

University of Nebraska - Lincoln

DigitalCommons@University of Nebraska - Lincoln

Proceedings of the North American Prairie
Conferences

North American Prairie Conference

2004

Adapting a Floral Biogeography Model to Prairie-Dependent Lepidoptera

Eric H. Metzler

The Ohio Lepidopterists

John A. Shuey

The Nature Conservancy

Leslie A. Ferge

Richard A. Henderson

Wisconsin Department of Natural Resources

Paul Z. Goldstein

Field Museum of Natural History

Follow this and additional works at: <https://digitalcommons.unl.edu/napcproceedings>



Part of the [International and Area Studies Commons](#)

Metzler, Eric H.; Shuey, John A.; Ferge, Leslie A.; Henderson, Richard A.; and Goldstein, Paul Z., "Adapting a Floral Biogeography Model to Prairie-Dependent Lepidoptera" (2004). *Proceedings of the North American Prairie Conferences*. 76.

<https://digitalcommons.unl.edu/napcproceedings/76>

This Article is brought to you for free and open access by the North American Prairie Conference at DigitalCommons@University of Nebraska - Lincoln. It has been accepted for inclusion in Proceedings of the North American Prairie Conferences by an authorized administrator of DigitalCommons@University of Nebraska - Lincoln.



Adapting a Floral Biogeography Model to Prairie-Dependent Lepidoptera

by Eric H. Metzler¹, John A. Shuey², Leslie A. Ferge³, Richard A. Henderson⁴ and Paul Z. Goldstein⁵

¹The Ohio Lepidopterists, 1241 Kildale Sq. N., Columbus, OH 43229; spruance@infinet.com

²The Nature Conservancy, Indiana Field Office, 1505 N Delaware St., Ste 200, Indianapolis, IN 46204; jshuey@TNC.ORG

³7119 Hubbard Avenue, Middleton, WI 53562; ferge@chorus.net

⁴Wisconsin Department of Natural Resources, Bureau of Research, 1350 Femrite Drive, Monona, WI 53716; hender@dnr.state.wi.us

⁵Division of Insects, Field Museum of Natural History, 1400 S. Lake Shore Drive, Chicago, IL 60605; pgstein@fmnh.org

Abstract

Analysis of data collected for a study of prairie dependent Lepidoptera in the northern tallgrass prairies showed four distributional patterns. A logical distributional pattern links species' distribution, i.e. *Catocala abbreviatella*, to larval host plants. Absence of larval host plant data, which is the case for most species of moths, requires inference based on habitat data of known specimens, i.e. *Tarachidia bimocula*, or in the case of infrequently encountered species, i.e. *Crambus murellus*, capture data for a limited number of specimens. A fourth distributional pattern, i.e. *Atrytone arogos*, can be explained by hypotheses which explain the immigration of native grassland species eastward into the Midwest before the last glacial maximum and northward into the Midwest and East Coast from Florida and the Gulf Coast following the last glacial maximum. The hypothesized distributional patterns can be used to predict the occurrence of species in yet-to-be discovered populations along the migration routes as well as explain their absence in other seemingly nearby localities. The widely disjunct distribution, i.e. East Coast and Midwest, of many species, including those not found in prairies, is easily explained by the hypotheses presented here.

Keywords: biogeography, Lepidoptera, phytogeography, tallgrass prairie

Introduction

From the earliest days of recorded natural history in North America to relatively recent times, the academic study of insect ecology and natural history in tallgrass prairies has been relatively ignored. Early exceptions to this lack of attention include Adams' (1915) "Ecological Study of Prairie and Forest Invertebrates" and Hendrickson's (1930) "Studies on the Insect Fauna of the Iowa Prairies."

In the past 20 years, Dana (1986, 1991), McCabe (1981), Orwig (1990), Panzer (1988, 1995), Panzer and his colleagues (1995), Schlicht and Orwig (1990), Swengel (1996, 1998, 1997, 2001), Swengel and Swengel (1997, 2001), and others examined lepidopterans in prairie habitats. Their studies were based on taxonomic groups (McCabe 1981; Dana 1986, 1991; Swengel 1997), local assemblages of habitats (Panzer 1988, Orwig 1990, Panzer 1995, Panzer and others 1995, Swengel and Swengel 1997), management practices (Panzer and DeMauro 1983; Panzer 1988; Swengel 1996, 1998; Panzer and Schwartz 2000; Swengel 2001; Swengel and Swengel 2001; Panzer 2002) or assemblages of vegetation (Panzer and Schwartz 1998). Researchers desiring to use lepidopterans as indicator species for purposes of management and restoration were required to use the lists developed for the Chicago region by Panzer and his colleagues (Panzer and others 1995, Panzer and Stillwaugh 1997). A panoptic examination of species of

Lepidoptera in prairies across the northern tallgrass region was needed.

In response to the need for more data about insects in tallgrass prairies, the Wisconsin Department of Natural Resources (WDNR) lead a consortium of academic institutions, and governmental and nongovernmental agencies in a 1995–2002 U.S. Fish and Wildlife Service's (USFWS) Partnerships for Wildlife (PFW) project to gather data about the insect fauna in the tallgrass prairie region of Illinois, Indiana, Iowa, Minnesota, Ohio, and Wisconsin (Figure 1). WDNR managed the PFW funds on behalf of the consortium. Our study is east of the 100th meridian.

Lepidoptera, one of the four largest orders of insects in number of species, is a practical group of organisms to study pertinent to prairies. Approximately one in 12 species of all known animals and plants on Earth is a lepidopteran (butterfly, moth, or skipper). Butterflies and moths are popular with amateur entomologists and naturalists. Lepidoptera are often collected, and a large number of historical specimens are available for examination. The popularity of Lepidoptera attracts attention from prairie managers and the general public. Accommodating the needs of Lepidoptera in management plans can be good for public support and for sustaining an important biological component of prairie habitats.

Not all species of Lepidoptera found in prairies are prairie dependent. Prior to widespread habitat degradation at the



hand of industrialized humankind, species that occur in many open habitats, including prairies, were perhaps grassland and prairie associates. Their widespread occurrences show broad tolerance and low fidelity to prairies. Prairie habitats are not critical for their survival. As such, these species are not prairie dependent (*sensu* Panzer and others 1997) throughout the study area.

