

A black and white photograph of two prairie skipper butterflies perched on a plant. The butterfly in the foreground is facing right, showing its wings with distinct dark markings. The second butterfly is behind it, also facing right. The background is dark and out of focus.

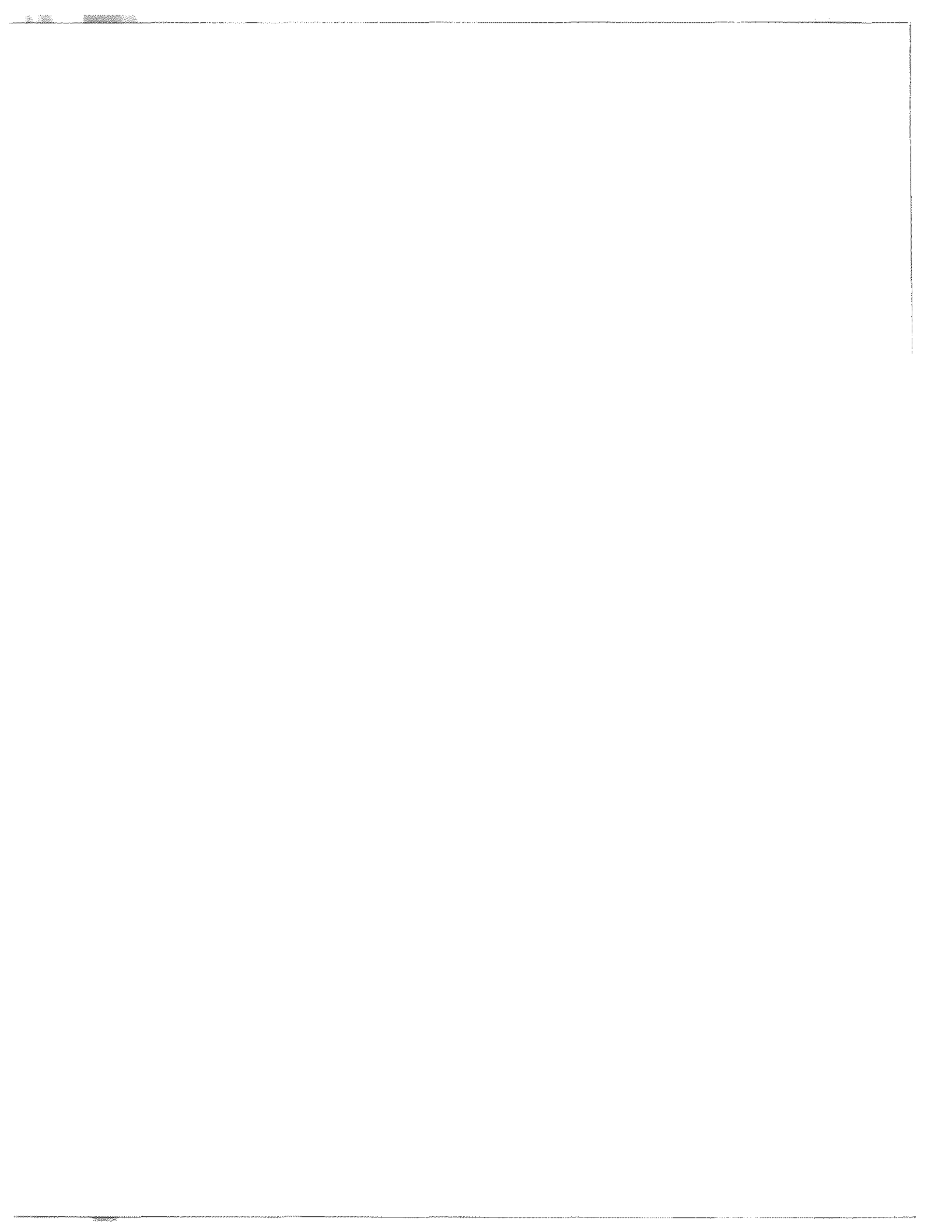
Conservation Management of the Prairie Skippers *Hesperia Dacotae* and *Hesperia Ottoe*

***Basic Biology and
Threat of Mortality
During Prescribed
Burning in Spring***

Robert P. Dana

UNIVERSITY OF MINNESOTA

*Station Bulletin 594-1991 (AD-SB-5511-S)
Minnesota Agricultural Experiment Station*



Conservation Management of the Prairie Skippers *Hesperia Dacotae and Hesperia Ottoe*

**Basic Biology and Threat of Mortality
During Prescribed Burning in Spring**

Robert P. Dana, Ph.D

**Station Bulletin 594–1991
Minnesota Agricultural Experiment Station
University of Minnesota**

St. Paul, Minnesota

The University of Minnesota, including the Minnesota Agricultural Experiment Station, is committed to the policy that all persons shall have equal access to its programs, facilities, and employment without regard to race, color, creed, religion, national origin, sex, age, marital status, disability, public assistance status, veteran status, or sexual orientation.

Author

This publication originated in 1989 as a thesis submitted to the faculty of the Graduate School of the University of Minnesota by Robert P. Dana in partial fulfillment of the requirements for the degree of Doctor of Philosophy. He is employed in conservation management by the Minnesota Department of Natural Resources.

Acknowledgements

Inspiration for this study came from Mark Heitlinger, then Director of Stewardship for the Minnesota Chapter of The Nature Conservancy, and his interest and encouragement played a major role in its realization. Donald Lawrence championed the need for the research, and thanks is extended to him and his wife Elizabeth for friendship and support. Thanks also to advisor William Miller for help during the design and execution phases of the work and for his thorough vetting of manuscript drafts. The final draft benefitted from criticism by Donald Alstad and David Andow. William Schmid and Steve Speech provided valuable assistance in measuring soil temperatures. Phillip Harein helped with advice and materials for plot fumigation. Frank Martin and Kathryn Chaloner provided advice regarding statistical analysis, but as they have not reviewed how that advice was used they are not implicated in any deficiencies. Herbert Kulman was instrumental in motivating the start on this project.

Writing could not have been completed without the flexible work schedule allowed while an employee of the Natural Heritage and Nongame Wildlife Programs of the Minnesota Department of Natural Resources. Barbara Coffin, Lee Pfannmuller, Keith Wendt, and Carmen Converse all generously accommodated time needs, and they and other colleagues at the DNR provided much needed moral support. Deep thanks is extended to spouse Mary Radford, for the many ways she helped, and especially for her companionship and patience.

Major funding came equally from an anonymous private source and the Minnesota Chapter of The Nature Conservancy, whose staff also assisted in various aspects of burning. Geoff Barnard and Peg Kohring are also singled out for special thanks. Additional financial support was provided by the World Wildlife Fund, the Xerces Society, and Mr. Robert Binger.

Station Bulletin series editing and design for the Minnesota Agricultural Experiment Station is by Larry A. Etkin, experiment station editor, Educational Development System, MES.

Disclaimer

Reference to commercial products or trade names is made with the understanding that no discrimination is intended and no endorsement by the Minnesota Agricultural Experiment Station or the University of Minnesota is implied.

Availability

For information on obtaining a copy of this publication contact the MES Distribution Center, University of Minnesota, Coffey Hall, 1420 Eckles Avenue, St. Paul, Minnesota, 55108-6064.

© Copyright 1991
Minnesota Agricultural Experiment Station, University of Minnesota and Robert Pelham Dana.

Printed on Recycled Paper

CONTENTS

Abstract	1
Introduction	2
Study Site	4
Physical Description	4
Soils	4
Climate	4
Vegetation	5
Surrounding Land Use	6
Site History	6
Methods	6
Life History, Population Studies	6
Immature Stages	6
Adults	7
Burning Studies	10
Field Procedures	10
Statistical Analysis	13
Computations	14
Results	14
Life History, Population Studies	14
Immature Stages	14
Adults	21
Burning Studies	38
Emergence Trap Study	38
Experiment I	38
Experiment II	41
Experiment III	44
Experiment IV	45
Discussion	46
Life History	46
Immature Stages	46
Adults	47
Population Aspects	51
Effects of Burning	54
Management Implications	55
Appendix: Tabashnik's Joint Residence-Catchability Test	57
References	58

TABLES

Table 1.	Stage lengths in captive reared <i>Hesperia dacotae</i> and <i>H. ottoe</i>	14
Table 2.	Sex ratios in adult skippers emerging in experimental field plots	16
Table 3.	Host plants used for oviposition by <i>Hesperia dacotae</i> and <i>H. ottoe</i> at Hole-in-the-Mountain Prairie	17
Table 4.	<i>Hesperia dacotae</i> survival to diapause on six major dry-mesic prairie grasses at Hole-in-the-Mountain Prairie	17
Table 5.	Analysis of variance of <i>Hesperia dacotae</i> larval dry-weights at diapause in field rearings on six grass species	18
Table 6.	Larval stage at diapause of <i>Hesperia dacotae</i> on six grass species in field rearings at Hole-in-the-Mountain Prairie	19
Table 7.	Flower visitation by <i>Hesperia dacotae</i> and <i>Hesperia ottoe</i> at Hole-in-the-Mountain Prairie during a three year mark-release-recapture study	21
Table 8.	Analysis of variance of counts of <i>Hesperia ottoe</i> ova on <i>Echinacea angustifolia</i> capitula at Hole-in-the-Mountain Prairie with respect to topographic position and habitat disturbance	29
Table 9.	Capture summary for three years of MRR study of <i>Hesperia dacotae</i> and <i>H. ottoe</i> adults at Hole-in-the-Mountain Prairie	30
Table 10.	Tests of between-sex differences in recapture probabilities for <i>Hesperia dacotae</i> and <i>H. ottoe</i> in three years of MRR study at Hole-in-the-Mountain Prairie	31
Table 11.	Tests of effect of marking on recapture probability of skipper adults at Hole-in-the-Mountain Prairie by comparison of recapture proportions between newly marked insects and those released at the same time bearing previous marks and not marked again	32
Table 12.	Likelihood of recapture as a factor of previous capture, July 9 through August 7, 1979	32
Table 13.	Tests of the Fisher-Ford assumption of independence of recapture probability and age in adult skippers studied by MRR at Hole-in-the-Mountain Prairie	34
Table 14.	Tests of the Fisher-Ford assumption of day-to-day constancy of adult residence rates in skippers studied by MRR at Hole-in-the-Mountain Prairie	34
Table 15.	Residence rate estimates for adult skippers from MRR study at Hole-in-the-Mountain Prairie	34
Table 16.	Adult generation estimates for <i>Hesperia dacotae</i> and <i>H. ottoe</i> at Hole-in-the-Mountain Prairie, based on Jolly-Seber and Fisher-Ford daily population estimates from MRR data	37
Table 17.	Analysis of variance of capture rates of adults in 3 years of MRR sampling of <i>Hesperia dacotae</i> and <i>H. ottoe</i> at Hole-in-the-Mountain Prairie	37
Table 18.	Relationship between intercapture distance and number of days elapsed between captures of adult skippers	39
Table 19.	Adult skipper emergence in previously burned and undisturbed prairie plots subjected to early and late spring burning (Experiment I)	41

Table 20. Analysis of variance of Experiment II data summarized in Figure 20	41
Table 21. Analysis of variance of Experiment III data summarized in Figure 2	42
Table 22. Analysis of variance of Experiment IV data summarized in Figure 23	43
Table 23. Analysis of variance of Experiment IV differential emergence data summarized in Figure 24	45

FIGURES

Figure 1. Study area at Hole-in-the-Mountain Prairie Preserve	5
Figure 2. Temporal pattern of adult emergence in skippers reared from hatching in prairie plots used in experiments on effects of burning at Hole-in-the-Mountain Prairie	15
Figure 3. Weight at diapause of <i>Hesperia dacotae</i> larvae reared from hatching on six prairie grasses under field conditions at Hole-in-the-Mountain Prairie	18
Figure 4. Hourly distribution of male skipper courtship pursuits of females at Hole-in-the-Mountain Prairie	23
Figure 5. Topographic distribution of male skipper courtship pursuits of females at Hole-in-the-Mountain Prairie	23
Figure 6. Hourly distribution of observed oviposition behavior (curving of abdomen, probing with tip in vegetation) of skippers at Hole-in-the-Mountain Prairie	25
Figure 7. Topographic distribution of observed oviposition behavior of skippers at Hole-in-the-Mountain Prairie	25
Figure 8. Age specific fecundity in three <i>Hesperia dacotae</i> females confined over prairie grasses in the field	26
Figure 9. Distribution of <i>Hesperia ottoe</i> ova on capitula of <i>Echinacea augustifolia</i> at Hole-in-the-Mountain Prairie with respect to topographic position and habitat differences produced by disturbances	28
Figure 10. Joint residence-catchability tests for male vs. female skippers at Hole-in-the-Mountain Prairie	31
Figure 11. Recapture decay plots for <i>Hesperia dacotae</i> and <i>H. ottoe</i> from MRR study at Hole-in-the-Mountain Prairie	33
Figure 12. Jolly-Seber estimates of residence rates (q_j) between sampling occasions for <i>Hesperia dacotae</i> and <i>H. ottoe</i> at Hole-in-the-Mountain Prairie	35
Figure 13. Estimates of adult <i>Hesperia dacotae</i> numbers at Hole-in-the-Mountain Prairie from MRR data	36
Figure 14. Estimates of adult <i>Hesperia ottoe</i> numbers at Hole-in-the-Mountain Prairie from MRR data. All symbols as in Figure 13. Data for females in 1980 were too sparse to warrant calculation of estimates	36

Figure 15. Capture rates of adult skippers in MRR sampling units at Hole-in-the-Mountain Prairie	38
Figure 16. Frequency distributions of distances between successive captures of adult skippers	39
Figure 17. Intercapture displacements of adult skippers in MRR study at Hole-in-the-Mountain Prairie with respect to sampling units (A–D)	40
Figure 18. Effect of spring burns in Experiment I prairie plots on temperature 5 mm below the soil surface as measured by thermocouple probe at plot center	42
Figure 19. Profiles of maximum temperature within a few centimeters above and below the soil surface during early and late spring burns in Experiment I prairie plots at Hole-in-the-Mountain Prairie	42
Figure 20. Effects of early spring burning of recently burned and undisturbed prairie plots on <i>Hesperia dacotae</i> larval survival as measured by adult emergence in Experiment II	43
Figure 21. Effects of early versus late spring burning of prairie plots with two fuel levels on <i>Hesperia dacotae</i> larval survival as measured by adult emergence in Experiment III	43
Figure 22. Temperatures 5 mm below the soil surface in spring burns of Experiment III temperature measurement plots	44
Figure 23. Effects of early versus late spring burning of prairie plots with light and medium fuel levels on skipper larval survival in Experiment IV	44
Figure 24. Experiment IV results expressed as burn treatment difference scores (number of treatment subplot survivors minus number of same whole plot control subplot survivors)	45

Conservation Management of the Prairie Skippers *Hesperia Dacotae* and *Hesperia Ottoe*

Basic Biology and Threat of Mortality During Prescribed Burning in Spring

Robert P. Dana, Ph.D

Minnesota Department of Natural Resources
Division of Fish and Wildlife

ABSTRACT

The life history and critical requirements of the scarce prairie-obligate skippers *Hesperia dacotae* and *H. ottoe* and mortality during prescribed fire in spring were investigated during 1978-83 at a site in southwest Minnesota.

Both species are univoltine, flying together at this site in early to mid-summer. No differences between the two in habitat use were apparent and adults spent almost all of their time in the same upland prairie where larval development occurred. Larvae of both feed on most of the grasses in this habitat, and females of both oviposit without apparent selectivity on grasses as well as on forbs. Both have the solitary, shelter dwelling larval habits of the genus. Shelters of *H. dacotae* are subsurface, burrow-like chambers until after the first postdiapause molt in spring, and then debris covered silk chambers on the surface. Habits of *H. ottoe* are identical from late summer on, but early stages make shelters up in the grass blades. These behavioral programs appear to be functional only in midheight, bunchgrass dominated vegetation. Both sexes are frequent flower visitors, water probably being the critical need.

Potential fecundity in both species appears to be

approximately 200 eggs, which are matured at a declining rate over a three week life span. A three year mark-release-recapture study of adults yielded estimates of average residence time within the site of between three and six days for males, and between three and ten days for females, in both species. *Hesperia dacotae* was the more abundant during the study, with annual cohorts estimated to be between 2,000 and 3,000 adults, compared with estimates between 600 and 1,200 for *H. ottoe*. Estimates for females were consistently lower than for males.

No difference between the species in the effects of spring burning in prairie plots was detectable. Fuel load strongly influenced mortality. Compared with unburned controls, mean survival in low-fuel plots was reduced 11% in the early spring burn when larvae were still in burrows, and 26% in the later burn when larvae were in surface shelters. The respective reductions in moderate-fuel plots were 78% and 100%. The fuel loads of 160 and 540 gm⁻² approximate natural extremes for the larval habitat. Although the higher mortality in the later burn is not statistically significant, further investigation of the effect of date of burn is recommended. Management implications of these results are discussed.

INTRODUCTION

Of the estimated 1.14×10^6 km² of tallgrass and mixed-grass prairie that existed in North America at the time of European settlement (Risser et al. 1981), probably less than 2% remains. The effects of this extreme habitat fragmentation and insularization on the arthropod fauna of the prairie are generally unknown, but in one of the better documented groups, the butterflies, several species have suffered significant declines (Opler 1981). Because the metapopulational balance between local establishment or reestablishment and local extinction (Ehrlich 1984) has probably been disrupted for prairie dependent organisms by this fragmentation, careful management of protected tracts to minimize the likelihood of local extinction is critically important (Goodman 1987). A particularly pressing question is whether the common use of prescribed burning in the conservation management of prairies may itself cause local extinctions (McCabe 1981, Opler 1981).

Two of the affected species are skippers in the genus *Hesperia*, a mostly North American group whose members inhabit various types of upland grassland habitats (Lindsey 1942, MacNeill 1964). The rarer of the two, the dakota skipper *Hesperia dacotae* (Skinner), historically occupied a limited range in the northern prairie, from Illinois and Iowa north through the Dakotas and Minnesota into southern Manitoba (McCabe 1981, Scott 1986). Except for a single colony in northwestern Iowa (Howe 1984) it has been extirpated in the southern part of this range, with surviving populations concentrated in the Dakotas and Minnesota (McCabe 1981). Two extant populations are known in Manitoba (Paul Klassen, letter to the author, Nov. 4, 1986). This skipper is restricted to prairie remnants scattered throughout this range.

Because of its rarity and the continuing loss of habitat, the U.S. Fish and Wildlife Service initiated formal proceedings to list this species as threatened (U.S. Dept. of Interior 1978). The proposed rulemaking was withdrawn without a determination after Congress amended the Endangered Species Act in 1979 (U.S. Dept. of Interior 1980), but the species remains a Category 2 candidate for listing (U.S. Dept. of Interior 1984).

The other species, the ottoe skipper *Hesperia ottoe* W.H. Edwards, is more widely distributed, from northern Texas to southern Manitoba, and from Colorado and eastern Montana to Michigan (Scott 1986), occurring in a wider variety of prairie types than *H. dacotae*. However, throughout this extensive range it appears to be highly local and generally uncommon to rare. It is much rarer in Minnesota than *H. dacotae*.

The frequency of fire in the North American prairie, and its importance in the development and

maintenance of the prairie, are well documented (Buell and Buell 1959, Kucera 1960, Kucera et al. 1963, Daubenmire 1968, Wells 1970, Bragg 1971, Moore 1972, Bragg and Hulbert 1976, Risser et al. 1981, Anderson 1982, Grimm 1983, 1984). The importance of fire in the natural ecosystem, along with its effectiveness in exotic species control, provide the rationale for the use of prescribed burning in prairie management (Christiansen 1972; Ehrenreich and Aikman 1963, Hulbert 1973, Henderson 1982).

Compared with the well studied effects of fire on prairie vegetation there is little research into its effects on prairie arthropods. There are a few studies reporting general reductions following burning of prairie habitats (Rice 1932, Reichert and Reeder 1972, Knutson and Campbell 1976), while others have found greater abundances in some groups, and reduced levels in others (Cancelado and Yonke 1970, Nagel 1973, Seastedt 1984). Postfire migration is not separable from actual mortality in most of these studies. Fire has occasionally been found effective in reducing populations of certain insects in agricultural and forestry situations (Miller 1979).

A general result seems to be that for insects unable to escape by flying or leaping, concealment in the soil or under rocks, etc., affords considerable protection (Reichert and Reeder 1972, Nagel 1973, Knutson and Campbell 1976, Seastedt 1984). Similar results have been reported for grasslands in South Africa and elsewhere (Bigalke and Willan 1984, Tainton and Mentis 1984). Although surface temperatures during grassland fires generally rise well into the lethal range, these fires move rapidly and the brief pulse of heat may not penetrate more than a few millimeters below the surface (Norton and McGarrity 1965, Reichert and Reeder 1972, Savage 1980, Wright and Bailey 1982).

Fuel load is a major factor in determining fire intensity (Stinson and Wright 1969, Wright and Bailey 1982), and average fuel load will vary considerably with the soil moisture regime (Whitman 1950, Redmann 1975). Hence, habitat selection may afford a degree of protection.

Apart from the issue of local extermination during prescribed burning, the long term persistence of isolated skipper populations will depend upon maintenance of the habitat conditions they require. In general, the primary determinants of a habitat's carrying capacity for a butterfly species are the abundance and quality of larval host plants and adult nectar plants, although many species have more "cryptic" requirements as well, such as ant symbionts, wet and mineral rich substrates, or vegetation structure (Murphy and Wilcox 1986, Thomas 1984). Different prairie management

regimes (burning, mowing, grazing, or various combinations) will produce differences in the species composition and structure of the vegetation, with possible effects upon the supply of both larval hosts and adult nectar flowers as well as on such things as larval microclimate, and natural enemy and pathogen populations.

Other aspects of skipper biology of potential significance for site management include adult movement patterns, individual longevity, fecundity, and "normal" population fluctuation (Ehrlich 1984).

It is not possible to make confident inferences, from the limited available information on the biology of these skippers, about either their vulnerability to fire at the times when prescribed burning is most commonly done (spring and fall) or the kind of management needed to maintain optimum habitat conditions.

McCabe (1981) inferred from its distribution pattern that *Hesperia dacotae* requires unproductive alkaline soils. He reported that the flowers of *Asclepias* and *Apocynum* species, which are avoided by cattle, are not utilized by adults, while flowers of species that tend to be eliminated by heavy grazing are favored. He suggested that this might be the basis for the absence of this skipper from grazed prairies in North Dakota. *H. dacotae* is a grass feeder, like all other members of the genus (MacNeill 1965). From the acceptance by captive larvae of several offered grasses and the nonselective oviposition behavior of females he concluded that larvae are generalist feeders on grasses. MacNeill (1964), however, found considerable host specificity in nature for a number of *Hesperia* species that readily accepted other grasses in captivity.

The habitat requirements of *H. ottoe* have not been described except that it is found only in native prairie. Nielsen (1958) reported the grass *Leptoloma cognatum* to be a larval host in Michigan, and McGuire (1982) has added several ovipositions on *Andropogon scoparius* from various parts of the range. (Plant nomenclature in this paper follows Great Plains Flora Association 1986.)

Lindsey (1942) commented that *H. ottoe* seemed to disappear when prairie was subjected to haying or grazing, and McCabe and Post (1977) attributed its rarity in the Badlands of North Dakota to grazing. Both McCabe and Post (1977) and Nielsen (1958) found adults to be avid flower visitors, but neither suggested any narrow requirements.

Hesperia larvae spend almost all their time within shelters or retreats (MacNeill 1964), and the location of the shelter will be an important factor in the risk of incineration. In the species he investigated, MacNeill (1964) found early instar shelters to be generally aerial (above the grass blade bases), whereas during the last two instars shelters of some species extend into the soil or are even entirely subterranean (he did not make any observations on *H. dacotae*

or *H. ottoe*). Larvae of *Hesperia comma assiniboia* (Lyman) often construct shelters beneath dried cattle droppings (McCabe and Post 1977).

McCabe (1981) provided a brief, somewhat vague description of the larval habits of *H. dacotae*, but he did not specify whether his observations were made on larvae in nature or in captivity. He reported shelters of newly hatched larvae to be at the soil surface, but he did not say where shelters of older larvae were constructed. He found this skipper to overwinter as a fourth instar, but no details about the overwintering shelter were given.

The only observations of the larval habits of *H. ottoe* are those of Nielsen (1958), who found a second instar in an aerial leafblade shelter. His other observations involved larvae crowded on a potted clump of grass; the one larva that survived into September had its shelter at the base of the clump, but this was not described in detail. This larva was accidentally killed when it wandered away from the pot so nothing was learned about overwintering behavior.

The impetus for this study was provided by The Nature Conservancy's acquisition of a prairie tract in southwestern Minnesota where *H. dacotae* and *H. ottoe* were present. The objectives of the study were to obtain basic information about the two skippers important for their conservation, and more specifically, to investigate the mortality risks posed by the use of prescribed burning in the management of their prairie habitat.

I investigated the life histories of the skippers through rearing and intensive field observation, including a three year mark-release-recapture (MRR) study of adults. Particular foci of attention were larval host plant and adult nutritional requirements. Clues to other habitat requirements or preferences were sought in the patterns of distribution of major adult activities determined during MRR sampling. I monitored larval behavior and development in seminatural and natural conditions. I also obtained some preliminary data on age specific and potential lifetime fecundities.

A major objective of the MRR study was to determine how much these skippers move about within the study site so that burn unit subdivision and rotation schedules can be planned to assure repopulation between burns. An original hope was that several independent demographic units of the skippers might occur within the site that could be subjected to experimental manipulation, but this proved not to be the case.

Another objective was to estimate the populations of the two skippers within the study site at the beginning of its establishment as a natural area preserve to provide a baseline for monitoring the effects of management. I repeated the MRR study for three consecutive years during which increasing proportions of the site (all the final year) were burned

in spring to see if this would have a detectable effect on population levels. The MRR study also supplied estimates of the average duration of residence of adults within the site. Potential lifespan was estimated from caged insects and maximum recapture intervals.

I directly investigated mortality during spring burning via a series of field experiments from 1979 through 1982. The first involved trapping newly emerging adults naturally present in burned and control areas, but low densities necessitated abandoning this in favor of artificially populated, enclosed areas of natural prairie as experimental plots in all four later experiments. Because of technical problems only two of the experiments yielded useful information.

I focused on spring burning because prescribed burning for prairie management is conducted primarily in spring to maximize the differential impact on exotic plants. These are cool season (C_3) species

that are vigorously growing at this time, whereas the dominant native grasses are warm season (C_4) species that are just beginning to shift reserves from roots to above ground production (Ode et al. 1980). Three of the experiments included early and late spring burn treatments to assess the effects of a change in the location of larval shelters during postdiapause development.

Because prairie fuel level and fire intensity can vary considerably, depending upon site soil-moisture regime and how long fuels have been accumulating, all experiments included two fuel levels. In two of the experiments I measured the rise in soil temperature produced during plot burning at the approximate depth of overwintering larvae.

The results of these investigations provide a substantial foundation for designing prairie management strategies that will ensure the persistence of these skippers.

STUDY SITE

PHYSICAL DESCRIPTION

This study was conducted at Hole-in-the-Mountain Prairie, a natural area preserve about 3 km south of the town of Lake Benton, Minnesota, (latitude $44^{\circ} 13' 45''$ N, longitude $96^{\circ} 18' 30''$ W) in the regional highland known as the Coteau des Prairies. The Late-Wisconsinan Bemis moraine, a massive ridge forming the crest of the Coteau, is breached here by a glacial meltwater gorge (Matsch 1972) whose sides have been deeply dissected by dendritic growth of tributary ravines. The preserve lies on the outer flank of the moraine, on the east side of the gorge at the confluence of a large tributary ravine (Figure 1).

Only the 63 ha portion of the preserve west of U.S. Highway 75 was utilized for the study. Most of the area consists of sideslopes of the main valley and tributary ravine, with long, moderately steep, northwest facing slopes predominating. The remainder is nearly level alluvial plain in the bottom of the valley.

Within the study area elevations range from 530 m above sea level on the valley floor to 565 m on the morainic surface in the southeast corner. There is a gradual rise to 585–590 m on the crest of the moraine about 1.6 km away.

SOILS

The soils of the steeply rolling upland portions of the site are almost all classified in the Buse series of

the fine-loamy, mixed, frigid family of Entic Udic Haploborolls. Buse soils are mildly alkaline and calcareous (U.S. Dept. of Agriculture, Soil Conservation Service Staff 1970). The parent glacial till here is very stony, and the surface is strewn with stones, ranging up to large boulders. Pebble pavements have formed on some exposures.

The small areas of level upland included on the south and east margins of the site are classified as well-drained silt loams in the Vienna and Kranzburg series, the latter formed in loess-mantled till. The valley bottom is occupied by poorly drained and very poorly drained silty clay loams in the Lamoure and Rauville series, respectively, both Cumulic Haplaquolls (U.S. Dept. of Agriculture, Soil Conservation Service Staff 1970).

CLIMATE

The climate is continental. The site is on the east edge of the dry subhumid climatic region of Thornthwaite (1941). Mean annual temperature at the weather station at Brookings, South Dakota, 40 km west of the site, is 5.8°C (1951–1980 normals). The summer (June–August) mean is 20.2°C , and the winter (December–February) mean is -9.9°C . The mean low and high for January, the coldest month, are -18.7°C and -6.6°C , respectively. The corresponding values for July, the warmest month, are 14.3°C and 28.7°C . The average degree-day accumulation above an 18.3°C base is 479.

Mean annual precipitation is 55.1 cm, with 80%

falling between April 1 and September 30 (U.S. Dept. of Commerce 1982b). Average annual snowfall is about 72 cm, almost all between November and April, with about 50% in February and March (U.S. Dept. of Commerce 1982a).

