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INSECTS AND THE NATIVE VEGETATION OF NEBRASKA

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ABSTRACT

The principal plant biomes in Nebraska are briefly reviewed. The relationships of insects, particularly scarab beetles and butterflies, to these biomes are discussed, especially as it relates to their distributions. Human-induced alteration of habitat has significantly influenced the present distributions of both plants and insects relative to their historical distributions at the time of Euro-american colonization of Nebraska in the mid-1800s. Examples of range expansion or contraction are presented for exemplar taxa of scarab beetles and butterflies

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An article on insects as they relate to the native vegetation in Nebraska is a challenge. On the one hand, we are dealing with a huge number of species when talking about insects —in fact, the most diverse group of organisms on the planet. There are more kinds of insects in Nebraska than all other kinds of animals *and* plants combined! Discussing even a tiny fraction of them in a single article is virtually impossible because there is *so much* that could be said.

On the other hand, there is little baseline data about the composition and distribution of the insect fauna in Nebraska prior to the conversion of native vegetation to intense agriculture, grazing, and urbanization conversion by mostly Euro-american settlers in the 1800s. Consequently, discussing even a tiny fraction of the insect fauna is virtually impossible because there are *so few* data available.

Our solution is to narrow the discussion to the two groups in which we specialize: butterflies for Hammond and scarab beetles for Ratcliffe. Both larval and adult butterflies feed on plants (usually quite specifically for the larvae and more generally for the nectar-sipping adults), and so correlations between plant communities and butterflies are easier to track. Within scarab beetles, the adults of many feed on leaves, flowers, or fruits while the larvae either feed on roots, especially those of grasses, or are detritivores living in rich organic matter. Scarabs, then, are not usually as closely associated with their adult food plants as are butterflies.

Although primarily a prairie state, Nebraska has many diverse habitats (Fig. 1) ranging from eastern deciduous forests to short and tallgrass prairies (actually six different grassland types), a large section of Sand Hills prairie (19,000 sq. mi.), and a small western component of Rocky Mountain forest. The vegetation in Nebraska has undergone considerable change since the pioneers first began settling here in the 1800s. Probably the three most significant changes are loss of many native prairies to agriculture, the introduction of trees in urban areas where once there were few, and the growth of woody vegetation in eastern Nebraska's gullies and draws. These changes in the flora have affected the insects because vegetation is a limiting factor for them, both as food and shelter. In some cases, floristic changes have been mirrored by the loss of insects to a particular habitat while in others it has resulted in a net gain in diversity. The interplay between plant and animal distribution is dynamic, and the human factor has substantially changed this relationship.

The sense of living in a prairie environment or being in a prairie state has been largely lost because of the almost complete destruction of the original prairie by modern agriculture. This is especially true in eastern Nebraska where the once-dominant tallgrass prairie, stretching as far as one could see, has been 99% eliminated by intense cultivation and urbanization. Concomitant with this has been a corresponding loss in the insects adapted to grassland habitats.

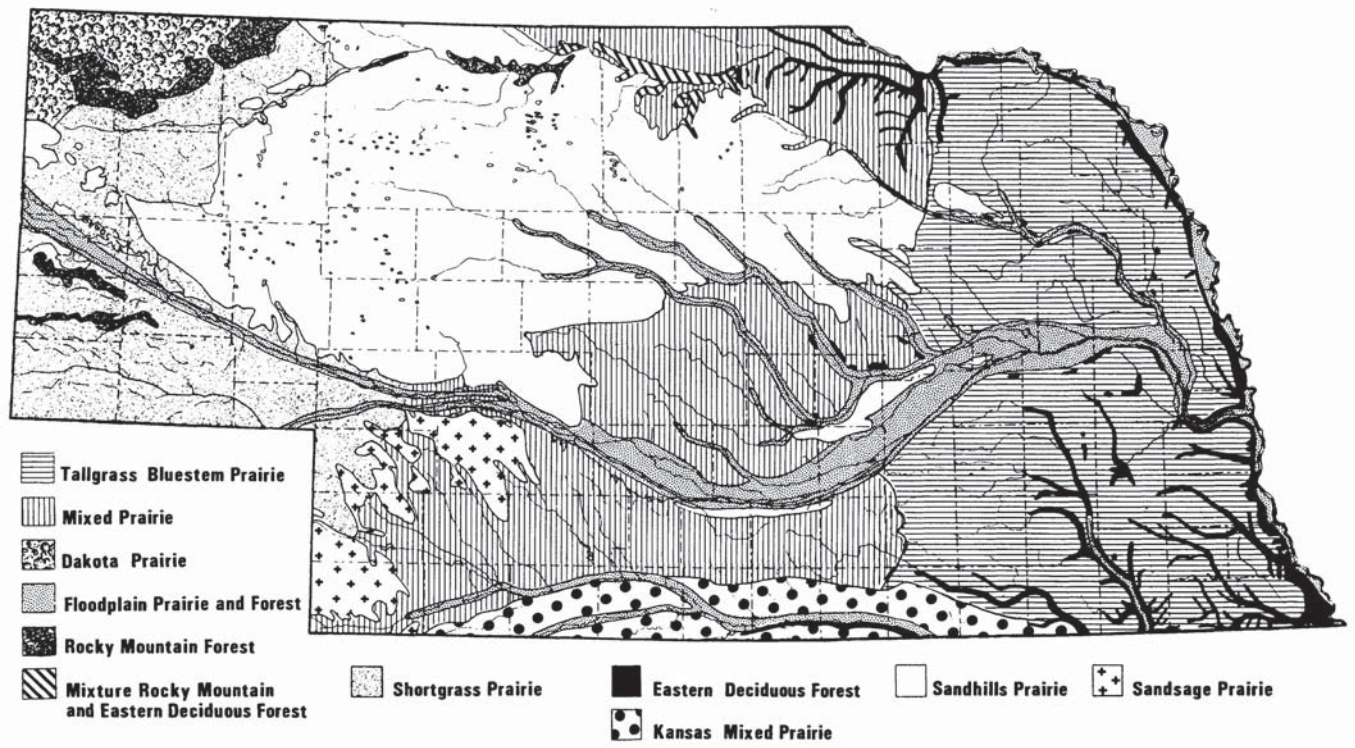

Figure 1. Vegetation of Nebraska ca. 1850 (after Kaul 1975).

Contrary to some popular anecdotes about midwestern prairie states having a "typical" or depauperate fauna, Nebraska has a diverse insect fauna reflecting the variety of vegetation types in the state. Critical to our understanding of the biotic diversity of today's fauna and flora is, of course, an understanding of what Nebraska was like in the past. Studies in paleoclimatology, paleogeography, and paleoecology have all contributed to a relatively clear picture of Nebraska since the Pleistocene glaciations although reconstructions of older times remain problematical.

According to Baker and Wain (1985) the history of the Great Plains grasslands is controversial. The controversy centers around the question of "did grasslands exist since the middle Tertiary (30 million years ago), or did they develop only after the glaciers retreated about 12,000 years ago?" While paleontological research continues to address the question of whether grasslands existed in the Tertiary, the fossil evidence does indicate that during the Pleistocene glacial maxima, the prairie was reduced to a remarkably small area and may, in fact, have been a savanna having only isolated areas of grass (Ross 1970).