Some species of Lepidoptera are not found outside prairie habitats, and these species are deemed to be prairie dependent. Not all of the factors limiting habitat utilization by lepidopterans are understood. Because nearly all species of Lepidoptera are herbivores, the distribution of plants is an obvious element of species requirements to consider in listing prairie dependent species of Lepidoptera.

The eastern tallgrass prairie (Figure 2), a subset of native grasslands in middle North America (Figure 3), is often characterized by its vegetative characteristics. A wealth of detailed, technically descriptive, complex, and precise information is available about native North American grasslands (see Transeau, 1935, Curtis 1959, Wright 1968, Langendoen and Maycock 1983, Pielou 1991, Vickery and Dunwiddie 1997, Henderson 1998). Grassland classification can be rigorous with respect to many characteristics such as soils, climate, moisture, plant composition, percent of cover, percent of canopy, and others. The data necessary to directly relate most prairie-dependent Lepidoptera to more precise grassland classifications are not available. For the purposes of this synthesis, our characterization is kept general. As an ecosystem, "tallgrass prairie" sufficiently describes the object of this study.

Methods and Materials

The study area is the six-state region (Figure 1) included in the PFW project. Data from the study area were supplemented with data from the United States and Canada east of the 100th meridian.

A preliminary list of 343 species of Lepidoptera to be evaluated for their dependency on prairies was created by examining the list of described Lepidoptera in North America (Hodges and others 1983), numerous unpublished documents and reports, representative faunal lists of Lepidoptera (Rings and others 1992), and information provided by 50 collaborating lepidopterists. These data were augmented by examining several hundred thousand lepidopteran specimens, taken in 800 samples from 39 prairie and nonprairie habitats in Indiana, Iowa, Ohio, and Wisconsin from 1992 through 2003.

We recorded lepidopteran distributional and habitat requirement data from several publications (e.g., Rockburne and Lafontaine 1976, Covell 1984, Scott 1986, Opler and Malikul 1992, Opler and Wright 1999). We also consulted many more publications, enumerated in Metzler and others (2005) for distributional and habitat requirement data on a more localized basis.

Specimen collection data were recorded from several thousand voucher specimens in 24 major research collections

(see Metzler and others 2005) in the eastern United States and Canada. We recorded the data with the specimens, but we did not attempt to specify locations more precisely than written on the specimen labels. Not all data were available for each specimen. We verified data from unpublished documents by locating the specimens. We eschewed sight records. Electronic databases from the Field Museum of Natural History, The Ohio Lepidopterists' Ohio Survey of Lepidoptera, and U. S. National Museum of Natural History were searched for specimen records. The peer-reviewed literature provided additional records.

Collaborating lepidopterists provided detailed comments and observations about the habitats where the species are found. The collaborators independently conducted surveys and other research in designated prairies both in the study area and in non-prairie habitats. We avoided generalizations and simplifications of habitat requirements when based on limited geographic observations.

Lepidopteran larval hostplant data were recorded from many references (e.g., Forbes 1906, 1923, 1948, 1954; Hessel 1954; Forbes 1960; Tietz 1972; Covell 1984; Opler and Malikul 1992; Hardwick 1996; Opler and Wright 1999; Robinson and others 2002). The field notes of Alex K. Wyatt (= Alex Kwiat), in the Field Museum of Natural History, revealed many larval hostplants based on rearing larvae caught in the wild on natural larval hostplants.

Plant names and distributions were recorded from several references (i.e., Rydberg 1965, Looman and Best 1979, Voigt and Mohlenbrock 1979, McGregor and others 1986, Gleason and Cronquist 1991, Ownbey and Morley 1991, Swink and Wilhelm 1994, Henderson 1998, Yatskievych 1999, Mohlenbrock 2002) and the published volumes of the *Flora of North America* (Flora of North America Editorial Committee 1993–2003).

Latitudinal and longitudinal data, when available, were recorded from specimen labels. Otherwise, several library and computer resources (i.e. Abate 1991) were used to convert locality data to latitude and longitude. We recorded the latitude and longitude data representing the geographic center of the locality on the label specimens.

Specimen records were plotted on maps by using latitude and longitude coordinates. We only plotted distributional data east of the 100th meridian, and we compared the distributions of the species of Lepidoptera with the schematic of eastern tallgrass prairies (Figure 2) and schematics of plant communities (Figure 4). The analysis of our data looked at animal and larval hostplant distributions concurrently.

Results

The thrust of research underlying this paper was to enumerate species of prairie dependent Lepidoptera in the states of Illinois, Indiana, Iowa, Minnesota, Ohio, and Wisconsin. We assembled considerable and elusive data to establish a baseline for further research, and to provide access to information not normally available in a single document. Fortunately, substantial collections with many historical data are available in



larger institutions, such as the American Museum of Natural History, Canadian National Collection, Field Museum of Natural History, U.S. National Museum, and many others.

As lepidopterans are herbivores it is logical their distributions will be congruent with distributions of their larval host plants, at least in part. It is noteworthy that many, if not most, butterflies and moths occupy only a small fraction of the range of their host plants. Additional factors, such as the specific features of prairies, may also limit the distributions of prairie dependent species of Lepidoptera.

Lepidopteran species, such as *Catocala abbreviatella* Grote, 1872 (Noctuidae) (Figure 5), which feed on prairie plants, leadplant (*Amorpha canescens* Pursh.) (Fabaceae), during their larval stage, and which occur only in prairies (Figure 6), are deemed to be prairie dependent.

In some cases, the distribution (Figure 7) of the lepidopteran species, such as *Tarachidia binocula* (Grote, 1875) (Noctuidae) (Figure 8) is congruent with tallgrass prairies, and all specimens are known to come from prairies, but the larval host plant(s) are not known. These species are deemed to be prairie dependent, but with reduced certainty. We hope larval host plant data will become available.