VEGETATION

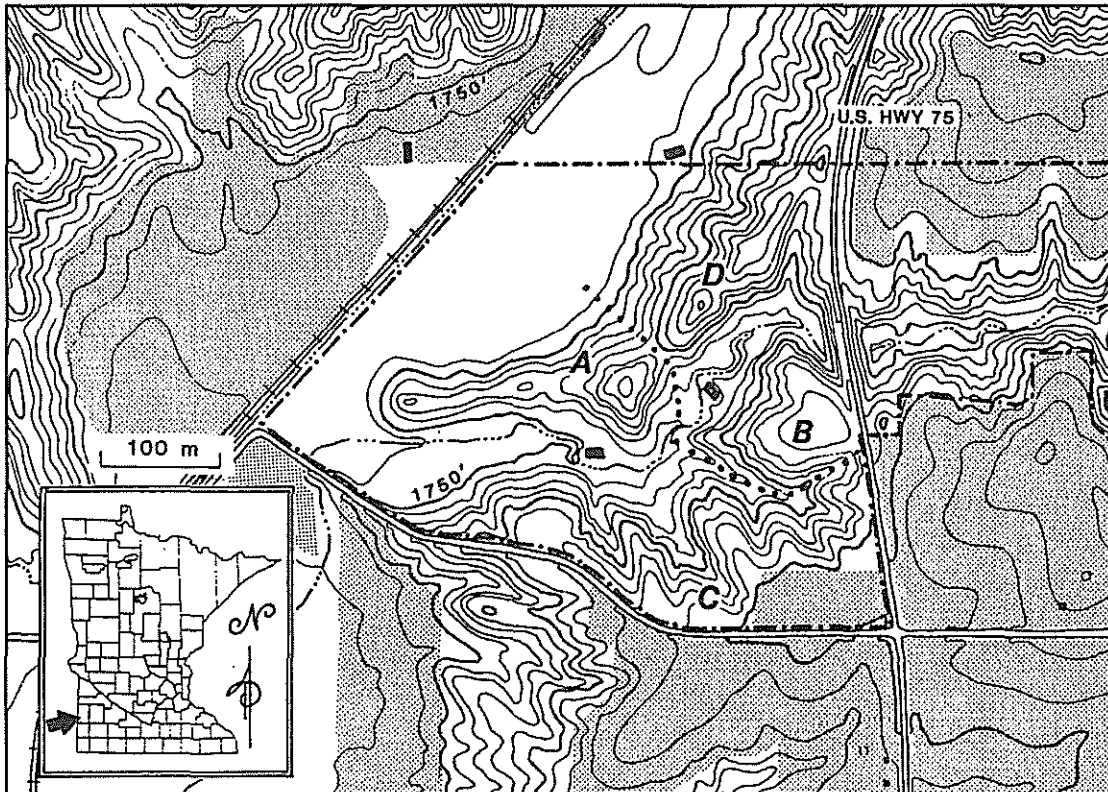
The site lies within the Tallgrass Prairie (Risser et al. 1981: fig. 2.1) or Bluestem Prairie (*Andropogon-Panicum-Sorghastrum*) (Küchler 1964). Most of the upland is dry-mesic prairie dominated by the midgrasses *Andropogon scoparius*, *Stipa spartea*, *Bouteloua curtipendula*, and *Sporobolus heterolepis*. (Description of the vegetation is based on personal observation, including intensive quantitative sampling in eight representative 15 x 30 m plots.)

The tallgrass *Andropogon gerardii* is common but generally of low stature in the drier habitat. Important secondary graminoids, most low growing species,

include *Koeleria pyramidata*, *Dichanthelium wilcoxianum*, *Carex heliophila*, and *Muhlenbergia cuspidata*, with *Stipa comata* and *Bouteloua gracilis* locally important. Taller stature prairie dominated by *Andropogon gerardii*, *Sorghastrum nutans*, *Stipa spartea* and *Bouteloua curtipendula* occurs on lower slopes and up shallow draws. Forb abundance and diversity are high, with Asteraceae and Fabaceae ranking first and second in numbers of species.

The drier prairie covers about 41 ha of the 63 ha total. Tallgrass vegetation occupies the alluvial plain west of the slopes and most of the bottom along the tributary ravine. The former is wet prairie dominated by *Spartina pectinata*, *Calamagrostis stricta*, and *Carex* spp., while that in the ravine is badly disturbed mesic and wet prairie full of weedy native and exotic species. Old field vegetation dominated by *Bromus inermis* and *Solidago* spp. occupies a narrow band on the footslope along the meadow margin and a larger area in the lower end of the tributary valley.

Figure 1. Study area at Hole-in-the-Mountain Prairie Preserve. Preserve boundary is indicated by dot-dash line. Study was limited to west side of Highway 75. The two *Hesperia* species investigated occurred only in drier prairie on slopes. Subdivisions of the uplands for mark-release-capture sampling are labelled A-D. Boundaries between divisions on either side of the ravine are indicated by dotted lines. Larger black rectangles are stockponds. Shaded areas were under cultivation during the study. Contour interval is five feet (1.524 m).



SURROUNDING LAND USE

The site is in a region of intensive agriculture, but several thousand hectares of dissected topography along the length of the gorge remain uncultivated. Most is prairie, but many of the large, deep ravines in the highest part of the moraine are wooded. All of the prairie has a long history of use as livestock pasture, and most has been badly damaged by overgrazing. At the time of the study almost all prairie outside the preserve was being heavily grazed, and most of the valley bottom was under cultivation.

SITE HISTORY

The Nature Conservancy acquired the study area in two separate transactions. The north tract (Units A, D, and most of B in Figure 1) was acquired in 1978, the south tract (Unit C and part of B) in 1979. Both had been used as pasture for domestic livestock

probably since the early 1900s when they were sold by the railroad out of its land grant. Although sheep probably were pastured in the north tract in the 1930s (Adrian Little, nephew of a former owner, personal communication), only cattle had been on either in recent decades.

Grazing in the north tract varied from heavy to light from 1974 through 1977, and was very heavy in the south tract from 1976 through 1978 (personal observation). Grazing levels before this are conjectural, although the north tract has suffered greater damage. Grazing was discontinued in the north tract after 1977 and in the south tract after 1978.

Fire had not occurred in the site for an indeterminate number of years. There is no tradition here of pasture burning, and accidental fires were probably infrequent, because heavy grazing would have kept fuel levels low.

METHODS

LIFE HISTORY, POPULATION STUDIES

IMMATURE STAGES

I incubated ova in covered plastic petri dishes lined with filter paper that was lightly moistened occasionally. *Hesperia dacotae* ova were obtained from caged females. Because *H. ottoe* females did not adjust well to confinement, most ova of this species were field collected from *Echinacea angustifolia* capitula, from which they were easily removed with a moistened fine artist's brush. Petri dishes were stored indoors, with exposure to natural daylight and forced ventilation but no air conditioning.

In 1978 I reared larvae in groups in polyethylene refrigerator storage containers. I subsequently reared larvae individually in 25 x 200 mm glass test tubes. A moistened layer of plaster of paris in the bottoms of these containers, and covers allowing limited gas exchange, maintained high enough humidities to prevent rapid desiccation of food plant material. Rearing containers were kept at ground level under an opaque sunshade on the study site in 1978. All later rearing occurred indoors, primarily in the same situation as incubating ova.

I provided larvae with excised culms and blades of various grasses. Fresh material was added every two to four days. Larvae always constructed shelters in the plant material, and I usually tried to leave as much of these intact as possible when removing

old material, although I periodically cleaned out all old material. I removed frass accumulation from the bottoms of containers every several days. I monitored development on a daily basis.

I transferred larvae at various points in prediapause development to potted grass clumps (*Andropogon scoparius*) which were embedded in the soil outdoors late in the fall for overwintering. I continued feeding many larvae indoors beyond the end of the natural growing season, transferring those that remained active into potted grasses (*Poa pratensis*) under fluorescent lights on a 16:8 LD cycle. I also attempted to overwinter diapausing larvae in individual containers held under humidified refrigeration. Postdiapause development of successfully overwintered larvae was monitored in individual rearing tubes.

Samples of ova, larvae, and pupae were preserved in 70% ethyl alcohol after killing in boiling water or KAAD (Peterson 1948). I retrieved cast head capsules and measured their width (across the widest part) under a dissecting microscope fitted with an ocular micrometer. Last instar head widths were measured on intact larvae, as the capsule splits apart in the larva-to-pupa moult.

I used the phenomenon, described by MacNeill (1964), of regular alternation between odd-instar and even-instar configurations of the "ring pores" on meso- and metathoracic and abdominal segments in *Hesperia* to aid in determining the instar of larvae whose complete developmental history was unknown. Examination of preserved larvae of known

instar confirmed that both these species, which were not studied by MacNeill, conform to the pattern.

Most larvae were reared on *Andropogon scoparius*, sometimes mixed with *Andropogon gerardii* and *Bouteloua curtipendula*. I conducted no-choice trials of several of the more common grasses in the habitat with hatching larvae, and I continued feeding larvae for several stages on those that were readily accepted.

I investigated host choice of *H. ottoe* larvae in the field in 1978 by tagging 600 *Echinacia angustifolia* plants having ova present and subsequently monitoring larval activity within about a 0.5m radius around each. These areas were closely searched on five occasions between August 11 and October 16. Searches were limited on all occasions after the first to areas in which surviving larvae had been found in the previous search.

I also monitored larval activity of both species in 1 m diameter prairie plots (not enclosed) into which I released larvae. Examination of enclosed plots used in the burning experiments, after adults had emerged, yielded additional information on larval host selection and behavior.

In 1982 I confined *H. dacotae* larvae individually from hatch to diapause on single species tufts of grass growing naturally in the prairie. Grass species included three native warm season (C_4) grasses (*Andropogon scoparius*, *Bouteloua curtipendula*, *Sporobolus heterolepis*), two native cool season (C_3) species (*Stipa spartea*, *Koeleria pyramidata*), and one non-native cool season species (*Poa pratensis*). Individual grass tufts were isolated within 10 cm diameter aluminum collars, 5 cm high, pushed 1 cm into the soil, with shoots of any other species present manually removed. A 20.5 cm high cylindrical cage of saran screen was fitted over the collar and cinched securely to it. I enclosed 15 tufts of each species within a fairly level area of dry-mesic midgrass prairie on a uniform soil, taking care that all species were well interspersed.

Larvae from five wild-caught female parents were distributed among the tufts, with three tufts of each species randomly assigned to offspring of each parent. I placed all larvae on their host grasses within five hours of hatching. All plots were stocked over six days in the third week of July and left undisturbed until October 25, after the onset of freezing temperatures, when I extracted survivors.

I placed survivors individually in 0.5 dm glass vials plugged with lengths of cellulose cigarette filter material and held them on ice two days before freezing them to -70°C . Frozen larvae were then transferred directly to a drying oven. After 90 hours at 75°C larvae were removed individually and weighed on an electronic balance to the nearest 0.01 mg. After all were weighed, head capsule width and ring pore configuration were determined for each.

The relationships of survival to host grass species and female parent were evaluated by log-linear contingency table analysis (Sokal and Rohlf 1969). The weight data from survivors was analyzed by ANOVA in a generalized randomized complete block design (Steel and Torrie 1980), with female parent as the blocking factor.

ADULTS

Mark-Release-Recapture Study

Field methods

I conducted an MRR study of adult populations of both skippers in the consecutive years 1979-1981 to obtain estimates of population sizes, and of residence periods and intrasite movements of individuals. I began sampling as soon as I observed the first adult skippers in the field in 1979 and 1981. For 1980 I began six days after the first sighting.

I discontinued sampling when capture rate had fallen to approximately one insect per hour or lower. Thus essentially the entire adult emergence periods of both species were spanned by the study each year except 1980 when the first several days of the emergence of *H. dacotae*, which begins earlier than that of *H. ottoe*, were missed.

I divided the upland portion of the study area into four units, designated A through D in Figure 1. The approximate habitat area within each unit was: A, 7 ha; B, 7 ha; C, 17 ha; D, 10 ha. Much smaller topographic subdivisions (not shown) permitted fairly precise localization of all captures.

All units were scheduled for sampling each day, with the order randomized. I attempted to spend approximately equal time in each (between 1 and 1.5 hours, most often about 1.25 hours), beginning about 0900 CST, and ceasing about 1630 (occasionally as late as 1900, the limit of flight activity).

Weather and other factors caused frequent deviations from the schedule. I did not do MRR work during prolonged periods of cloudiness and/or cool temperatures when flight activity was suppressed.

I captured insects opportunistically with a standard insect net having a 45 cm diameter net ring and a 1.21 m long handle. I made some effort to sample throughout each unit, but more productive parts were disproportionately sampled.

On first capture, insects were individually numbered with permanent felt tip marking pens using the coding system of Ehrlich and Davidson (1960) with the 2 and 20 marks moved from the anal angle of the forewing to the base of the hindwing. I gently restrained insects in a fold of the net, grasping the thorax between thumb and forefinger, and applied

the marks to the ventral wing surfaces through the net fabric. Insects were released at the point of capture immediately after marking.

For each capture I recorded species, sex, wing wear (using the five-point system of Watt et al. 1977), missing appendages or other injury and whether damage occurred during handling, subunit where captured, time and date, and behavior just before capture. Behavior categories were:

- 1) perching and chasing (male mate-seeking behavior),
- 2) search flight (male mate-seeking behavior),
- 3) courtship interaction (male-female),
- 4) copulation,
- 5) oviposition search flight,
- 6) oviposition (substrate was recorded),
- 7) basking, and
- 8) nectaring or other adult feeding/drinking activity (nectar-flower species recorded).

Insects that appeared to be badly injured were recorded as killed on capture.

Parameter Estimation

I calculated estimates of population parameters by both the Fisher-Ford and Jolly-Seber methods (Begon 1979). I used Bailey's correction, as given in Blower et al. (1981), in calculating the estimated number of marked insects available for capture on each sampling occasion in the Jolly-Seber model, because daily samples were small and contained few recaptures.

Recaptures of insects captured earlier the same day were not included in the data used to estimate population parameters. They were omitted in order to remain approximately faithful to the assumption that each sampling occasion is instantaneous. I did, however, use the same day recapture data in behavior analyses.

I calculated daily population size estimates and an estimate of the assumed constant residence rate θ by the Fisher-Ford method. This factor is called "residence rate" rather than the traditional "survival rate" because losses were due to emigration as well as death. From the Jolly-Seber procedure I obtained daily population estimates with their standard errors and estimates of a daily θ (which is allowed to fluctuate stochastically in this model) with standard errors.

I also calculated a weighted average of the Jolly-Seber $\hat{\theta}_i$'s according to the method of Scott (1973b):

$$\hat{\theta} = \frac{\sum_{i=1}^{k-2} (\hat{\theta}_i)^{1/d_i} W_i}{\sum_{i=1}^{k-2} W_i}$$

where k is the total number of sampling occasions, and d_i is the number of days between the i th and $(i + 1)$ th sampling occasions on which the $\hat{\theta}_i$ is based. This converts all $\hat{\theta}_i$ to a common daily basis. The weights (W_i) are the estimated numbers of marked insects present immediately after each sampling occasion (the estimated number present before the start of sampling, calculated from the data, plus the actual number of newly marked ones released after the sampling).

From both the estimated constant θ s of Fisher-Ford and the Jolly-Seber averages I calculated corresponding estimates of the average length of individual residence (Cook et al. 1967):

$$R_{AV} = - (\text{Log}_e \hat{\theta})^{-1}$$

I calculated the number of adults present in the annual generation using the formula of Blower et al. (1981)

$$\hat{N}_{TOT} = (1 - \hat{\theta}) \sum_{i=1}^{k-1} \hat{N}_i + \hat{N}_k$$

With the Jolly-Seber \hat{N}_i I used the weighted average of the $\hat{\theta}_i$ for $\hat{\theta}$. I followed Watt et al. (1977) in obtaining values for \hat{N}_i and \hat{N}_k , which the Jolly-Seber procedure itself does not produce. Because in most cases sampling began when only a few adults had emerged and ended after all had emerged and most died, values for these two days had little influence on the estimated total. Missing \hat{N}_i in the series were filled in by averaging surrounding \hat{N}_i , usually four values.

Assumptions Testing

To determine whether males and females should be analyzed as separate populations I used a test devised by Tabashnik (1980). It permits simultaneous but separate evaluations of whether the sexes differ in catchability and residence rate. Under the assumptions that the ratios of male to female catchability and male to female residence rate (α , λ respectively) are both constant from day to day, least squares regression is used to estimate these parameters from the ratios of the proportions of each sex recaptured t days after release (${}^mR_{ij} / {}^fR_{ij}$, $j - i = t$):

$$\text{Log} (\sum {}^mR_{ij} / \sum {}^fR_{ij}) = t \text{Log } \lambda + \text{Log } \alpha$$

The prefixed superscripts m , f , indicate male or female, respectively. The sums are over all different intervals of length t . An intercept of 0 indicates equal catchabilities ($\alpha = 1$) and a slope of 0, equal

residence rates ($\lambda = 1$). A more complete account of this test is provided in the Appendix.

Because this test could be performed for only three of the six species-year combinations, I also used standard contingency table techniques to test whether recapture likelihood was independent of sex. Each day's release was classified by sex and by whether the individual was subsequently recaptured, and a Chi-square was calculated under the assumption of independence, with the sum of these Chi-squares being the test statistic (Begon 1979). Since recapture probability is the product of catchability and residence rate, it can be used to test equality of one only if the other is either known or assumed to be equal.

I evaluated the Fisher-Ford assumption of a constant θ with two tests. These were a test of day-to-day constancy, and a test of age independence. The first is a Chi-square goodness-of-fit test comparing the sequence of observed number of days survived by marks with the sequence of values expected under the assumption of a constant θ , using the estimated value of the parameter (Begon 1979). The second test calculates the expected numbers of recaptured marks of ages 1, 2, 3, . . . , n days under the assumption that age has no effect and compares them with observed numbers by Chi-square tests (Begon 1979).

Additional qualitative evidence on whether residence rates changed with age was provided by "recapture decay plotting" (Watt et al. 1977), in which the logarithm of the number in a "cohort" of recaptured insects still alive (not yet recaptured for the last time) is plotted against the number of days between initial release and final recapture. A linear relationship indicates a constant θ . I made separate plots for insects young at first capture (wing-wear rating less than 3) and for those older (rating 3 or greater).

I tested whether marking itself affected probability of recapture by dividing insects released on any given day into two groups. The groups were those actually marked just before release and those that already had marks from a previous capture and were released without being marked again. I calculated a Chi-square statistic from the proportions of recaptures in each under the assumption of independence. The Chi-square statistics for individual days are summed for the test (Begon 1979).

Begon (1979) gives a similar test for the independence of recapture probability from previous capture history. A Chi-square statistic is calculated from the proportions of recaptures of insects released on a given day that had been previously captured 0, 1, 2, etc. times, and the several statistics are then summed for the test. I could make this test only on males of one species in one year because of the general infrequency of multiple recapture.

Distribution and Movement

I measured the straight line distance between the approximate locations of successive captures of individual insects on a map of the site (scale 1:3720). I tested the possibility of a relationship between these distances and the number of days between captures with Spearman's coefficient of rank correlation (Steel and Torrie 1980) because the distribution of distances was strongly nonnormal. I calculated this statistic for each sex of each species on an annual basis.

I evaluated differences in intercapture distances among years with a Kruskal-Wallis K-sample test, and between sexes (on a per species basis) and between species (on a per sex basis) with Wilcoxon-Mann-Whitney two sample tests (Steel and Torrie 1980).

I evaluated differences between sexes and species in the likelihood of recapture in a different versus the same unit as the preceding capture with Chi-square tests. Differences in the likelihood of inter-unit movement crossing the large tributary valley versus remaining on the same side of it were similarly evaluated.

To evaluate the relationships between adult densities and unit, I computed mean per-minute capture rates for each sex of each species in each unit each year. These means were calculated from the total numbers of captures and the total minutes of capture effort in each unit, from the day of the first capture to the day of last capture. Data were not used from days on which sampling conditions were poor. All means were based on nearly equal numbers of days (average = 25). I analyzed the resulting data by analysis of variance (ANOVA) in a three way factorial design (sex x species x unit) in randomized complete blocks (years). Data were transformed before ANOVA by taking square roots.

Ancillary Investigations

In addition to recording behaviors of captured insects during the MRR study, I noted details of significant behaviors of noncaptured ones observed both while conducting MRR sampling and outside sampling periods. Some similar data came from preliminary field work in 1978 involving observation along regular transects as well as from less structured observations. During 1978 I attempted to investigate habitat and host plant selection and other behaviors of ovipositing females by prolonged, continuous observation of individuals, but most data on these aspects of life history came from brief observational episodes involving different females. These usually began with the sighting of a female in preovipositional search flight and ended after one oviposition.

In 1979 I investigated the distribution of *H. ottoa* ova

on *Echinacea angustifolia* capitula by counting ova on random samples of 50 capitula each in upper and lower slope positions in each of six subdivisions of the preserve on five regularly spaced occasions spanning the peak egg laying period, between July 18-30. I restricted sampling to capitula in anthesis, as only these were selected by females.

Sampling units were: Unit A, the unburned part of Unit D, Unit B, the burned part of D, and two approximately equal subdivisions of Unit C. The first two were unburned and in the second growing season since termination of intermittent grazing. The second two had the same grazing history as the first two but had been burned in spring, 1979. The last two were unburned and in their first growing season after a period of heavy grazing had ended.

To evaluate the treatment (grazing, burning, no recent disturbance) and slope position effects, I summed the counts over all five sampling occasions, and analyzed the resulting data by ANOVA as a split plot design, with treatments as the whole-plot factor and slope position the subplot factor. Counts were high enough that no transformation was needed to satisfy the assumption of normality.

I supplemented field observation of courtship and mating behaviors with observation of insects in small flight cages set up in the natural habitat. These were net enclosures over plots in Experiments II and III. I put newly emerged and sometimes older unmated females into cages with field-caught males, or in a few instances, with recently emerged, reared males. Usually one to three males were included with a single female, but sometimes more than one female was put in with several males. I also released a few virgin females into the prairie where males were active.

I obtained daily egg production data from females held in small open bottom net cages placed over grass clumps in the prairie. Cages were provisioned with cut flowers in water and additional moisture supplied by misting the cage and enclosed vegetation with water from a trigger sprayer at intervals during the day. I removed all eggs daily at dusk. Most females were field-caught and ranged from young (little wing wear) to old (worn, frayed wings) at capture, but three reared *H. dacotae* females, mated in cages, were also included.

I dissected females to obtain additional data on egg maturation and potential fecundity. Specimens were dissected in 0.05% saline after anaesthetization in ethyl acetate vapor. Excised reproductive organs were stained lightly with Delafield's hematoxylin to aid visualization of oocytes in the distal portions of ovarioles and to render chorionation evident. I counted developing oocytes under a binocular dissecting microscope (maximum magnification of 60). Dissected specimens included many of the females held in confinement for egg production data, freshly emerged females, and fresh to worn field-caught females.

To obtain data on female mating frequency, I counted spermatophores in field-caught specimens dissected for other purposes, as well as in a sample of various ages taken for this purpose. Dissection procedures were the same in all cases.

BURNING STUDIES

FIELD PROCEDURES

Emergence Trap Study

A prescribed burn of unit B was conducted on May 6, 1979. To evaluate the effects of the burn on the number of adults subsequently emerging, I set out 180 emergence traps in burned and unburned habitat June 24-30. This was just before the appearance of the first *H. dacotae* adults. Six 9 x 13 m sampling plots were located in each of the three units then part of the preserve (A, B, and D), with three plots in mesic habitat dominated by tallgrass vegetation and three in drier, midgrass dominated habitat.

Each plot was gridded into a 10 x 10 array of 0.9 x 1.3 m subplots, and emergence traps were placed over a randomly chosen sample of 10 of these subplots. Traps were tent shaped constructions of green nylon mesh fabric suspended over a wire frame with the bottom edge worked down among the grasses and pinned to the soil.

I checked all traps at least once a day from July 1 through August 11, usually in the late morning. I recorded the species and sex of skippers emerging in the traps and removed them.

Experiment I

In this and the following experiments, artificially populated enclosures set up in natural prairie served as plots. These were established at the natural beginning of the annual generational cycle and burned the following spring. Plots were open-burned in all experiments but III, in which a closed-burning approach (Miller 1979) was employed. Fire-caused mortality was measured by comparison of postfire numbers in burned plots with those in unburned controls.

Although all plots were populated with the same number of hatchling larvae, an undetermined number of these had died by the time of burning several months later. I used this approach, despite the experimental error introduced, to insure that larval circumstances in the plots, which involve the construction of concealed shelters, were representative of those of larvae in nature. I did not try to reduce this error by determining the number of larvae actually present just before burning because of the severe disturbance to larvae and shelters this would have required. I did not attempt

to extract all larvae, both survivors and those killed, right after burning because death from fire injury might not be immediate and the effects of removal, including a substantial risk of mechanical injury, could obscure delayed fire-mortality. I also wished to include deaths that might result from subsequent starvation or desiccation among those attributable to burning. By the time I scored survivors (emerging adults, or in the last experiment, last instars and pupae), the remains of dead larvae could not reliably be found nor time of death (preburn or postburn) always determined.

Experiment I plots were 1.5 m² squares enclosed by 9 cm high sheet-metal barrier strips inserted vertically approximately 2 cm into the soil and covered with 65 cm high removable cages. Cages were made of white polyester marquisette fabric stretched over the tops and sides of unpainted pine frames. The bottom edge of the frame fit snugly against the inside of the barrier strip and rested on the soil surface.

Plots were laid out in midgrass prairie in blocks of four arranged in squares with 2 m between adjacent sides of plots. Five blocks were in Unit A, which had been burned earlier in the spring, and five were in unburned Unit D where there was a substantial accumulation of litter. Three randomly chosen plots in each block were fumigated with hydrogen phosphide prior to stocking to reduce populations of natural enemies. These fumigated plots were randomly assigned to three treatments: no burn (control), early spring burn, and late spring burn. Unfumigated plots were left unburned.

For fumigation, I placed Phostoxin[®] tablets in the plots and covered them for three days with 0.15 mm thick polyethylene film taped to the metal barrier strips. Opaque sunshades were suspended over the plots during this period. I included small screen topped vials containing ten larvae of *Dermestes caninus* Germar with a supply of food to provide an indication of the effectiveness of fumigation. Cages were installed over the plots immediately after the fumigation materials were removed.

I began stocking plots two weeks later, in mid-July, 1980. I put 20 hatchling larvae of *H. dacotae* in each plot, from ova obtained from a number of wild-caught females. Stocking was done by blocks, with larvae randomly assigned to plots as they hatched. I had not planned to include *H. ottoa* in the experiment because of difficulties in obtaining ova from captive females, but when ova proved to be readily obtainable from the wild, I substituted ten larvae of this species in each plot for ten of the initially planned 30 *H. dacotae* larvae.

Cages were removed from plots for the winter in October following several hard freezes and were replaced after all experimental burning was completed the next spring.

A firebreak was mowed around each block and

along the center of the dividing strips within each, leaving each plot in a slightly larger area of prairie surrounded by a break. I burned plots individually by firing part of the perimeter of the surrounding area and allowing the flame front to move across the plot.

I conducted the early spring burns on April 25, 1981, when larvae were still in buried shelters, and the later spring ones on May 30, when they were in shelters on the surface. Before burning each plot, I recorded the air temperature just above the vegetation with a mercury thermometer held in my shadow. To obtain information about temperatures larvae were exposed to during burning, I buried an iron-constantan thermocouple probe 5 mm below the soil surface in the middle of each plot and recorded temperature before ignition and at the maximum following ignition. This depth was an estimate of the average location of larvae in buried shelters.

To obtain information about approximate maximum temperatures over a greater range of distances from the soil surface, I also inserted four 95 x 115 x 0.635 mm aluminum oxide ceramic wafers (3M AlSiMag 838[®]), vertically striped with specific-melting-point fusible paints (Tempilaq[®]), into the soil to a depth of 35 mm at selected spots within each plot. A second, blank wafer protected the painted surface of the first. This device recorded that part of the measured profile from 60 mm above the soil surface to 35 mm below it that was exposed during burning to temperatures as high or higher than the fusion temperature of each indicator paint (38°, 41°, 45°, 52°, 59°, 62°, 69°, 79°, and 93° C).

I checked the plots for emerging adults daily (usually twice a day) from June 17 through August 31, recording the species and sex of each and removing it from the cage.

I analyzed the experiment as a split plot design, with the blocks as whole plots (preburned and not preburned), and the individual plots as subplots. Data were analyzed for each species separately, and for species combined.

Experiment II

Four blocks of plots from Experiment I, all in the unburned unit D, were used for a second experiment. Two plots in each block had been burned as part of Experiment I in spring 1981, and two had been left unburned. The latter had a rather heavy litter accumulation. I randomly selected one of each condition for burning in this experiment, the other two being no-burn plots.

I stocked each plot with 10 first-instar *H. dacotae* in mid-July, 1981, while still monitoring them for Experiment I adults. Procedures were the same as those in Experiment I. Cages remained over the plots until removal for winter in late November. These were replaced in the spring with a redesigned cage that more effectively prevented larval escape

during prepupation wandering. These were made of the same marquisette fabric, but the free bottom edge of the fabric fit around the outside of the metal border where it was held securely in place with strips of flexible magnetic material.

Burning was done on April 30, 1982, (early spring in this year). Fire burned naturally through the treatment plots when a Nature Conservancy crew burned all of Unit D. The no-burn plots were kept from burning by wetting the vegetation within and covering them with sheet-metal just before the start of the burn. No temperature measurements were made. I removed the sheet-metal covers from the no-burn plots immediately after the fire had passed through all blocks and installed cages over all plots three days later.

I checked plots for emerging adults daily from June 21 through August 2, usually once in the morning and again in the afternoon. The experiment was analyzed as a two way factorial design (two preburn conditions combined with two burn treatments) in randomized blocks.

Experiment III

Plots in this experiment were 0.07 m² circles in midgrass prairie. These were enclosed with 15 cm high white vinyl rings cut from wastebaskets. The bottom edge was pushed about 1.5 cm into the soil and the top covered with a removable lid screened with polyester marquisette fabric.

I laid the experiment out in ten blocks of six plots. Experimental treatments consisted of two fuel load levels (moderate and heavy) combined factorially with two burning dates (early and late spring). These, plus two no-burn "treatments" were randomized among plots in each block.

I stocked each plot with six hatchling *H. dacotae* larvae during the first half of July 1981. Methods of obtaining ova and stocking plots were the same as in the previous experiments. I removed the screened lids of the enclosures in late November, after light snowfall. Lids were replaced after completion of the late spring burn.

Plots were burned one at a time, with the order of the two fuel levels randomized in each block, and with the block order the same on both dates. A 57 cm diameter, 53 cm high expanded steel mesh ring was centered on the plot. This was surrounded by a 76 cm diameter, 46 cm high sheet-metal fire barrier ring perforated 15 cm above its base to allow inflow of air. I then removed the vinyl enclosure, added a measured quantity of dry fuel (harvested from the site) within the mesh ring, and ignited the fuel at a point on the outside edge. As soon as there was no more visible flame I removed the barrier ring, and when no further combustion was evident I removed the mesh ring and replaced the vinyl enclosure in its original position.