During the Pleistocene, four vast continental glaciers (Nebraskan, Kansan, Illinoian, and Wisconsin) were each followed by a comparatively warm, dry period (Aftonian, Yarmouth, Sangamon, and Recent). These events clearly affected the distribution of all insects in Nebraska. Assemblages of plants and insects were displaced, not necessarily intact, southward ahead of the advancing glaciers, and they then shifted northward again during interglacial times.

Near the end of the Pleistocene glaciations, much of Nebraska was covered by boreal coniferous forests (spruce, *Picea* spp. and pines, *Pinus* spp.) and boreal parkland. Palynological data as well as fossils of Late Pleistocene forest mammals (musk-ox, stagmoose, and jaguar) indicate the presence of spruce taiga in north-central Nebraska (Schultz *et al.* 1985). Deciduous forests were present in the eastern plains (Bradbury 1980; Delcourt and Delcourt 1981; Wright 1976). Following the late glacial dominance of boreal forests, prairie grasslands developed and spread about 12,000 years ago as the climate became warmer and drier in post-Wisconsin times. These grasslands are, therefore, relatively young. The boreal forests shifted northward although relict stands are found in the North Platte and Niobrara river valleys and in the Pine Ridge escarpment. The forest-prairie ecotone moved eastward from the Niobrara Valley and Sand Hills area 11,000–9,000 years ago (Bernabo and Webb 1977). Wright (1970) indicated that evidence of prairie can be detected as occurring in Kansas about 10,000 years ago and reached eastern Minnesota as prairie openings about 7,000 years ago. Beginning 5-4,000 years ago, deciduous forests began expanding in the upper Midwest at the expense of grasslands. This trend toward forest

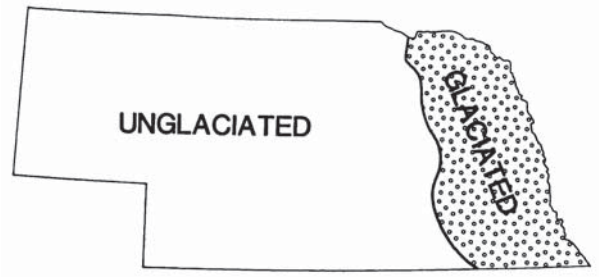

Figure 2. Extent of Pleistocene glaciation in Nebraska.

expansion continues to the present, due not only to a gradual shift in climate but also to the activities of humans.

The insect fauna of North America was well-developed before the Pleistocene, with most genera probably present in the Miocene. The glaciations of the Pleistocene affected the insects present in Nebraska at that time. The eastern fifth of the state was glaciated (Fig. 2), and much of the fauna retreated to the south, west, or east of the ice sheets. Following the retreat of glacial ice and boreal forests, Nebraska was re-colonized from the south, west, and east by an insect fauna characterized by taxa that had not occurred here in the first place as well as by those whose ancestors had previously been driven out by glaciation. Nebraska is a pivotal state for insects and plants because eastern and western faunas and floras, as well as northern and southern, converge here as in no other state.

At the time of Euro-american settlement, Nebraska was mostly prairie. The prairie (Fig. 3) is a land of waving grasses and broad-leaved forbs. Asteraceae and Fabaceae are the most diverse plant families while the many grasses are the most dominant plants found in the prairie. John Weaver, a noted Nebraska scholar of the prairie habitat, observed (1954) that the prairie appears almost monotonous in the general uniformity of its plant cover — but that it also has a special grandeur in its open expanses and in the

Figure 3. Prairie at Rowe Sanctuary near Gibbon in south-central Nebraska. Photo courtesy of NEBRASKAland/ Nebraska Game and Parks Commission.

abundance of its varicolored flowers. The dominance of perennial grasses, the paucity of shrubs, the absence of trees (except along rivers and streams), and a characteristic drought-enduring flora constitute its main features. Prairie is the name given to the vast expanse of grasslands in central North America. Similar grasslands in Eurasia are called "steppe," whereas in southern South America they are referred to as "pampas," and in southern Africa they are known as "veld." The insects living in this habitat are adapted to feeding on grasses (especially their roots) and herbaceous vegetation. Grasses are wind-pollinated, and so insects have a much larger role in pollinating forbs and woody shrubs.

The dominant grasses of North American prairies change along an east-west gradient of decreasing precipitation. This can be seen clearly in a vegetation map of Nebraska. The eastern fourth of the state is (or was) tallgrass prairie (Fig. 4), so called because the grasses there may reach a height of seven feet during moist years. The principal grasses are big bluestem (*Andropogon gerardii* Vit.), switchgrass (*Panicum virgatum* L.), and Indian grass (*Sorghastrum nutans* (L.) Nash). The western border of tallgrass prairie approximates the line of 23 inches of annual precipitation (Jones 1964).

Tallgrass prairie grades westward into mixed prairie (Fig. 5) where the dominant grasses are bluestems (*Andropogon* spp.), grama grasses (*Bouteloua* spp.), and buffalo grass (*Buchloe dactyloides* Nutt.). According to Weaver and Clements (1938), this association owes its name to the fact that its climax vegetation is composed of short and longer grasses in almost equal diversity. Jones (1964) observed that mixed prairie covers the largest area of any of the grassland associations in North America. It is *the* grassland of the Great Plains.

Grasshoppers (Fig. 6) are among the most noticeable insects in prairie grasslands. As many as 24 species have been found on a single mixed grass prairie site in Wyoming (Pfadt 1994). Of this total, 14 were grass feeders, six were mixed feeders, and four fed on forbs. The grass-feeding species comprised 85% of the total population. How can so many different species live in one place at the same time? According to Pfadt (1994), differences in population density and species diversity are correlated with differences in the microhabitat of the site in conjunction with differences in requirements of the grasshoppers. Within a single patch of prairie, there may be differences in soil, slope, and exposure to wind and sun; these all affect significantly the type of vegetation occurring there which, in turn,

Figure 4. Tallgrass prairie in Webster Co. in south-central Nebraska. Photo by PCH.

Figure 5. Mixed prairie in Sarpy Co. in eastern Nebraska. Photo courtesy of NEBRASKAland/Nebraska Game and Parks Commission.

affects the species of grasshoppers feeding on the vegetation. It should also be noted, however, that most species of grasshoppers will feed on many different species of grasses and forbs. As parts of the prairie became converted to agriculture, grasshoppers often became severe pests as they moved into cultivated fields. This was particularly acute in Nebraska in the 1800s when the migratory grasshopper, *Melanoplus sanguinipes* (Fabr.), reached plague proportions. With densities of 60–100 adults per square yard, their forage quickly became exhausted, and the grasshoppers were forced to fly to new areas of vegetation until, finally, huge swarms of these insects were on the move seeking out new food plants.

Figure 6. Threebanded grasshopper, *Hadrotettix trifasciatus* (Say), commonly found in shortgrass and mixed grass prairies.