In some cases, the distribution of the lepidopteran species (Figure 9) is congruent with tallgrass prairies, and some specimens of Lepidoptera, such as *Neodactria murellus* (Dyar, 1904) (Crambidae) (Figure 10), are known to come from prairies, and larval hosts are probably Poaceae (Landry 1995). Because of incomplete specimen label data, it cannot be stated for certain that all historical specimens came from prairies. With decreased certainty we deem these species to be prairie dependent and encourage the search for clarifying data.

Based on distributional data, larval host data, and known habitats where the species are found, we identified approximately 50 lepidopteran species appearing to be prairie dependent in the mid-western part of North America. However, an additional 54 species which are dependent on midwestern northern tallgrass prairies, as illustrated by *Atrytone arogos* (Boisduval and Leconte 1837) (Hesperiidae) (Figure 11), also occur in native grasslands and sand habitats along the East Coast, from as far north as Nova Scotia south to Florida, along the Gulf Coast from Florida to Texas and north as far as Mississippi's Black Belt prairies, in glades in northern Georgia, and from Texas north along the Mississippi River to western Ohio, west to New Mexico, and northwest to Wyoming (Figure 12). In spite of their wider distributions, the high degree of fidelity of these species to northern tallgrass prairies in the Upper Midwest compelled further analysis.

Peattie (1922) noted a Great Lakes/Atlantic Coastal Plain plant association, and European settlers found heath- and scrub-like conditions on coastal Massachusetts and near today's Washington, DC. Peattie discussed several options accounting for the disjunct populations and noted (1922: 83) that "there is little zoological evidence which is corroborative of that of the plants."

Shapiro (1970) discussed several options to explain disjunct populations of species of butterflies and skippers. Shapiro examined a several species specializing on marsh

habitats, and although some of his habitat types coincided with Peattie's examples, others did not. Peattie, Shapiro, and others necessarily associated current distributions of plants and Lepidoptera with northward migration routes facilitated by postglacial climate changes.

Our study provides several examples of zoological evidence coinciding with Peattie's observations and supporting one of Shapiro's proposed migration routes which combined a Mississippi River valley route and an East Coast route northward from refugia along the Gulf Coast states and in Florida. We focused on a subset of Lepidoptera associated with prairies, a few of which were noted by Shapiro. Several species of Lepidoptera, e.g. *Digrammia ordinata* (Walker 1862) and *Chortodes enervata* (Guenée 1852), exhibit the same distributional pattern pointed out by Peattie for plants.

An unpublished manuscript by Leland L. Martin (1963) proposed an idea useful in our efforts to understand the biogeography of several supposed prairie species. Martin concluded that *Euphyes dukesi* (Lindsey 1923) found refuge along the Gulf Coast during the last glacial maximum and followed the retreating glaciers northward up the East Coast and the Mississippi River valley (Figure 13). Although *E. dukesi* is a marshland, not a prairie species, the distribution noted by Martin is closely similar to the distributional patterns of several species of Lepidoptera that, were it not for their occurrence along the Gulf Coast and/or the East Coast, would easily be considered as dependent on northern tallgrass prairies.

The phytogeography of eastern North America as described and illustrated in *Flora of North America Volume 1* (Thorne 1993) (Figure 4), and the distribution of other plants noted by McCormac (1993a, 1993b; McCormac and others 1995) is closely similar to the distribution of *E. dukesi* illustrated by Martin (1963) (Figure 13). The notion that lepidopteran distributions coincide with plant distributions is logical, and the notion that prairie dependent species could also occur along the Gulf Coast and/or the East Coast lepidopteran supports Martin's hypothesis while reflecting known distributions of plants and their communities.

Brown (2003) analyzed distributions of Lepidoptera and other insects in Mississippi's Black Belt prairies and found several species with apparent disjunct distributions in the Great Plains. Brown hypothesized that, along with the ranges of grasslands contracting and expanding many times during the glacial and interglacial periods of the Quaternary period (Braun 1928, Delcourt and others 1986), a grassland corridor between the Great Plains and the Black Belt existed before the Wisconsin glaciation that allowed dispersal of some western species to Mississippi [and although not implicitly stated in the hypothesis, for eastern species to disperse to the Great Plains (Brown in lit.)]. Brown (2003 and in lit.) further speculated that the Mississippi Black Belt was a refugium for grassland species during the Wisconsin glaciation and that the current fauna in the tallgrass prairies was equally derived from the Black Belt and southwestern United States or southern Texas. Fifty-four percent of the species we deem to be prairie-dependent have distributions coinciding with Martin's



hypothesis and 46% have distributions exclusive of the Gulf Coast and/or East Coast.

A sequence of events by which prairie-dependent species moved in the Black Belt prairies (Figure 14), followed by the last glacial maximum which forced prairie dependent species to find refuge in the Black Belt, along the Gulf Coast, and in the Florida peninsula is logical. The sequence continued with the retreat of the last glacial maximum and subsequent northern migration of many species of plants and animals, including prairie-dependent species, up the East Coast in native grasslands, and up the Mississippi corridor, also in grasslands logically follows (Figure 15). The sequence is supported by the distributions of many plants and animals, including several which are prairie dependent. A depiction (Figure 16) of a combination of the northern tallgrass prairies (Figure 2), phytogeographic regions of eastern North America (Figure 4), and depiction of northern migration from Martin's manuscript (Figure 15) shows strong convergence.

The distributional pattern illustrated in Figure 12 was useful for distinguishing previously undetected prairie species, e.g., *Diviana eudoreella* Ragonot, 1888 (Pylalidae) (Figures 17 and 18).

Discussion

Our observations result from the analysis of the distribution of several hundred thousand lepidopteran specimens compared to the distributions of northern tallgrass prairie, distributions of plants and phytogeographic regions of eastern North America. Our study did not include any designed experiments. More study is needed.

The larval hostplants of many more species of Lepidoptera, especially moths, is needed. The habitat requirements of the species of Lepidoptera without known larval hosts are highly educated guesses based on observations of field caught specimens, but without experimental data.

We support the notion that there are prairie-dependent lepidopteran species in the Upper Midwest. We provide zoological data consistent with the observations of Peattie (1922), the phytogeographic regions illustrated by Thorne (1993), and our evidence supports ideas advanced by Leland L. Martin in 1963 and Brown (2003). We submit that several species of prairie-dependent species of Lepidoptera moved east into Ohio, southern Michigan, and southeastern Ontario during the Hypsithermal. Some populations remained in the pockets of prairie that remained when the prairies retreated to the west of Ohio.