The amounts of added fuel were 75 g for the moderate level, and 175 g for the heavy level. With the estimated 140–150 gm⁻² fuel naturally present, these fuel loads were equivalent to 430–440 gm⁻² and 830–840 gm⁻², respectively. The lower value was close to the mean fuel load of 410 gm⁻² measured about one week earlier in a very similar prairie 13.5 km southeast of the study site. This prairie had not been grazed or burned for at least four years and the fuel load was probably the maximum or equilibrium level for this dry-mesic habitat type. The higher value was chosen as fairly representative of fuel levels found in mesic tallgrass prairie habitat (Kucera and Ehrenreich 1962, Hulbert 1969).

I conducted the early burn on May 1, and the late burn on June 5, 1982. All plots were burned within a four hour period on each date. I measured air and soil temperatures at the beginning, midpoint, and end of each period with an iron-constantan thermocouple. Air temperature measurements were made with the probe tip held above the vegetation in my shadow. For soil temperature measurements I inserted the probe tip about 5 mm into the soil. On each measuring occasion I took six soil readings, half in spots shaded by vegetation, half in bare, insolated spots.

I measured soil temperatures during burns with a thermocouple buried so that the probe tip was about 5 mm below the soil surface at plot center, recording the temperature every ten seconds from ignition until the maximum was reached. Because of the risk of disturbing or injuring larvae during burial of the probe and lead wires, I made these measurements in a separate set of plots identical to those with larvae, burned the day after each experimental burn under similar ambient conditions. On each date I burned five plots with each fuel load level, in alternating sequence.

I began daily, usually twice daily, monitoring of plots June 21, with a thorough initial search of each for adults that had emerged earlier and died. All plots were dismantled during the third week of July; each was exhaustively searched, and adult remains or pupal cases not accounted for by recorded adult emergences were tallied as additional emergences. The experiment was analyzed as a randomized complete block design, with a two way factorial treatment structure and two controls.

Experiment IV

Experiment IV was a modified version of Experiment III. *Hesperia ottoe* and *H. dacotae* were both included in this experiment. An open burning technique similar to the approach in Experiment II was used instead of the closed burning technique of Experiment III. Fuel levels were also lowered.

Plot enclosures were similar to those used in Experiment III. The only difference was the

marquisette fabric in the covers was replaced with saran screen. In early summer, 1982, I set up 72 plots in 24 blocks of three, divided evenly between two areas of midgrass habitat about 70 m apart. Both of these areas were in Unit D, which had been burned in early spring. They appeared similar in character except for the direction of slope (northwest versus southwest).

One of the three plots in each block was designated as a no-burn control. The two burn plots were distributed between the two fuel levels (light and moderate). All designations were made randomly.

Whole blocks were the experimental units for species and date of burning (early spring, late spring), in factorial combination. Blocks were randomly assigned to species until they were equally divided between the two species in both areas. The logistics of open burning made random assignment of blocks to date impractical. Instead, all blocks in one area were assigned the same date so the whole area containing them could be burned.

I stocked plots between July 10 and August 1, putting five hatchling larvae into each. Ova were obtained as previously: for *H. dacotae*, by confining wild-caught females; for *H. ottoe*, by collecting wild-laid ova in the field. I stocked plots by pairs of blocks, one from each area, randomly distributing available larvae among the six plots in the pair until all had the full complement. In most cases, all plots in a pair were stocked in one day, but two days were occasionally required. I removed enclosure lids for the winter in late October and replaced them in the third week of April, before larval feeding activity resumed.

I ringed each of the two large areas within which blocks were dispersed with a firebreak and burned plots by firing the large area and allowing the flame front to move across the plots. Just before the burn, I removed all enclosures from the plots in the area.

To protect the controls from fire, I clipped all fuels in and around the plot to a height of about 5 cm, centered a 54 cm diameter sheet metal barrier ring 10 cm high around it, over which I placed a sheet-metal cover after wetting the remaining fuels in and around the ring.

Fuels in the light fuel load plots consisted of the naturally present standing-dead material from the single previous season's growth (with significant amounts of live new growth for the late spring burn). The amount was estimated by clipping and weighing material in ten 0.25 m² circular areas near the plots to be approximately 160 gm⁻² on both dates. To create a moderate fuel load I centered 58 cm diameter chicken-wire rings around plots and added to each, 100 g of loose, dry fuel collected at the site. With naturally present fuels, this produced the equivalent of about 540 gm⁻². Immediately after each burn, I replaced the enclosures and covers.

The early spring burn in this experiment was on May 16, 1983; the late-spring burn on June 5. Before ignition I measured air temperatures with a mercury thermometer as in Experiment II, and soil temperature with the bulb of the same thermometer inserted to a soil depth of approximately 10 mm at several places. I made no soil temperature measurements during burning or afterward.

I searched all plots on June 16, for live larvae and pupae. I removed these to individual containers and allowed their development to proceed. I left the enclosures in place until 17 July, when I made a thorough search of each for evidence of survivors missed in the first search (dead adults and pupal cases not accounted for by adult remains). These were added to the count of live insects found in the earlier search to determine the total number of survivors.

I analyzed this experiment as a split plot design, with a two-way factorial treatment structure (burn date x species), applied to blocks as whole plots, and with fuel load levels plus no-burn control applied to individual plots as subplots.

Because of the method of assigning blocks to burn date, an area effect could have been confounded with the effect of date. Therefore, I also analyzed a derived data set created by subtracting from the burn-plot scores in a block the score of the control plot in that block. These data, consisting of differential survival scores for the burned plots only, permit the evaluation of date effect free of area effect if there was no interaction between the two (that is, if area affected only non-burn-related mortality.)

STATISTICAL ANALYSIS

For all ANOVA's I transformed the counts of survivors to their square roots, after adding 0.5 to each, as recommended to avoid overcorrection when values are very small and there are zeros (Steel and Torrie 1980). This generally seemed to give better conformity to ANOVA assumptions than angular transformation of the proportions. Substantive conclusions do not depend on the transformation.

Because derivation of the difference scores from Experiment IV involves the subtraction of the same control plot score from both treatment plot scores in each whole plot, errors may be correlated. These difference scores can be regarded as analogous to data from an experiment in which two treatments are applied to each subject. Ordinary ANOVA procedures apply because the covariance matrix of the subplot treatment errors satisfy the condition of compound symmetry (Morrison 1976, Milliken and Johnson 1984), which in the present case is equivalent to homoscedasticity. Before taking square roots of the difference scores for ANOVA, I added a constant to make all scores positive.

COMPUTATIONS

All MRR calculations were performed on a programmable hand calculator. Least squares line fitting, Chi-square, and log-linear contingency table analysis were also done on a calculator. The

Kruskal-Wallis and Wilcoxon-Mann-Whitney tests were done on a microcomputer using StatPro® software. All ANOVA's were run on a mainframe computer using IVAN except that from the *H. dacotae* host plant experiment, which was done using the GLM routine in SAS®.

RESULTS

LIFE HISTORY, POPULATION STUDIES

IMMATURE STAGES

Hesperia dacotae

Development

The *Hesperia dacotae* egg, which has not been previously described, is approximately hemispherical. Its walls rise vertically from the circular base for about one-fourth of the total height of the egg, then curve smoothly to a barely flattened summit (basal diameter 1.21 mm, height 0.95 mm, N = 3). The surface is nearly smooth, even under

40x magnification. In shape and surface character it closely resembles the egg of *Hesperia pahaska martini* as figured in MacNeill (1964). It is a gleaming, semi-translucent white when newly laid, becoming slightly duller in a few hours, but with little noticeable color change.

All eggs hatched on completion of embryogenesis. Larval growth was relatively slow, with an interruption by winter diapause. Table 1 summarizes stage-length data obtained in captive rearings under natural photoperiod and uncontrolled but approximately natural temperature regimes.

Feeding and growth of captive larvae slowed noticeably in the fourth stage, and only one larva kept indoors under artificial long-day illumination completed development. Some of these larvae

Table 1. Stage lengths in captive reared *Hesperia dacotae* and *H. ottoe*. Rearings were conducted under the natural photoperiodic regime; temperature was not controlled and probably averaged slightly warmer, with less diel variation, than in nature. Prediapause development took place from July into October, postdiapause in May and June.

Stage	<i>H. dacotae</i>		<i>H. ottoe</i>	
	N	Range (days)	N	Range (days)
Prediapause				
Egg	21	8-12	12	12-13
1st Larval ^a	34	8-14	18	7-14
2d Larval	29	6-14	13	11-18
3d Larval	24	9-18	12	9-26
4th Larval	19	16-35	4	14-36
Postdiapause^b				
Penultimate Larval	3	14-19	2	8-13
Ultimate Larval	8	15-21	22	17-25
Pupal	10	13-19	6	12-19

^aLarval stage lengths were measured from the completion of one molt to the completion of the next and recorded to the nearest whole day.

^bActual instar number of the postdiapause stages was not known for any of the animals from which data were obtained. *H. dacotae* diapauses as both fourth and fifth instars, with two postdiapause stages completed before pupation in either case. The same appeared to be true of *H. ottoe* larvae in these rearings.

molted to the fifth stage, but feeding appeared to nearly cease and death eventually followed. These observations suggest that diapause is obligatory.

Diapause occurred in fifth and, to a lesser extent, fourth instars under field conditions. All larvae removed in late October from the host plant experiment field enclosures had no food in their guts and appeared to be in diapause. Twelve were in an even-numbered stage, and 54 were in an odd-numbered stage, as determined by ring-pore configuration. These larvae were clearly fourth and fifth instars based on comparison of the width of their head capsules with that of capsules from known instars.

Fourth and pre-diapause fifth instars differed very little in size. On average, fifth instar head capsules were slightly wider than fourth instar capsules in both captive and field-reared groups. However, overlap was extensive, and mean dry weights of the two instars in the host plant experiment were nearly identical (fourth = 4.956 g; fifth = 4.943 g).

Postdiapause observations were more limited, but these indicated that two additional larval stages was the norm following a molt shortly after feeding resumed. I did not obtain a complete record of molts for any of the larvae that successfully overwintered, but assuming that these included both fourth and fifth stage diapausers, pupation took place after both six and seven stages. As determined by ring pore configurations, the stage of 31 final instars from Experiment IV field plots was an odd numbered one, while that of six was even numbered. Most were final instars when removed from the plots, with a few penultimate instars.

This ratio is consistent with the ratio of fifth to fourth instar diapause in the host plant experiment. The one larva that completed development indoors without diapausing pupated after the seventh instar.

The number of stages was not related to sex in reared larvae. The difference between the sexes in the proportions of larvae pupating after an odd—versus an even—numbered final stage in the sample removed from Experiment IV plots is not statistically significant (males: 2 even, 19 odd; females: 4 even, 12 odd; Chi-square = 1.601, $P = 0.21$). There was no obvious difference in size between even and odd numbered last-instars of the same sex; I did not observe a large enough sample to warrant statistical evaluation of quantitative measurements.

Adult emergence in field plots occurred over a three week period, with males emerging on average about five days earlier than females (Figure 2). This pattern was also seen in the wild population. Similar protandry in pupation of larvae from Experiment IV plots suggests that longer larval development time for females was responsible, rather than a longer pupal stage. Captive rearings were not conducted carefully enough to demonstrate this. McCabe's (1981) assertion that males and females emerge at

the same time is in error insofar as this implies no protandry, although it does accurately reflect the considerable overlap in emergence.

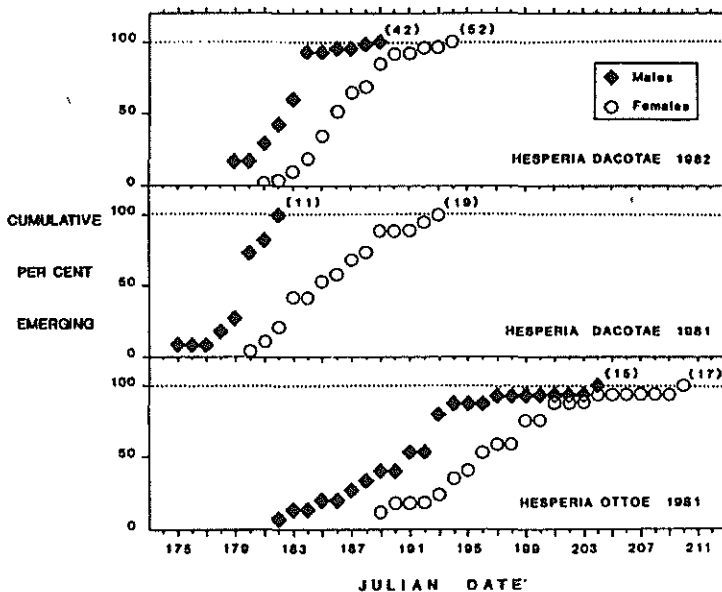
The proportion of males at emergence in five field-plot-reared populations ranged from 0.33 to 0.62. Log-linear contingency table analysis indicates no inconsistency with a 1:1 ratio (Table 2).

Habits

Three to four days before eggs hatched, the darkening head capsule became evident through the chorion. Larvae ate away a circular exit hole at the apex of the egg and crawled out as soon as this would allow the head capsule to pass. About 24 hours usually elapsed between the first visible breach in the chorion (without magnification) and larval escape.

Immediately after hatching, larvae turned and finished eating the chorion, leaving only the attached base. The only exceptions occurred when larvae were repeatedly disturbed by other wandering larvae in crowded Petri dishes, or when fungal growth had developed on the chorion surface.

Figure 2. Temporal pattern of adult emergence in skippers reared from hatching in prairie plots used in experiments on effects of burning at Hole-in-the-Mountain Prairie. Most of the data is from unburned control plots. The N for each sample is shown in parentheses at the top of the curve. Kolmogorov-Smirnov tests of the identity of the two distributions against the one-sided alternative that males are earlier, from top to bottom: $D = 0.736$, $P < 0.005$; $D = 0.789$, $P < 0.005$; $D = 0.514$, $P < 0.01$ (Steel and Torrie 1980).



After eating the chorion, larvae did not ordinarily begin to feed on plant tissue until they had completed shelters. In Petri dishes they crawled beneath grass blade fragments or beneath the filter-paper liners and began making shelters of these materials.

When placed on grass plants shortly after hatching, they quickly crawled down among the culm bases where their small size (about 3 mm long) and the dense tangle of vegetation and litter made nondisruptive observation very difficult. Observed shelters of first instars were small chambers not much larger than the larva, made by fastening various plant materials together with silk. These were at the bases of grass stems, at or below the soil surface.

Within bunchgrass clumps, where larvae most frequently made shelters, the soil surface is less well defined than it is between clumps. However there is an identifiable boundary between an above ground zone of grass stems and the dense, persistent basal material of dead and living stems, with soil usually present in the interstices. The surface within clumps is generally a bit higher than the surrounding soil

surface, up to a few centimeters in larger clumps, but anything clearly below this boundary is effectively below ground. Fire usually leaves the material below this surface unburned.

Shelters were most frequently constructed between closely appressed stems in a clump or between a stem and litter fragments. Sometimes the space formed between a stem and diverging leaf blade just above the ligule was used, but only if this junction was at the soil surface. Natural shelters of second and later instars up through diapause were steeply angled tubular chambers mostly or entirely down in the soil or basal mass of a grass clump. Often there was a tube of silk and grass stems extending the entrance a bit above the surface. Frass was deposited in the lower end of the shelter, and larvae constructed two, possibly three, successively larger shelters by diapause.

At some point after diapause, probably right after the first postdiapause molt, larvae shifted from buried shelters to horizontal ones on the soil surface (although often partially concealed by overhanging stones, basal material of grass clumps, etc). These were made of silk with a covering of soil and litter and were sometimes serpentine affairs several centimeters long. Frass was deposited in a cache in the blind end. Larvae appeared to construct at least two of these shelters before pupating, based on fecal pellets size in the caches.

Pupation was usually in chambers newly constructed for that purpose, although pupation in the last larval shelter sometimes occurred (perhaps owing to confinement). Pupal shelters were similar to those of late instars but only long enough to conceal the pupa, and without an entrance. Pupal shelters were well impregnated with the flocculent material from the ventral glandular patches of the last instar; shelters I completely submerged in water trapped large masses of air around the pupae, which could not be wetted. Larvae also always constructed shelters in rearing containers, making tubes of the grass material provided as food.

In natural settings, most feeding activity took place within shelters, on grass blade segments that larvae cut off and pulled back into them. Only first-instars appeared to feed in more conventional lepidopteran fashion on foliage in situ. I observed only a few harvesting forays of older larvae. These forays may take place mainly at night, as feeding in other *Hesperia* is reported to be nocturnal (MacNeill 1964). The instances I witnessed were at sunset, or in overcast weather. Foraging larvae constructed trails of matted silk similar to those made by other *Hesperia* (MacNeill 1964), but these were flimsy and difficult to find until the last two stages, and even then only evident where they converged at the shelter entrance.

During diapause, shelter entrances were closed with a loose meshwork of silk. I never observed any evidence of cannibalism or other intraspecific

Table 2. Sex ratios in adult skippers emerging in experimental field plots. Data are mostly from unburned control plots except for Experiment IV. Ratios in Experiment IV adults remain almost unchanged if data from burned plots is excluded. *Hesperia ottoe* was not included in Experiments II and III. Heterogeneity among the different experiments is not statistically significant for either species: $G = 5.45$, 4 df, $P = 0.24$ (*H. dacotae*); $G = 2.02$, 2 df, $P = 0.37$ (*H. ottoe*). Sex ratio in the pooled data set is not significantly different from 1:1 for either species: $G = 0.21$, 1 df, $P = 0.65$ (*H. dacotae*); $G = 1.57$, 1 df, $P = 0.21$ (*H. ottoe*).

Experiment	Year	N σ :N ρ	$\frac{N\sigma}{N\sigma+N\rho}$
<i>Hesperia dacotae</i>			
P ^a	1981	5:10	0.333
I	1981	7:9	0.438
II	1982	13:15	0.464
III	1982	29:37	0.439
IV	1983	29:18	0.617
<i>Hesperia ottoe</i>			
P	1981	11:13	0.458
I	1981	5:4	0.556
IV	1983	28:16	0.636

^aExperiment P, not described in text, employed small circular plots like those in Experiments III and IV, but a propane flaming device was used to burn treatment plots.

aggression in *H. dacotae* larvae, even under crowded conditions.

Host plants

Females oviposited on a variety of plants at this site, both grasses and forbs (Table 3), not just on forbs as reported by McCabe (1981) for another population. In field plots used in various burning experiments, larvae fed mostly on the common C₄ grasses, *Andropogon scoparius*, *A. gerardii*, *Sporobolus heterolepis*, and *Bouteloua curtipendula*, and to some extent upon two common (but secondary in terms of biomass) C₃ grasses, *Dichanthelium wilcoxianum* and *Poa pratensis*. One common small sedge, *Carex heliophila*, showed evidence of occasional use. The major native C₃ grasses here were avoided, either altogether (*Koeleria pyramidata*), or partially (*Stipa spartea*). Only postdiapause instars appeared to make much use of *S. spartea*, whose thick, tough leaves probably pose mechanical problems for small larvae. Except for the avoided species, larvae appeared to feed on whatever grasses were close to shelter entrances, usually including more than one species.

Several common grasses of the upland prairie did not occur in these plots, precluding observations on acceptability. These included *Sorghastrum nutans*, *Stipa comata*, *Bouteloua gracilis*, *Bouteloua hirsuta*, and *Muhlenbergia cuspidata*.

Captive larvae in no-choice situations fed readily on the same grasses that were used in field plots and also on a naturalized Eurasian C₃ species, *Bromus inermis*, which did not occur in plots. Early instars did not accept *K. pyramidata* or *S. spartea*, but I did not test older larvae. None of the other grasses or the sedge were offered to captive larvae.

In the host plant study the proportion of larvae surviving was lowest on *K. pyramidata*, next lowest on *S. spartea*, but the relationship between mortality and host species is not statistically significant (Table 4). Offspring of female 2 suffered conspicuously higher mortality than those of other females, possibly because a heavy thunderstorm occurring a few hours after female-2 larvae were put into the enclosures drowned those that had not completed secure shelters. Elimination of these data reduces differences among the grasses (Table 4).

Mean dry weight was lower for larvae surviving to diapause on *K. pyramidata* and *S. spartea*, but within-species variation was high (Figure 3), and the F-ratio for host-species effect is not significant (Table 5). Interaction was included in the model because the P-value of the F-ratio exceeds 0.25 (Bancroft 1968). However, leaving interaction out of the model does not change the result. Strong lack of balance precluded incorporating larval stage as a factor in the model, but fourth-instar weights showed no apparent tendency to be lower than those of fifth instars. Females are larger than males at pupation

Table 3. Host plants used for oviposition by *Hesperia dacotae* and *H. ottoe* at Hole-in-the-Mountain Prairie. Data were collected during a three year mark-release-recapture study.

Host Species	Number of Ovipositions Observed	
	<i>H. dacotae</i>	<i>H. ottoe</i>
Graminoids		
<i>Andropogon scoparius</i>	7	6
<i>Andropogon gerardii</i>	4	3
<i>Bouteloua curtipendula</i>	4	1
<i>Sporobolus heterolepis</i>	2	0
<i>Stipa spartea</i>	2	0
<i>Dichanthelium wilcoxianum</i>	0	1
Total	19	11
Forbs		
13 species (vegetative parts)	15	3
<i>Echinacea augustifolia</i> (capitula)	0	16
Total	15	19

Table 4. *Hesperia dacotae* survival to diapause on six major dry-mesic prairie grasses at Hole-in-the-Mountain Prairie. Newly hatched larvae were confined individually within small enclosures over tufts of each host species growing naturally in the prairie. Ova were obtained from five wild-inseminated females. There were three replicates of each parent-host combination. All surviving larvae were in diapause when removed October 25, following onset of freezing temperatures.

Host Grass	All Larvae ^a		Female 2 Larvae Omitted ^b	
	Alive	Dead	Alive	Dead
<i>Andropogon scoparius</i>	13	2	10	2
<i>Bouteloua curtipendula</i>	11	4	10	2
<i>Sporobolus heterolepis</i>	11	4	10	2
<i>Poa pratensis</i>	10	5	9	3
<i>Stipa spartea</i>	9	6	9	3
<i>Koeleria pyramidata</i>	7	8	6	6

^aG = 6.5474, 5 df, P = 0.256
^bG = 4.9068, 5 df, P = 0.427

and it is possible that the difference is expressed as early as the fourth and fifth stages, but I could not reliably sex larvae this young without dissecting them

Figure 3. Weight at diapause of *Hesperia decotae* larvae reared from hatching on six prairie grasses under field conditions at Hole-in-the-Mountain Prairie (methods described in Table 4). Host-grass abbreviations are: SS, *Stipa spartea*; KP, *Koeleria pyramidata*; BC, *Bouteloua curtipendula*; AS, *Andropogon scoparius*; PP, *Poa pratensis*; SH, *Sporobolus heterolepis*. Larvae were killed after removal from host grasses in late October by freezing to -70°C and oven dried for 90 h at 75°C before weighing. Mean weights of surviving larvae from each female parent (identified by symbol pattern) are plotted, with the mean of the means indicated by dashed line. Heterogeneity among host means is not statistically significant (Table 5). Female 2 is represented by open circles.

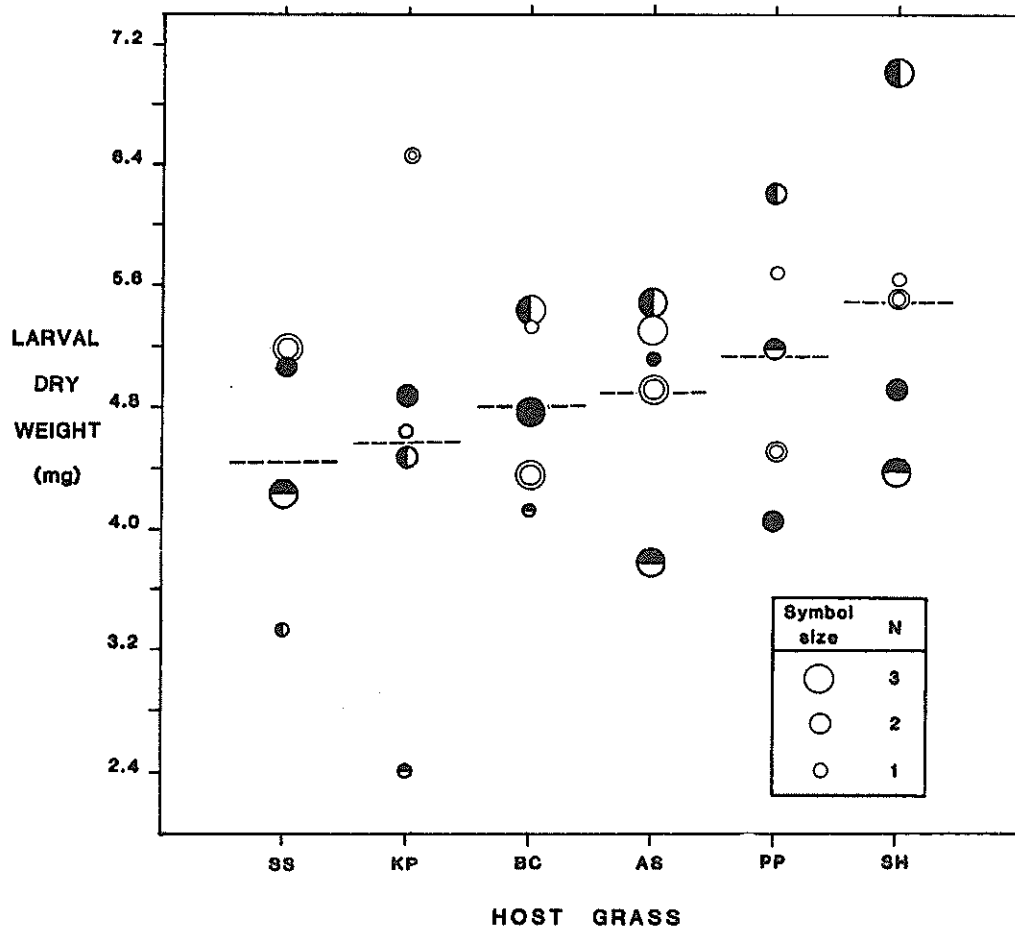


Table 5. Analysis of variance of *Hesperia decotae* larval dry-weights at diapause in field rearings on six grass species. Data summarized in Figure 3.

Source	df	Sum of Squares ^a	Mean Square	F	P
Female Parent	4	16.1053	4.0263	6.01	0.001
Host Species	5	5.7190	1.1438	1.71	0.163
Female X Host	19	20.6976	1.0893	1.63	0.112
Error	31	20.7806	0.6703		

^aSAS® Type IV sums of squares are presented because no offspring of Female 2 survived on one host grass.

in freshly-killed condition, making it impossible to control for the sex of larvae.

The proportion of survivors diapausing as fourth instars was greater on *A. scoparius* than on any other host but the deviation from expectation under the hypothesis of independence is not statistically significant (Table 6).

Mortality factors

Table 6. Larval stage at diapause of *Hesperia dacotae* on six grass species in field rearings at Hole-in-the-Mountain Prairie (methods described in Table 4). Chi-square = 9.213, P = 0.10.

Host Grass	Number of Larvae	
	Fourth Stage	Fifth Stage
<i>Andropogon scoparius</i>	4	9
<i>Poa pratensis</i>	2	7
<i>Bouteloua curtipendula</i>	1	10
<i>Sporobolus heterolepis</i>	0	11
<i>Stipa spartea</i>	0	9
<i>Koeleria pyramidata</i>	0	7

Only a few natural enemies were incidentally noted. A small parasitoid, *Ooencyrtus* sp. (Hymenoptera: Encyrtidae) emerged from a couple of field-collected ova. I found a hemerobiid larva (Neuroptera) feeding on an early-instar *Hesperia* (probably *H. dacotae*). On a few occasions *Myrmica americana* Weber (Hymenoptera: Formicidae) seized wandering hatchling larvae just after I had placed them on grasses.

Disease was infrequent in captive rearings despite high humidities in the rearing containers and only moderate attention to sanitation. I did not determine the pathogens responsible. The cause of death in larvae I tried to rear continuously through to maturity appeared to be dehydration or starvation rather than disease. The cadavers of larvae refrigerated for diapause were covered with fungal mycelia when removed, but I do not know if the fungus was pathogenic or saprophytic.

In both Experiment III and Experiment IV, mortality from hatch to adult emergence was about 50% in control plots. I never found remains in shelters; larvae killed by fire in burned plots frequently remained intact on the surface until the final plot search, but perhaps denaturing by heat and drier conditions on the surface than in shelters inhibited decay. In the host plant study about 30% of the

larvae disappeared by diapause. Two dead fourth or fifth instars shrouded in fungal mycelia were present in shelters, but again the fungus could have been saprophytic. No other remains were found, and even shelter remnants were seldom found, suggesting that most losses occurred shortly after hatchlings were put into the enclosures.

Hesperia ottoa

Development

The egg of this species has also not been previously described. It is nearly identical to that of *H. dacotae* in shape and surface texture, but about 30% larger (basal diameter 1.31 mm, height 1 mm, N = 3). It is gleaming white when newly laid, sometimes with a greenish tinge, turning duller white to creamy yellow after a couple of days.

Development from egg to adult was very similar to that observed in *H. dacotae*. Stage-length data are summarized in Table 1. I did not determine the stage of any diapausing larvae that had developed under natural conditions. Feeding and growth in rearing containers usually slowed noticeably in the fourth stage as in *H. dacotae*. The small sample of prediapause fifth-instar head capsules I obtained suggests that as in *H. dacotae* there is little increase in size at this molt.

Most larvae were transferred to grass clumps for outdoor wintering while still in the fourth stage, between one and 35 days after molting, and were no longer monitored. Four did molt to the fifth stage while still under observation, two after two weeks, and two after four to five weeks (the latter were held in conditions more like those experienced by larvae in the field than the former). These were also subsequently transferred to overwintering arrangements after from one to 22 days. All appeared to have nearly ceased feeding.

I did not obtain a complete record of molts from any *H. ottoa* larva. Most of the few larvae I removed early from overwintering shelters completed two stages before pupating, but one completed three. The prediapause history of none of these larvae was known.

Of the 36 larvae of this species removed from Experiment IV field plots that pupated, 13 were even numbered last instars and 23 odd numbered ones, as determined by ring-pore configuration. It is most likely that these were sixth and seventh instars, as in *H. dacotae*. The proportions of the two instars differed significantly between the sexes (males: 12 even, 10 odd; females: 1 even, 13 odd; Chi-square = 8.33, P = 0.004). There was no evident difference in head capsule widths of the odd numbered versus the even numbered final instars in a preserved sample of three larvae of each type.