Although almost entirely grassland, Nebraska is dissected by riverbottom forests (Fig. 7) that provide natural pathways for forest-adapted species to enter the plains. Consequently, related eastern and western species (previously isolated by climate and/or Pleistocene glaciations) are now coming together forming a broad band of overlap. The insect fauna of Nebraska is, for the most part, a recent amalgam of other faunas, both eastern and western, northern and southern, that are near the limits of their respective ranges. An insect fauna unique to Nebraska or, for that matter, the Great Plains does not exist although a few relictual or isolated taxa may occasionally be found there. Kaul (1986) observed that the flora was also ad-


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ventive in origin with nearly all of the species having colonized from elsewhere, especially from the southwest and southeast. Many eastern species of both plants and animals extend west to approximately 100° west longitude in Nebraska (about the middle of the state), and many western species dispersed eastward to roughly that same meridian.

Beginning in the mid-1800s, the landscape of Nebraska began to change radically as native prairies were converted to agriculture, grazing, transportation corridors, and settlement. This was especially noticeable in the tallgrass and mixed grass prairies in the eastern half of Nebraska where, today, only a few isolated remnants of native vegetation remains (Kaul and Rolfsmeier 1993; Samson and Knopf 1994). The short-grass and Sand Hills prairies have not been altered as much, but they have still been changed by fire suppression, introduction of exotic plants, and elimination of the large, native herbivores (bison, elk) that once lived there (Benedict *et al.* 2000; Bogan *et al.* 1995). By contrast, riparian woodlands (especially) and forests have expanded due to a variety of factors, including those just mentioned above (Bragg 1995; Johnson 1994).

As a consequence of all of these anthropogenic-induced changes to the native vegetation, the distributions of insects inhabiting these biotopes have also changed, either by expanding or contracting, because most insects are closely associated with their respective plant communities where they seek food, shelter, and breeding places. What follows is a brief review of some of those changes in insect distribution using exemplar taxa of scarab beetles and butterflies.

Figure 9. Upland deciduous forest on sheltered east-facing slope along Missouri River in Richardson Co. in southeastern Nebraska. Photo courtesy of NEBRASKAland/Nebraska Game and Parks Commission.

THE SCARAB BEETLES

There are 201 species of Scarabaeidae in Nebraska (Ratcliffe 1991). Scarab beetles associated with eastern deciduous forests (Fig. 8) comprise about 25% of the fauna. Most of these species are found in the eastern third of the state, and many of those are in gallery forests that extend well into areas of former tallgrass prairie. Nebraska's eastern deciduous, hardwood forests are largely restricted to the southeast corner of the state, the west bank of the Missouri River, and the Niobrara River in its eastern third. Within these riverine strips of forest, steep and undulating ridges contain dense upland forests (Fig. 9) dominated by the drought resistant bur oak (*Quercus macrocarpa* Michx.), shagbark hickory (*Carya ovata* (P. Mill.) K. Koch), and basswoods (*Tilia americana* L.). The deep ravines provide shelter from drying prairie winds permitting many species of broadleaf trees to survive. About 44 species of deciduous trees are native to southeastern Nebraska (Pool 1929). These hardwood forests extend west along rivers well out into the grasslands where they become impoverished in species (Kaul 1986). Considering that only 3% of the state's land area is covered by eastern deciduous forests, the large number of scarab beetles and other insects occurring there will give some idea as to the rich biotic diversity supported by woodlands. Partly accounting for this is that the life history of the majority of scarabs is based on leaf and flower-feeding as adults and compost and root-feeding as larvae. Deciduous forests provide the greatest number of feeding niches for these kinds of food preferences. All the species occurring in Nebraska's deciduous forests dispersed there from either the south (primarily) or east (Ratcliffe 1990).

The eastern Niobrara River valley (Fig. 10) in north-central Nebraska contains disjunct and relictual elements of both plant and animal species that were

Figures 7 and 8. 7. Seasonally dry riverbed with gallery forest along Platte River in Hall Co. in central Nebraska. Photo by BCR. 8. Eastern deciduous forest adjacent to Missouri River in Richardson Co. in southeastern Nebraska. Photo courtesy of NEBRASKAland/Nebraska Game and Parks Commission.

Figure 10. Niobrara River valley in Keya Paha Co. in northeastern Nebraska. Photo by PCH.

Figure 11. *Xyloryctes jamaicensis* (Drury), Nebraska's only "rhinoceros beetle." Illustration by Mark Marcuson.

probably widespread during cooler, wetter Pleistocene and Holocene times and that today occur well to the west, north, or east. Post-Wisconsin climatic shifts are probably responsible for causing the isolation of these taxa in the Niobrara Valley. Other species have colonized the Valley since the retreat of the glaciers, but some undoubtedly vanished from there as well when the climate warmed and dried in the Holocene Hypisthermal Interval (Kaul *et al.* 1988). Kaul *et al.* concluded that the Niobrara Valley is a glacial and postglacial refugium in the central plains of North America. The congruence of various extant plant and animal distributions, in addition to the macro- and microfossil data, strongly suggests historical factors rather than dispersal events to account for the observed distributional patterns of many species. Among the Scarabaeidae, *Xyloryctes jamaicensis* Drury, a small, horned, rhinoceros beetle (Fig. 11) found in extreme southeastern Nebraska and the Niobrara River valley, is the best example of a disjunct population isolated from its normal range, which is in the deciduous forests well to the south and east of Nebraska.

Scarab beetles associated with the coniferous, evergreen trees of the western Rocky Mountain forests and woodlands (Fig. 12) are found only in the northwest

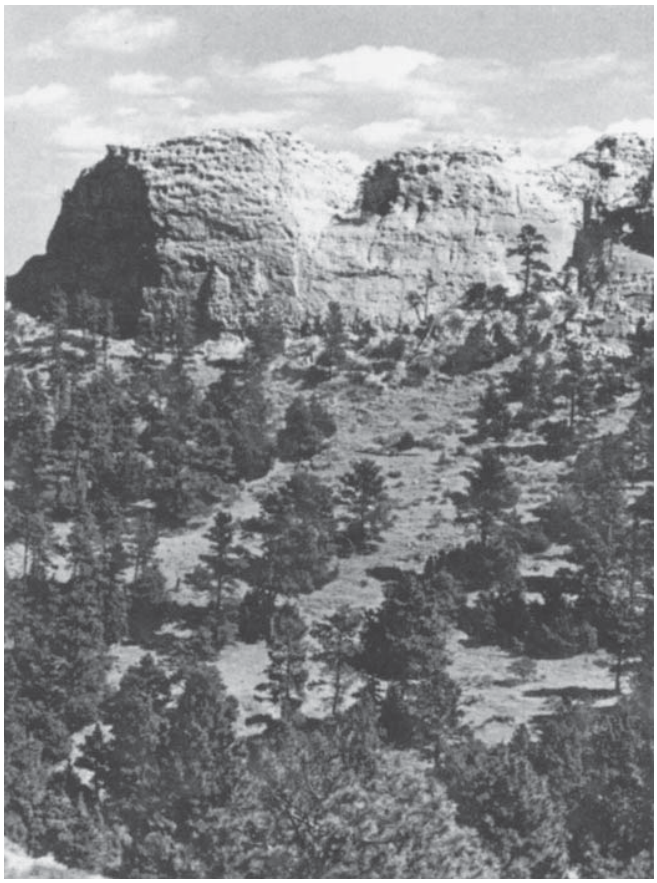


Figure 12. Rocky Mountain forest near Chadron in Dawes Co. in northwestern Nebraska. Photo courtesy of NEBRASKAland/Nebraska Game and Parks Commission.