Acknowledgments

This paper was made possible by substantial data provided by collaborators: James K. Adams, David Adamski, George J. Balogh, Susan S. Borkin, Robert J. Borth, Vernon A. Brou, Jr., John W. Brown, Richard L. Brown, John M. Burns, Floyd B. Catchpole, Lars G. Crabo, Robert P. Dana, Donald R. Davis, Diane M. Debinski, George J. Derkovitz, Jr., Charles A. Ely, Gerald M. Fauske, Douglas C. Ferguson, Lawrence F. Gall,

Loran D. Gibson, Karl J. Gnaedinger, Charles E. Harp, Terry Harrison, J. Richard Heitzman, Ronald W. Hodges, Ronald L. Huber, Douglas M. Ladd, J. Donald Lafontaine, Jean-François Landry, Ron H. Leuschner, Timothy L. McCabe, William E. Miller, Mogens C. Nielsen, Paul A. Opler, Ron Panzer, David K. Parshall, John W. Peacock, Michael G. Pogue, Eric L. Quinter, John E. Rawlins, Steven M. Roble, Michael Sabourin, Dennis W. Schlicht, James A. Scott, Jay C. Shaffer, M. Alma Solis, Stephen M. Spomer, Douglas J. Taron, James T. Troubridge, James P. Tuttle, James T. Vargo, and James R. Wiker.

The efforts of many people contributed to this paper. In addition to the extraordinary amount of information and assistance of the collaborators, this project benefited from the help of many organizations and individuals including Brian J. Armitage, Larry E. Berger, Richard O. Bray, Michael J. Budzik, Denis S. Case, Philip J. Clausen, Philip J. DeVries, Fred W. Dierkes, Carol B. Ferge, Robert J. Ford, Ronald R. Gattelle, Jocelyn D. Gill, Steven A. Gray, Chris Grinter, Richard A. Henderson, John B. Heppner, E. Richard Hoebecke, Jeffrey D. Hooper, Catherine Lundeen Huber, Hugo L. Kons Jr., Steven J. Krauth, Marleen L. Kromer, Jon A. Lewis, James K. Liebherr, James Louderman, Terri L. Lucas, Bryant Mather, James S. McCormac, Patricia A. Metzler, Jacqueline Y. Miller, Lee D. Miller, Dave Minney, Herb H. Neunzig, Norman R. Pearson, Carla M. Penz, David M. Pollock, Gregg A. Pressler, Eric Rickey, Charlene L. Riley, John F. Riley, Frederick H. Rindge, David L. Risley, Robert K. Robbins, Thomas A. Rocheleau, Ronald A. Royer, Patrick M. Ruble, Dale F. Schweitzer, Terry Siedel, Hisa Shigematsu, Judy A. Shuey, Jeffrey R. Slotten, Suzanne A. Smailes, J. Boling Sullivan, Ann B. Swengel, David L. Wagner, Reed A. Watkins, Jason D. Weintraub, Andrew H. Williams, Donald J. Wright, Jennifer M. Zaspel, and Roger A. Zebold provided valuable assistance and professional courtesies.

Special praise goes to Carolyn Caldwell for unending support and application of administrative skills to ensure the success of this project.

Thomas Meyer of the Bureau of Endangered Resources, Wisconsin Department of Natural Resources; John A. Shuey, Indiana Field Office of The Nature Conservancy; Marleen L. Kromer, Ohio Chapter of The Nature Conservancy; Guy L. Denny, Ohio Division of Natural Areas and Preserves; Michael J. Budzik, Carolyn Caldwell, J. William Moody, and Richard B. Pierce, Ohio Division of Wildlife; John W. Fleckenstein and Daryl L. Howell, Iowa Department of Natural Resources Division of Parks, Recreation and Preserves, John A. Bacone, Lee A. Casebere, Gary Doxtater, and Cloyce L. Hedge, Indiana Department of Natural Resources Division of Nature Preserves, Joseph P. Croy, Toledo Metropolitan Park District, facilitated collecting specimens on lands under their care.

We are indebted to Nancy Braker, Charles C. King, Jerry A. Powell, Tim Simmons, and Keith S. Summerville and anonymous reviewers for suggestions that improved the manuscript.

Most of the information presented here is derived from "Contributions to the Understanding of Tallgrass Prairie-Dependent Butterflies and Moths (Lepidoptera) and their Biogeography in the United States" (Metzler and others 2005), and is reproduced with the permission of the Ohio Biological Survey, Inc., Columbus, Ohio.