Protandry in adult emergence in field plots was

similar to that observed in *H. dacotae*, but emergence of both sexes was considerably more protracted (Figure 2). These features were also observed in the wild population. The proportion of males at adult emergence in the three field-plot-reared populations ranged from 0.46 to 0.64 but none is significantly inconsistent with a 1:1 ratio (Table 2).

Habits

Darkening of the summit of the egg by the developing larval head occurred as in *H. dacotae*. The sequence of events in hatching was identical, including consumption of all of the chorion but the base, with shelter construction preceding further feeding. However, natural early-instar larval shelters (in living grass plants) were very different from those of *H. dacotae*.

These shelters were made by fastening two or more blades of grass together with silk into a narrow tube several centimeters above the soil surface. The most commonly observed type incorporated two or three blades from a vegetative shoot of *Andropogon scoparius*, pulled together from their points of divergence from the stem, with the distal portions of the blades free.

Newly hatched larvae crawled about in the grasses until they found a naturally occurring structure that could easily be modified into a shelter. Most hatching larvae I observed settled into the space at the juncture of a sharply creased, ascending blade and the culm of *A. scoparius*. They exhibited no tendency to descend to the bases of grass stems.

Larvae fed on the free distal portions of the blades forming the shelter and filled the lower end with frass. The shelter was abandoned when these two processes converged, leaving a frass filled tube usually 4–6 cm long, and a new one begun. Larvae constructed two, possibly three, leaf-blade shelters before moving in late summer to buried shelters identical to those made by *H. dacotae*, in which they eventually entered diapause.

Postdiapause larval and pupal shelters were indistinguishable from those of *H. dacotae* in construction, although the pupal chambers were not waterproof, as *H. ottoe* does not produce a hydrofuge secretion in the last stage before pupation. The number of successive postdiapause shelters was not determined, but fecal pellet sizes indicated more than one.

The move from leaf blade to buried shelters appeared to occur principally during the fourth stadium, but third stadium moves may also have been frequent. The cast head capsules recovered from leaf blade shelters came from first through third instars, based on comparison with capsules from known instars, indicating that larvae commonly completed the third molt in them. The two capsules

recovered from empty buried shelters (prediapause) were probably from third instars, based on width comparisons. One third instar immediately constructed a buried shelter when transferred to a grass clump from a rearing container (this was the only such release monitored).

Monitoring of larval activity in the field in 1978 indicated that the move to buried shelters took place in late August and early September. I found the first buried shelter during the August 15 search, several others on August 26, and many on September 10. On the last date I found only two occupied leaf blade shelters, and none on the last search, September 25.

Feeding behavior of larvae in natural circumstances was similar to that of *H. dacotae* larvae, although I observed more exposed feeding on plant tissue in situ during the leaf-shelter period, and more diurnal activity. Behavior in rearing containers was indistinguishable from that of *H. dacotae*, including the absence of cannibalism or other forms of aggression.

Host plants

Observed ovipositions were distributed among a variety of grasses and forbs (Table 3). Over half were on capitula of *Echinacea angustifolia* (erroneously reported in Dana 1981 as *E. pallida*). After hatching, larvae dropped off capitula, which are elevated above the grass canopy, rather than crawling down (Dana 1981). Ovipositions on other forbs were on leaves within the grass canopy.

Early instars in captive, no-choice situations accepted and refused the same grasses as *H. dacotae*, and utilization of grasses in experimental field plots was also qualitatively similar to that of *H. dacotae*. Leaf blade shelters found around *E. angustifolia* plants in the 1978 searches were in *Andropogon scoparius* (62), *Bouteloua curtipendula* (27), *Andropogon gerardii* (14), and *Dichanthelium wilcoxianum* (11).

Sometimes shelters incorporated more than one grass species, and feeding on nearby grasses different from the shelter species was frequent. What appeared to be the successive shelters of a larva were often in different species. Buried shelters found in these searches were associated with *A. scoparius* (12), *B. curtipendula* (5), and *Bouteloua hirsuta* (4), and feeding on other species near the shelter entrance was common.

Mortality factors

A small percentage of ova collected from purple coneflower capitula was parasitized. The parasitoid in most cases was a *Trichogramma* sp. (Hymenoptera: Trichogrammatidae), with a small unidentified scelionid wasp (Hymenoptera:

Scelionidae) emerging in a few cases. Ova on capitula were also destroyed by a predator that cleanly evacuated the contents through a minute puncture in the chorion. I observed predation by damsel bugs (Hemiptera: Nabidae) on ova of *Hesperia leonardus pawnee* Dodge that left identical remains.

I found one probably third-stage larva in a leaf blade shelter that had been killed by a parasitoid. One of the three cocoons in the shelter with the carcass yielded an adult wasp, probably a species of *Apanteles* (Hymenoptera: Braconidae). The larva of a soft-winged flower beetle (Coleoptera: Melyridae) was found feeding on a second instar in a leaf blade shelter. The incidence of disease in captive rearings was comparable with that in *H. dacotae*. Again, I did not identify the pathogens responsible. Mortality in burn-experiment control plots was 50–60%, about the same as for *H. dacotae* in the same type of plot.

ADULTS

General Biology and Behavior

Hesperia dacotae

Feeding. Both males and females visited flowers regularly throughout the day. Brief as well as more prolonged feeding bouts were interspersed with other major activities (mate-seeking for males, oviposition for females) and occurred in the same habitat as the other activities. I recorded visits to flowers of 25 species (Table 7), but four of these (*E. angustifolia*, *A. adsurgens*, *V. stricta*, and *O. lambertii*) accounted for more than 90% of the visits. The purple coneflower, *Echinacea angustifolia*, was overwhelmingly the most important nectar source for both sexes.

I never saw *H. dacotae* visit flowers of several common species, notably *Dalea purpurea*, *D. candida* var. *oligophylla*, *Amorpha canescens*, *Symphoricarpos occidentalis*, *Asclepias syriaca*, and *Ratibida columnifera*. Despite the abundant floral resource in lowland habitats, I never encountered adults in these areas, nor did I ever see males imbibing from the wet soils regularly visited by males of other similar skipper species (muddy stockpond margins, rain-soaked gravel road along the south boundary of the site).

Courtship and mating. Mate seeking dominated the daily flight period of male skippers. Most mate seeking was of the “waiting” or “perching” type (Magnus 1963, Scott 1974b), but some behavior suggestive of a “search” strategy was also observed. When perching, males sat nearly motionless but in a flight-ready, vigilant-looking posture. They were highly reactive to insects flying nearby and darted in pursuit of a wide variety belonging to several orders. After pursuits they frequently returned to the same or a nearby perch, often after a brief episode of low,

Table 7. Flower visitation by *Hesperia dacotae* and *Hesperia ottoe* at Hole-in-the-Mountain Prairie during a three year mark-release-recapture study. An adult was scored as nectaring if it extended its proboscis and probed within flowers. Abbreviations are: V = very common (many hundreds, not enumerated); C = Common (about 35); F = frequent (11–25); O = occasional (5–10); R = rare (2–4); S = single. A single visit each was recorded to: *Asclepias verticillata*, *Cirsium arvense*, *Linum rigidum*, *Phlox pilosa*, *Senecio pauperculus*, *Tragopogon dubius* (*H. dacotae* males); *Achillea millefolium*, *Carduus nutans*, *Erysimum inconspicuum* (*H. dacotae* females); *Dalea candida* (*H. ottoe* female).

Flower Species	Frequency of use			
	<i>H. dacotae</i>		<i>H. ottoe</i>	
	Males	Females	Males	Females
<i>Echinacea angustifolia</i>	V	V	V	V
<i>Verbena stricta</i>	O	F	F	O
<i>Astragalus adsurgens</i>	C	F	S	–
<i>Cirsium flodmanii</i>	–	S	O	O
<i>Oxytropis lambertii</i>	F	R	S	–
<i>Asclepias viridiflora</i>	S	–	O	R
<i>Calylophus serrulatus</i>	R	R	–	–
<i>Lactuca oblongifolia</i>	S	–	R	R
<i>Erigeron strigosus</i>	R	R	–	–
<i>Trifolium hybridum</i>	R	R	–	–
<i>Liatris punctata</i>	–	–	R	R
<i>Agoseris glauca</i>	R	–	–	–
<i>Monarda fistulosa</i>	–	–	R	–
<i>Mellilotus officinalis</i>	–	R	–	–
<i>Dalea purpurea</i>	–	–	S	S

rapid flight back and forth over the area.

I did not record how long individuals remained at particular perching spots, but on the several occasions I monitored activity in approximately 100-m² areas, when several males were usually perching within them, the spots occupied by males moved around and the number of males present fluctuated during the 20-minute periods. Under most conditions perches were on tips of vegetation slightly above the grass canopy (0.3–0.5 m), but lower perches were used under cooler, windy conditions. Capitula of *E. angustifolia* were the most frequently used perching platforms.

The apparent search behavior I occasionally observed consisted of a relatively slow “fluttering” flight weaving along just above the grasses, similar to the behavior of males of skippers that obtain mating opportunities by searching for receptive

females waiting in the vegetation. I never saw an encounter between a male exhibiting this behavior and a female.

Male skippers were the objects of most pursuits by perching males that I observed (excluding pursuits of non-skipper insects). The majority of these were conspecifics, but males of other perching species were almost as frequently involved.

Pursuits of male skippers quickly developed into aerial engagements in which the two insects whirled about each other. The engaged males tended to gradually ascend 2–3 m, but lateral displacements were more pronounced. One or more additional males frequently became involved when the original pair passed over them. Participants would abruptly break away in high velocity returns to the perching area, but re-engagements before landing were common. I was unable to determine if there are any consistent differences between conspecific engagements and those involving participants of different species. Observation was greatly handicapped by the small size and cryptic coloration of the insects, and their very fast flight.

Pursuits of conspecific females produced a fairly stereotyped sequence. On being overtaken, females descended quickly into the vegetation without any attempt at evasion. Males appeared to fly slightly above and ahead of females during at least part of the descent phase, but I could not clearly resolve the details of this typically brief, less than three second episode. The male alighted nearly simultaneously with the female and quickly crawled alongside her, curving his abdomen around with claspers spread in an effort to initiate copulation.

Males did not engage in any obvious post-alighting courtship behaviors; when observed pursuits did end with copulation this was effected within two to three seconds after landing. In unsuccessful courtships, the majority observed, the female held her abdomen up between closed wings and periodically jerked the wings forward with enough force to send a tremor through the vegetation on which the insects were resting (the wings did not appear to open at all in these jerks). This is clearly a rejection signal by unreceptive females; similar rejection signals have been reported for other skippers, including *Hesperia pahaska* (Leussler) (Scott 1973a, Shapiro 1975).

Sometimes males departed quickly after eliciting a rejection signal, but often they were more persistent, clambering after the female and hindering her efforts to climb up to an unobstructed point for taking flight. If a female succeeded in flying off before the male had departed, this usually triggered another pursuit by the male and a repeat of the whole process. The vigor of a male's efforts and his persistence were inversely related to the age of the female. A similar relationship was observed between the intensity of courtship and age of the target when the latter was a heterospecific female, and even when it was another male, suggesting that the stimulus is probably short-

lived odors associated with emergence rather than a species specific female pheromone.

Pursuit of females of other species produced similar sequences, including descent by the female, but females always rejected male copulatory advances. Typically, males did not persist in courtship efforts as long as with conspecific females, but female age was also a factor in these cases. One *H. dacotae* male continued to attempt copulation with an apparently recently-emerged female *Polites themistocles* (Latreille) in the net after both were captured during courtship.

Flushed noctuid moths were often pursued. They reacted by suddenly plunging to rest in the grass. Though the pursuing male landed with the moth on a number of occasions, it always flew off quickly without making any further courtship overtures.

A few times I observed three to five *H. dacotae* males flying along together just above and among the grass stems in a tumbling fashion. McCabe (1981) reported a similar phenomenon, which he described as involving pursuit of a "submissive" male. The pursued males may actually have been general. The weak flight of a general male resembles the descent flight of pursued females, and if there is an odor associated with emergence this would provide an additional stimulus.

In the field cages, flight behavior by a female usually initiated male pursuit and courtship. Sometimes mere proximity to a female on the cage netting would stimulate copulatory advances. Typically, the female responded with rejection signals while the male crawled after and around her on the netting, sometimes spasmodically fluttering his wings. When females crawled about upside down on the top of the cage, males sometimes hovered closely below. Most copulations followed almost immediately after an in-flight interaction, but occasionally mating occurred suddenly during a prolonged bout of courtship activity on the cage netting. The frequency of unsuccessful aerial pursuits in the cages, which contrasted with the almost invariable acceptance of the first pursuing male by virgin females released into the field, may have been due to insufficient space in the small cages for the normal in-flight courtship events.

In cages, males pursued other males, especially after stimulation by interaction with a female, sometimes abandoning courtship of a female to fly after another male. Copulatory advances frequently followed landing in these homosexual pursuits, although they were briefer than when a female was involved. Courted males gave rejection signals similar to those of females, though weaker. Virgin *H. ottoe* females were also pursued and courted vigorously and persistently.

Males engaged in mate seeking behavior throughout most of the daily flight period. Figure 4 shows the hourly distribution of pursuits of conspecific females

observed during MRR sampling. I did not record all pursuit activity of perching males, but the temporal pattern was similar.

During longer bouts of nectaring, males were unresponsive to the nearby flight activities of other skippers; these bouts were scattered throughout the day. The uncommon search mode of mate seeking and the tumbling groups of males were both seen only in the mornings, up to about midday. Copulations were observed from midmorning to early afternoon (Figure 4). All females were recently emerged (no visible wing wear), while male age varied.

Perch/pursuit activity was more common in the mid

to upper slope and summit zones than lower on slopes. This is reflected in the relative numbers of observed pursuits of conspecific females in the different zones (Figure 5). Although sampling time in the lower zone was less than in the other two, the difference was not enough to account for the difference in numbers of observed pursuits. The more extensive level areas back from the rim of slopes in units B and C were infrequently occupied by perching males. Search behavior did not appear to be associated with topographic prominences. Three of the observed copulations occurred in the upper slope zone. The fourth pair was encountered in copula about midslope, but the pair could have flown to this point during courtship from an upper slope encounter point.

Figure 4. Hourly distribution of male skipper courtship pursuits of females at Hole-in-the-Mountain Prairie. Pursuits ending in copulation are shaded. Data are from three year MRR study and 1978 transect observation. Intensity of observation was approximately equal in all intervals except the last two, in which it was lower by about one-fourth. The temporal distribution of total pursuits does not differ between the two species ($X^2 = 4.744, P = 0.78$, first two and last two intervals each combined).

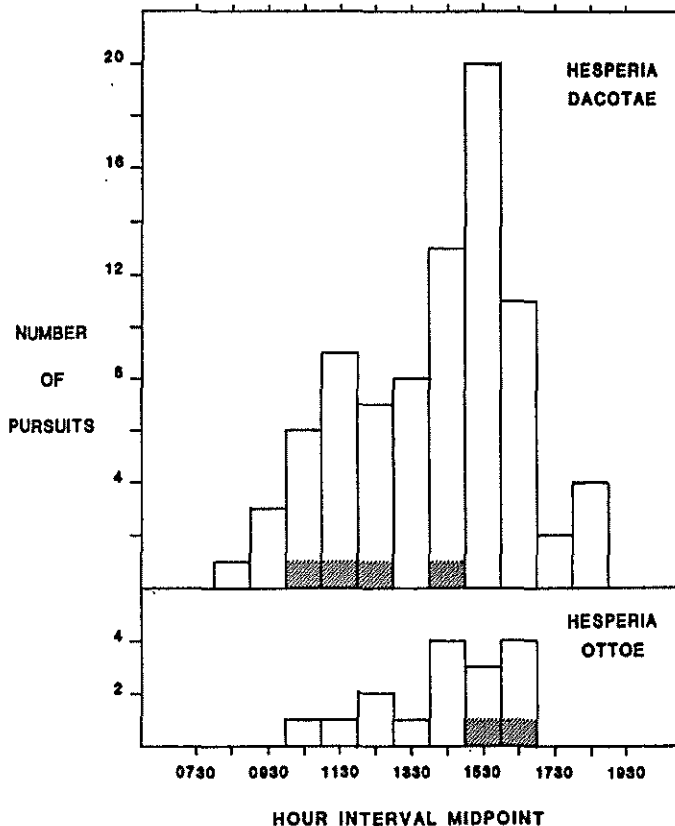
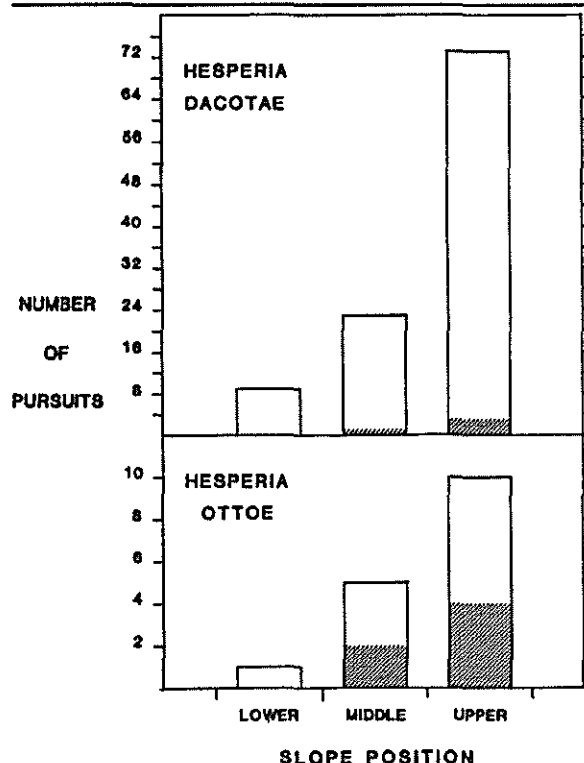


Figure 5. Topographic distribution of male skipper courtship pursuits of females at Hole-in-the-Mountain Prairie. Pursuits ending in copulation shaded. Source of data as in Figure 4. Numbers in upper slope category are adjusted to put them on an equal-area basis with the other two categories (actual count X 1.44, rounded to nearest integer). Intensity of observation was slightly less in the lower slope position than in the others, but the difference was not quantified. There is no difference between the two species in the distribution of total pursuits among slope positions ($X^2 = 0.340, P = 0.84$). Note different scale for the two species.



Copulating pairs remained quiescent in the vegetation; if disturbed, the female flew, carrying the male. One copulation whose beginning and end were witnessed (in a field cage) lasted 45 minutes. Other copulations lasted at least 45 but not more than 75 minutes.

Females mated readily on the same day they emerged. One reared male mated in a field cage on the day of its emergence, while two others did not respond to virgin females on the day of emergence but did mate when tested again on the third day of adult life.

Thirty-one females were dissected over three years. Twenty-two had one spermatophore, and nine had two. I recorded the wing-wear index of age for 19 of these, and in this group there was no association between age and number of spermatophores. The ratio of one to two spermatophores in young females (wing-wear index ≤ 3) was 4:2, and in the older group (index > 3) it was 9:4.

Where only one spermatophore was present it was typically globular, abruptly constricted to a slender neck, and with a broad, low protuberance cephalad. The main part was pearlescent white to yellowish-white, with the protuberance a brighter, grainier white. The flattened to sometimes slightly concave underside was more transparent. The collum extended into the ductus bursae, terminating in a large, lumpy plug at the mouth of the ductus, with a slender, transparent "tail" extending well out into the ostium. A few variants were seen, including two longitudinally compressed, discoid-shaped examples, and one that was rather small and round. Except for these variants, the spermatophores appeared to fill the corpus bursae to its full extent. All were firm and unyielding when pressed (freshly killed material in 0.05% saline).

I found no evidence that spermatophores change in size, shape, color, or consistency with age, where minimum age was determined by the length of the period of female captivity. One, from a female held 12 days in an oviposition cage after capture, was thus at least this old when examined. Moreover, the appearance of spermatophores did not vary with the age, as determined by wing-wear, of females dissected right after capture.

Spermatophore shape and size were more variable in individuals that had two. In four females the two were side by side and flattened closely against each other. In two of these cases, the spermatophores were subequal in size, and in the other two, one was approximately normal in volume while the other was quite small. In the other five doubly mated females one spermatophore was above the other in the corpus bursae, with the upper one always approximately normal in size and shape and the lower smaller to much smaller and highly irregular in shape. The smaller appeared to have been formed against the larger, with little deformation of the latter.

When two spermatophores were present, their total volume appeared to be about the same as or slightly larger than that of normal solitary ones. There were no color or consistency differences suggestive of differing ages. Although I could not dissect apart the necks of these paired spermatophores, there were in all but one case clearly two "tails" extending out of the genital plug confirming separate copulations.

Oviposition behavior. Eggs were affixed singly, usually to the underside of leaves, sometimes to the upper surface of erect grass blades. Most of those found were within 1–4 cm of the soil surface. Some on forbs were higher, but all were within the grass stratum.

Females about to oviposit flew in a distinctive slow, hesitant manner just above the grasses. They alighted most frequently on small bare spots of soil or on stones, and crawled either immediately or after a period of basking into the grasses. Once in the vegetation they usually clambered about, curving the abdomen beneath and forward to explore surfaces with the tip several times before ovipositing. Sometimes oviposition was almost immediate, and sometimes after prolonged efforts the female climbed up and flew on to a new spot without ovipositing.

When the female found an acceptable substrate, she remained motionless 2–3 seconds while extruding and affixing the egg. Typically the female then climbed up and flew, either rapidly away from the area (most cases), or a short distance to a flower for nectaring or some resting spot for basking. However, bouts of a few ovipositions in quick succession were observed. In a few of these cases, the female resumed a search flight, landing and ovipositing again nearby. Twice I observed a female crawl a few centimeters away from the first egg and oviposit again before flying; in one of these cases the female flew only a short distance after the first pair of ovipositions and repeated the sequence of two ovipositions before leaving the area.

Female behavior did not suggest any effort to determine chemical properties of plants during oviposition activity. Contact chemoreceptors on antennae or tarsi are commonly employed by butterflies for this purpose, and females often tap or drum these appendages on plants to determine their suitability as larval hosts (Chew and Robbins 1984). I saw no behaviors of this kind in *H. dacotae*. Moreover, females made no effort, as far as I could determine, to place the egg on the same plants they were clasping and in fact frequently oviposited on a different one. Reliable information about the actual substrate could be provided by chemoreceptors on the papillae anales, as these necessarily contact it during oviposition. Some Lepidoptera have these (Chew and Robbins 1984), but nothing is known about their occurrence in the HesperIIDae.

Oviposition occurred throughout most of the daily activity period, possibly declining in frequency in

late afternoon (Figure 6). Females may have favored middle and upper slope zones for oviposition (Figure 7), but the smaller amount of observation time in the lower zone could account for the lower number of ovipositions observed there.

Ovarian Dynamics and Fecundity. I did not kill and dissect any females right after emergence, but one killed 8–10 hours later had one fully formed ovum in the pedicel of each ovariole, and another in each above the sphincter. Ovarioles were filled with a long train of gradually enlarging follicles terminating at the lower end with a short sequence of rapidly enlarging ones.

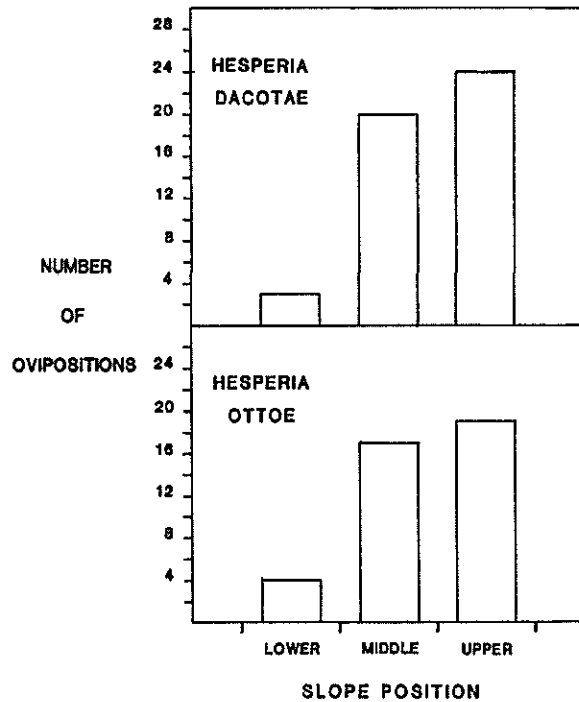
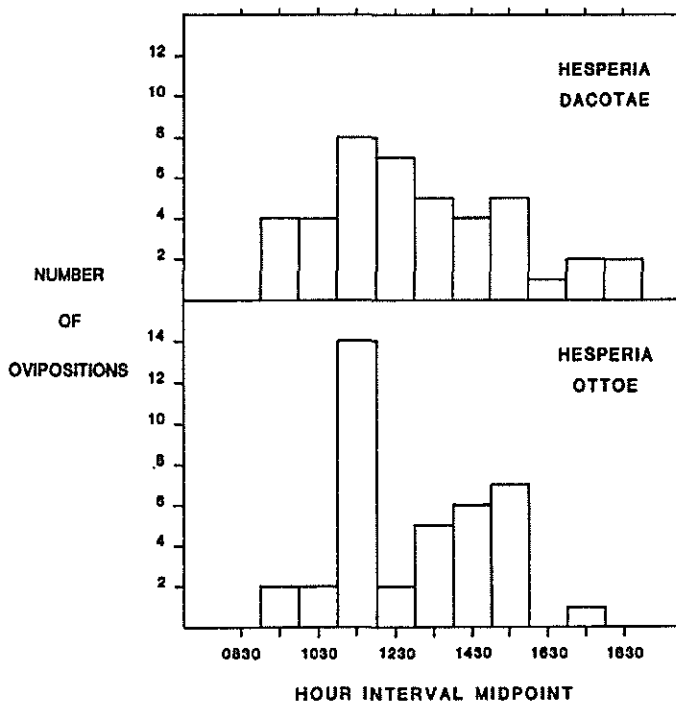
Ova are apparently released into the pedicel shortly after completion of chorionation and disappearance of the follicular epithelium. There is no buildup of mature ova in the ovarioles as reported for a pierid butterfly, *Colias eurytheme* Boisduval (Stern and Smith 1960). I never found more than one fully developed ovum above the sphincter in an ovariole. This was true even in a reared virgin female held for

nearly two weeks after emergence (refrigerated the final week), during which time it laid no eggs. This female had 32 ova in pedicels and lateral and common oviducts, a much smaller number than would have been produced by a mated, ovipositing female during the same period, suggesting that development rate is responsive to mating status and/or backlog of unlaid eggs in the oviducts (unmated females oviposited very reluctantly). I found no evidence of resorption of oocytes.

Females may be capable of beginning oviposition the day they emerge. Although I did not confine any captive-mated females the day they emerged and mated, all confined in oviposition cages the next day immediately began laying eggs. Egg production began at the maximum rate, gradually decreasing over the female's lifetime. Three substantially complete records of lifetime daily production followed this pattern (Figure 8A), although one female with gut abnormalities that probably were responsible for its shortened life gave a steeper decline than the others. Daily production was 20–30

Figure 6. Hourly distribution of observed oviposition behavior (curving of abdomen, probing with tip in vegetation) of skippers at Hole-in-the-Mountain Prairie (an ovum was found in about 80 percent of the cases). Data from three year MRR study and 1978 transect observation. Intensity of observation as in Figure 4. The difference between the two species is not statistically significant ($X^2 = 9.049$, $P = 0.25$, last three intervals combined).

Figure 7. Topographic distribution of observed oviposition behavior of skippers at Hole-in-the-Mountain Prairie. Source of data as in Figure 6. Upper slope values adjusted to an equal-area basis as in Figure 5. Intensity of observation less in lower slope position as noted also in Figure 5. The difference between the two species is not statistically significant ($X^2 = 0.407$, $P = 0.82$).



eggs the first couple of days, declining almost linearly to very small numbers per day towards the end of the second week. The same data plotted as cumulative percentages (Figure 8B) show that in

two normal females about 50% of the total output occurred in the first week, and about 90% in two weeks.

Females can live long enough to mature their entire complement of oocytes. Several were dissected in which the distal portion of all ovarioles was empty, with only a short train of developing follicles remaining in the lower part. These females included a few very worn, field-caught individuals, as well as ones held in oviposition cages.

Potential fecundity is probably between 180 and 250 eggs. The maximum lifetime production obtained was 200 eggs, from a field-caught, wild-inseminated female held for 19 days in a small oviposition cage in the field. This female was confined on the first, or at most second, day of adult life, as inferred from the absence of wing wear at capture. Unfortunately, it disappeared from the cage during the 19th day so I do not know whether it had exhausted its egg supply.

Two reared, captive-mated females caged in the same way produced, respectively, 154 eggs in 17 days, with about 35 oocytes remaining when killed, and 110 eggs in 10 days, with 116 remaining oocytes. The reared, virgin female killed 8–10 hours after emergence contained 240 discriminable developing oocytes in addition to 8 fully formed ova. A field-caught virgin had at least 180 oocytes, including ripe eggs.

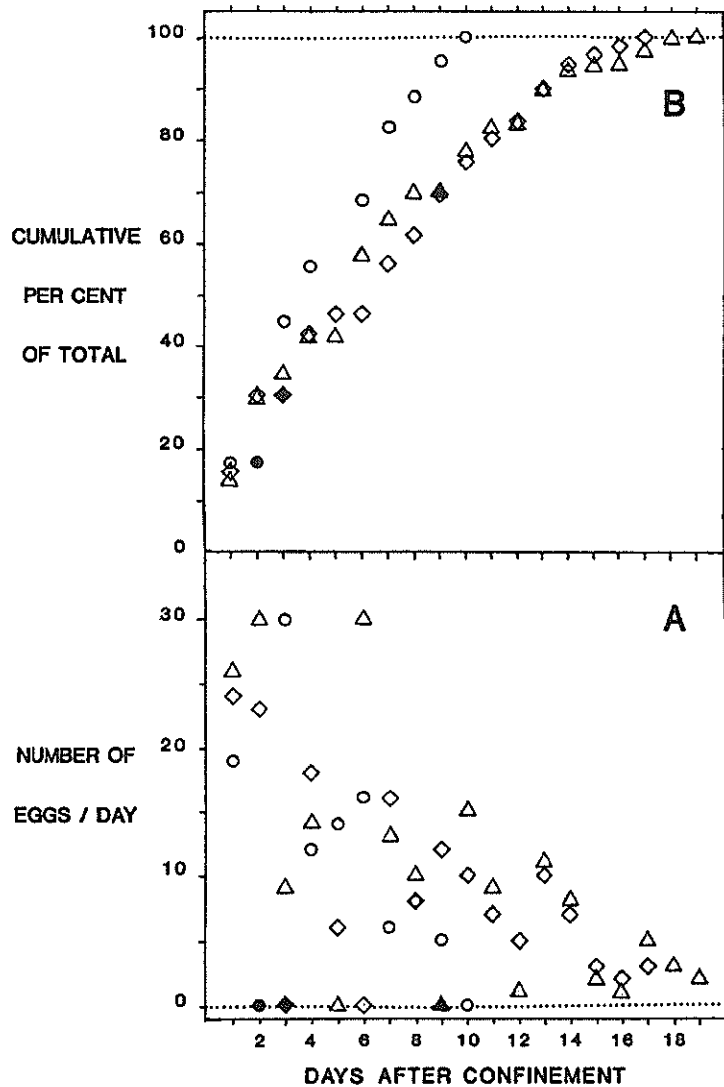
Fat body, as visually estimated in freshly killed individuals dissected in 0.05% saline, was nearly depleted in females nearing the end of egg production, both in very worn, field-caught individuals as well as those that had been held in cages. There appeared to be a slight decrease in egg size with age in caged females, but I did not weigh eggs to confirm this.

