kill violets. Comparisons between areas of prairie that had been hayed or burned the previous year and areas that had remained undisturbed for one to two years revealed that violet density was significantly reduced in the more recently disturbed locales, especially the burned sites. Debinski and Kelly (1998), Hammond and McCorkle (1984) and Kelly and Debinski (1998) suggest that larval food limitation may be an important factor in the decline of *S. idalia* in many parts of its range.) But violets are early succession or pioneer species that are easily smothered out by tall, dense vegetation and the accumulation of thick layers of ground thatch (Hammond and McCorkle (1984)). Therefore, violets require periodic disturbances such as fire to clear the ground in order to thrive over extended periods.

But there is another consideration: nectar sources. My research with *S. idalia* in Missouri and my ongoing investigations beginning in 1991 with the Diana fritillary, *Speyeria diana* (Cramer), in Arkansas (Ross, 2003b, 2004b; Ross and Henk, 2004), convince me that these two species of butterflies are very dependent upon specific nectar plants. In the past, the canonical thesis regarding



Fig. 16. Haying (mowing) is routinely used in prairie management to reduce shrubs that otherwise would quickly invade prairie landscapes. To minimize impact on flowering species, haying follows a predetermined grid. Photograph illustrates division between cut (left) and uncut (right) sectors. Regrettably, haying occurred during the height of bloom for rough blazing star (*Liatris aspera*) (Asteraceae), a favorite nectar source for many species of butterflies, particularly the regal fritillary, *Speyeria idalia* (Nymphalidae).

nectar plant/butterfly relationship held that nectars in general simply supplied butterflies with sugars to generate metabolic energy. And research by Boggs and Ross (1993) has shown that the fecundity of females of *Speyeria mormonia* (Boisduval), a western relative of *S. idalia* and *S. diana*, is very much influenced by food availability. Recently, physiologists and nutritionists have been turning their attention to the role of phytochemicals and micronutrients in human metabolism. Their conclusions prompt the manifest question: How are these substances being used throughout the plant and animal kingdoms?

Answers are coming slowly (see Einem, 2004; Pitchersky, 2004). For examples: We now know that the males of many species of butterflies supplement their normal diets of nectar by puddling in order to acquire specific minerals and salts that they not only use in sperm production but also transfer to females in their spermatophores during mating (Boggs and Gilbert, 1979; Boggs, 1998; Ross, 1998b); butterflies of the genus *Heliconius* (Nymphalidae: Heliconiinae) are able to acquire amino acids by dissolving pollen gathered from various plants. The amino acids are used to promote general longevity and increase fecundity in females (Boggs *et al.*, 1981; Dunlap-Pianka, 1979; Dunlap-Pianka *et al.*, 1977). The addition of amino acids to the diet of captive butterflies in butterfly conservatories is now sometimes used to increase individual life spans; and finally, the addition of amino acids or protein to the diet of captive regal fritillaries increases life span, female fecundity, and egg fertility (Williams, 1995).

Therefore, I theorize that the nectar sources that are preferred by both *S. idalia* and *S. diana* contain specific micronutrients and/or phytochemicals that are necessary for sustaining the insects, unusually lengthy and fecund life cycle (Ross, 2003b, 2004b; Ross and Henk, 2004). As such, the viability of populations of *S. idalia* (and *S. diana* as well) is determined by not only the availability of host plants but also by the accessibility of nectar sources. This idea is supported by an increasing body of published conjecture. For example, research on prairie violet distribution and population sizes of *S. idalia* (Britten and Riley, 1994; Kelly and Debinski, 1998; Swengel, 1997) has consistently shown that the distribution of *S. idalia* cannot be regulated totally by the availability of violets. These authors conclude that other factors, e.g., nectar plant density and area of suitable microhabitat, seem to be important factors in the long-term persistence of the butterfly.

On the Wah'Kon-Tah, the meadows hosting the greatest concentrations of *Asclepias tuberosa*, *Cirsium discolor* and *C. altissimum*, *E. pallida*, *Liatris pycnostachya* and *L. aspera*, *P. tenuifolium*, and *Vernonia* spp., hosted the greatest density of regals. These habitats had experienced a controlled burn either the previous year or two years prior. Consequently, when considering prairie management for *S. idalia*, burning must be considered. Three questions are critical: How often should a prairie be burned? How much habitat is necessary to maintain threshold densities for host plants and nectar plants? And, what are optimal times for burning?