ern corner of Nebraska in the Pine Ridge escarpment and, to a lesser extent, in the western reaches of the Niobrara River valley. These forests extend eastward to approximately the 100th meridian on the north-facing slopes of the Niobrara River valley and its spring-fed tributaries. They meet the westward extensions of the eastern deciduous forests only in this region of north-central Nebraska. Ponderosa pine (*Pinus ponderosa* Lawson) and narrow-leaf cottonwood (*Populus angustifolia* James) are common Rocky Mountain trees that are found in this region of the state. Quaking aspen (*Populus tremuloides* Michx.) and western black birch (*Betula occidentalis* Hook.) also indicate the montane floral affinities of the Pine Ridge. These species probably occurred widely over much of the western part of the state in post-Wisconsin times, and the areas remaining when Europeans first reached western Nebraska were relics of this former widespread distribution (Jones 1964). Scarab beetles associated with this kind of vegetation account for less than 1% of the Scarabaeidae in Nebraska but, considering that boreal coniferous forests are relatively depauperate of scarabs in the first place, this is not surprising.

Because the Sand Hills are, for the most part, a treeless landscape of grass-covered sand dunes, most of the insects that occur there are adapted to sandy habitats and a dry, continental climate as well as to the kinds of plants and other animals that live there. Compared to some forest-adapted species, insects in the Sand Hills tolerate drier and windier conditions and greater solar radiation. They have also been successful in surviving the periodic fires that are so necessary for maintaining native grasslands. In fact, the mosaic of habitats partially created by fire has probably contributed to increased insect diversity in the Sand Hills. With the introduction of monoculture row crops (often with irrigation) in the Sand Hills, a few insect species that formerly occurred there in relatively low numbers now occasionally reach economic thresholds (Wedberg *et al.* 1975). On the other hand, some species have now disappeared from native prairie because of the severe disturbance caused by agriculture.

Approximately 13% of Nebraska's Scarabaeidae have close associations with Sand Hills prairie (Ratcliffe 1990, 1991, 1998) (Fig. 13), the particular plant/sand association confined almost entirely to Nebraska. The vegetation of the Sand Hills is surprisingly diverse. It is also unique — not because it consists of many unusual species, but because it is a mixture of so many different types of vegetation. It is a "borrowed" vegetation in that most plants probably moved into the area from elsewhere during and after retreat of the glaciers (Kaul 1989).

Some of the most characteristic plants of the Sand Hills are bluestem grasses, sandreed grass (*Calamovilfa longifolia* Hook.), needle grass (*Stipa* spp.), and yucca (*Yucca* spp.). The grass cover of the sand dunes comprising this area is fragile and susceptible to erosion. Excessive cultivation during the drought years of the 1930s caused erosion and some sand movement. Although the dunes are stabilized by plant cover today, local blowouts remain common. A few species of scarabs are found only in sandy habitats (*Polyphylla* species, Fig. 14; *Stephanucha pilipennis* Kraatz, Fig. 15) while others seem to be adventive.

Scarab beetles with affinities to the deserts of the Southwest (*e. g. Bradycinetulus fossatus* (Haldeman, Fig. 16) are found in areas of sandsage prairie (Fig. 17) and shortgrass prairie (Fig. 18) in the southwestern part of the state and constitute about 6% of the scarab fauna. The shortgrass prairie is dominated by blue grama grass (*Bouteloua gracilis* Kunth) and buffalo grass (*Buchloe dactyloides* Nutt.). Shortgrass prairie is found in much of Nebraska's panhandle. Sandsage prairie is characterized by species of sage (*Artemisia* spp.) as well as by sandreed grass (*Calamovilfa longifolia* Hook.) and bluestems (*Andropogon* spp.); this prairie type is found

Figure 13. Sand Hills prairie in Arthur Co. in western Nebraska. Photo by BCR.

Figure 14 The ten-lined June beetle, *Polyphylla decemlineata* (Say), the largest scarab beetle in the Sand Hills. Illustration by Mark Marcuson.

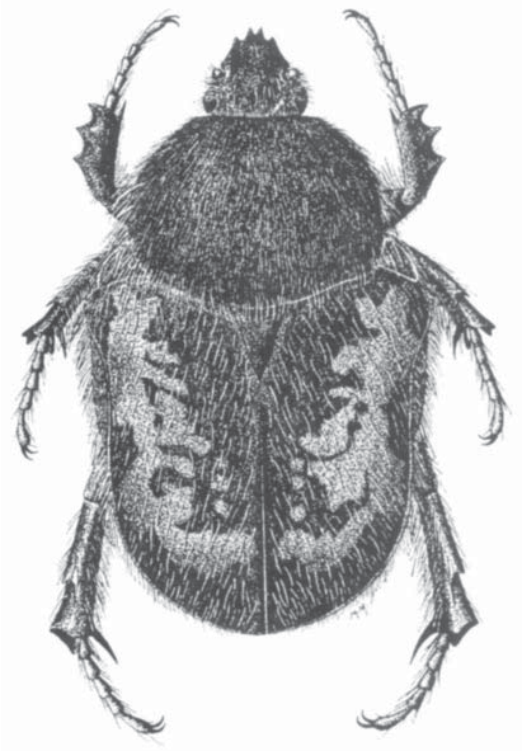


Figure 15. *Stephanucha pilipenrus* Kraatz, a cetoniine scarab restricted to sandy habitats like Sand Hills prairie. Illustration by Mark Marcuson.

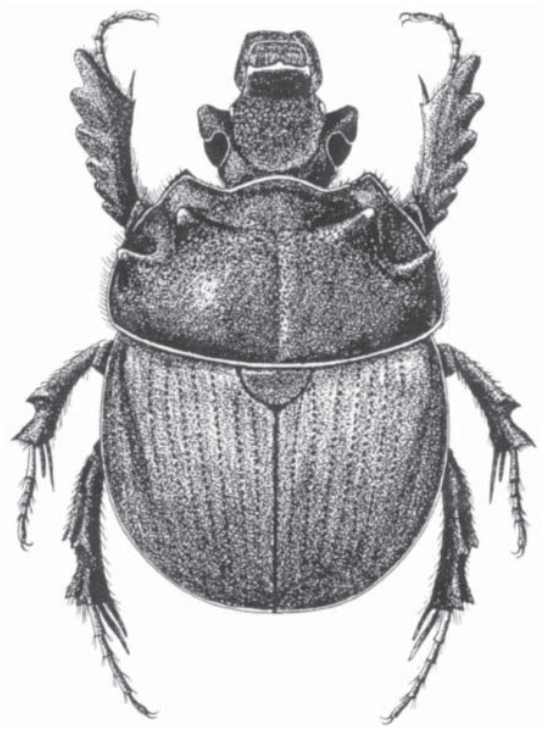


Figure 16. *Bradycinetulus fossatus* (Haldeman), a geotrupid found in the sandsage prairie of southwestern Nebraska, occurs more commonly in the southwestern United States. Illustration by Mark Marcuson.

in the southwestern corner of Nebraska. Unlike the plant colonists, the low percentage of scarab beetles indicates that the source of most of the scarab beetles species in the state is from the southeast and not the southwest.