Shape and chorion-surface abnormalities often appeared after a female had been caged several days, but these may have been somehow the result of caging rather than female age as I did not find these abnormalities in eggs laid by newly captured and confined old females. I made no careful study of hatching rate as a function of female age, but no obvious decline occurred.

Mortality factors. I found four males and three females that had been captured by large, white crab spiders (Araneida: Thomisidae) on purple coneflower capitula. All six of the spiders I collected proved to be *Misumenops carletonicus* Dendale and Fedner. A dead female was found beneath an *Astragalus* inflorescence occupied by an unidentified white crab spider. These spiders (probably more than one species) were common on coneflower capitula as well as on other important nectar sources for this skipper.

Ambush bugs, *Phymata* sp. or spp. (Hemiptera: Phymatidae) were also common on the same

Figure 8. Age specific fecundity in three *Hesperia dacotae* females confined over prairie grasses in the field. Cut flowers, renewed daily, were provided for nectaring, and supplemental drinking water was supplied by spray-misting the cage and vegetation several times daily. Female (Δ) was field caught when recently emerged (little wing wear); the other two were reared and captive mated. Female (\circ) had a gut malformation that may have interfered with nutrition and caused its death after only 10 days. A: Absolute daily egg production (eggs removed each day at dusk). A severely stormy day when females were removed from cages for protection is indicated by filled symbols. B: Same data as cumulative percentage of total output.



flowers, and I found two male skippers taken by them on coneflower capitula. I captured a robber fly, *Promachus fitchii* O.S. (Diptera: Asilidae), with a male it had taken prey, and I observed captures by unidentified large robber flies of a female *H. dacotae* and a female of a very similar skipper, *Polites mystic* (W. H. Edwards). Large robber flies (belonging to at least three species) were common throughout the flight period.

All the captured butterflies were moderately to quite worn. I saw many unsuccessful attacks by both crab spiders and robber flies on young, unworn skippers.

I occasionally observed injured skippers that appeared from the severity of injury to have been victims of vertebrate attack. Three of the swallows that foraged in large numbers over the prairie during the study, bank (*Riparia riparia* (L.)), barn (*Hirundo rustica* L.), and roughwinged (*Stelgidopteryx ruficollis* (Vieillot)), are known to take adult Lepidoptera and other insects in the size class of the skippers (Bent 1942). Eastern kingbirds (*Tyrannus tyrannus* (L.)) also hunted in the upland prairie. I observed one capture a *Colias* butterfly (Pieridae), but I could not determine if they attempted to capture skippers.

Lederhouse et al. (1987) suggest that the primary cause of adult mortality for many butterflies may be predation on roosting individuals. The western meadowlark (*Sturnella neglecta* (Audubon)) and other insectivorous birds that forage mainly on the ground may be able to take roosting skippers early or late in the day or during cool, cloudy conditions. Small mammals may also take roosting skippers, although mainly at night when most forage. I found no evidence that either species of *Hesperia* roosts in taller vegetation where it would be less accessible to these predators.

Hesperia ottoe

Feeding. Flower visiting activity was similar in spatial and temporal aspects to that in *H. dacotae*, although males were observed on a few occasions visiting flowers in lowland areas. I recorded visits to eight species, with three accounting for most (Table 7). *Echinacea angustifolia* was also the predominant nectar source for both sexes of this species.

Males commonly visited the muddy margins of the two stockponds in the tributary valley, and I occasionally saw them on the gravel road along the south boundary after rains. One or two males were usually present on the stockpond margins at any time during the day. These were invariably young, with little or no evident wing wear.

Courtship and mating. Mate seeking and courtship behaviors resembled those of *H. dacotae* in most respects. Perching dominated male mate seeking activity, but what seemed clearly to be a form of

search was observed with some frequency. The perching and pursuit behaviors were similar to those of *H. dacotae*, including the use of purple coneflower capitula as the major perching platform. Pursuits often took males greater distances from their perches, which may have contributed to an apparently greater tendency for *H. ottoe* males not to return to the perch site. The rapid forays over the perch area when returning were more common and prolonged than in *H. dacotae*.

In the mate seeking type of search, males flew rapidly from coneflower to coneflower, making brief "bobbing" inspections around each without landing. Several encounters with individuals of the skipper *Oarisma poweshiek* (Parker) nectaring on capitula resulted in longer inspections than usual.

I observed only one encounter between a searching male and a nectaring conspecific female. The female flew as soon as the male landed beside her, initiating a standard courtship sequence (unsuccessful). On a few occasions I observed solitary males in a low, slow search-type flight similar to that seen in *H. dacotae* males, and once I saw two males pursuing each other rather slowly just above the grasses, with occasional interruptions for basking.

Aerial engagements between perching males were similar in general features to *H. dacotae* engagements, but they were more wide-ranging and frequently rose to considerable heights. Interactions with males of other skipper species, which outnumbered those with conspecifics, were briefer and remained closer to the ground. Encounters between males searching coneflower capitula resulted in aerial engagements similar to those initiated from perches.

I observed a behavior in males of this species that had no obvious counterpart in *H. dacotae*. Single individuals often "spontaneously" flew up at a steep angle to what seemed like a considerable height (5 m or more) and began a kind of skipping or "dancing" flight back and forth in a limited area. This sometimes continued for many seconds, once for nearly two minutes. Typically, one or more other males rose rapidly from perches below and entered into a very high velocity engagement that I could not visually follow.

The behavior of pursued females was indistinguishable from that of *H. dacotae*, and the courtship interactions were similar, including the wing-jerking rejection signal. In all courtships I witnessed that resulted in copulation, pairing occurred almost immediately after landing. All observed matings involved unworn, probably recently emerged females. The behavior of copulating pairs was identical to that of *H. dacotae* pairs. I did not determine the duration of copulation.

Males commonly pursued and courted females of other skipper species, most frequently *H. dacotae*.

Again, the vigor and duration of the male's efforts were dependent upon the age of the female. A marked, recently emerged virgin *H. dacotae* female released in the field was immediately pursued by a male of *H. ottoe*, which courted persistently, pursuing the female each time she flew away. I lost sight of the pair in one of these flights, but rediscovered them about a half hour later, the male still courting. I inadvertently terminated the courtship by capturing the pair before realizing its identity.

I was unable to observe courtship in the flight cages as males spent all their time flying against the netting or agitatedly crawling around on it and did not react to females.

Perching mate seeking behavior occurred throughout the daily flight period, as represented by the observed pursuits of conspecific females (Figure 4), again only a small fraction of the perching behavior observed. Searching was observed from late morning to late afternoon. Copulating pairs were encountered throughout the day (Figure 4).

Males of this species also favored upper slopes and

summits for perch/pursuit activity; the distribution of observed pursuits of conspecific females in Figure 5 is representative. The more extensive level upland areas were as rarely used by *H. ottoe* as by *H. dacotae*. Searching males ranged widely across the habitat, wherever purple coneflowers occurred. Copulations were observed in both upper and middle slope zones.

I did not dissect any mated females of this species to determine mating frequency.

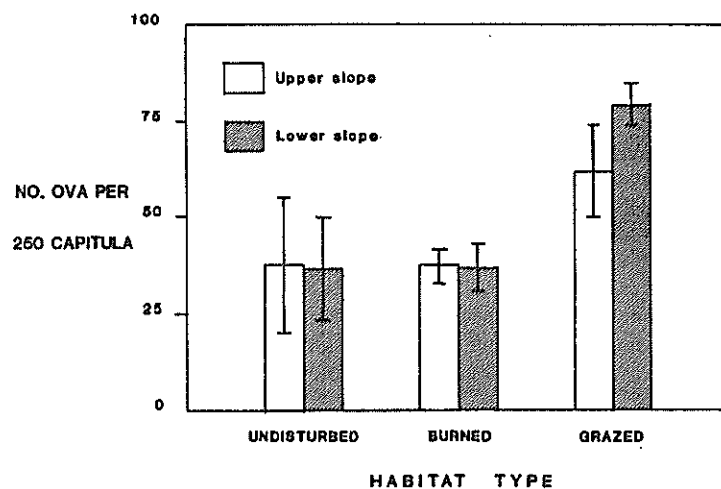
Oviposition behavior. The oviposition behavior of *H. ottoe* was very similar to that of *H. dacotae* except when the substrate was a coneflower capitulum. In the instances of oviposition on coneflowers that I observed, females flew rapidly and directly to capitula, in the same manner as females seeking nectar, and short bouts of nectaring often occurred before oviposition. Sometimes a female engaged in some exploratory probing with the tip of her abdomen before ovipositing, but usually she simply curved her abdomen down and affixed an egg in a single, unhesitant sequence. In all observed cases, the female left immediately after laying one egg, but in three instances the flight was directly to another capitulum where another oviposition occurred. In one of these cases, the female oviposited in this manner on four capitula in rapid succession.

Eggs on capitula were usually affixed to the outward-facing, convex undersides of the firm receptacular bracts that extend several millimeters beyond the disk florets they subtend. Occasionally they were attached to the upper, concave surfaces of these bracts, and rarely, to the bases of ray florets (Dana 1981). The placement of eggs on the other substrates was quite similar to that described for *H. dacotae*.

Ovipositions (on all substrates) were observed throughout the same nine hour period of the day as those of *H. dacotae* (Figure 6). I obtained no evidence that different substrate types might be favored during different parts of the day. The topographic distribution of observed ovipositions (on all substrates) was also similar to that in the *H. dacotae* sample (Figure 7).

The number of ova in the samples of 50 capitula taken in 1979 increased on average with successive sampling dates, but there was considerable variation among the sampling units in this regard. Increases were strong in the two subdivisions of the recently grazed Unit C, and in the unburned part of Unit D, but only moderate to weak in the other sampling units. The mean combined counts for the zone-treatment combinations are shown in Figure 9. Differences between upper and lower zone counts within units were very small and not statistically significant, and the average of the two was used in the analysis of disturbance effects (Table 8). Although the mean average count was greater in recently grazed prairie than in the other two types,

Figure 9. Distribution of *Hesperia ottoe* ova on capitula of *Echinacea angustifolia* at Hole-in-the-Mountain Prairie with respect to topographic position and habitat differences produced by disturbances. Undisturbed habitat had a heavy litter accumulation and a low density of *Echinacea* capitula. Habitat burned in early spring was free of litter and had a high density of capitula. Litter amounts were low and capitulum density moderately high in habitat subjected to heavy season-long grazing the previous year. Data totals are from five independent random samples of 50 capitula taken at regular intervals spanning the peak egg laying period in two units of each habitat type. Means of the two totals and standard errors are shown. Analysis is presented in Table 8.



the effect of disturbance type is not statistically significant (Figure 9). The error term was inflated by highly divergent values for the two undisturbed units.

It should be noted that even though the per capitulum rate did not differ between burned and unburned habitat, because the density of capitula was much greater in the burned prairie the number of eggs per unit area was greater in burned than in undisturbed prairie. Capitulum density was slightly lower in the grazed habitat than in burned, but the number of eggs per unit area may have been about the same because of the possibly higher per capitulum number. Capitulum densities also tended to be higher in the upper slope zone than in the lower, so that the number of eggs per unit area should have been greater in the former. Only qualitative characterization of these differences has been possible as I did not measure capitulum densities.

Most sampled capitula had no ova, with successively smaller numbers having one, two, three and four (capitula with five were seen in casual observation but did not occur in any samples). A tendency towards weak aggregation is found in the combined data from all samples on each date. The variance-mean ratio exceeds unity for all dates, but the deviation from a Poisson distribution is significant only for the last two (Chi-square = 20.29, 6.89 for fourth and fifth dates, respectively; $P < 0.01$ in both cases). Since females apparently rarely if ever lay more than one egg on a capitulum during a visit, multiple visits to more attractive capitula is suggested.

Ovarian Dynamics and Fecundity. There were no mature oocytes in two reared females dissected about eight hours after eclosion; the lowest oocyte in

each ovariole was still clothed in follicular epithelium. A reared female dissected about 36 hours after eclosion had only one fully mature ovum in each ovariole.

Females of this species did not adjust to the oviposition cages, but quickly battered themselves in persistent efforts to escape, so I was not able to obtain daily production data comparable to what was obtained for *H. dacotae*. The maximum single day's production from a captive female was 28 eggs, laid on the second day of confinement following no oviposition the first day (the female was captured and confined in the morning.) In several cases, young females laid about 15 eggs in a day (no old individuals were confined). These observations suggest that this species may not begin oviposition as quickly after emergence as *H. dacotae* and may lay fewer eggs per day.

The only estimate of potential lifetime fecundity was obtained from the female dissected about 36 hours after eclosion. There were 225 distinguishable oocytes in this female. Although eggs are slightly larger than those of *H. dacotae*, females are larger by roughly the same proportion, suggesting that potential fecundity is similar.

Mortality factors. I observed a number of unsuccessful attempts by crab spiders and ambush bugs to capture adults on coneflower capitula. The only capture I witnessed was of a worn male by an ambush bug (*Phymata* sp.). I watched a robber fly (probably *Promachus* sp.) repeatedly attack a pair on a coneflower capitulum (nectaring female being courted by a male). After each unsuccessful attack the skippers returned to the capitulum until finally the male and the robber fly disappeared. No bird predation was observed but severe wing damage

Table 8. Analysis of variance of counts of *Hesperia ottoe* ova on *Echinacea angustifolia* capitula at Hole-in-the-Mountain Prairie with respect to topographic position and habitat disturbance (data summarized in Figure 9). Untransformed data were used in this analysis.

Source	df	Sum of Squares	Mean Square	F	P
Model Including Slope Zone					
Disturbance Type	2	3037.500	1518.750	3.593	0.16
Whole-plot Error	3	1268.250	422.750		
Slope Zone	1	80.083	80.083	1.516	0.31
Disturbance X Slope	2	228.167	114.084	2.163	0.26
Subplot Error	3	158.250	52.750		
Model Without Slope Zone					
Disturbance Type	2	1507.583	753.792	3.563	0.16
Error	3	634.750	211.583		

suggestive of vertebrate attack was occasionally encountered.

Mark-Release-Recapture Study

Tests of Assumptions

The numbers of insects captured and recaptured in each year of MRR sampling are shown in Table 9. In all years of the study the number of females ever captured was smaller than the number of conspecific males, and the number of *H. ottoe* was always smaller than the number of *H. dacotae* of the same sex. Recapture rates were fairly low. They were similar in the two species, with the rate for females lower than the rate for the respective group of males in all but one case. The lower capture totals and recapture percentages in 1980 resulted from the reduced sampling effort that year.

The differences between the sexes in recapture likelihood are not statistically significant (Table 10). As mentioned in Methods, recapture probability combines the effects of catchability and residence rate. Equal recapture probabilities between the sexes could result from opposing differences in the two component factors.

There were enough recaptures to permit meaningful evaluation by Tabashnik's method of between-sex differences in catchability and residence rate for *H. dacotae* in 1979 and 1981, but only in 1979 for *H. ottoe* (Figure 10). This test provides no evidence that the sexes of *H. dacotae* differed in either factor, but it suggests that in 1979 *H. ottoe* males were more catchable than females. The negative regression coefficient, indicating a greater female residence rate, is very close to significance, but the strongly influential point at $t = 11$ days is based on only two ratios ${}^mR_{ij}/{}^fR_{ij}$, while the other points are based on between 5 and 11 ratios.

Although these tests indicate that analysis of the sexes as separate populations is probably necessary only for *H. ottoe*, I have analyzed them separately in all cases because a difference in catchability is made likely by the pronounced differences in the behavior of males and females, while the power of the tests to detect it is probably low with my data.

No effect of marking on recapture likelihood could be detected by comparison with recapture rates in insects recaptured and released without additional marking (Table 11). The sensitivity of these tests is limited by the low numbers of multiple recaptures,

Table 9. Capture summary for three years of MRR study of *Hesperia dacotae* and *H. ottoe* adults at Hole-in-the-Mountain Prairie.

Year	Sex	Number captured and released at least:				% Releases Recaptured
		1 time	2 times	3 times	4 times ^a	
<i>Hesperia dacotae</i>						
1979	M	248 (1) ^b	24	3	0	9.8
	F	169 (1)	21	1	0	11.5
1980	M	177 (4)	8	0	0	4.3
	F	88 (36)	3	0	0	3.3
1981	M	266 (4)	21	1	0	7.6
	F	156 (25)	8	0	0	4.9
<i>Hesperia ottoe</i>						
1979	M	216 (3)	35	6	0	16.0
	F	77 (2)	6	1	1	9.4
1980	M	129 (1)	13	1	0	9.8
	F	34 (9)	1	0	0	2.9
1981	M	145 (0)	10	1	0	7.1
	F	72 (0)	5	0	0	6.5

^aNo insect was ever captured more than four times.

^bNumbers in parentheses are additional captures not released. In 1980 and 1981 many females were held for ova or dissected to determine mating frequency.

Table 10. Tests of between-sex differences in recapture probabilities for *Hesperia dacotae* and *H. ottoe* in three years of MRR study at Hole-in-the-Mountain Prairie.

Year	Sum of Chi-squares ^a	df	P
<i>Hesperia dacotae</i>			
1979	18.854	18	0.40
1980	8.267	7	0.31
1981	8.584	11	0.66
<i>Hesperia ottoe</i>			
1979	14.853	20	0.78
1980	1.860	5	0.87
1981	11.381	8	0.18

^aIndependent Chi-squares calculated for each day where both sexes were captured and released.

and they would detect only effects whose expression was limited to a brief period after marking.

Capture and marking could have reduced residence rate in several ways. Handling skippers during marking inevitably produced injuries, but these were mostly minor and behavioral impairment was seldom evident. Only five skippers during the three years were unable to fly when released; all but one of these recovered flight capability in a few minutes, and one was recaptured in good health seven days later. Loss of labial palps was the most frequent injury (mainly in *H. ottoe*). Comparisons of recapture rates for palp-injured insects with those for uninjured ones by contingency-table techniques yielded no significant Chi-square values. Leg loss also occurred, but too rarely to test. Some of the vestiture of the thorax was always removed, which could have reduced the probability of escape from predators, but the amount lost was small in most cases.

Dye in the marking ink penetrated the wing cuticle and circulated in the haemolymph, appearing in the chorion of eggs one to two days after females were marked. This raises the possibility that marking had toxic effects. Longevity in marked females held for eggs was not obviously reduced compared with that in unmarked ones, but a carefully controlled experiment would be needed to detect subtle but still biologically significant effects.

The possibility that the number of previous captures of an insect might affect the likelihood of recapture could be tested only with 1979 data from male *H. ottoe*. There is no evidence in these data that

capture history influenced the likelihood of recapture (Table 12).

None of the tests of the Fisher-Ford assumption of age-independence of θ provides support for rejection (Table 13). In the two cases where the Chi-square approaches significance, the pattern of departures from expected values is not consistent with age-dependence. Tests of whether day-to-day constancy of θ is a reasonable assumption give more equivocal results (Table 14). Three of the four possible tests for *H. ottoe* are significant at the 0.05 level or better. None of the *H. dacotae* tests is significant at this level, but one is fairly close.

Figure 10. Joint residence-catchability tests for male vs. female skippers at Hole-in-the-Mountain Prairie. Tests were not performed for data sets with few recaptures. The R_{ij} are recapture proportions on day j of day i releases for males (m) and females (f). Lines are least-squares regressions; slope ($\ln \lambda$) $\neq 0$ indicates unequal residence rates (positive if male greater, negative if female), and intercept ($\ln \alpha$) $\neq 0$ indicates unequal catchabilities (positive if male, negative if female). Regression estimates for *H. dacotae* are: (1979) $\ln \lambda = 0.014$ ($t = 0.11$, $P = 0.92$), $\ln \alpha = -0.46$ ($t = -0.64$, $P = 0.54$); (1981) $\ln \lambda = 0.002$ ($t = 0.02$, $P = 0.99$), $\ln \alpha = -0.17$ ($t = -0.22$, $P = 0.84$). For *H. ottoe* these are: $\ln \lambda = -0.19$ ($t = -2.66$, $P = 0.08$), $\ln \alpha = 1.33$ ($t = 3.19$, $P = 0.050$).

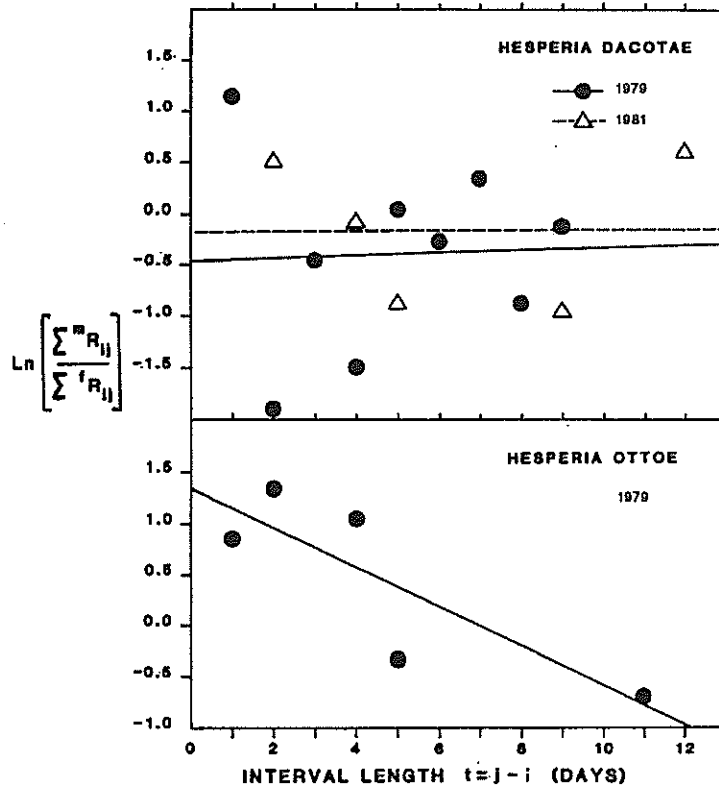


Table 11. Tests of effect of marking on recapture probability of skipper adults at Hole-in-the-Mountain Prairie by comparison of recapture proportions between newly marked insects and those released at the same time bearing previous marks and not marked again. Data from individual days were pooled until all expected values were greater than 1, and independent Chi-squares were summed. Recaptures of females in 1980 were too few to allow meaningful tests.

Year	Sex	Chi-square	df	P
<i>Hesperia dacotae</i>				
1979	M	1.275	2	0.53
	F	2.764	2	0.25
1980	M	0.397	1	0.53
	F	—	—	—
1981	M	1.381	2	0.50
	F	0.487	1	0.48
<i>Hesperia ottoe</i>				
1979	M	1.524	3	0.68
	F	1.815	1	0.18
1980	M	0.307	1	0.58
	F	—	—	—
1981	M	0.188	1	0.66
	F	0.275	1	0.60

Table 12. Test of effect of number of previous captures on recapture probability of *Hesperia ottoe* males. Data for 1979. Chi-square = 1.138, 2 df, P >> 0.05.

	Number of previous captures		
	0	1	2
Recaptured	35	6	0
Not recaptured	162	25	5

The recapture-decay plots (Figure 11) show a fairly good fit to a constant θ in all cases if the first data point, the number of insects captured but never recaptured, is excluded. Slopes are slightly steeper for older cohorts than for younger in all but one case, an indication that residence rate may have declined with age. Significance tests are not possible because the assumption of independent errors is violated.

Inasmuch as Fisher-Ford is fairly robust unless variations in residence rate are quite large (Manly 1970, cited in Begon 1979), these tests do not provide a strong basis for rejecting this model in favor of Jolly-Seber, especially as Fisher-Ford is likely to be the more accurate when there are low sampling intensities (<12 percent) and/or small population sizes (<1,000) (Begon 1979).

Residence rate

The Jolly-Seber $\hat{\theta}_i$ are plotted in Figure 12. Variation is pronounced, with the majority of values below 0.50, and a substantial number greater than 1.0. The variation probably reflects vagaries of sampling more than real changes in residence rate. Except for occasional thunderstorms, weather variations were moderate and unlikely to have produced day-to-day fluctuations of this magnitude. Values greater than one represent sampling error.

The Fisher-Ford and weighted-average Jolly-Seber residence rate estimates are presented in Table 15. The Fisher-Ford estimates are consistently higher than the corresponding Jolly-Seber values, a surprising result in light of Bishop and Sheppard's (1973) finding that Jolly-Seber tends to seriously overestimate θ when data are sparse, while Fisher-Ford is free of this bias. The recapture-decay values (Figure 11) are generally closer to the Fisher-Ford estimates. There is no clear basis for regarding either the Fisher-Ford values or those from Jolly-Seber as the more plausible in general (although the value of the former for male *H. ottoe* in 1980 is clearly unrealistic).

There was no difference between the two species in residence rate, based on either the Jolly-Seber average or Fisher-Ford constant rate estimates. Year to year variation was small and not consistent across groups, either within models or between them, suggesting that there were no strong annual effects on residence rate. Average rate, from the Jolly-Seber model, was consistently higher in males than in females. The constant residence rate from the Fisher-Ford model, however, was greater in males one year and in females another.

Expected periods of residence corresponding to the estimates of θ or average θ , were mostly between two and seven days. Observed durations were mostly less than one week, although a few periods of residence of more than two weeks were observed, including one of 19 days following initial capture. The latter, a male of *H. ottoe*, and the *H. dacotae* female that lived 19 days in an oviposition cage after capture, indicate a potential adult life span of at least three weeks under normal conditions.

Population size

Jolly-Seber and Fisher-Ford daily population size estimates \hat{N}_i for *H. dacotae* are plotted in Figure 13

and those for *H. ottoe* in Figure 14. Standard errors are shown where these could be calculated (no previously marked insects in the *i*-th sample, or no subsequent recapture of any of the insects in that sample, produces a denominator of zero in the expression for the standard error of \hat{N}_i). The per hour capture rate is also plotted in these figures for comparative purposes.

The Fisher-Ford \hat{N}_i is generally higher than the corresponding Jolly-Seber estimate. On average, the former is higher by 10 or more individuals on 70% of the days in a data set, with the latter higher by 10 or more on only 20% of the days. This reflects the rather low Jolly-Seber estimates of θ_i compared with the Fisher-Ford estimates of θ .

There is considerable fluctuation in the \hat{N}_i , reflecting the well known sensitivity of the estimate to sampling variation. The Jolly-Seber standard errors are strongly correlated with the \hat{N}_i , another well-known phenomenon (Roff 1973), and for larger values of \hat{N}_i , these standard errors are quite large.

The capture rate followed a smoother course of change over the flight period. Daily fluctuations were closely tied to weather conditions affecting skipper catchability, such as cloudy or very windy conditions. Capture rate probably tracked population density rather well at low to moderate levels, but handling-time constraints would have made the relationship nonlinear over the range of densities encountered. Despite this, it does provide a basis

Figure 11. Recapture decay plots for *Hesperia dacotae* and *H. ottoe* from MRR study at Hole-in-the-Mountain Prairie. Adults young at first capture (●) and older at first capture (Δ), as determined by wing-wear index values, are treated as separate cohorts. Lines are fitted by least squares regression to all data points but the first (insects never recaptured). Linear decay corresponds to a constant residence rate (θ), estimated by the antilog of the slope of the regression line. No plots are shown for *H. dacotae* in 1980 because of sampling gaps. Only one *H. ottoe* female was recaptured in 1980.