My comments and recommendations can be summarized as fol-



Fig. 17. Hay is critical for livestock during winter months. Generally, a prairie will be mowed, burned, or grazed every third or fifth year to discourage woody species. Because natural fires and native wildlife such as bison, pronghorn, and elk have all been extirpated from the Tallgrass Prairie Ecosystem, prairie lands today would quickly succeed to forest. As such, Tallgrass Prairie today is the only ecosystem in North America that must be artificially maintained.

follows: First, both burning and haying on prairie lands appear to be necessary to retard the invasion of woody species and to create fertile ground for rejuvenation of obligate pioneer plant species utilized by *S. idalia* during its life cycle. Still, burning appears to pose the greater risk to the butterfly. But because *S. idalia* seems now to be dependent upon both types of intrusions, the answer is not either/or but balance involving short-term rotational regimes designed so that no given section of prairie is burned or hayed each year. Second, reductions in burn/mow areas from what are currently employed would create a more diverse checkerboard, thereby increasing the availability of precise microhabitats, e.g., extensive patches of violet host plants and specific nectar sources, needed by adult butterflies. Third, haying and burning should be avoided between early September of one year and mid July of the following in order to reduce destruction of the immature stages of *S. idalia*. (This probably will constitute the greatest dilemma for prairie managers.)

Grazing and Browsing by Herbivores (Native and Domestic Livestock)

One other factor should be considered in future conservation strategies: controlled grazing and browsing by livestock. As with fire, the effect of grazing and browsing on butterfly diversity is difficult to document under controlled conditions (Swengel, 2001). In the past, prairie conservationists have regarded domesticated animals of any sort as an anathema to good prairie management. The literature abounds with stories describing the disastrous effects

of overgrazing in open habitats throughout the world (Swengel, 2001). Yet, we must not overlook the fact that native grazers (grass-feeders) and browsers (shrub and small tree feeders) historically were an integral part of the prairie's web of life (Collins and Steinauer, 1998; Duncan, 1979; Hartnett and Fay, 1998; Kendeigh, 1961; Kaufman and Fay *et al.*, 1998; Kaufman and Kaufman *et al.*, 1998; Madson, 1993, 1995; Reichman, 1987; Shelford, 1963).

Shelford (1963) states that in 1600 the interior North American prairies supported at least 45,000,000 bison (American buffalo), 15,000,000 pronghorns (American antelope), and untold numbers of elk (wapiti), and deer. Of these, the bison was the largest, attaining weights between 1000 to 2000 pounds (Anon., 1967) and is often regarded as the symbol of the Midwest (Fig. 19). Responsible accounts describe single herds of bison commonly contained 20,000 individuals (one report, Seton, 1909, describes a herd with 4,000,000 individuals). Bison typically are grazers, whereas pronghorn, elk, and deer feed not only on grass but browse on taller, more woody vegetation. Madson (1995) suggests that Tallgrass Prairie was always marginal habitat for bison (the ungulates seem to be better adapted to the lands farther west where the grasses were shorter in stature), and in Missouri the animals were never plentiful. Nevertheless, Reichman (1987) states that a herd of more than 4,000,000 individuals was recorded in the southwestern portion of Kansas. Historic records dating back to 1639 place bison as far eastward as the banks of the Potomac River (Madson, 1995).