THE BUTTERFLIES

As with many other insects, the butterfly fauna of Nebraska has greatly changed in abundance and distribution patterns as a consequence of European settlement and development of the state (Hammond 1995; Johnson 1973, 1986). These changes in the butterflies have taken place in concordance with the vegetational alterations across the state during the past 150 years because most butterflies are highly monophagous and closely associated with their larval foodplants. Many species declined in abundance and distribution during this time, and a few are completely extinct in Nebraska today. By contrast, other species have greatly expanded their ranges and abundance due to the anthropogenic changes to the state's landscape.

Good examples that serve to illustrate these changing patterns are found among the fritillary butterflies of the genus *Speyeria* and the swallowtail butterflies of the genera *Papilio* and *Eurytides.* These species include some of the largest and most spectacular of Nebraska's

Figure 17. Sandsage prairie near Parks in Dundy Co. in southwestern Nebraska. Photo courtesy of NEBRASKAland/Nebraska Game and Parks Commission

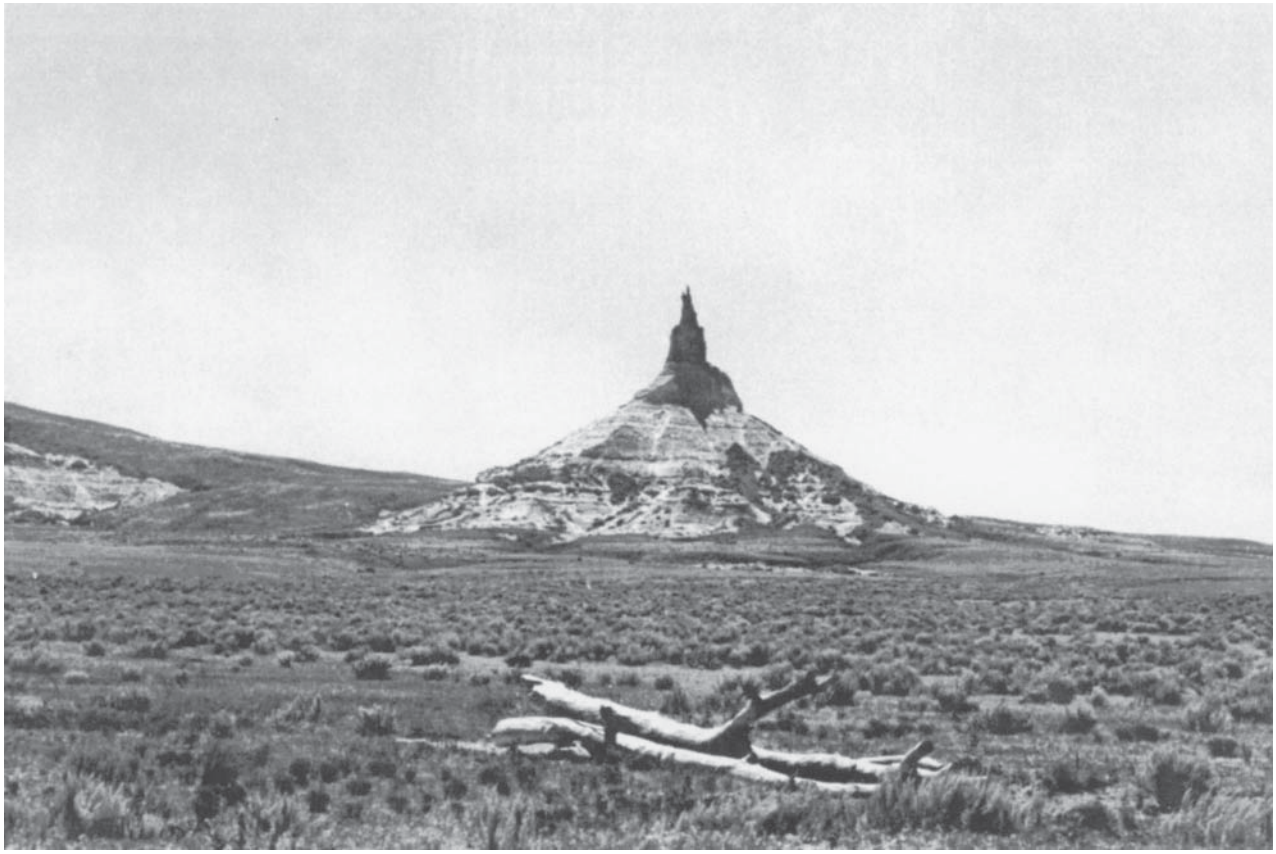


Figure 18. Shortgrass prairie at Chimney Rock in Morrill Co. in western Nebraska. Photo courtesy of NEBRASKAland/ Nebraska Game and Parks Commission.

native butterfly fauna. The caterpillars of fritillary butterflies feed exclusively on violets (*Viola* spp., Violaceae). These herbs include many species that live in a wide diversity of habitat types. Most vegetational communities are characterized by particular species of violet and fritillary butterfly, including both native prairie and forest habitats across the state.

The tallgrass bluestem prairie occupied much of eastern Nebraska about 150 years ago. This prairie segregates into wet tallgrass and dry tallgrass habitat types. The wet tallgrass prairie usually has consistent soil moisture throughout the summer and supports many mesic-adapted plants and insects that have no toleration for summer drought. This prairie type is more characteristic of Illinois and eastern Iowa but extends westward through western Iowa and eastern Nebraska in low, wet bottomland sites. Characteristic of this mesic habitat is the Alcestis fritillary butterfly (*Speyeria aphrodite alcestis* (Edw.)) and its larval foodplants, the large blue violets of the *Viola sororia* complex, including both *V. pratincola* Greene and *V. nephrophylla* Greene. This butterfly is still common on native prairie preserves throughout Iowa and Illinois, and it was probably common on wet bottomland sites throughout eastern Nebraska in 1850. We have historical specimens preserved in the University of Nebraska State Museum that were collected at West Point and Lincoln around 1894, but, unfortunately, the Alcestis fritillary is now thought to be extinct in Nebraska today.

The dry tallgrass prairie habitat occupies the drier, upland hills through western Iowa and eastern Nebraska. Mesic-adapted plants and insects are mostly excluded from this prairie due to periodic summer drought during many years. The regal fritillary (*Speyeria idalia* (Drury)) and its larval foodplant, the blue prairie violet (*Viola pedatifida* G. Don), are characteristic of this habitat. Today, this prairie and these organisms have almost completely disappeared from most of eastern Nebraska due to agriculture, and they survive in only a few prairie preserves. However, larger tracts of dry tallgrass prairie still survive on the rugged Buckskin Hills bordering the Missouri River in Dixon, Cedar, and Knox counties.

Westward, both the regal fritillary and *V. pedatifida* are still common on the mixed prairie and Sand Hills prairie of central Nebraska when the habitat is not overgrazed by livestock. However, both species are mostly absent from the drier upland prairie and are strongly restricted to moist bottomland sites, particularly the moist floodplain prairie along rivers and creeks. The

regal fritillary also uses *V. pratincola* and *V. nephrophylla* in boggy "fens" and floodplain prairie throughout the Nebraska Sand Hills. It should be noted that the regal fritillary is mostly absent from prairie heavily grazed by domestic livestock.