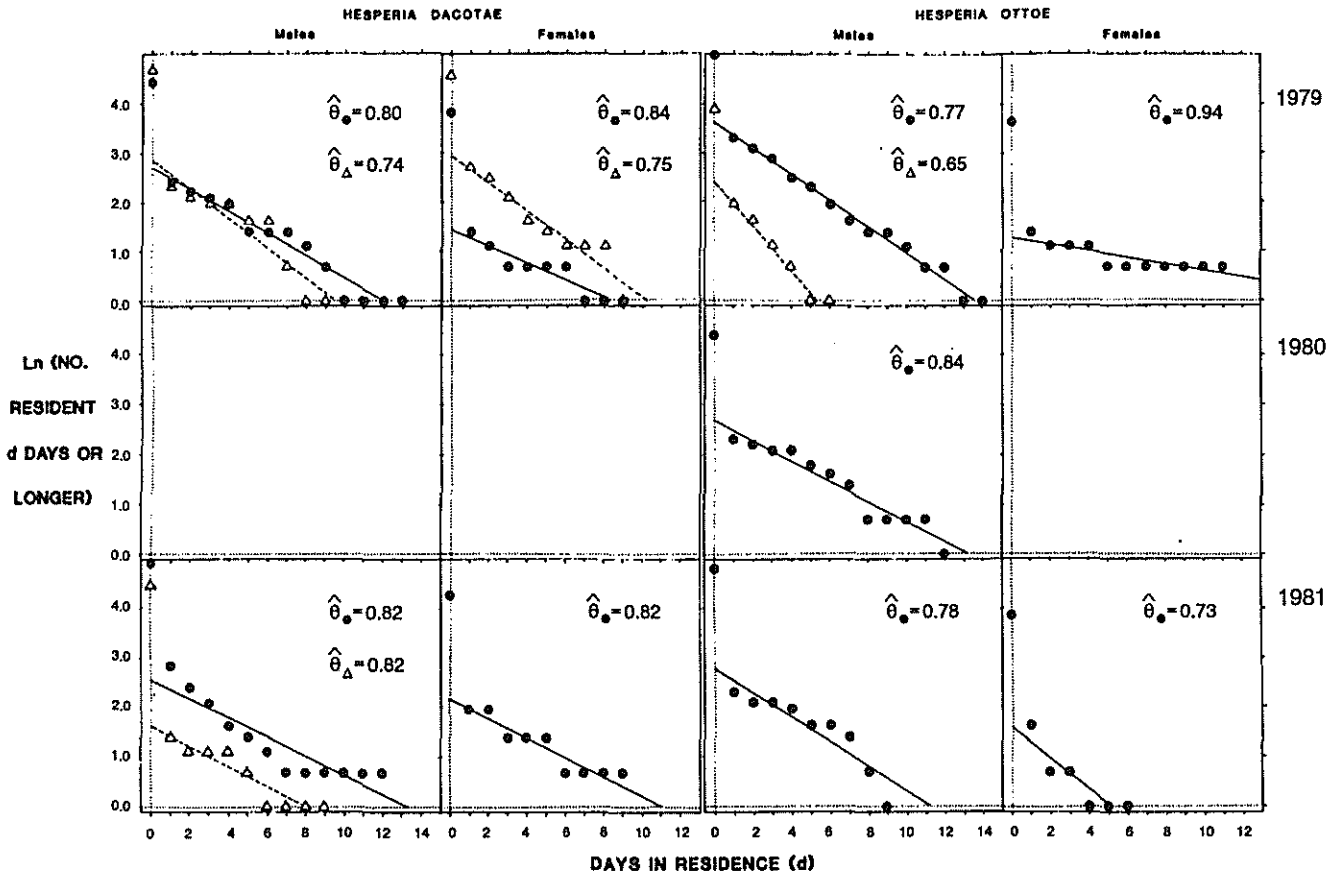


Table 13. Tests of the Fisher-Ford assumption of independence of recapture probability and age in adult skippers studied by MRR at Hole-in-the-Mountain Prairie. Expected recaptures of marks of various ages calculated under the assumption of independence were compared with the numbers observed (residence length classes were combined so that no expectation was less than 2), and the resulting Chi-squares summed (Begon 1979). The age of "marks," not insects, is used, an insect being considered to carry a mark corresponding to each time it was captured and released.

Year	Sex	No. Marks		Chi-square	df	P
		Recaptured				
<i>Hesperia dacotae</i>						
1979	M	23		7.222	10	0.70
	F	21		6.965	8	0.54
1980	M	8		insufficient data		
	F	3		insufficient data		
1981	M	22		6.786	8	0.65
	F	8		insufficient data		
<i>Hesperia ottoe</i>						
1979	M	43		11.768	9	0.23
	F	10		12.825	9	0.17
1980	M	15		10.870	10	0.37
	F	1		insufficient data		
1981	M	12		14.532	9	0.11
	F	5		insufficient data		

Table 14. Tests of the Fisher-Ford assumption of day-to-day constancy of adult residence rates in skippers studied by MRR at Hole-in-the-Mountain Prairie. The sequence of observed number of days survived by marks (not insects) taken in daily samples was compared for goodness of fit with the sequence of values expected under the assumption of constancy (Begon 1979). The degrees of freedom are one less than the number of days on which marked insects were captured.

Year	Sex	Chi-square	df	P
<i>Hesperia dacotae</i>				
1979	M	17.706	12	0.13
	F	8.802	11	0.64
1980	M	—		
	F	—		
1981	M	14.066	8	0.08
	F	—		
<i>Hesperia ottoe</i>				
1979	M	27.775	17	0.048
	F	22.991	5	<0.001
1980	M	22.964	8	<0.01
	F	—		
1981	M	9.164	8	0.33
	F	—		

Table 15. Residence rate estimates for adult skippers from MRR study at Hole-in-the-Mountain Prairie. Residence rates are the estimated probabilities of remaining alive within the study area for one day intervals. Figures within parentheses are the expected periods of residence in days corresponding to these (Cook et al. 1967). Estimates from the Fisher-Ford model are of assumed constant rates; the Jolly-Seber values shown are weighted averages (Scott 1973b) of the individual estimates for each one-day interval produced by this model. Data were too sparse for females in 1980 to support comparable estimates.

Year	Males				Females			
	Jolly-Seber		Fisher-Ford		Jolly-Seber		Fisher-Ford	
<i>Hesperia dacotae</i>								
1979	0.78	(4.1)	0.84	(5.9)	0.59	(1.9)	0.74	(3.4)
1980	0.56	(1.7)	0.81	(4.6)	—	—	—	—
1981	0.67	(2.5)	0.83	(5.2)	0.60	(2.0)	0.92	(11.4)
<i>Hesperia ottoe</i>								
1979	0.70	(2.8)	0.76	(3.6)	0.57	(1.8)	0.91	(11.2)
1980	0.68	(2.6)	0.996	(256.0)	—	—	—	—
1981	0.64	(2.2)	0.88	(7.5)	0.37	(1.0)	0.63	(2.2)

for discounting some of the fluctuations in \hat{N}_t .

On average *H. ottoe* numbers peaked about 20 days later than the *H. dacotae* peak, after the latter species had nearly disappeared. However, *H. ottoe* adults were present throughout most of the flight period of *H. dacotae*. Protandry in both species and the more protracted emergence of *H. ottoe* seen in the plot-emergence data (Figure 2) were evident in the field populations also.

The estimates of annual adult generation size are

given in Table 16. No value is included for *H. dacotae* in 1980 because of the large gap in sampling that occurred in the middle of its flight period (effects of gaps in sampling on the estimation of θ , which in turn affects estimation of total population, are discussed by Watt et al. 1977). The estimated total was larger for *H. dacotae* than for the respective sex of *H. ottoe* in both years that all were obtained. In 1979 and 1981, respectively, the estimated number of *H. dacotae* males was 1.4 and 1.5 (Jolly-Seber) or 1.8 and 2.1 (Fisher-Ford) times the number of *H. ottoe* males. The corresponding

Figure 12. Jolly-Seber estimates of residence rates (θ_t) between sampling occasions for *Hesperia dacotae* and *H. ottoe* at Hole-in-the-Mountain Prairie. Males = \diamond , females = \bullet ; where they could be calculated standard errors are shown by vertical bars. Days marked with X were not sampled or data were excluded from calculations because of poor sampling conditions. Otherwise, all rates are for one day intervals. Weighted average one day rates (Scott 1973b) are shown by horizontal bars at the right of each graph.

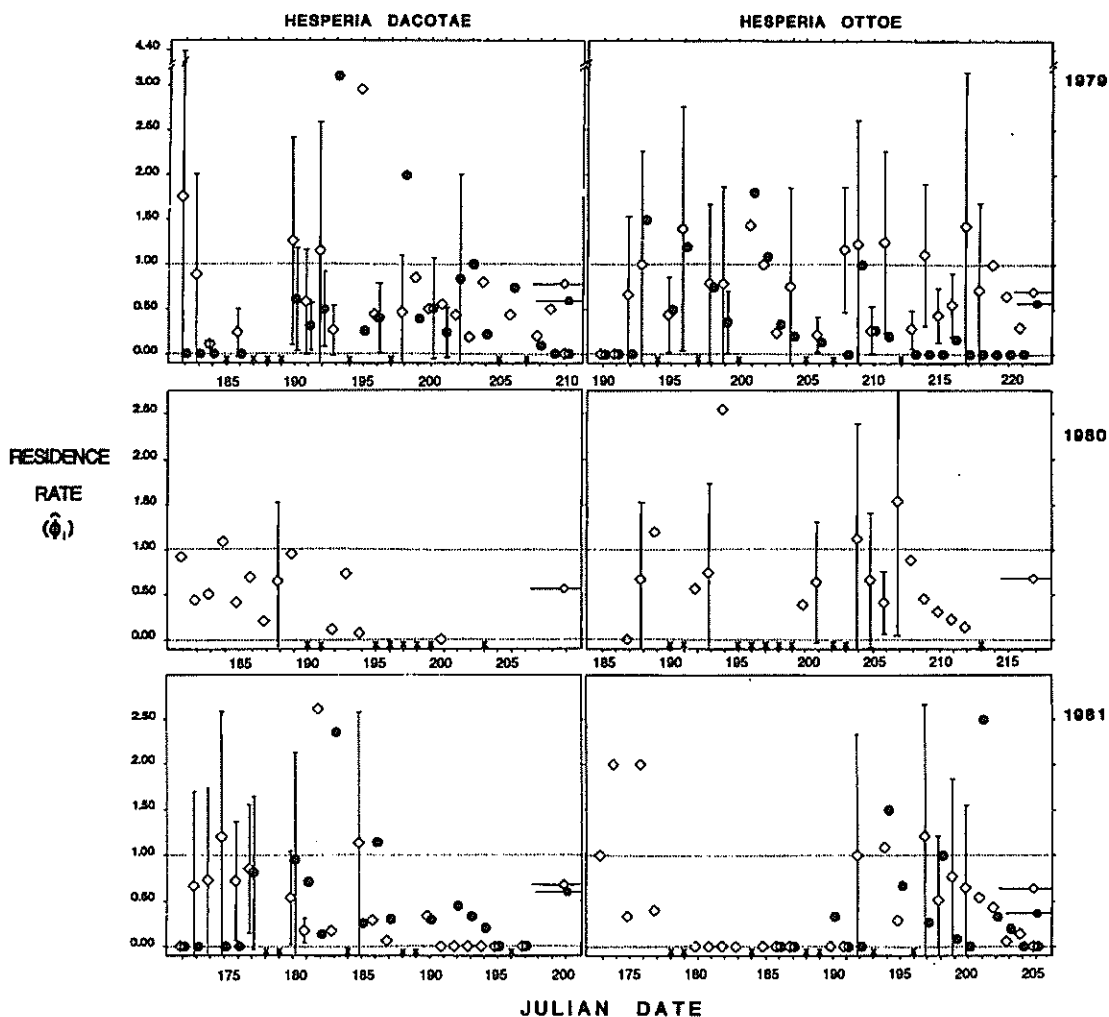


Figure 13. Estimates of adult *Hesperia dacotae* numbers at Hole-in-the-Mountain Prairie from MRR data. Open symbols are Jolly-Seber estimates (vertical bars are standard errors); filled symbols are Fisher-Ford estimates. Days marked X were not sampled or data was excluded from calculations because of poor sampling conditions. Daily capture rate (Δ) is shown in upper parts of graphs for comparison with population estimates. Data for females in 1980 were too sparse to warrant calculation of estimates.

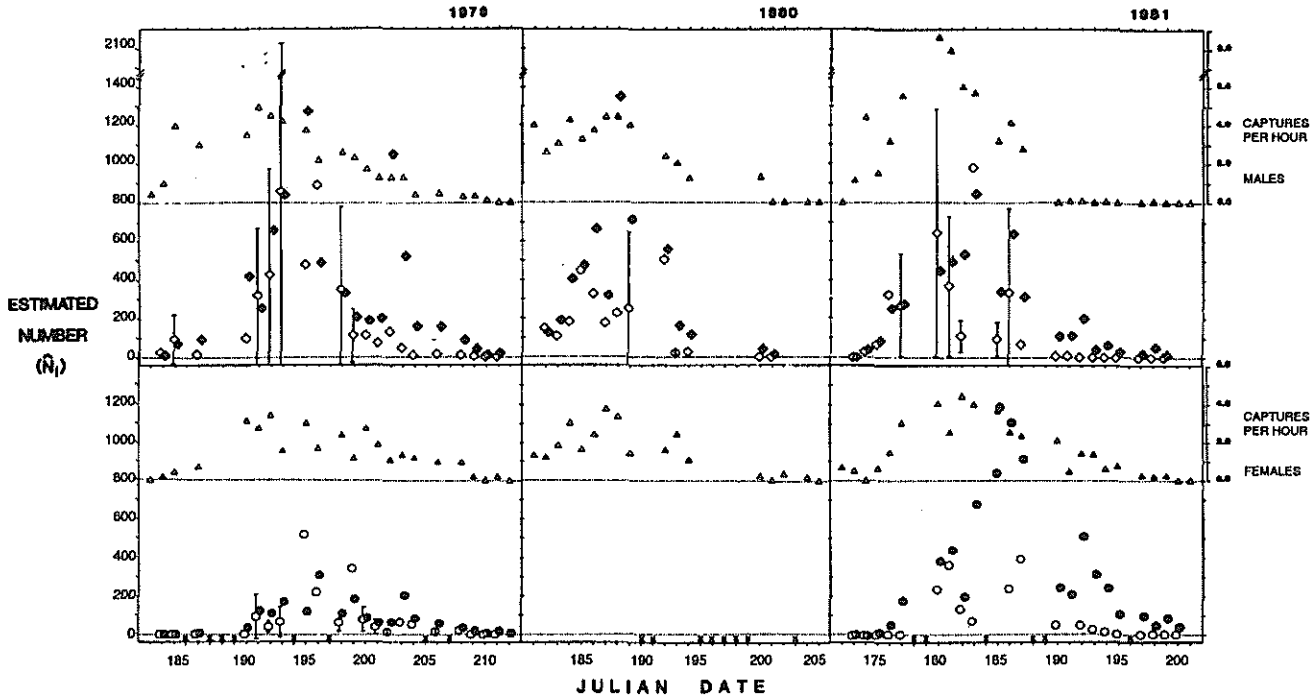
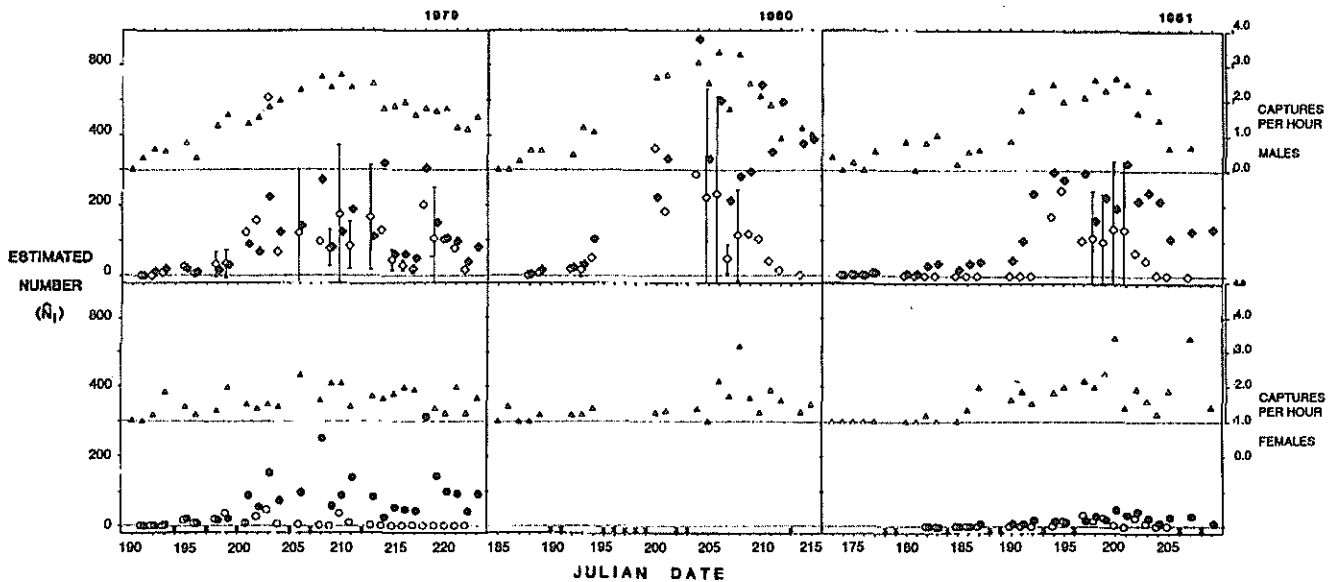


Figure 14. Estimates of adult *Hesperia ottoe* numbers at Hole-in-the-Mountain Prairie from MRR data. All symbols as in Figure 13. Data for females in 1980 were too sparse to warrant calculation of estimates.



values for females were 6.6 and 14.0 (Jolly-Seber) or 2.0 and 7.6 (Fisher-Ford) times as many *H. dacotae* as *H. ottoe*. For both species the estimated number of males in a generation was always greater than the number of females (the "realized sex ratio" of Ehrlich et al. 1984). These ratios for *H. dacotae* were, in 1979 and 1981, respectively, 1.4:1 and 1.1:1 (Jolly-Seber) or 2.4:1 and 1.4:1 (Fisher-Ford). The corresponding ratios for *H. ottoe* were 6.6:1 and 5.4:1 (Jolly-Seber) or 2.6:1 and 5.1:1 (Fisher-Ford).

Jolly-Seber estimates were higher in 1981 than 1979 for both sexes of *H. dacotae*, while Fisher-Ford estimates showed the same pattern for females but the reverse for males. Changes from the 1979

values were about 25% except for the 60% increase in the Jolly-Seber estimates for females. The estimates for *H. ottoe* were consistently lower in 1981 than in 1979, about 40% lower for males in both models, 25% in Jolly-Seber, 70% in Fisher-Ford, for females.

Evaluation of these differences is necessarily speculative without estimates of the precision of the estimated totals. However, supporting evidence for a decline in *H. ottoe* numbers in 1981 relative to 1979, without a corresponding decrease in *H. dacotae*, is provided by the season-average capture rates for the whole site. These were 40% and 30% lower in 1981 than in 1979 for males and females, respectively, of *H. ottoe*, while being only about 10% lower for both sexes of *H. dacotae*.

Distribution and movement

Capture rates varied considerably among the four units (Figure 15). The effect of unit was not uniform over species or sex, however (Table 17). *Hesperia dacotae* densities were clearly highest in D and A, intermediate in B, and quite low in C, with both sexes showing approximately the same pattern. Males of *H. ottoe* were also most abundant in D and A, but they were more frequent in C than in B, while females were captured at an almost uniformly low rate in all units. This among-unit pattern of capture rates was fairly constant over the three years despite year-to-year differences in the units burned.

Table 16. Adult generation estimates for *Hesperia dacotae* and *H. ottoe* at Hole-in-the-Mountain Prairie, based on Jolly-Seber and Fisher-Ford daily population estimates from MRR data. Each daily estimate up to the final one was multiplied by the estimated one day loss rate and the products, plus the final day's estimate, summed (Blower et al. 1981). Daily population estimates from each model were multiplied by the loss rate estimate (the converse of residence rate) from the same model; for the J-S model, this was a weighted average (Scott 1973b) of the daily rate estimates. No estimate is given for *H. dacotae* in 1980 because a significant part of the flight period was not sampled, or for *H. ottoe* females the same year because recaptures were too few to permit meaningful estimation of daily numbers.

Year	Number of Adults			
	Males		Females	
	Jolly-Seber	Fisher-Ford	Jolly-Seber	Fisher-Ford
<i>Hesperia dacotae</i>				
1979	1248	1547	896	649
1980	—	—	—	—
1981	1540	1165	1431	818
<i>Hesperia ottoe</i>				
1979	892	877	136	331
1980	1014	433	— ^a	—
1981	547	544	102	107

^aThere were at least 43 females, as this many were captured.

Table 17. Analysis of variance of capture rates of adults in 3 years of MRR sampling of *Hesperia dacotae* and *H. ottoe* at Hole-in-the-Mountain Prairie. Data are season-average rates for sampling units based on ca. 1.25 h/day capture effort for 12 - 20 days spanning most of the flight period, excluding periods when conditions were unfavorable for skipper activity. A square-root transformation was applied to the data before analysis.

Source	df	Sum of Squares	Mean Square	F	P
Block (Year)	2	3.30	1.65	0.35	0.71
<i>dacotae</i> vs <i>ottoe</i>	1	357.91	357.91	75.05	<0.001
Males vs Females	1	197.11	197.11	41.33	<0.001
Unit	3	494.83	164.94	34.59	<0.001
Species X Sex	1	8.02	8.02	1.68	0.20
Species X Unit	3	253.70	84.57	17.33	<0.001
Sex X Unit	3	84.58	28.19	5.91	<0.01
Species X Sex X Unit	3	7.41	2.47	0.52	0.67
Error	30	143.06	4.77		

Means of intercapture distances and intercapture intervals (days) are presented in Table 18. Intercapture distance did not increase with the number of days between captures. Spearman rank order correlation coefficients are generally low and in no case significantly different from zero. There was no relationship between age at first capture and intercapture distance.

Frequencies of intercapture distances are shown in Figure 16. For both sexes of *H. dacotae* and for male *H. ottoe*, the mean intercapture distance was greater in 1980 than in the other two years, the means of which were similar (a three-year comparison for *H. ottoe* females is not possible because only a single recapture was made in 1980). With all data from each year combined, the mean distance was greater in 1980 than in the other years (246 m vs 158 m, 163 m), and the heterogeneity among years is statistically significant (Kruskal-Wallis H corrected for ties = 6.824, 2 df., $P = 0.03$).

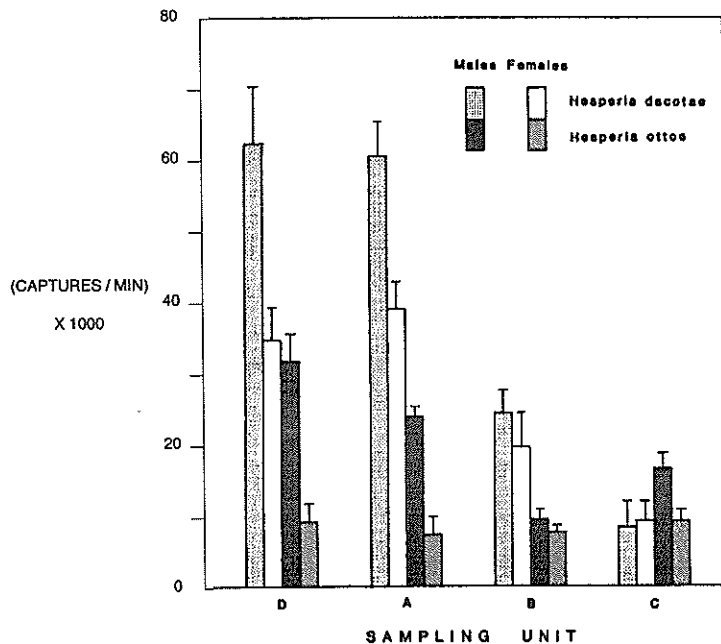
Management burning created greater among-unit habitat heterogeneity in 1980 than in the other years but interunit transfers were no more frequent in that year than in the others, suggesting this

heterogeneity was not the cause of the greater intercapture distances. Annual *H. ottoe* means were higher than *H. dacotae* means (of the same sex) in all cases. Three-year combined means were higher for *H. ottoe* than for *H. dacotae* in both sexes, but only the difference between males is statistically significant (Wilcoxon-Mann-Whitney $U = 1311.5$, $P = 0.016$ for males, $U = 200.5$, $P = 0.69$ for females).

There is no consistent pattern in the differences between sexes. Annual means for females exceeded those for males more often than the reverse, but the three-year combined mean for males was greater than for females of both species. Neither of the latter differences is statistically significant ($U = 978.0$, $P = 0.93$ for *H. dacotae*, $U = 530.5$, $P = 0.24$ for *H. ottoe*).

Intercapture movements are mapped diagrammatically in Figure 17. On the whole, most recaptures were in the same unit as the preceding capture, but moves between units were common, including moves across the large tributary valley. With the data from all three years combined, the proportions of recaptures involving any move between units and of those involving a move across the tributary valley were both slightly greater for *H. ottoe* than for *H. dacotae*. Of the 87 *H. dacotae* recaptures 32% involved interunit moves, and 29% of the interunit moves crossed the valley. For *H. ottoe*, 43% of 76 recaptures were interunit and 38% of the latter crossed the valley. None of the differences is statistically significant, however. The proportion of recaptures involving a move between units and the proportion of interunit moves that crossed the valley were both nearly equal for males and females within each species. Year-to-year variations do not suggest any pattern.

Figure 15. Capture rates of adult skippers in MRR sampling units at Hole-in-the-Mountain Prairie. Means of three season-average rates are shown (thin vertical bars are standard errors). The difference in unit effects between species (averaged over sex) and between males and females (averaged over species) are statistically significant (Table 17).



BURNING STUDIES

EMERGENCE TRAP STUDY

The 180 emergence traps set out to sample adults emerging in burned and unburned parts of the site captured only six skippers, all *H. dacotae*. All emerged between July 3 and July 9. Two (a male and a female) emerged in the 60 traps in burned habitat while four (three males and a female) emerged in the 120 traps in unburned habitat. All but one emerged in sampling plots in midgrass habitat, and the one emerging in a tallgrass habitat sampling plot was in a trap in habitat actually transitional between the two types. Two males emerged in one trap, with all other emergences solitary.

EXPERIMENT I

In this experiment the effects of early and late spring burnings were compared using large (1.5 m²) enclosed prairie plots that had each been stocked

Figure 16. Frequency distributions of distances between successive captures of adult skippers. Dotted bars in upper panel show distributions for all three years combined. The maximum distance observable was ca. 800 m.

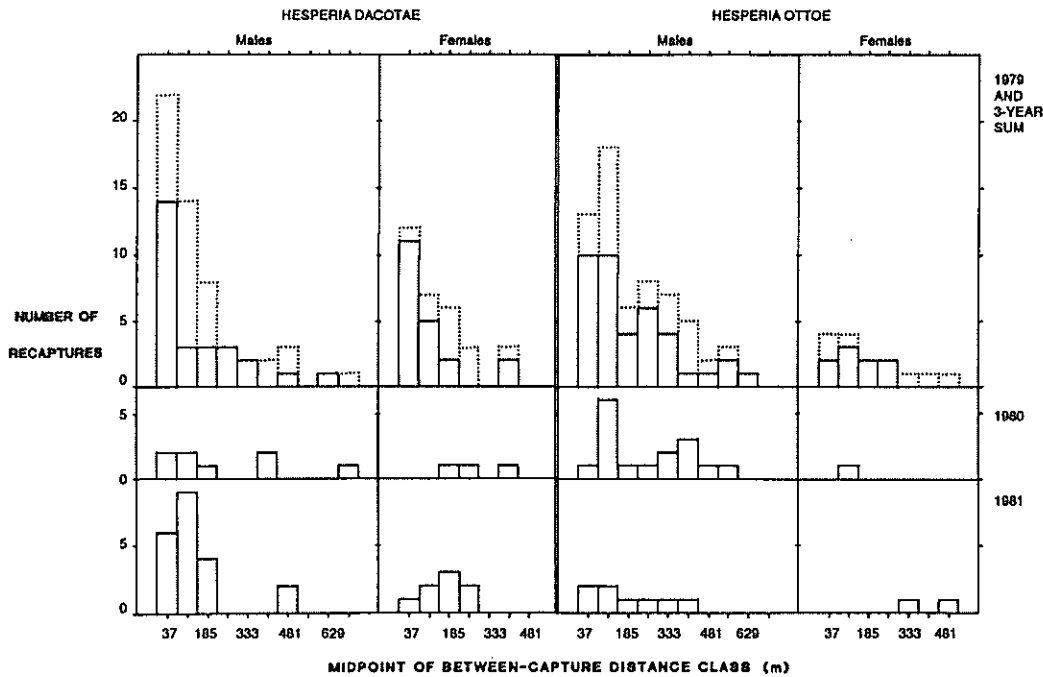
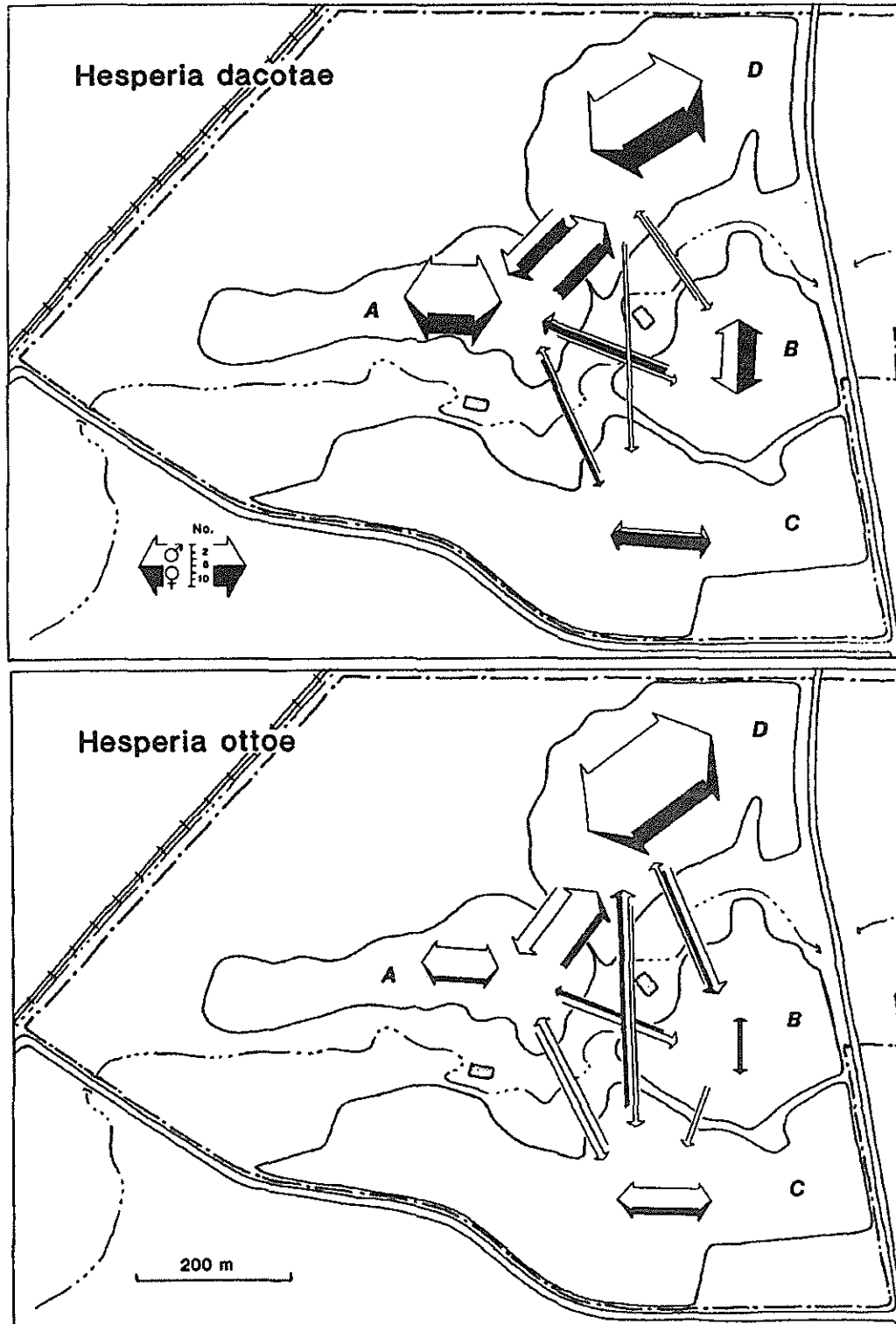


Table 18. Relationship between intercapture distance and number of days elapsed between captures of adult skippers. Time measured in whole day units. Distances measured as straight lines between approximate capture points on a site map (scale 1:3720) and converted to meters. Only successive intervals were used from multiply-recaptured insects, i.e., the intervals including an intervening recapture were not included. Means are given with their standard errors. Tests are two-tailed.