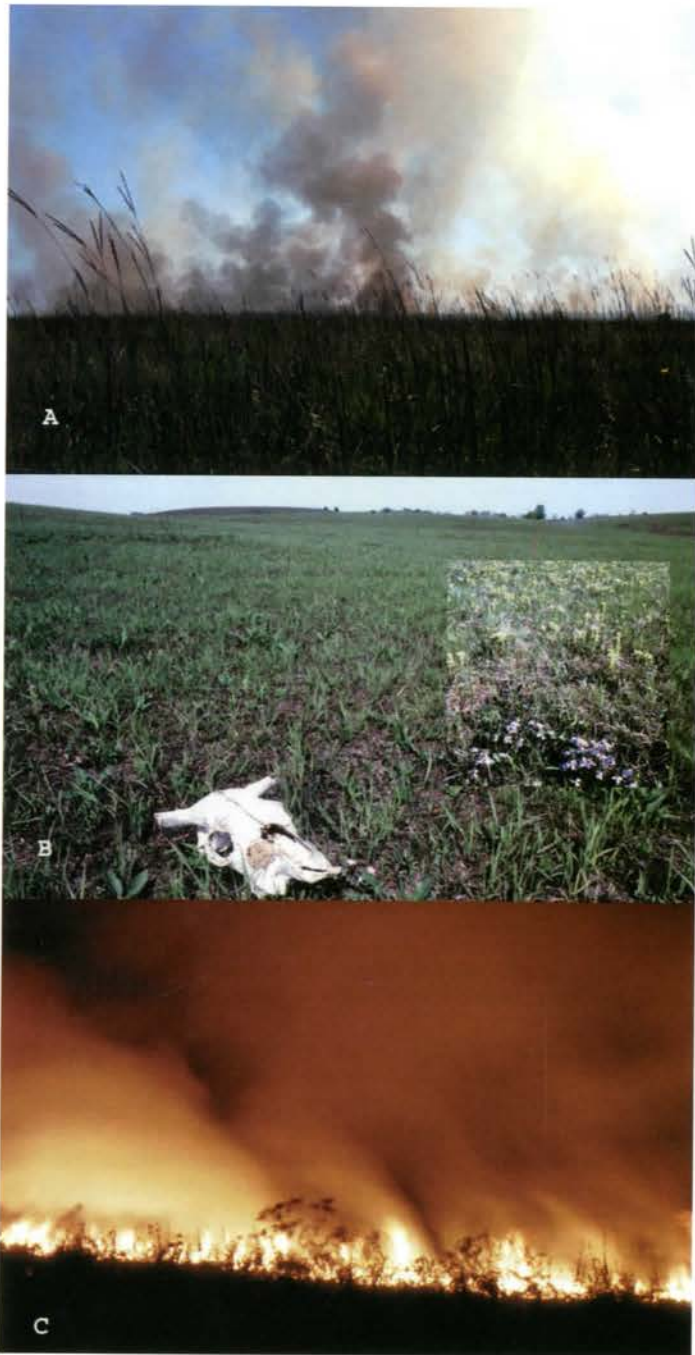


Fig. 18. Prairie management consists of periodic controlled burns to retard woody species: A and C. In the past, shrubs and trees were held at bay in part by fires set by lightning and nomadic Indian tribes. B. Fire is a trigger for many spring forbs, some of which are particularly important as nectar sources for butterflies; inset illustrates bird's foot violet (*Viola pedata*) and arrow-leaved violet (*V. sagittata*) (Violaceae) and wood betony or lousewort (*Pedicularis canadensis*) (Scrophulariaceae), two species that often cover extensive acreage. Without periodic controlled burns on the Wah'Kon-Tah, the violet host plants for the regal fritillary (*Speyeria idalia*) (Nymphalidae) would soon be smothered out by competing vegetation.

Consequently, most authors conclude that large herbivores were a significant feature of the tallgrass lands (Collins and Steinauer, 1998). Reichman (1987) states that regardless of their abundance, bison and well as many other ungulates were a "dominant factor in shaping the prairie community." Collins and Benning (1996) suggest that bison serve as "keystone engineers" in grassland ecosystems (keystone engineers being those species that modulate available

resources by causing physical state changes in biotic and abiotic systems (Jones *et al.* 1994)).

Consider the following. Monocots such as grasses seem to be extremely tolerant to moderate amounts of grazing (and firings). The meristems of grasses are underground. Therefore the plants can easily recover from having above-surface leaves and stems cropped. (In contrast, dicots are characterized by having terminal meristems, and therefore can be severely damaged by cropping.) When the above ground portion of a monocot is removed, regrowth is stimulated so that, the total amount of herbage produced in a given year is greater in grazed lands than in those ungrazed (Reichman, 1987). In addition, grazing promotes clonal expansion by stimulating the production of new growth from underground lateral shoots. Because of this difference in growth habits, monocots have a distinct advantage in habitats that are subjected to periodic surface alterations. As such, grasslands, fires, and ungulates have interacted over the millennia in what might be considered an evolutionary codependency.