A special biogeographic region of Nebraska is found on the steep hills and rugged canyonlands bordering the Niobrara River in eastern Cherry and Keya Paha counties. Within this area, eastern and western species of plants and insects freely mix. For example, the ponderosa pine/bur oak forests represent a mixing of Rocky Mountain and eastern deciduous forest types. On the open, mixed grass prairie of these hills, the western yellow prairie violet (*Viola nuttallii* Pursh) is often extremely abundant and extends far eastward to Holt County, beyond its normal range on the shortgrass prairies. This violet supports very large populations of the regal fritillary on the hills bordering the Niobrara River.

Because the regal fritillary is mostly restricted to native tallgrass and mixed prairie, it has disappeared from most of its former range across North America, and it is now a candidate for federal listing under the Endangered Species Act. It is especially significant that some of the largest surviving populations of *Speyeria idalia* in North America today are found on the mixed prairie of the Nebraska Sand Hills and Niobrara River hills.

In western Nebraska, the mixed prairie is gradually replaced by a semi-desert steppe that receives very little summer rainfall. This is the shortgrass prairie plus the Dakota prairie in the northwest corner of the state. The primary violet that occupies this prairie is *Viola nuttallii,* and this species is mostly absent from the Sand Hills prairie.

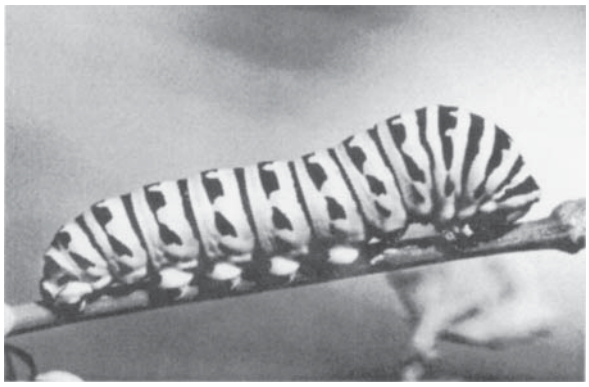
Viola nuttallii is the larval foodplant for large populations of Edward's fritillary (*Speyeria edwardsii* (Reakirt)) on the shortgrass and Dakota prairies. This butterfly is specially adapted to the arid environment, and it is one of the few species of *Speyeria* that engages in migration to avoid mid-summer drought. Adult butterflies emerge from their pupae on the shortgrass prairie during May and June and are then believed to migrate westward to the Rocky Mountain forests at higher elevations to spend the summer without laying eggs. After nectaring on wildflowers in the mountains during July and August, the female butterflies are thought to migrate eastward again in late August and September to lay their eggs on the shortgrass prairie. In this way, the newly-hatched larvae are not exposed to the mid-summer heat and drought of the shortgrass prairie.

Figure 19. Great Spangled Fritillary, *Speyeria cybele* (Fabr.). Photo by Steven Spomer, University of Nebraska–Lincoln.

Edward's fritillary butterflies probably travel up to several hundred miles during their migrations, although no marking experiments have been done to trace these migratory movements. We suspect that most Nebraska Edward's fritillaries spend the summer within the Rocky Mountain forests of the Pine Ridge and Wildcat Hills, but some may migrate to the Laramie Mountains in Wyoming or Black Hills in South Dakota. The eastward migration by females to lay eggs in the fall does not extend much past the shortgrass prairie in most years, but, during exceptional years, breeding may extend as far east as the Niobrara River hills in Keya Paha County.

Fritillary butterflies also feed on violets growing in forest habitats across Nebraska. The most common species is the great spangled fritillary (*Speyeria cybele* (Fabr.), Fig. 19). It occupies forest and brushland habitats throughout the eastern deciduous forest region of North America but also uses wetlands with tall vegetation on native tallgrass prairie. The primary larval foodplants are the large blue violets of the *Viola sororia* complex such as *V. pratincola* and *V. nephrophylla,* but it also uses various forest species such as downy blue violet (V. *sororia* Willd.), downy yellow violet (*V. pubescens* Ait.), Missouri violet (*V. missouriensis* Greene), and Canada white violet (V. *canadensis* L.).

In 1850, the great spangled fritillary was probably restricted to the eastern part of the state, where it used wetlands on the tallgrass prairie and the eastern deciduous forests along the Missouri River and smaller tributary rivers. Affording it a significant western extension of its range was the mixed ponderosa pine/ bur oak forest along the Niobrara River of Keya Paha and Cherry counties. Today, with the elimination of prairie fires, the great spangled fritillary has greatly expanded its range across the entire state as forests have spread along all the rivers and creeks and in towns and other



Figs 20–21. Larva and adult of the Black Swallowtail, *Papilio polyxenes* Fabr. All photos on this page by Leon Higley, University of Nebraska–Lincoln.

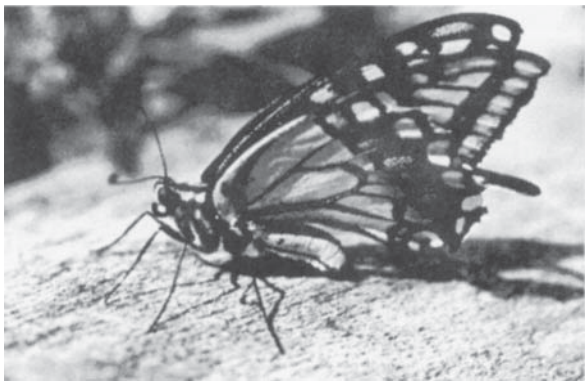


Figure 22. Baird's Swallowtail, *Papilio bairdii* Edwards, is adapted to semi-arid regions.

Figure 23. *Colias eurytheme* Boisduval, a sulfur butterfly prefers disturbed habitats.

Figure 24. The Cabbage Butterfly, *Pieris rapae* (L.), is a wide-ranging species introduced from Europe.

Figure 25. The Monarch Butterfly, *Danaus plexippus* (L), was originally a native of tallgrass prairie, but it has greatly expanded its habitat preference to other areas.

urban areas. This is an example of a butterfly that has greatly benefited from European settlement and development of the Nebraska landscape.

The other important forest type for butterflies in Nebraska is the Rocky Mountain forest that is found in the Pine Ridge and Wildcat Hills. It actually consists of two habitat types in the Black Hills of South Dakota, the Laramie Mountains of Wyoming, and southward along the Colorado Front Range. One type consists of open, dry ponderosa pine forest, and it is the prevailing type of the two habitats in Nebraska, both in the past and today. The second type consists of dense, moist quaking aspen forest, usually on north-facing slopes and in moist, sheltered canyons.

The Coronis fritillary (*Speyeria coronis* (Behr)) is the primary fritillary butterfly that breeds in open, dry pine forests of the Pine Ridge and Wildcat Hills, and it is probably as common in these areas today as in the past. The larval foodplant is *Viola nuttallii.*

However, the quaking aspen forest is far more restricted in Nebraska. Mesic-adapted violets, such as *Viola canadensis,* occur in this type of forest and serve as larval foodplants for the Hesperis fritillary (*Speyeria atlantis hesperis* (Edw.)). We have specimens of this butterfly preserved in the University of Nebraska State Museum collections that were collected in Sioux County in 1901. Although this butterfly is still common in the Laramie Mountains and Colorado Front Range, we believe it is extinct in Nebraska today.