References

- Adams, Charles C. 1915. An ecological study of prairie and forest invertebrates. *Bulletin Illinois State Laboratory of Natural History* 11(2):33–280.
- Braun, E. Lucy. 1928. Glacial and post-glacial plant migrations indicated by relic colonies in southern Ohio. *Ecology* 9:284–302
- Brown, Richard L. 2003. Paleoenvironment and Biogeography of the Mississippi Black Belt evidence from insects. Pp. 11–26 in Evan Peacock and Timothy Schauwecker (eds.), *Blackland prairies of the Gulf Coastal Plain*. Tuscaloosa: The University of Alabama Press. 148 p.
- Covell, Charles V., Jr. 1984. *A field guide to the moths of Eastern North America*. (Peterson Field Guide Series). Boston: Houghton Mifflin Company.
- Curtis, John T. 1959. *The vegetation of Wisconsin*. Madison: University of Wisconsin Press.
- Dana, Robert P. 1986. Habitat management and the Dakota Skipper. *Ecology Forum* 59:24–26.
- _____. 1991. Conservation management of the Prairie Skippers *Hesperia dacotae* and *Hesperia ottoe*. Minnesota Agricultural Experiment Station Bulletin 594–1991. 63 p.
- Delcourt, Hazel R., Paul A. Delcourt, G. R. Wilkins and E. Newman Smith, Jr. 1986. Vegetational history of the cedar glades region of Tennessee, Kentucky, and Missouri during the past 30,000 years. *Association of Southeastern Biologists Bulletin* 33:128–137.
- Flora of North America Editorial Committee. 1993–2003. *Flora of North America*, various volumes. New York: Oxford University Press.
- Forbes, William T.M. 1906. *Field tables of Lepidoptera*. Boston: Stanhope Press.
- _____. 1923. The Lepidoptera of New York and neighboring states. Primitive forms, Microlepidoptera, Pyraloids, Bombyces. Cornell University Agricultural Experiment Station Memoir No. 68.
- _____. 1948. The Lepidoptera of New York and neighboring states, Part II. Geometridae, Sphingidae, Notodontidae, Lymantriidae. Cornell University Agricultural Experiment Station Memoir No. 274.
- _____. 1954. The Lepidoptera of New York and neighboring states, Part III. Noctuidae. Cornell University Agricultural Experiment Station Memoir No. 329.
- _____. 1960. The Lepidoptera of New York and neighboring states, Part IV. Agaristidae through Nymphalidae, including Butterflies. Cornell University Agricultural Experiment Station Memoir No. 371.
- Gleason, Henry A. and Arthur Cronquist. 1991. *Manual of vascular plants of northeastern United States and adjacent Canada*, 2nd Edition. Bronx, NY: The New York Botanical Garden.
- Hardwick, David F. 1996. *A monograph to the North American Heliothentinae*. Published by the author, Ottawa, Ontario.
- Henderson, Richard A. 1998. Plant species composition of Wisconsin prairies: An aid to selecting species for plantings and restorations based upon University of Wisconsin–Madison Plant Ecology Laboratory Data. 2nd Edition. Wisconsin Department of Natural Resources Technical Bulletin 188, Madison, Wisconsin.
- Hendrickson, George O. 1930. Studies on the insect fauna of the Iowa Prairies. *Iowa State College Journal of Science*. 4(2):49–179.
- Hessel, Sidney A. 1954. A guide to collecting the plant-boring larvae of the genus *Papaipema* (Noctuidae). *The Lepidopterists' News* 8(3–4):57–63.
- Hodges, Ronald W., Tatiana Dominick, Donald R. Davis, Douglas C. Ferguson, John G. Franclemont, Eugene Munroe and Jerry A. Powell. 1983. *Check list of the Lepidoptera of America North of Mexico including Greenland*. London: E. W. Classey Ltd. and The Wedge Entomological Research Foundation.
- Landry, Bernard. 1995. *A phylogenetic analysis of the major lineages of the Crambinae and the genera of Crambini of North America (Lepidoptera: Pyralidae)*. Gainesville, FL: Associated Publishers.
- Langendoen, Don and Paul F. Maycock. 1983. Preliminary observations on the distribution and ecology of tallgrass prairie in southern Ontario. Pages 92–97 in Richard Brewer (ed.), *Proceedings of the Eighth North American Prairie Conference*. Western Michigan University, Kalamazoo, Michigan.
- Looman, J. and K. F. Best. 1979. Budd's flora of the Canadian Prairie Provinces. Hull, Quebec. Agriculture Canada Publication 1662.
- Martin, L.A. 1963. A specialized scientific paper in two parts. Part I—a new occurrence of *Atrytone dukesi* (Hesperiidae) in Ohio. Part II—a theory on the northern distribution of *Atrytone dukesi* (Hesperiidae). Unpublished. Wellington, Ohio.
- McCabe, Timothy L. 1981. The Dakota skipper, *Hesperia dacotae* (Skinner): range and biology, with special reference to North Dakota. *Journal of The Lepidopterists' Society* 35:179–193.
- McCormac, James S. 1993a. First record of *Leersia lenticularis* Michx. in the Great Lakes drainage. *Castanea* 58(1):54–58.
- _____. 1993b. Swamp cottonwood (*Populus heterophylla*) in Ohio. *The Michigan Botanist* 32:35–39.
- McCormac, James S., James K. Bissell and Stanley J. Stine, Jr. 1995. The status of *Fraxinus tomentosa* (Oleaceae) in Ohio with notes on its occurrence in Michigan and Pennsylvania. *Castanea* 60(1):70–78.
- McGregor, Ronald L., Theodore Mitchell Barkley, Ralph E. Brooks and Eileen K. Schofield. 1986. *Flora of the Great Plains*. Lawrence, KS: University Press of Kansas.
- Metzler, Eric H., John A. Shuey, Leslie A. Ferguson, Richard A. Henderson and Paul Z. Goldstein. 2005. Contributions to the understanding of tallgrass prairie-dependent butterflies and moths (Lepidoptera) and their biogeography in the United States. Ohio Biological Survey Bulletin New Series.
- Mohlenbrock, Robert H. 2002. *Vascular flora of Illinois*. Carbondale, IL: Southern Illinois University Press.
- Opler, Paul A. and Vichai Malikul. 1992. *A field guide to eastern butterflies*. Boston: Houghton Mifflin Company. 396 p.
- Opler, Paul A. and Amy Bartlett Wright. 1999. *A field guide to western butterflies*. Boston: Houghton Mifflin Company.
- Orwig, Timothy T. 1990. Loess hills prairies as butterfly survival: opportunities and challenges. Pages 131–135 in *Proceedings of the Twelfth North American Prairie Conference*.
- Ownbey, Gerald B. and Thomas Morley. 1991. *Vascular plants of Minnesota: A checklist and atlas*. Minneapolis: University of Minnesota Press.
- Panzer, Ron. 1988. Managing prairie remnants for insect conservation. *Natural Areas Journal* 8(2):83–90.
- _____. 1995. Remnant dependence among prairie- and savanna-inhabiting insects. *Natural Areas Journal* 15(4):290–292.