But grazing encourages the growth of forbs, too. Collins and Steinauer (1998) state that "grazing tends to create considerable heterogeneity in both grass and forb cover." Furthermore, these authors conclude that grazing by bison "is a disorganizing force in this (Konza) grassland that tends to reverse the impacts of frequent burning." Grazing reduces the abundance of the dominant C4 grasses and leads to higher plant species diversity and community heterogeneity, greater temporal variation in plant community composition, and increase nutrient retention. In addition, bison redistribute N in feces and urine and reduce N losses during burning. And even after death, the organic matter produced by the decomposition of massive bodies would have enhanced soils and subsequent prairie vegetation, particularly since the ecosystem's scanty rainfall reduces natural leaching.

Finally, the actual physical impact upon land resulting from millions of animals walking about should not be considered lightly. For example, bison are notorious for creating long-standing migratory trails and buffalo wallows (barren patches or basins where bison traditionally bathed or dust-rolled). Some of these are in evidence today. But even the simple impact of millions of hoofs on the ground tends to churn and aerate soils, producing ideal conditions for pioneer species of plants. All in all, these physical assaults upon the land influenced surrounding vegetation (Madson, 1995).

Although ungulates were certainly the dominant animal life on the prairie, one should not discount the role of animals of lesser stature, either. For example, Shelford (1963) mentions that prairie dogs, ground squirrels, prairie chickens, mice, voles, and even jack rabbits were abundant and must have played a significant role in soil aeration and soil fertilization. And of course, there were the insects, abundant in both numbers and in biomass. Shelford (1963) mentions that by late August "they sometimes reach 10 million individuals per acre" (25 million/hectare). Once again, the organic matter in the form of excretory products and dead bodies produced by these invertebrates must have proven extremely beneficial to prairie soils. Of course, the role of Rocky Mountain locust, or Rocky Mountain grasshopper (*Melanoplus spretus*, Orthoptera), now extinct but whose numbers once exceeded those of any known species, can scarcely be imagined (Lockwood, 2001).

As would be expected, the rapid degradation of native prairies correlates well with the extirpation of native ungulates and other herbivores. In 1987, bison were reintroduced to what is now the Konza Prairie Research Natural Area in Kansas. Carefully monitoring of rotational grazing regimes over the years has provided unequivocal data to support the theory that ungulates are indeed vital for long-term prairie life (Collins and Steinauer, 1998; Kaufman and Fay *et al.*, 1998; Kaufman and Kaufman *et al.*, 1998).



Fig. 19. Bison (American buffalo) once roamed the American prairies by the hundreds of thousands. Activities of these large ungulates were critical for maintaining a healthy grass dominated landscape. Today, however, all Tallgrass Prairie lands are behind fences on either federal or private lands. While still controversial, an increasing number of land stewards are advocating that native prairie lands should be grazed and browsed for short periods of time by cattle and goats, in essence, simulating historic land use. (Photograph from Prairie State Park, Barton County.)

Later introductions of domesticated livestock such as cattle, sheep, and goats with uncontrolled practices of grazing continued to accelerate the deterioration of prairie landscapes (Fig. 6A,C). But while intensive herbivory can have disastrous negative effects on native plant diversity, the total removal of livestock can cause significant damage to grassland communities, too. For example, Launer *et al.* (1992) report that the deliberate exclusion of livestock from the coastal prairie in California has probably been responsible for the loss of both native and non-native species.

Land subject to grazing by livestock has produced mixed results for butterflies (see Swengel, 2001), indicating that different grazing practices affect individual prairie butterfly species differently. This suggests that each species must be considered on a one-on-one basis. For the regal fritillary we shall require a substantially new manner of thinking. Specifically, prudent conservation planning should consider the inclusion of both grazing and browsing livestock such as cattle, sheep and goats to fill the void created by the historic loss of native ungulates. Just as the reintroduction of fire has been marginally successful with regal fritillaries, the reintroduction of livestock could also prove beneficial. Swengel (1997) also advocates unintensive grazing to replace burning. [NOTE: The extreme northeast section of the Thoreson Ranch, consisting of approximately 10 acres, had been grazed both by cattle and goats on a rotational basis several years prior to my 1998 study (Fig. 10). Haying and burning had not occurred for over 12 years. While several woody species were gaining foothold, native grasses and forbs continued to thrive. Interestingly, the area had one of the

highest densities of *S. idalia* of any sites on the Wah'Kon-Tah preserve.]