Year	Sex	N ^a	Days	Distance (m)	r _s ^b	t	P
<i>Hesperia dacotae</i>							
1979	M	27	3.9 ± 0.62	151 ± 30	0.122	0.615	0.54
	F	20	3.8 ± 0.62	104 ± 2	0.163	0.702	0.49
1980	M	8	4.4 ± 0.92	246 ± 84	0.101	0.249	0.81
	F	3	6.7 ± 2.91	272 ± 58	—	—	—
1981	M	21	3.7 ± 0.74	131 ± 29	0.399	1.895	0.07
	F	8	4.9 ± 1.11	169 ± 26	0.613	1.901	0.11
<i>Hesperia ottoe</i>							
1979	M	39	3.5 ± 0.48	195 ± 26	0.243	1.523	0.14
	F	8	4.6 ± 1.48	143 ± 38	-0.304	-0.780	0.47
1980	M	14	6.3 ± 1.43	256 ± 44	0.221	0.785	0.45
	F	1	1	41	—	—	—
1981	M	10	4.7 ± 0.93	198 ± 38	0.039	0.112	0.91
	F	4	2.2 ± 1.25	231 ± 105	—	—	—

^aNot all recaptures recorded in Table 9 were usable owing to occasional failure to record capture location precisely.
^bSpearman's coefficient of rank correlation.

Figure 17. Intercapture displacements of adult skippers in MRR study at Hole-in-the-Mountain Prairie with respect to sampling units (A–D). Data from three years is combined. Arrows indicate direction of movement; bidirectional arrows represent recaptures within the same unit as previous capture. Arrow width indicates number of displacements. Arrow length has no significance.



with 20 *H. dacotae* and 10 *H. ottoe* larvae. Plots were open burned.

Table 19 presents the numbers of skippers emerging in the plot enclosures. Analysis of variance (not presented) showed no statistically significant effects when species were considered separately or combined. These results are rendered meaningless, however, by the probability that larvae escaped from the enclosures.

Comparison of the proportion of stocked larvae that emerged in unburned control plots in this experiment with the proportions from subsequent ones where larval escape was made more difficult or impossible (0.02 versus 0.14, 0.51, 0.41) strongly suggests that this happened. Apparently the cage frame resting on the surface within the metal barrier strip formed an ineffective deterrent to larval emigration. Alternatively, the unusually high density of larvae within the plots may have attracted arthropod predators, which found that enclosure presented little impediment to entry.

The temperature measurements made during burning of these plots are of interest despite the lack of mortality data. They provide some indication of conditions that would be produced during management burns, and it is possible to draw inferences regarding likely mortality. Thermocouple measurements are summarized in Figure 18. Although air temperatures averaged slightly higher during the early burn (26° versus 21° C), ambient soil temperatures were about 10° C higher at the time of the late burn.

On both dates preignition soil temperatures averaged 6–7° C warmer in previously burned plots than in unburned ones where the heavy mulch greatly reduced insolation of the soil. Maximum soil temperatures reached during burning were strongly influenced by ambient soil temperature. Despite apparently much hotter fires in the heavier fuel loads of the previously-unburned plots, maxima in these plots averaged lower than in the previously-burned plots by about the same amount as the difference in ambient temperatures. The maxima measured in this way were well below levels likely to be lethal to skipper larvae. Only one potentially lethal maximum was recorded (67° C), but the probe tip may have been right at the soil surface rather than at the intended 5 mm depth.

Measurements made using the fusible paints on ceramic wafers present a slightly different picture (Figure 19). Fusion depths generally indicate greater buffering by the cooler soil during the early burn, but the fuel level differences between preburned and not preburned plots had little discernible effect. This technique suggests that potentially lethal temperatures occurred fairly frequently at larval depths in late-burned plots of either pretreatment type. On average, the soil 4 mm below the surface reached 52° C in these plots, as determined by the depth to which this indicator-paint stripe was fused.

Table 19. Adult skipper emergence in previously burned and undisturbed prairie plots subjected to early and late spring burning (Experiment I). Plots arranged as four subplots in whole plots were stocked the previous summer with 20 *Hesperia dacotae* and 10 *H. ottoe* hatchling larvae each. Undisturbed whole plots had moderately heavy litter, while those burned in spring before stocking were cleared of litter and had low fuel levels for experimental burning. Burn treatment subplots and one control in each whole plot were fumigated with PH just before stocking to reduce natural enemy numbers. The early burn was on April 25, the late burn on May 30. Each number is the total from five subplots. Larval escape from plot enclosures was probably responsible for the very low numbers of adults.

Subplot Treatment	Whole-Plot Type			
	Previously Burned		Not Previously Burned	
	<i>dacotae</i>	<i>ottoe</i>	<i>dacotae</i>	<i>ottoe</i>
Nonfumigated Control	2	1	4	0
Fumigated Control	1	2	3	1
Early Spring Burn	2	1	1	3
Late Spring Burn	1	0	2	1
Total	6	4	10	5

Table 20. Analysis of variance of Experiment II data summarized in Figure 20. Data were subjected to a square-root transformation for analysis.

Source	df	Sum of Squares	Mean Square	F ^a	P
Blocks	3	0.4131	0.1377	0.412	0.54
Pretreatment	1	0.5909	0.5909	1.768	0.21
Burn vs Control	1	0.2488	0.2488	0.744	0.41
Interaction	1	0.0136	0.0136	0.037	0.85
Error	9	3.3286	0.3698		

^aInteraction was combined with error to test the significance of main effects.

The discrepancy between this and the thermocouple measurements may have resulted from conduction of heat through the ceramic wafer itself from the part above the surface that was exposed to very high temperatures.

EXPERIMENT II

Four blocks of plots from experiment I, subsequently stocked with 10 *H. dacotae* larvae each and fitted

Figure 18. Effect of spring burns in Experiment I prairie plots on temperature 5 mm below the soil surface as measured by thermocouple probe at plot center. Only preignition and postignition maximum temperatures were recorded. Plots burned in spring the previous year had low fuel levels (standing dead material from one growing season), while those not previously burned had a moderately heavy litter accumulation. Plots were open burned. Dates of burning were April 25 and May 30, with air temperatures of 26° and 21°C, respectively. Means are from five plots each (vertical bars are standard errors).

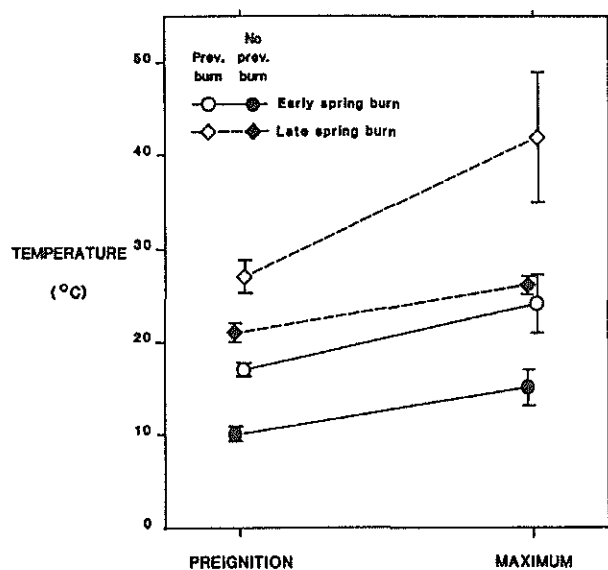


Figure 19. Profiles of maximum temperature within a few centimeters above and below the soil surface during early and late spring burns in Experiment I prairie plots at Hole-in-the-Mountain Prairie. Measurements were made using stripes of specific-melting-point paints on ceramic wafers that were inserted into the soil with stripes normal to the surface. Approximately 35 mm of the strip was below the surface, with 80 mm above it. Melting always extended down from the top edge of the wafer, indicating that the zone of most intense heat was above this level. Means and standard errors (vertical bars) are based on four measurements (subsamples) in each of five plots.

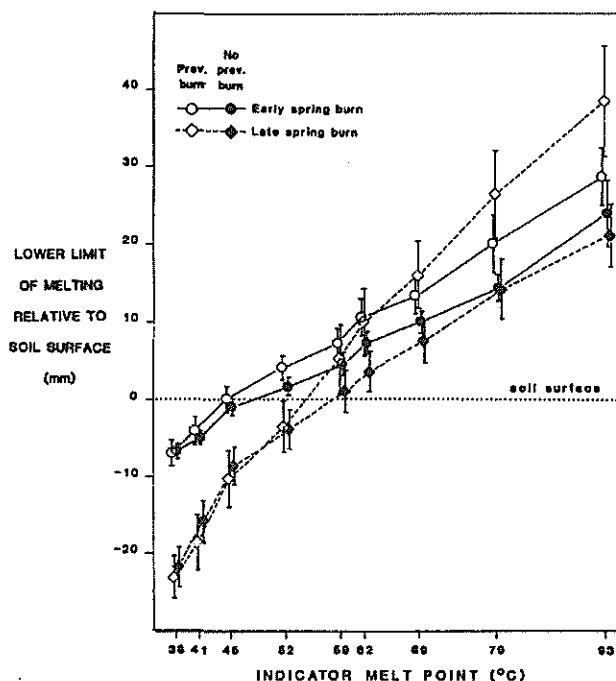


Table 21. Analysis of variance of Experiment III data summarized in Figure 21. Data were subjected to a square-root transformation for analysis.

Source	df	Sum of Squares	Mean Square	F	P
Blocks	9	1.4031	0.1159	1.212	0.31
Treatments	5	15.9693	3.1939	33.409	<0.001
Control vs Burn	1	14.5227	14.5227	151.911	<<0.001
Moderate vs Heavy Fuel	1	0.1472	0.1472	1.540	0.22
Early vs Late Spring	1	0.0484	0.0484	0.506	0.48
Fuel X Date	1	0.0484	0.0484	0.506	0.48
Error	45	4.3038	0.0956		

Table 22. Analysis of variance of Experiment IV data summarized in Figure 23. Data were subjected to a square-root transformation for analysis. Abbreviations are: C = control (not burned); LF = low fuel load (approximately 160 gm⁻²); MF = moderate fuel load (about 540 gm⁻²).

Source	df	Sum of Squares	Mean Square	F	P
Early vs Late Burning ^a	1	0.3974	0.3974	1.719	0.20
Whole Plot Error	22	5.0863	0.2312		
Burn Treatment	2	6.8854	3.4427	17.718	<<0.001
LF vs C	1	0.3177	0.3177	1.635	0.21
MF vs (C+LF)	1	6.5677	6.5677	33.802	<<0.001
Burn X Date	2	1.0028	0.5014	2.581	0.09
(LF vs C) X Date	1	0.1514	0.1514	0.779	0.38
[MF vs (C+LF)] X Date	1	0.8515	0.8515	4.382	0.04
Subplot Error	44	8.5508	0.1943		

^aWhole plots were not randomized between dates.

Figure 20. Effects of early spring burning of recently burned and undisturbed prairie plots on *Hesperia dacotae* larval survival as measured by adult emergence in Experiment II. Plots were stocked with ten hatchling larvae the previous summer. Previously burned plots (spring before stocking) had low fuel levels at the time of experimental burning, while undisturbed plots had a moderately heavy litter accumulation. Treatment plots were open burned April 30, with controls left unburned. All means are from four plots (vertical bars are standard errors). No differences are statistically significant (Table 19).

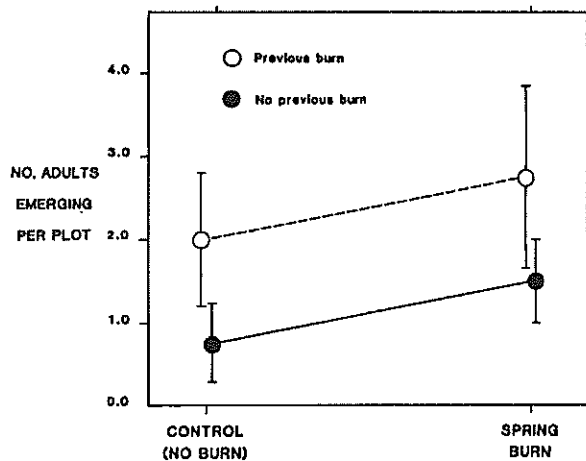


Figure 21. Effects of early versus late spring burning of prairie plots with two fuel levels on *Hesperia dacotae* larval survival as measured by adult emergence in Experiment III. Plots were stocked with six hatchling larvae the previous summer. All plots were in prairie burned in spring before stocking. In situ fuels were augmented with similar material just before experimental burning to produce medium and heavy fuel loads of about 435 and 835 gm⁻², respectively. Plots were closed burned individually within a metal barrier ring. Burn dates were May 1 and June 5. The control mean is from 20 plots and all treatment means are from ten plots (vertical bars are standard errors). Emergence in controls is statistically significantly greater than in burned plots, but no differences among the burn treatments are significant (Table 20).

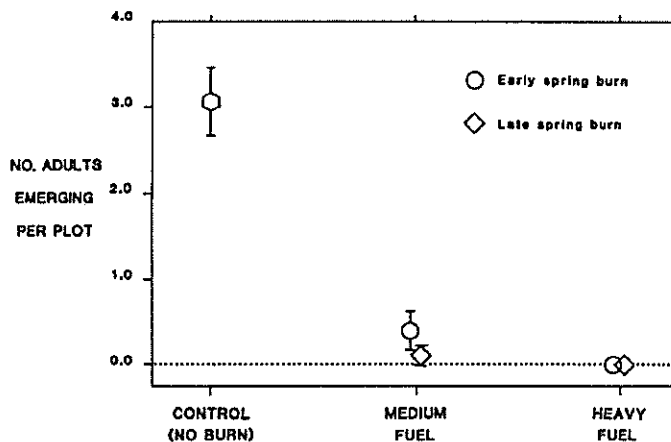
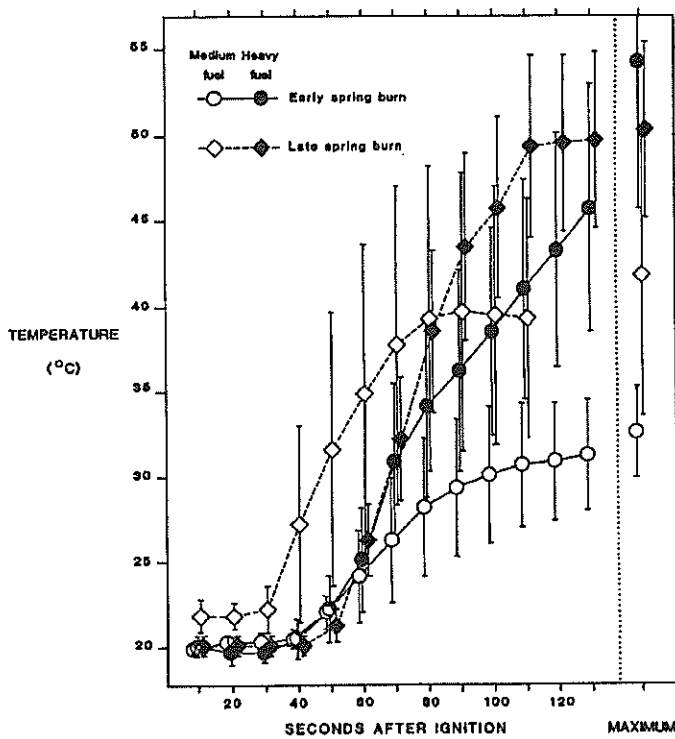
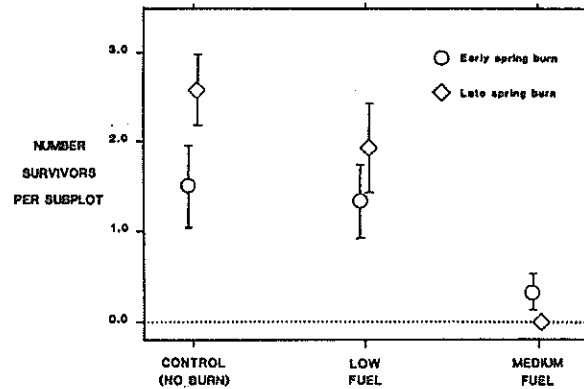


Figure 22. Temperatures 5 mm below the soil surface in spring burns of Experiment III temperature measurement plots. Procedures were identical to those for experimental plots with skipper larvae (see Figure 21 legend), but burns were one day later (May 2 and June 6 for early and late spring treatments, respectively). Temperature was measured with a thermocouple probe buried at plot center, and readings were recorded every 10 s after ignition until there was no further perceptible rise up to 130 s. If temperature was still increasing at 130 s, the final maximum was recorded. Maxima without regard to the time of occurrence were used in calculating mean maximum values. Air temperatures were 26–27° and 19–23°C during early and late burns, respectively. All means are based on ten readings (vertical bars are standard errors).



with an improved enclosure, were used to compare the effects of two fuel levels in an early spring, open burn. The data are summarized in Figure 20. Mean emergence was slightly higher in burned than unburned control plots under both high and low fuel levels (preburned and not preburned). Means for the low fuel plots were higher than those for high fuel plots. However, analysis of variance (Table 20) fails to justify rejection of any null hypothesis at the 0.05 level of significance. Variability in emergence within treatment combinations was relatively large. The use of the old design "leaky" enclosures during the prediapause part of larval development may have

Figure 23. Effects of early versus late spring burning of prairie plots with light and medium fuel levels on skipper larval survival in Experiment IV. Whole plots of three clustered subplots were stocked the previous summer with hatchling larvae of *Hesperia dacotae* or *H. ottoe*, five larvae per subplot. Date of burning was also a whole plot factor. All plots were in prairie burned the spring before stocking. In situ fuels, and augmentation with similar materials just before burning provided fuel levels of about 160 and 540 gm⁻², respectively. Whole plots were open burned (control subplots protected) on May 16 and June 5 for early and late spring treatments, respectively. Survivors (larvae and pupae) were retrieved from all plots 11 days after the late burn. Differences between the two species were minor and not statistically significant, and combined data are shown here. All means are based on 12 values (vertical bars are standard errors). Whole plots were divided between two separate areas of prairie and each area was burned as a whole on one of the two dates. The difference between control means for the whole plot date treatments exceeds the LSD for $\alpha = 0.05$, indicating a probable location effect that is confounded with the effects of interest (see Table 21 for ANOVA).



contributed to this. Despite the effectively sealed enclosures installed before resumption of activity the next spring, the average proportion of stocked insects emerging as adults in controls was only 0.14, much lower than for the two experiments using escape-proof enclosures throughout.

EXPERIMENT III

This experiment, conducted at the same time as Experiment II, employed smaller (0.07 m²) plots stocked with six *H. dacotae* larvae each and a closed burning technique to evaluate the effects

of both early spring versus late spring fire, and two fuel levels, in factorial combination. The data are summarized in Figure 21. Mean emergence was dramatically lower in burned plots than in controls. No adults emerged in the heavy fuel load plots, and only four emerged in all of the moderate load plots. The effect of burning versus controls is highly significant statistically, but neither the two fuel levels nor the two burn dates differed significantly from each other (Table 21).

Soil temperature data from the 5 mm deep thermocouple probes in test plots are summarized in Figure 22. On both burn dates temperatures rose well into the potentially lethal range in the heavy fuel load plots, and these temperatures typically persisted for several minutes. In the moderate fuel load plots, lethal temperatures were infrequently reached and means were well below lethal levels. On the basis of these data, it seems unlikely that exposure to high temperatures in shelters could have caused all the mortality observed in early burned, moderate fuel load plots.

EXPERIMENT IV

The three way factorial combination of early versus late spring burning, two fuel levels, and *H. dacotae* versus *H. ottoa* was investigated in this experiment using the same plot design as Experiment III, but with an open instead of a closed burning technique, and with lower fuel levels. Five instead of six larvae were stocked in each plot. On the basis of a preliminary ANOVA, which showed the effect of species and all interactions involving species to be insignificant statistically, the data from the two species were combined for analysis of other treatment effects. The combined data are summarized graphically in Figure 23, and the analysis of variance is presented in Table 22.

Most of the highly significant burn treatment effect was due to the moderate fuel level. Survival was not statistically significantly lower in the light fuel plots than in controls, while the moderate fuel plot mean was significantly lower than the combined mean of control and light fuel load plots.

Comparison of the differences at each date in mean emergence between the light fuel plots and their associated controls, and between the light and moderate fuel plots, suggest that late burning had a greater impact than early burning. The overall interaction term is just short of statistical significance, while one orthogonal partition of it yields a statistically significant interaction between date and moderate fuel level versus the control-light fuel average. Mean emergence in late-burn area controls exceeded that in early-burn controls by more than the LSD for $\alpha = 0.05$, suggesting that nonburn-related mortality was lower in all plots in the former area. Absence of an overall date effect, then, could be the result of opposing differences in burn and nonburn-related mortalities in the two areas.

Figure 24. Experiment IV results expressed as burn treatment difference scores (number of treatment subplot survivors minus number of same whole plot control subplot survivors). Actual survival in controls and treatments is shown in Figure 23. Larger negative difference values indicate greater treatment mortality relative to controls. Direction of the difference was chosen to make relationships readily comparable to their depiction in Figure 23. Note that early burn means have been shifted upwards relative to late burn means, compared with their positions in Figure 23, suggesting that had the effect of location of nonburn related survival been properly controlled for, the expected less severe impact of early burning would have been confirmed. Only the effect of fuel level is statistically significant in these data, however (Table 23).

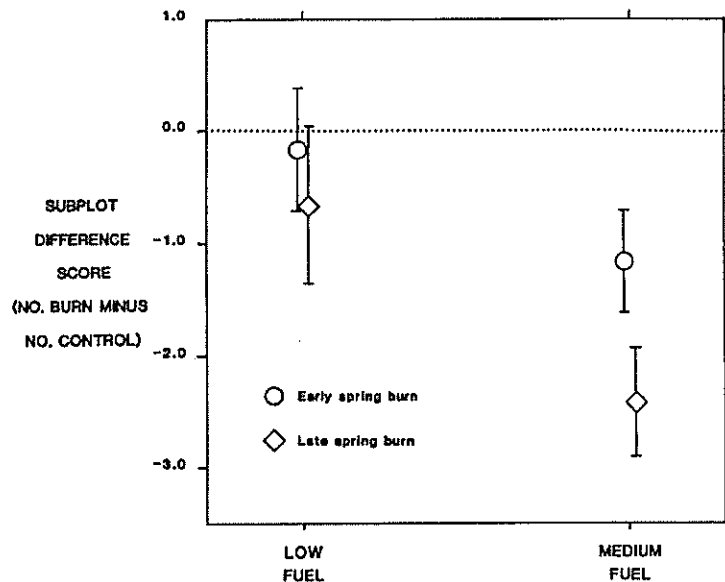


Table 23. Analysis of variance of Experiment IV differential emergence data summarized in Figure 24. A square root transformation was applied to the data (after addition of a constant to make all scores positive) before analysis.

Source	df	Sum of Squares	Mean Square	F	P
Early vs Late Burning	1	0.9337	0.9337	2.242	0.15
Whole Plot Error	22	9.1570	0.4162		
Light vs Moderate Fuel	1	1.4774	1.4774	19.992	<0.001
Date X Fuel	1	0.1784	0.1784	2.414	0.13
Subplot Error	22	1.6256	0.0739		

The differential survival data, corrected for the nonburn-related location effect, are summarized in Figure 24, and the analysis of variance is presented in Table 23. Late burn means were lower than early

burn means for both fuel levels, with the difference greater for the moderate level. However, both the overall date effect and the interaction between date and fuel level fall short of statistical significance.

DISCUSSION

LIFE HISTORY

IMMATURE STAGES

Development in both species is generally similar to that described for other *Hesperia*, although the number of larval stadia is greater than typical (six normal, five the common variant) (MacNeill 1964). The factors responsible for variation in the number of larval stages to pupation have not been identified for any *Hesperia*. In *H. dacotae* it seems clear that it is the number of pre-diapause stadia that varies (four or five), while post-diapause development consists of two additional larval stadia regardless of the diapausing instar.

The nearly identical size of fourth and fifth instar head capsules in *H. dacotae* suggests that the fourth instar size is critical for entering diapause and that a larva reaching this point well before the onset of cold weather will continue to feed enough to support metabolic needs and undergo another stationary molt before diapausing. McCabe (1981) reports the fourth to be the usual overwintering instar, perhaps reflecting the higher latitude of his study sites where the average interval between the third molt and cold weather would be shorter.

The sample of pre-diapause fifth instar head capsules from *H. ottoe* suggests that a fourth molt before diapause is a stationary one in this species also, but the data are too limited (N = 5, all from captive reared larvae) to be convincing. The greater temporal spread of adult emergence in *H. ottoe* may involve the ability of third instars to enter diapause. Eggs laid late in the flight period hatch in late August and early September, and it is doubtful that all can complete the third stadium before the end of the season.

The minimum time to the third larval molt in captive rearing was about 35 days from hatch, and under the cooler field conditions significantly longer could have been required. Non-senescent warm season grass tissue became increasingly scarce during late September and unavailable by mid-October in the years of the study. If larvae not making it into the fourth stadium by winter died, greater synchrony in adult emergence should have been observed, similar to that in *H. dacotae*.

The pattern of oligophagy within the Poaceae that

I found in these skippers is a common one in grass feeding specialists, probably related to the minor role played by chemical defenses in this plant family (Bernays and Barbehenn 1987). In contrast, MacNeill (1964) found considerable fidelity within local populations of the *Hesperia* he investigated to single grass species in nature, despite their ready acceptance of other grasses in captivity. He found bunchgrasses invariably to be the hosts in nature, and he proposed that the basis for the observed specificity is adaptation of larval habits to the architecture of bunchgrasses. The dense cluster of erect blades and the mass of persistent basal material may be requirements for successful shelter construction, and the close proximity to the shelter of an abundance of edible grass blades minimizes the exposure to natural enemies of larvae foraging for food.

The greater diversity of grasses used in nature by the two *Hesperia* in my study may reflect differences in the character of the vegetation between this prairie grassland type and the western grasslands where MacNeill worked. A notable feature of the dry-mesic prairie here is the diversity and fine-scale interspersed grass species, with several bunchgrasses predominating. It would be interesting to compare the host-use pattern of *H. ottoe* in the less diverse, structurally rather different sand prairies where it also occurs.

The particular shelter dwelling habits of these two skippers are probably important determinants of their restriction to dry and dry-mesic native grassland habitats within their ranges. The dominant grasses of mesic tallgrass prairie, *Andropogon gerardii* and *Sorghastrum nutans*, would appear to pose formidable challenges to early instar survival. The usual large stature of these grasses would require the slow-moving larvae to travel considerable distances from shelters to food, and the frequent hairiness of stems and sheaths in the former species would further impede their progress (personal observation). The size of blades would also make harvesting difficult or impossible.

Larvae would probably not be able to survive grassland where the exotic *Bromus inermis* dominates because of similar problems with its size and because the structure of widely spaced stems at the soil surface resulting from its strongly rhizomatous habit may reduce the effectiveness of shelters. Furthermore, this is a C₃ grass that

becomes senescent during mid and late summer, or even completely dormant in dry years (personal observation).

The other major dominant of disturbed upland grasslands in the midwest, *Poa pratensis*, although of a more appropriate size for these skippers, is also a C₃ species with the same pattern of midsummer senescence or dormancy.

The different types of shelters constructed by the two species during their early stages could produce different patterns of host use, resulting in differences in the habitats each can exploit. In particular, the elevated leaf-blade shelters of *H. ottoe* might allow it to be more successful in mesic prairie as travel problems from shelter to food would be less than for *H. dacotae*. However, I never observed evidence of oviposition in the mesic parts of the study site by *H. ottoe*, nor does the species seem ever to occur in true tallgrass prairie. The larva of *H. ottoe* is unusual in the genus (perhaps unique) in not producing hydrofuge material during the stadium before pupation, which suggests a close association with very well-drained habitats.

ADULTS

The only substrate characteristic that appears to be important to ovipositing *H. dacotae* is a surface wide and smooth enough for the relatively large egg to adhere firmly to. Leaving out oviposition on *E. angustifolia*, the same appears to be true for *H. ottoe*. This again differs from the pattern in the *Hesperia* MacNeill (1964) studied, which in most cases oviposit selectively on the particular grass that serves as the larval host. It is probably related to the difference in host-use patterns of larvae of MacNeill's species compared to the two in my study.

Similar oviposition without regard to host potential of the actual substrate has been reported for several grass feeding satyrid butterflies that apparently feed opportunistically on a number of grasses in nature (Wiklund 1984, Shreeve 1986). Wiklund (1984) concluded that the "superabundance" of suitable hosts in the grassy habitat where these butterflies occur makes the costs associated with leaving larvae to find their own way to food smaller than the costs in oviposition time for females to place eggs only on suitable hosts.

For the two *Hesperia* in my study, a newly hatched larva placed at random in dry-mesic prairie habitat would have a very high probability of being on a suitable host. Since females probably cannot precisely locate a good initial shelter site, their best strategy may be to simply find a good surface for securely affixing the egg within the right habitat. The other *Hesperia* that occurs at this site, *H. l. pawnee*, also oviposits here on a wide variety of grasses and forbs in the dry and dry-mesic habitat.

The use of *E. angustifolia* capitula by *H. ottoe* seems

to be something of a specialization, but its function is obscure. It is reminiscent of the behavior of certain California populations of *Hesperia lindseyi* (Holland) that oviposit on an arboreal lichen (MacNeill 1964) and *Hesperia comma leussleri* Lindsey, which oviposit on woody stems of nonhost species (McGuire 1982), although in these cases the nonhost substrates are the only ones used.

The behavior in these two taxa may be related to their overwintering in the egg stage. All eight species of Swedish butterflies that feed on herbaceous perennial hosts and overwinter as eggs avoid ovipositing on green parts of their hosts. They usually select instead sturdy substrates in the vicinity of host plants, apparently an adaptation to prevent the eggs from being displaced away from the host during the winter (Wiklund 1984).