- _____. 2002. Compatibility of prescribed burning with the conservation of insects in small, isolated prairie reserves. *Conservation Biology* 16:1296–1307.
- Panzer, Ron and M. DeMauro. 1983. Native prairie insects, fire studied on prairie remnant (Illinois). *Restoration and Management Notes* 1(4):17–18.
- Panzer, Ron, Don Stillwaugh, Rich Gnaedinger and George Derkovitz. 1995. Prevalence of remnant dependence among the prairie and savanna inhabiting insects of the Chicago region. *Natural Areas Journal* 15:101–116.
- Panzer, Ron, John A. Shuey and Don Stillwaugh. 1997. Characterizing insects within fragmented landscapes. *Natural Areas Journal* 17(1):53–55.
- Panzer, Ron and Mark W. Schwartz. 1998. Effectiveness of a vegetation-based approach to insect conservation. *Conservation Biology* 12(3):693–702.
- _____. 2000. Effects of management burning on prairie insect species richness within a system of small, highly fragmented reserves. *Biological Conservation* 96:363–369.
- Peattie, Donald C. 1922. The Atlantic Coastal Plains element in the flora of the Great Lakes. *Rhodora* 24: 57–70, 80–88.
- Pielou, Evelyn C. 1991. *After the Ice Age: The return of life to glaciated North America*. Chicago: University of Chicago Press.
- Rings, Roy W., Eric H. Metzler, Fred J. Arnold and David H. Harris. 1992. *The owl moths of Ohio Order Lepidoptera Family Noctuidae*. Bulletin of the Ohio Biological Survey New Series 9.
- Robinson, Gaden S., P. R. Ackery, Ian J. Kitching, G. W. Beccaloni and L. M. Hernandez. 2002. Hostplants of the moth and butterfly caterpillars of America north of Mexico. *Memoirs of the American Entomological Institute*. Volume 69.
- Rockburne, E.W. and J.D. Lafontaine 1976. The cutworm moths of Ontario and Quebec. Canada Department of Agriculture, Ottawa, Ontario.
- Rydberg, Axel. 1965. *Flora of the prairies and plains of central North America*, Facsimile of 1932 Edition. New York: Hafner Publishing Company.
- Schlicht, Dennis W. and Timothy T. Orwig. 1990. Sequential use of niche by prairie obligate skipper butterflies (Lepidoptera: Hesperidae) with implications for management. Pages 137–139 in the Proceedings of the Twelfth North American Prairie Conference.
- Scott, James A. 1986. *The butterflies of North America*. Palo Alto, CA: Stanford University Press.
- Shapiro, Arthur M. 1970. Postglacial biogeography and the distribution of *Poanes viator* (Hesperidae) and other marsh skippers. *Journal of Research on the Lepidoptera*. 9(3):125–155.
- Swengel, Ann B. 1996. Effects of fire and hay management on abundance of prairie butterflies. *Biological Conservation* 76:73–85.
- _____. 1997. Habitat associations of sympatric violet-feeding fritillarids (*Euptoieta*, *Speyeria*, *Boloria*) (Lepidoptera: Nymphalidae) in tallgrass prairie. *Great Lakes Entomologist* 30:1–18.
- _____. 1998. Effects of management on butterfly abundance in tallgrass prairie and pine barrens. *Biological Conservation* 83:77–89.
- _____. 2001. A literature review of insect responses to fire, compared to other conservation managements of open habitat. *Biodiversity and Conservation* 10:1141–1169.
- Swengel, Ann B. and Scott R. Swengel. 1997. Co-occurrence of prairie and barrens butterflies: applications to ecosystem conservation. *Journal of Insect Conservation* 1:131–144.
- _____. 2001. Effects of prairie and barrens management on butterfly faunal composition. *Biodiversity and Conservation* 10:1757–1785.
- Swink, Floyd and Gerould S. Wilhelm. 1994. *Plants of the Chicago Region*, 4th Edition. Indianapolis: Indiana Academy of Science.
- Thorne, Robert F. 1993. Phytogeography. Pages 132–153 in *Flora of North America North of Mexico Volume 1 Introduction*. Flora of North America Editorial Committee (ed.). New York: Oxford University Press.
- Tietz, Harrison M. 1972. *An index to the described life histories, early stages and hosts of the Macrolepidoptera of the continental United States and Canada. Parts I & II*. Sarasota, FL: Allyn Museum of Entomology.
- Transeau, Edgar N. 1935. The prairie peninsula. *Ecology* 16:423–437.
- Vickery, P. D. and P. W. Dunwiddie (eds.). 1997. *Grasslands of north-eastern North America*. Lincoln, MA: Massachusetts Audubon Society.
- Voigt, John W. and Robert H. Mohlenbrock. 1979. Prairie plants of Illinois. Illinois Department of Conservation, Division of Forestry, Springfield, Illinois.
- Wright, Herbert E., Jr. 1968. History of the prairie peninsula. Pages 78–80 in Robert E. Bergstrom (ed.), *The Quaternary of Illinois: A symposium in observance of the Centennial of the University of Illinois*. University of Illinois College of Agriculture Special Publication 14.
- Yatskievych, George. 1999. Steyermark's flora of Missouri, volume 1, Revised Edition. Missouri Department of Conservation, Jefferson City, Missouri.