As with fire, the impact of livestock would have to be carefully monitored. Special emphasis should be placed on the percentage of prairie to be grazed as well as the timetable for grazing (e.g., length of grazing time and season for grazing).

Speyeria idalia and the future

Speyeria idalia, the regal fritillary, is a living legacy of the magnificent Tallgrass Prairie ecosystem of America's Midwest. Surveys of butterflies in the Midwest (see Opler and Swengel, 1994; Swengel, 2002; Swengel and Opler, 1995, 1996, 1997, 1998, 1999, 2000, 2001; Swengel and Swengel, 2003) have shown that the butterfly species continues to exist in reasonable numbers, but only on those prairie lands that are being managed for the control of invasive woody species. During its evolution, the butterfly developed complex morphological, physiological and behavioral adaptations to deal with periods of intense radiation and summer drought followed by icy winters, cyclical fires, and periodic trampling by large herbivorous mammals. These adaptations have now obligated the butterfly to the vagrancies of its unique ecological niche. Modern man, however, has obliterated the natural Tallgrass Prairie ecosystem. In response, *S. idalia* must cope with a new regime of environmental parameters.

In conclusion, if *S. idalia* is to be sustained for future generations of mankind, preserves or sections of preserves will have to be managed in accordance with the specific requirements of that butt-



Fig. 20. A female regal fritillary (*Speyeria idalia*) (Nymphalidae) nectars atop a favorite summer food source, pale purple coneflower (*Echinacea pallida*) (Asteraceae). The combination symbolizes the beauty and fragility of the Wah'Kon-Tah Preserve as well as the entire Tallgrass Prairie Ecosystem.

erfly species. Simply setting aside land as preserves will surely fail. Likewise, ecosystem management that does not consider the specific feeding and reproductive requirements of this particular butterfly will fail. We have too little land; it is that simple. As professed stewards of the environment, we would be very wise not to be lulled into a sense of complacency based on what some might regard as recent stories of success. Clearly, *S. idalia* walks the proverbial tight rope, constantly teetering between survival and extinction in a microenvironment that by and large is now totally man-managed. What a pity to lose *Speyeria idalia*, the resplendent butterfly we endearingly refer to as the regal fritillary, at the very time the species is emerging as a "poster child" for North America's unique Tallgrass Prairie (Fig. 20).

"It is our task in our time and in our generation, to hand down undiminished to those who come after us, as was handed down to us by those who went before, the natural wealth and beauty which is ours."

John F. Kennedy

ACKNOWLEDGEMENTS

I would like to express my appreciation to the following for their contributions. The Nature Conservancy, Missouri Office (St. Louis), Mr. Roger L. Still, Director (1998-2001), for financial support and encouragement during my 1998 residency on the Wah'Kon-Tah; Missouri Department of Conservation (El Dorado Springs office), Mr. Jack Shatford, Director, for generous assistance and hospitality during my visits and residency in El

Dorado Springs; Powell Gardens (Kingsville), Mr. Eric N. Tschanz, President, for foresight to contract with me in 1997 to develop a butterfly festival (with an emphasis on prairie butterflies); the residents of El Dorado Springs (especially Mr. Bill Bishop, Mrs. Helen Bishop, Mr. and Mrs. John L. Eslinger, Dr. and Mrs. Bill Neale, Mr. Dean Smith, Mr. and Mrs. Bennett Thoreson) along with Mrs. R. D. Gurley and her son Mike (Appleton City), for overwhelming hospitality, friendship, and assistance with my numerous requests for assistance with photographic projects; Mr. Kenny Long, editor of the *El Dorado Springs Sun* newspaper, for providing good media coverage of my activities on the Wah'Kon-Tah Prairie; Mr. Mervin Wallace, President, Missouri Wildflowers Nursery, for introducing me to his special technique for harvesting prairie wildflower seeds; to Mr. James Schlachta, Dr. Andrei Sourakov and Dr. John Heppner (Gainesville, FL) for assistance with the electronic preparation of the manuscript and photographic plates; and lastly, a very special thanks to Ted and Sue Thoreson and their four children (especially Tannen), who from the very first moment of my arrival in 1998 adopted me into their family, providing not only personal friendship, invaluable insight into the complex world of prairie/pasture management, but also "Babe" and "Ike," two unusual canine pets, to keep me company during residency in my "little house on the prairie."

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