The swallowtail butterflies of the genus *Papilio* include the largest butterflies in North America. Like the fritillaries, swallowtails serve to represent the butterfly fauna that associates with the major vegetational communities across Nebraska, and they serve as indicators of change resulting from European settlement.

Caterpillars of the black swallowtail (*Papilio polyxenes* Fabr., Figs. 20, 21) feed exclusively upon umbellifers (Apiaceae). Before European settlement, the black swallowtail was probably confined to the eastern part of Nebraska where the larvae fed on the native golden alexanders (*Zizia aurea* (L.) Koch) that grew in moist bottomland sites of the tallgrass bluestem prairie. With the demise of this habitat due to the conversion to agriculture, the black swallowtail could have become extinct in Nebraska like the Alcestis fritillary, which occupies the same type of wet tallgrass prairie. However, early settlers also planted gardens in towns and on farms all over the state and cultivated many types of domesticated umbellifers used by the black swallowtail as larval foodplants. These included carrots, parsley, dill, and celery. Instead of becoming extinct, black swallowtail populations actually expanded and spread over the entire state, and the species is now one of the more common urban butterflies in Nebraska. This is an example of a native prairie insect that has found an entirely new habitat and has greatly benefited from the European settlement.

The closely related Baird's swallowtail (*Papilio bairdii* Edwards, Fig. 22) is a western species adapted to life in arid semi-desert regions. Its caterpillars feed almost exclusively upon green sage (*Artemisia dracunculus* L., Asteraceae). This species is still widely distributed in the canyonlands of western and central Nebraska but is probably less common today than in the past due to agriculture and heavy livestock grazing. However, in disturbed areas with significant soil erosion and along man-made canals, both green sage and Baird's swallowtail have probably increased in abundance.

Three swallowtail species are characteristic of the eastern deciduous forests along the Missouri River. The zebra swallowtail (*Eurytides marcellus* (Cramer)) feeds exclusively on the pawpaw (*Asimina triloba* (L.) Dunal, Annonaceae). This butterfly and plant have a very restricted distribution in the state, confined to the forests of extreme southeastern Nebraska. By contrast, the giant swallowtail (*Papilio cresphontes* (Cramer)) and its larval foodplant, prickly ash (*Zanthoxylum americanum* Mill., Rutaceae), are more widely distributed in the forests of the Missouri River hills, extending north to Dakota County. Together with the giant swallowtail, prickly ash also extends westward along the Niobrara River to the mixed ponderosa pine/ bur oak forests of Keya Paha County and up the Platte to Hall County. The distributions of the zebra and giant swallowtails in Nebraska today are probably much the same as in the pre-settlement period.

The third species of eastern deciduous forests is the tiger swallowtail (*Papilio glaucus* (L.)). Its caterpillars feed on various Rosaceae, such as chokecherry (*Prunus virginiana* L.) and wild plum (P. *americana* Marsh.) and also on various ash trees (*Fraxinus* spp., Oleaceae). Around 1850, the tiger swallowtail was probably limited to the extreme eastern part of Nebraska, primarily within the forests along the Missouri River and its tributaries. A likely western extension of its range may have included the pine/oak forests along the Niobrara River in Keya Paha and Cherry counties.

With European settlement, ash trees increased over their natural abundance along rivers and creeks as they were planted on farmsteads and in towns throughout the state, and the tiger swallowtail was able to extend its range dramatically over virtually all of Nebraska. Today, it is frequently one of the more common urban butterflies and is another example of a species that has greatly benefited from European settlement.

Table 1. Nebraska butterflies that have seriously declined during the past 150 years.

HESPERIIDAE	
Atrytone arogos (Boisduval & LeConte)	Arogos skipper
Atrytonopsis hianna (Scudder)	dusted skipper
Erynnis martialis (Scudder)	mottled dusky wing
Euphyes bimacula (Grote & Robinson)	two-spotted skipper
Euphyes conspicua (Edwards)	black dash
Euphyes dion (Edwards)	Dion skipper
Hesperia leonardus leonardus Harris	Leonard's skipper
Hesperia leonardus pawnee Dodge	Pawnee skipper
Hesperia ottoe Edwards	Ottoe skipper
Poanes viator (Edwards)	broad-winged skipper
Polites mystic (Edwards)	long dash
Polites origenes (Fabridus)	crossline skipper
Thorybes bathyllus (Smith)	southern cloudy wing
PAPILIONIDAE	
Papilio bairdii Edwards	Baird's swallowtail
NYMPHALIDAE	
Boloria bellona (Fabridus)	meadow fritillary
Boloria selene nebraskensis (Holland)	silver-bordered fritillary
Speyeria aphrodite alcestis (Edwards)	Alcestis fritillary
Speyeria atlantis hesperis (Edwards)	Hesperis fritillary
Speyeria callippe (Boisduval)	Callippe fritillary
Speyeria idalia (Drury)	regal fritillary
Speyeria mormonia (Boisduval)	Mormon fritillary
SATYRIDAE	
Satyrodes eurydice (Johansson)	eyed brown

Mention should also be made of the two-tailed swallowtail (*Papilio multicaudatus* Kirby) of western North America. Like the closely related tiger swallowtail, this species feeds on chokecherry and ash trees. It was probably limited to the canyonlands of western Nebraska prior to European settlement, extending eastward from the Pine Ridge and Wildcat Hills along the North Platte and Niobrara rivers to Keith and Cherry counties. Like the tiger swallowtail, this species has greatly increased in abundance today and is often a common urban butterfly in towns across the Nebraska panhandle due to the cultivation of ash trees. The two-tailed and giant swallowtails are the largest butterflies found in the United States.

Two other swallowtail butterflies of the eastern deciduous forests probably lived in eastern Nebraska during prehistoric times and are still common in eastern Kansas and Missouri today. The spicebush swallowtail (*Papilio troilus* (L.)) feeds on spicebush (*Lindera benzoin* (L.) Blume) and sassafras (*Sassafras albidum* (Nutt.) Nees, Lauraceae), while the pipevine swallowtail (*Battus philenor* (L.)) feeds on pipevines (*Aristolochia* spp., Aristolochiaceae). These plants probably disappeared from eastern Nebraska during Pleistocene glaciations, and the adult butterflies rarely stray into the state today from adjacent states to the south. These plants and butterflies serve to emphasize the relative decrease in the flora and fauna of Nebraska's eastern deciduous forest resulting from Pleistocene climatic disruptions in the past.

Of the approximately 155 species of butterflies that regularly occur in Nebraska (Johnson 1973), including common migratory species, about 88 species (or 57% of the fauna) probably remain as common today as 150 years ago, or they have experienced only modest declines in range and abundance as a result of European

settlement. Most of these inhabit the eastern deciduous forests, the Rocky Mountain forests, or the rugged hills and canyonlands of the Pine Ridge and Wildcat Hills.