Figure 1. Six-state study area



Figure 2. Conceptual map of eastern tallgrass Prairie Peninsula

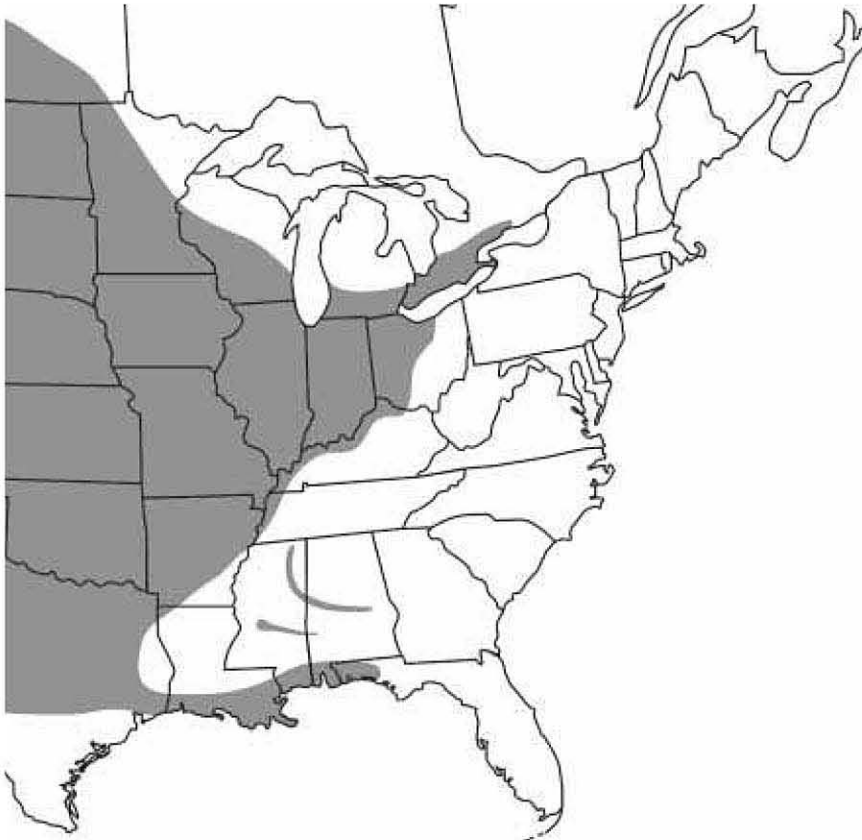


Figure 3. Native grasslands in middle North America

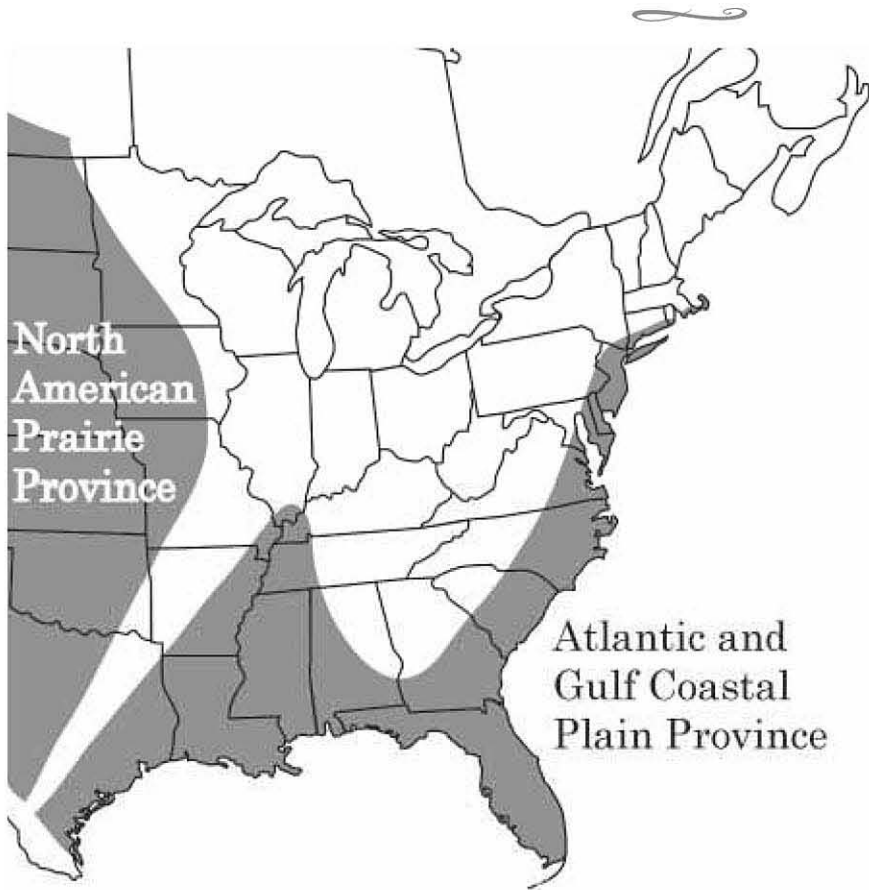


Figure 4. Prairie and coastal phytogeographic regions of eastern North America

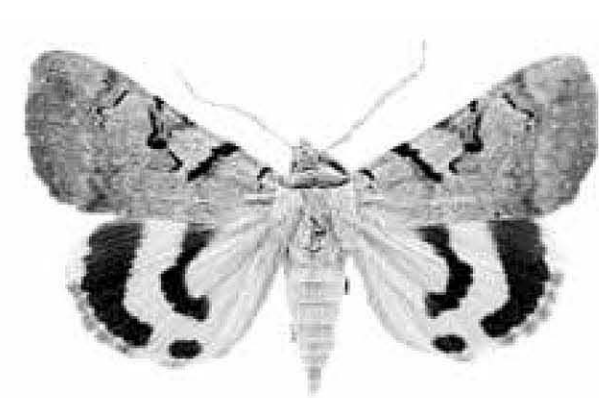


Figure 5. *Catocala abbreviatella*



Figure 6. *Catocala abbreviatella* distribution map



Figure 7. *Tarachidia binocula* distribution map



Figure 8. *Tarachidia binocula*



Figure 9. *Neodactria murellus* distribution map

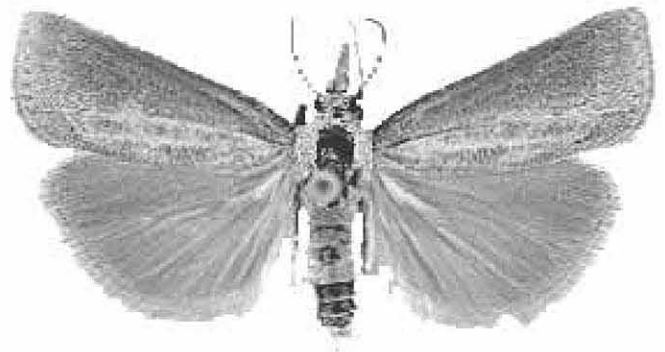


Figure 10. *Neodactria murellus*

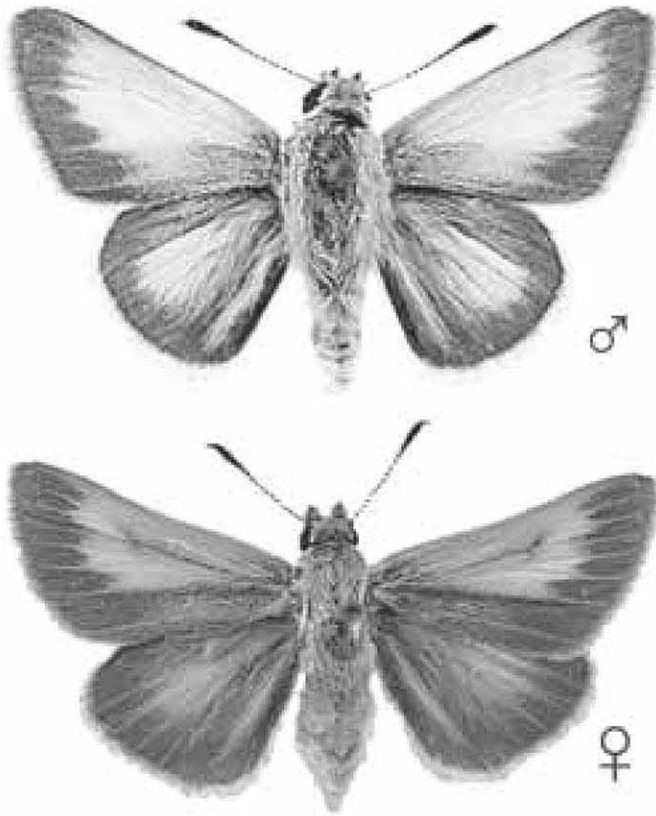


Figure 11. *Atrytone arogos*

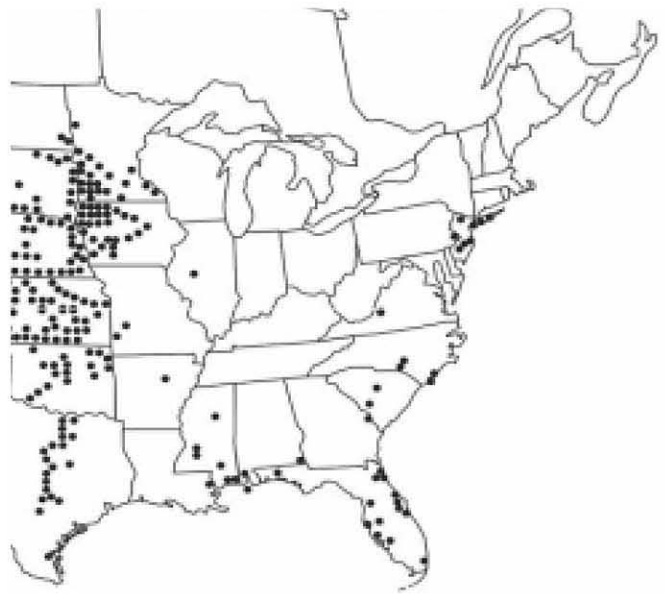


Figure 12. *Atrytone arogos* distribution map



Figure 13. Distribution of *Euphyes dukesi*



Figure 14. Species from dry western areas migrated to Mississippi and the Gulf Coast (Brown 2003).

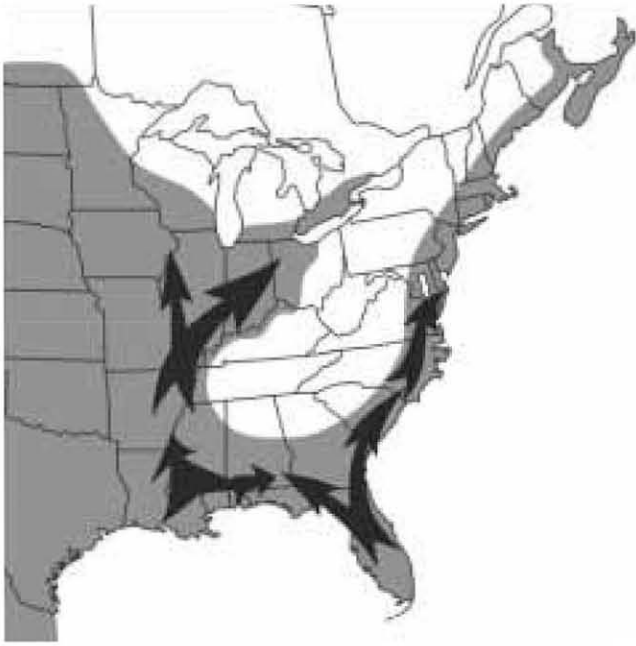


Figure 15. Martin's hypothesis of northward migration from the Gulf Coast following the last glacial maximum.

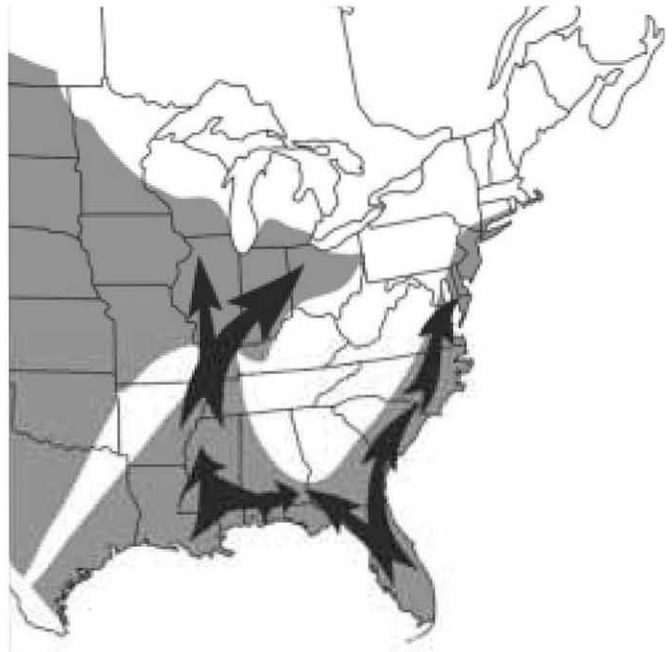


Figure 16. Figures 2, 4, and 15 combined to show schematic of biogeography of many prairie-dependent species.



Figure 17. *Diviana eudoreella* distribution map



Figure 18. *Diviana eudoreella*