By contrast, 44 species (28%) have greatly expanded in range and abundance as a result of European settlement. In addition to the forest species mentioned above, there are also species that prefer disturbed habitats. The sulfur butterflies (*Colias eurytheme* Boisduval (Fig. 23) and *C. philodice* Godart) and the introduced European cabbage butterfly (*Pieris rapae* (L.), Fig. 24) are good examples. The monarch (*Danaus plexippus* (L.), Fig. 25) has undoubtedly expanded from its original habitat on the native tallgrass prairie to utilize weedy milkweeds (*Asclepias* spp., Asclepiadaceae) along roadsides throughout the state.

Approximately 23 species (15%) of butterflies have greatly declined in range and abundance or are completely extinct in Nebraska today. Most of these are native prairie species that have not been able to find new habitats across the state's altered landscape. Thus, for 85% of the Nebraska butterfly fauna, European settlement and development of the state have been beneficial or have had relatively little effect. However, special conservation efforts should be directed toward the remaining 15% of mostly prairie species that have not been able to survive in alternative habitats.

Table 1 lists the 23 species of Nebraska butterflies that have seriously declined during the past 150 years. Most of these declines have taken place in eastern Nebraska due to the elimination of the tallgrass bluestem prairie for agriculture and the drainage of wetlands. Some species, such as *Euphyes conspicua* Edwards, are almost extinct in the state, while others, such as *Speyeria aphrodite alcestis* and *Hesperia leonardus leonardus* Harris are totally extinct. A number of species, like *Speyeria idalia* and *Boloria selene* D. & S., are still common in wet areas of Sand Hills prairie but are now very rare or extinct in much of eastern Nebraska. In western Nebraska, butterflies such as *Papilio bairdii, Speyeria callippe* (Boisduval), and *Neominois ridingsii* (Edwards) have probably suffered major declines on the shortgrass prairie due to agriculture and heavy livestock grazing.

OTHER INSECTS

It should be noted that many other types of insects have greatly expanded their ranges over most of the state as a consequence of European settlement and the spread of forests. Giant silkmoths (Saturniidae), such as the polyphemus moth (*Antheraea polyphemus* (Cramer), Fig. 26) and cecropia moth (*Hyalophora cecropia* (L.)), are widely distributed today. Among the underwing moths of the genus *Catocala* (Noctuidae), the small, prairie-inhabiting species have probably declined, but the large forest species have increased in abundance and distribution. This is also true of various wood-boring insects. The horntail wasp (*Tremex columba* (L.), Siricidae) has larvae that bore into the trunks of many deciduous trees, and they are eaten in turn by the parasitoid ichneumon wasp (*Megarhyssa lunator* (Fabr.), Ichneumonidae). Both wasps are widely distributed across Nebraska today in forest and urban areas. The same story applies to the *Tibicen* cicadas (Cicadidae; Fig. 27) that feed on the roots of various

Figure 26. Polyphemus moth, *Antheraea polyphemus* (Cramer), now widely distributed in Nebraska. Photo by Leon Higley, University of Nebraska–Lincoln.

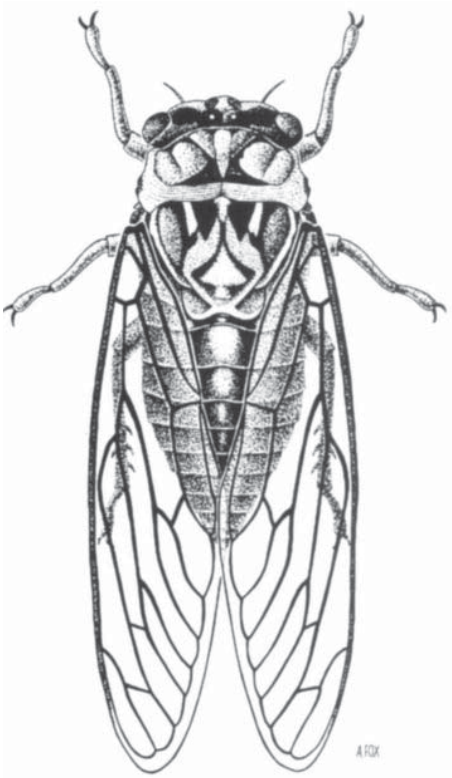


Figure 27. Cicada, *Tibicen* sp. Nymphs of cicadas feed on the roots of trees. As trees expand their ranges in Nebraska as a result of human activities, so too do the cicadas. Illustration by Angie Fox (University of Nebraska–Lincoln).

Figure 28. A bumblebee, *Bombus* sp., the principal pollinator of many prairie plants. Photo by Jim Kalisch, University of Nebraska–Lincoln.

deciduous trees, and the cicada-killer wasp (*Sphecius speciosus* (Drury), Sphecidae) that feeds on the cicadas. Indeed, the spread of trees along rivers, creeks, and in urban areas has been accompanied by an entire food-web of associated arthropods, passerine songbirds, and small mammals (such as squirrels).

In the Sand Hills, wild bees and bumblebees are the most important pollinators of native prairie flowers. The large bumblebees (*Bombus* spp.. Fig. 28) are social insects (like honeybees) whereas wild bees are all solitary. According to LaBerge and Webb (1962), various species *of Bombus* are probably the principal pollinators of various prairie plants in Nebraska such as prairie clovers (*Dalea* spp.), milk-vetches (*Astragalus* spp.), thistles (*Cirsium* spp.), mints (*Monarda* spp.), the introduced sweet clovers (*Melilotus* spp.), and sunflowers (*Helianthus* spp.). Wild bees (sand bees, sweat bees, leafcutter bees, alkalai bees) are ground-nesting, but their burrows may be so close together so as to form colonies. The introduced European honeybee (*Apis mellifera* L.) has become an important pollinator of crops introduced into the Sand Hills, such as alfalfa and other fruit and vegetable producing plants, but it is not native to the Sand Hills.

The yucca moth (*Tegeticula yuccasella* (Riley), family Prodoxidae) is the sole pollinator of the many yucca plants in the Sand Hills. Both moth and plant rely on each other exclusively for their existence. Female moths insert their eggs into the ovary of the yucca flower and then force a wad of pollen they have collected from other yuccas into the long, funnel-shaped stigma. The moth larvae eat some of the developing seeds that result from cross fertilization, but enough seeds are left uneaten to ensure survival of the yucca.

SUMMARY

In conclusion, Nebraska supports a highly diverse flora and insect fauna derived from both eastern and western North America. As our examples have illustrated, the Niobrara River serves as a major biogeographic conduit across northern Nebraska through which eastern and western species mix together into entirely new associations. Butterflies, moths, and many other insects that feed on the leaves of trees and shrubs have a lower diversity in the Sand Hills than the do in the rest of the state. There are several reasons for this, but principal among them is the predominance of grasses instead of broadleaf plants upon which these insects customarily feed.

In some areas of Nebraska, the native vegetation has not been as heavily altered by human activity, and the insects associated with these plants have not changed substantially in their diversity or numbers in the last century. In the majority of the state, however, agriculture and urbanization have radically altered the native vegetation and its associated insect fauna. In some cases, certain species of insects have prospered as a result, and the distributions have expanded. In many other cases, insect species have declined or become extinct as their habitats or food plants were eliminated by human activities.

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