This hypothesis does not apply to the use by *H. ottoe* of *E. angustifolia* capitula, as eggs of this skipper do not overwinter. An alternate possibility is that this plant is a reliable indicator of good larval habitat. Another is that being close to that plant's flowering stems reduces the risk of early instars being eaten by grazing ungulates. Personal observation indicates that cattle tend to avoid these stems when they have ample forage. Bison may have behaved similarly. Neither explanation obviously requires that eggs be placed on capitula, however. Yet another possibility is that eggs thus elevated above the vegetation are subject to reduced mortality from predators and parasitoids. Oviposition on *Echinacea pallida* in Illinois (McGuire 1982) suggests that this behavior may occur throughout much of the range of *H. ottoe*, but the relationship is not obligatory as the skipper occurs where no *Echinacea* species is present (personal observation).

Regular access by adults to nectar is clearly important for both skippers. Water is the most critical need. *H. l. pawnee* females inadvertently denied access to any water while confined in field cages for oviposition died within a few hours on a hot, windy day. Desiccation, not starvation, was the cause of death of these insects, which were recently emerged and had ample fat body remaining.

Carbohydrates obtained from nectar are probably also important, but the effects of deprivation would be less dramatic. In these skippers, the fat body depot of nutrients acquired during larval development is substantial at adult emergence, but the energetic demands of flight activity would probably exhaust the reserves quickly in the absence of a dietary supply of carbohydrates. For females this would divert resources from egg production (Willers et al. 1987).

It has been shown experimentally that adult carbohydrate intake significantly increases realized fecundity compared with water alone in a number of Lepidoptera (Norris 1935, Stern and Smith 1960, Watt et al. 1974, Murphy et al. 1983, Leather 1984,

Taylor and Sands 1986, Miller 1987). Age specific fecundity in these skippers declines gradually enough that adult nutrition can have a substantial impact on realized fecundities (Boggs 1986).

Amino acids are also frequently present in floral nectars (Baker and Baker 1983). Murphy et al. (1983) found that in the nymphalid butterfly *Euphydryas editha* (Boisduval), a species in which larval survival is positively correlated with egg weight, addition of amino acids to the sugar water diet of adult females reduced egg weight decline with age compared with that in females fed sugar water only. Much more research is needed, however, to determine whether this is a general phenomenon. Amino acids are present in the nectar of *E. angustifolia*, as revealed by ninhydrin staining (Baker and Baker 1973) of dried residues of nectar that I extracted, although I did not determine concentration.

The most commonly visited nectar flowers here all have relatively concealed nectar, accessible only to insects with a slender trophic apparatus about 5mm long or longer. As a result, the standing crop of nectar in these flowers is probably greater than in those flowers with more accessible nectar, making foraging on them more likely to be profitable. Available evidence indicates that both skippers are at least moderately opportunistic. In 1975, when the study area was being fairly heavily grazed and *E. angustifolia* inflorescences were uncommon, *H. dacotae* frequently visited *Cirsium arvense* (personal observation), a species that was virtually ignored during the study. The two most frequently visited species at the Felton Prairie (McCabe 1981) were infrequently (*Erigeron strigosus*) or never (*Ratibida columnifera*) utilized at Hole-in-the-Mountain despite being common. Both produce at most small quantities of nectar (I could detect none in *R. columnifera*) and their corolla tubes are short, giving an enormous population of small insects access to what there is.

With the copious supply of high quality nectar sources at my study site, there was no reason for visits to these probably quite poor nectar sources. Although McCabe (1981) presented his ranking of species on the basis of frequency of visit as a preference ranking, it may have simply reflected a scarcity of better quality sources and a superabundance of these lesser quality ones. He provided no information about relative availabilities.

The claim that *H. dacotae* does not exploit milkweeds (McCabe 1981) is not completely correct, as revealed by the two observations of visits to small *Asclepias* species and by milkweed pollinia found attached to the tarsi of several individuals. However, I never saw any use of the common, weedy milkweed *Asclepias syriaca* despite frequent checks of large patches in areas where skippers were active. I never saw *H. ottoe* visit *A. syriaca* either, even though visits to *A. viridiflora* were occasional. *Asclepias syriaca* is highly attractive to butterflies,

including many skippers, and I have no explanation for its avoidance by these *Hesperia*.

The habit of *H. ottoe* males of imbibing from moist soil may imply an additional resource requirement for this species. There is some evidence that nutrients (mineral salts, amino acids), not simply moisture, are the object of this common behavior among male butterflies (Arms et al. 1974, Sevastopulo 1974, Adler and Pearson 1982). The apparent absence of this behavior in *H. dacotae* is puzzling. All the other skippers present in this habitat except *Oarisma poweshiek* were observed on the stockpond margins.

Transfer of nutrients from males to females via the spermatophore has been found in a number of Lepidoptera (Rutowski et al. 1978, Boggs and Gilbert 1979, Boggs and Watt 1981, Rutowski 1984, Suzuki and Zalucki 1986), but generally this is accompanied by loss of the spermatophore's structural integrity, something that does not occur in *H. dacotae*. Loss of fertility with time after mating, another basis for multiple mating, does not seem to occur either. If females mate again to secure additional nutrients or to renew their sperm supply, the incidence of multiple mating should increase with female age, yet this was not true in my sample (age indexed by wing wear). Additionally, I never observed a female in copula that exhibited any scale wear, strongly suggesting all were recently emerged.

An alternative explanation is that second matings occur immediately after termination of the first, during the brief period before the female becomes refractory (Ehrlich and Ehrlich 1978). As Labine (1964) finds in *Euphydryas editha*, the physical barriers to further mating deposited by the first male (spermatophore collum and genital plug) may not be fully hardened and effective right after the insects separate. Given the density of perching *H. dacotae* males here, any female taking wing during this "window" would have a high probability of being pursued and courted. The disparity in size between the two spermatophores in many multiply-mated females in my sample is consistent with this hypothesis, as an already-filled bursa will not accommodate a second full-sized spermatophore.

This, however, suggests another possible explanation for second matings: transference of an undersized spermatophore by the first male, as will happen if the male has recently mated (Rutowski 1984, Svård 1985, Svård and Wiklund 1986, Rutowski and Gilchrist 1986). Females receiving small spermatophores may remain receptive as the result of insufficiency in the mechanical or hormonal stimuli that induce refractoriness (Labine 1964, Taylor 1968, Sugawara 1979, Stringer et al. 1985). As the condition or relative position of the two spermatophores provided no clues to the sequence of deposition, I could not determine which of the possibilities is more likely.

These aspects of female mating behavior are probably very similar in *H. ottoo*. The frequencies of multiple mating in the two other *Hesperia* species that have been investigated are close to what I found for *H. dacotae* (Burns 1968, Scott 1973a).

The persistent courtship of unmated heterospecific (even heterogeneric) females makes it clear that it is the female that determines whether copulation takes place, contrary to MacNeill (1964). Although direct proof is lacking, it is almost certain that a pheromone carried by the androconial particles from the forewing "brands" or stigmata (actually pouches) of the male acts as a species-specific chemical password without which the female will not copulate. These particles, 10 to 12 micron long segments of specialized scales, are porous and impregnated with the pheromone substance, which is probably active only in the liquid phase and so requires direct contact with the antennal sensilla of the female (Barth 1952, Sellier 1972).

Sellier (1972) concluded from indirect evidence that the antenna of the female has to contact the male stigma for the particles to reach their target, but no phase of the courtship of these skippers provides any opportunity for such contact. Airborne dispersal seems to be the more likely mode of transference to the female's antennae, with the male somehow opening or everting the pouch during wing strokes and fanning particles toward the female. The highly modified structure of the androconial scales assuring their fragmentation into minute adhesive particles would seem to be an adaptation for just this mode of transfer.

In both the studied *Hesperia*, as well as in *H. l. pawnee*, the dispersal of androconia apparently takes place during flight. Except in the cages, I never observed any post-landing wing fanning or fluttering, as reported in another "branded" skipper, *Hylephila phylaeus* (Drury) (Shapiro 1975). When *H. l. pawnee* males discovered virgin females sitting on *Solidago* inflorescence (where I had put them), they alighted and began nudging or bumping the females until they flew, and copulation occurred immediately upon termination of the ensuing pursuit flight.

Pursuits in the cages reinforced my impression from unconfined pursuits that *H. dacotae* males attempt to get just above and ahead of the female during the descent flight, a position from which the male could fan androconial particles over the female. The fluttering behavior of males around females after landing, seen in the cages, may have occurred because the normal in-flight transfer was often thwarted by the abbreviated flights possible there.

McCabe (1981) interpreted the behavior of perching males of *H. dacotae* as involving aggressive defense of mating territories. This common interpretation of the perch-chase mode of mate seeking has been challenged in general by Scott (1974b) on the grounds that males move about too freely and their intent in pursuits is not aggressive but investigative.

These were conclusions MacNeill (1964) had earlier reached regarding *Hesperia* in particular.

Both MacNeill and Scott allow that interactions between males may produce a nonrandom (over-dispersed) distribution of perching males as an incidental result. This is enough for some authors to count the behavior as territorial (Pitelka 1959, Schoener 1968, Davies 1978), but Brown (1975) argues that a distinction between behavior involving defense of fixed areas (including "ritual" defense) and other spacing producing behaviors (e.g., maintenance of an individual space or distance) is useful. While some studies conclude that the perch-chase mate seeking behavior of males of particular species of butterflies does involve territoriality in the stricter sense (Davies 1978, Lederhouse 1982, Baker 1983, Wickman and Wiklund 1983, Alcock 1983, 1985, Dennis and Williams 1987), other studies indicate that this behavior is not always territorial (Shreeve 1984, Suzuki 1976).

One indicator of whether perch-chase behavior involves territoriality is the degree of individual fidelity to perch sites. According to MacNeill (1964) perch fidelity in the *Hesperia* he investigated seems to be inversely related to male density, with a continuous circulation of individuals among perch sites being the typical pattern when densities are high. McCabe (1981) reported that *H. dacotae* males "often" return to their original perches following interactions with other males, but he did not quantify this.

My own impression from the continuous observation of fixed areas I occasionally made, during which *H. dacotae* male density was moderately high, was of something like MacNeill's "continuous circulation," but marked insects were never present to allow me to confirm this. The MRF movement data cannot be interpreted as evidence against significant periods of fixed-area occupancy because of the probability that capture (with or without marking) was disruptive of normal behavior.

However, some theoretical considerations weigh against the occurrence of territoriality in these skippers. Perches used by these skippers are abundant and do not vary in any obvious way that would affect their possessors' chances in the scramble for mates. Emerging females are widely dispersed and unpredictable in space. Even if they tend to move after emerging towards summits for mating, as has been reported in other butterflies (Shields 1967), uppermost males do not necessarily have the most favorable positions (Ehrlich and Wheye 1986, Courtney and Anderson 1986). The modeling exercises of Courtney and Anderson (1986) suggest that frequent moves up and down slope will be favored if females do not choose among males but simply mate with the first one encountered. This is a condition that the simple, very brief courtships of these skippers suggest they meet.

Whether the pursuits of other males by perching

individuals involves aggression is also controversial. Motion picture photography of male-male encounters in a satyrid butterfly have been reported to show actual physical assaults (Wickman and Wiklund 1983), but the format (Super 8) and camera speed (24 frames per second) leave room for doubt about the interpretation. MacNeill (1964) suggested that pursuing male *Hesperia* are trying to elicit a female response from the pursued insect and that the whirling engagements result when a pursued male responds to its pursuer with the same intent.

My hypothesis that the male is attempting to get just above and ahead of a pursued female to disperse androconia towards it involves only modification in detail of MacNeill's (1964) suggestion. In male-male engagements an effort by each to do this should produce a whirling ascent. Pursuits of other males in flight cages were pretty clearly courtship efforts and not aggression, as copulatory attempts usually followed landing.

On balance, the evidence seems to favor interpreting the mating systems of the *Hesperia* in this study as a form of scramble competition polygyny (Thornhill and Alcock 1983) rather than as involving territoriality. The territoriality-like features of male behavior can be explained more simply as products of indiscriminate mating effort, itself resulting from the combination of a high premium on being the first male to engage a receptive female in flight and limited visual powers. Further research is obviously needed to convincingly resolve the issue. Major areas needing study are the spatio-temporal aspects of perch occupancy by males, the details of behavior in aerial interaction, the frequency and function of multiple mating in females, and movement patterns of receptive females and whether they exercise any active mate choice.

The occurrence of mate searching in both species was unexpected, as perching has been the only mode of mate seeking reported for *Hesperia* with the exception of *H. lindseyi*, in which both kinds of behavior have been reported (MacNeill 1964, Scott 1975b, 1982). The occurrence of both mate locating tactics in one species may actually be more frequent in *Hesperia* than realized. In addition to its primary strategy of perching, *Hesperia leonardus pawnee* at my study site also commonly made rapid flying inspections of inflorescences of favored nectar plants quite similar to the inspections of *E. angustifolia* capitula made by *H. ottoe*.

The employment of more than one kind of mate seeking behavior by males within a population has been studied in at least three butterflies. Wickman (1985) found that mate seeking behavior in a grassland satyrid, *Coenonympha pamphilus* (L.), tended to vary with ambient temperature, perching predominating when temperatures were low and searching when they were high. *Ochlodes venata* (Bremer & Grey), a skipper investigated by Dennis and Williams (1987), tended to perch in the early morning and afternoon and to search during the

middle part of the day. Scott (1974a) found that the nymphalid *Poladryas minuta* (W. H. Edwards) perched on ridges and hilltops until about midday and searched near flowers more widely throughout the habitat in the afternoon.

Wickman (1985) proposed that continuous search flight in cool conditions would be inefficient or impossible because of convective heat loss from the insect's body, while basking in the boundary layer during perching could elevate body temperature enough to permit short bursts of flight. Dennis and Williams (1987) related the change of tactics in the skipper to the diel cycle of availability of newly emerged females, with energetically more costly searching reserved for the midday period of greatest likelihood of encounter. Scott (1974a) suggested that diel changes in both ambient temperatures and the distribution of receptive females might be involved.

Neither hypothesis seems satisfactory to account for the polymorphism in the *Hesperia* I studied. In *H. dacotae* searching was observed during the cooler morning hours while the late-morning to late-afternoon period in which *H. ottoe* was seen searching extends well beyond the time when newly emerged females are most likely to be encountered. Further, only a small fraction of the males adopted the search mode in these *Hesperia*, whereas in the cited studies the shifts were general throughout the populations. An intensive investigation of this phenomenon might shed some light on the factors that lead to the evolution of one or the other behavior as the predominant mode of mate locating for a species, as is typically the case (Ehrlich 1984).

In all the *Hesperia* he studied, MacNeill (1964) found mating, feeding, and oviposition to occur in different parts of the habitat, although some overlap was occasional. This was not the case with either skipper in my study. Oviposition occurred throughout the upland habitat, with no evidence that areas where male perching activity was concentrated were avoided. Almost all nectaring also occurred throughout the same habitat.

The difference between my observations and those of MacNeill may reflect differences between the distribution of critical resources in the prairie habitat here and that in typical habitats of the species he studied. *H. l. pawnee*, not investigated by MacNeill, exhibited the same degree of spatial overlap in its major activities here as did *H. dacotae* and *H. ottoe*.

The higher densities of males of both species in Units A and D in all three years of the MRR study were probably related to topographic preferences for mate seeking. The only "hill tops" in the study area occur in these units as peaks along a somewhat dissected ridge line. In all other units the slopes head onto expanses of more or less level upland, although in C there are several long, ridge-like spurs in the side slopes. I do not have any explanation for the apparent preference of *H. dacotae* females for Units A and D. Larval habitat did not appear

obviously different than in other units, nor was the density of nectar flowers always greater. Once mated, females should have no reason to remain where males are aggregated, and I would expect a more even distribution among all units, as *H. ottoa* females in fact exhibited.

The low densities of *H. dacotae*, especially males, in Unit C is puzzling. Nectar resources were probably greater in this unit than in any of the others; diversity was certainly highest here. Unit C should have been more attractive to perching males than B on account of the long spurs in the side slopes, absent from B. The *H. ottoa* males were in fact more common in C than in B, perching most frequently along the spurs. If the scarcity of *H. dacotae* here was the result of elimination during the preceding episode of heavy grazing, then either *H. ottoa* is less sensitive to grazing, or it reestablished immediately, indicating greater vagility.

While the movement data are consistent with greater vagility in *H. ottoa*, the difference is not of a magnitude that would seem to explain the difference in numbers, especially after three years. Another possibility is that the lower vigor of the grasses and sparser cover the first year after grazing were more attractive to *H. ottoa*, and less attractive to *H. dacotae*, than the rested prairie in the other units. However, by the third year of the MRR study recovery of the grasses had eliminated any obvious difference between C and the others in this regard and there was still no increase in *H. dacotae* relative to *H. ottoa*.

The capture rate data do not reveal an effect of burning on habitat attractiveness despite the much greater densities of nectar flowers in burned units than in those with a heavy litter accumulation. However, the burn unit divisions and the schedule of burning were not well designed to separate the effects of burning from the influence of topography and past land use. The greater per-unit-area oviposition rates on *E. angustifolia* capitula by *H. ottoa* in the burned and grazed habitat compared with the undisturbed one are inconclusive as indicating female preference for the former because I could obtain no data on the relationship between use of capitula and total oviposition in an area. Definite answers to questions about the relationship between habitat quality and fire rotation will probably require finding an efficient (and unbiased) sampling method for immature stages.

POPULATION ASPECTS

The MRR data afford a very limited view of adult movements. Because of the infrequency of multiple recaptures, little can be inferred from these data about typical ambits of activity or lifetime tracks. The evidence does suggest that *H. ottoa* moved about the whole site rather freely, but even though *H. dacotae* may have been more reluctant to cross the large tributary ravine, crossings were not rare,

making it unlikely that either skipper occurred as independent demographic units in the two separated areas.

Because I did not conduct MRR sampling outside the site boundary, I obtained no direct evidence regarding movement across the boundary. It is possible that the skipper "populations" in the site were in fact constantly changing local samples of much more extensively distributed populations of highly vagile adults.

This type of population structure has been documented in the grassland satyrid butterfly *Erebia epipsodea* Butler (Brussard and Ehrlich 1970a,b), and two common satyrids at this site whose size and flight behavior make their movements easy to observe appeared to fit this pattern also. In all three of these satyrids, males never perch but continuously search for newly emerged females (Brussard and Ehrlich 1970b, and personal observation). At least in *E. epipsodea* there is no evidence of aggregation for mating purposes (Brussard and Ehrlich 1970a).

In the case of the skippers, males may have aggregated within the site from a more extensive area and remained there for extended periods, whereas females dispersed shortly after mating. Scott (1975a) found evidence for just such a behavioral difference between the sexes of several butterflies in the greater vagility indices of females than males obtained by MRR techniques. Intercapture distances in my study were not consistently greater for females in either *Hesperia*, but the sampling area may have been too small for these distances to reflect the hypothesized behavioral difference. However, a difference in residence rates should have been detectable, and none was.

The scarcity of these skippers nearly everywhere I checked outside the study area provided circumstantial evidence against substantial exchange with neighboring grassland habitat. In the heavily grazed stretch continuing for about 1.5 km north of the preserve I never saw any skippers, even right across the fence, although they were present in a large, moderately grazed pasture farther north. To the south there was an approximately 4 ha area immediately adjoining the preserve where densities were comparable to those in the study area, but beyond this for another 1.5 km both skippers were extremely scarce. They were also quite scarce along the tributary valley east of the study area. Although I never checked the slopes across the main valley, almost all were very heavily grazed during the study.

The skippers in the small area just south of the preserve were almost certainly part of the populations estimated by the MRR study. Habitat is continuous along part of the boundary with the preserve, separated only by a narrow gravel road that creates no deterrent to movement. Males of

H. l. pawnee perched on vegetation along its edges and even on stones in the road itself, chasing freely back and forth across it. I observed one marked *H. dacotae* female in this area south of the road during one of the infrequent, brief checks I made.

Two factors probably contributed to the abundance of skippers in the small area just south of the preserve, compared with their very low densities in the rest of the pasture continuing south. One was the better condition of the prairie vegetation, which was similar to that within the preserve, while exotic grasses were more common and nectar flowers sparse in the rest of the pasture. These differences were the result of past differences in grazing management.

The second factor was topography. A long, ridge-like spur occupies much of the area where the skippers were (see Figure 1), and they were concentrated along it. Although the only evidence I have is the one incidentally observed, marked female that had moved from the study area, it seems likely that skipper densities in this small area were maintained by immigration from the study area.

The approximate age independence of θ (residence rate) over most of the adult life span is similar to findings in other butterflies (Douwes 1970, Watt et al. 1977, Brown and Ehrlich 1980, Brakefield 1982, Gall 1984). Most of these studies also noted a tendency for the rate to decline towards the end. None of the other studies included insects never recaptured after initial capture (0 days in residence) in their analysis of recapture decay rate, but this number can be determined in several of these from other data provided in the reports, and it is always well above the regression line through the other points as in my data sets.

Two possibilities for the anomalously high initial loss rate are that marking produced a brief increase in the probability of death or emigration, or that the sampled populations consisted of two kinds of individuals, one dispersing widely and the other staying put. Tests of the effect of marking on recapture probability were negative, but as noted, the small numbers of multiple recaptures limits the sensitivity of these tests. There is no suggestion of bimodality in the distributions of intercapture distances (Figure 16) as one might expect under the second hypothesis, but an effective test would require a greatly expanded sampling area.

From all of the estimates of residence rates—Jolly-Seber, Fisher-Ford, and residence decay analysis—a value for males between 0.70 and 0.85, corresponding to an average residence time between three and six days, seems most plausible for both species. The estimates for females are more variable, being based on sparser data, but most are between 0.70 and 0.90, with no species difference apparent. The corresponding expected residence times, between three and ten days, would permit females to lay on average between 40 and 70

percent of their potential egg supply, or 80–170 eggs, based on the preliminary age-specific fecundity curve obtained for *H. dacotae* (Figure 8).

These residence values fall within the range of residence expectancy estimates in Scott (1973c) for non-diapausing adults of a number of temperate butterflies. In the latter, expectancies of less than four days are associated with high rates of emigration, and given the estimated potential life span of three weeks for the skippers in this study, average residence times toward the low end of the range of estimates I obtained strongly suggest substantial emigration.

The discrepancy between the balanced sex ratios at adult emergence in the reared material and male bias in the estimated realized ratios of the field populations is similar to results obtained in studies of many butterflies (Ehrlich 1984). In several cases the imbalance in the field has been found to be only apparent, the result of lower female catchability (Ehrlich 1984). In my study, the imbalance is considerably greater in *H. ottoe*, for which I have evidence that female catchability is lower, than in *H. dacotae*, for which unequal catchabilities are not indicated. It does appear, then, that the smaller estimates of adult generation size in females than in males are at least partly the product of lower female catchability in *H. ottoe*.

However, a real difference in numbers could easily have resulted from a combination of higher pre-adult and adult mortalities in females, as Ehrlich et al. (1984) found to be the case in *Euphydryas editha*. The additional mortality occurring during the longer female development time in this butterfly resulted in fewer female than male adults emerging. They also found evidence for higher female mortality during the teneral period following emergence.

Development time in the skippers is 4–6 days longer for females than males, providing the opportunity for additional pre-emergence mortality in the former. The plot enclosures minimized this in the reared groups by excluding most natural enemies. Skipper females may also suffer higher mortality than males after emergence because their greater weight requires wing hardening be more complete than in males for effective flight to be possible. Differential mortality this early in adult life would not be reflected in the residence rate estimates because it would have occurred before adults usually appeared in MRR samples.

Although lower catchabilities may have played some role in depressing the estimates of *H. ottoe* numbers relative to those of *H. dacotae*, there is no doubt that there was a real difference in the abundance of the two species. Behavioral differences between males, especially, were too small to explain the magnitude of the difference in capture rates evident from comparison of Figures 13 and 14, nor were the recapture rates for males of the two species evidently different.

I did not determine the basis for the difference in population size, but comparison of the life history details of the two is suggestive. Potential fecundity does not appear to be lower in *H. ottoe* than in *H. dacotae*, nor were resource levels obviously lower for the former. Nothing I observed suggested competitive suppression of *H. ottoe* by the other.

Behavioral differences could result in greater mortality in *H. ottoe* during development. Oviposition on *E. angustifolia* and the more exposed shelters of early stage larvae are the most obvious ways in which this skipper differs from *H. dacotae*, and both differences would plausibly increase the likelihood of loss. Greater overwintering mortality in *H. ottoe* is also possible, as the species is near its northern range limit in this area. The limit appears to be climatic, as appropriate habitat is found much farther north, and this skipper may not be as well-adapted to the seasonal regime as the more northerly *H. dacotae*, which is in the center of its range at this site.

The possibility that a fraction of the larvae of *H. ottoe* fail to reach the fourth stadium and are unable to diapause before food becomes unavailable would be a manifestation of its relatively poorer climatic adaptation. More speculatively, *H. ottoe* could have a greater tendency, perhaps density dependent, to disperse. Although the MRR residence rate estimates do not indicate a difference of this kind, my data are not good enough to rule it out.

McCabe (1981) reported that *H. dacotae* does not seem to fluctuate in abundance very much from year to year, and the results of this study, although from too brief a period to effectively test McCabe's observation, are at least consistent with it. I have not found any reference to fluctuation or lack of it in *H. ottoe*. That the latter decreased during the study, while *H. dacotae* did not, lends a bit of additional support to the supposition that *H. ottoe* is more susceptible to several mortality factors during larval development, as this would make it also more responsive to variations in their levels.

This study presented no obvious candidate for the cause of the decrease in *H. ottoe*. In particular, greater overwinter mortality in the years 1980 and 1981, compared to 1979, is unlikely. Late fall and winter regimes in the area were milder in these two years than in 1979. Longer term monitoring of dynamic trends in *H. dacotae* and *H. ottoe* could contribute significantly to an understanding of their ecology.

I did not learn enough about natural enemies to afford any basis for speculation about their role in skipper population dynamics. It is at least plausible that prairie burning reduces natural enemy population levels. One probably significant predator on adults, the ambush bug (*Phryma* sp.), suffered nearly total mortality in spring burns. By the time winged adults had developed and begun to migrate into burned areas, the skippers' flight periods were

substantially over. On the other hand, crab spider numbers were not obviously depressed in burned areas.

Fluctuations in litter levels could affect skipper abundance in several ways. Soil moisture and atmospheric relative humidity near the soil surface increase with litter buildup in prairie, and soil temperatures are significantly lowered (Ehrenreich and Aikman 1963, Old 1969). McCabe (1981) asserts that high humidity is an important cause of mortality in *H. dacotae* larvae, but his basis for this is only the remark in MacNeill (1964) that *Hesperia* larvae in that study (which did not include *H. dacotae*) often developed a bacterial septicaemia when reared under very humid conditions.

Humidity induced disease was not a significant problem in my rearing of either species, and it seems implausible that high humidity should be a problem for them as most of their larval development is spent in shelters where the atmosphere is probably close to saturation most of the time. However, lower temperatures may be an important factor even if disease is not, as larval growth rates are strongly influenced by temperature (Scriber and Lederhouse 1983). In some Lepidoptera, temperature optima for larval growth have been found to be as high as 30–35° C (Porter 1982). For the *Hesperia* species in this study, prolongation of growth and metamorphosis in the spring, where heavy litter retards soil warming, could result in higher mortality from the longer exposure to mortality factors.

Skipper population levels could be affected by the cycle of litter buildup and removal, through the probable effects of the latter on the quantity and quality of critical resources (Dempster and Pollard 1981). The likelihood of newly hatched larvae quickly finding good shelter sites when litter levels are high may be considerably lower than in recently burned prairie because of lower grass stem densities and longer, more slender leaves and stems under the former condition (Hulbert 1969). Nutritional quality of grasses in stagnant prairie is also poorer than in recently burned prairie (Smith and Young 1959).

Flowering rates in most forbs are suppressed by litter buildup. Following the first prescribed burn of Unit D the number of flowering stems of *E. angustifolia* in two 15 m x 30 m permanent plots increased tenfold from the level of the previous year when the litter level had been moderately heavy.

Reduced local availability of nectar has been found to increase the likelihood of female dispersal in *Euphydryas editha* (Ehrlich et al. 1984), and a similar effect is probable in the skippers given their need for water during the day. Because the decline in age specific fecundity in the skippers is moderately gradual, changes in residence expectancy have the potential to significantly affect realized fecundities within the site.

Longer term changes in the character of the habitat at this site that could lead to declines in the populations of the two skippers are possible with the complete exclusion of large animal grazing. Both species are reported to be intolerant of grazing (Lindsey 1942, McCabe and Post 1977, McCabe 1981), but this needs qualification. Both do apparently decline or disappear during heavy grazing, probably owing importantly to the scarcity of nectar flowers, and they are permanently eliminated by the vegetation changes induced by prolonged overgrazing. These changes include the replacement of the native bunchgrasses by rhizomatous C_3 exotics (especially *Poa* species), or by native shortgrasses on more xeric sites farther west, and a marked reduction in forb diversity (Voight and Weaver 1951).

Prairie on steeper topography is more resilient than on level sites (Herbel and Anderson 1959). The effect of moderate grazing in steeper sites is to increase the importance of midgrasses relative to tallgrasses (Drew 1947, Kelting 1954, Dix 1959, Herbel and Anderson 1959), an effect that may be favorable for the skippers.

Although the midgrass aspect of the prairie along the Hole-in-the-Mountain valley slopes predates the pasturing of domestic livestock on it (Sheldon 1910), there is a decidedly greater tallgrass component in a few small areas that have remained outside pasture fences than in equivalent sites within pastures, and midgrasses are also taller and more robust. A strong recovery of tallgrass vigor in the more mesic parts of slopes in the study area had become evident only five seasons after grazing had been ended. These observations indicate that without any grazing there will be a general increase in canopy height and a significant fraction of the area that was suitable for the skippers during my study will develop a tallgrass character.

There may also be a long term reduction in the floral resource for adults. Several of the more frequently used nectar plants during the study, notably *Verbena stricta*, are favored by some grazing disturbance (Voight and Weaver 1951) and had begun to decline noticeably during the research. The abundance of *Echinacea angustifolia* at the time of my study may have owed something to the site's grazing history. Weaver (1954) classifies this species as a decreaser with grazing, but Smith (1940) reports it to be more common in "overgrazed" prairie pastures than in "good" ones in Oklahoma.

Finally, without cattle activity the broad, muddy margins of the stockpounds will revegetate, and loss of this resource for male "puddling" could adversely affect *H. ottoe*. Murphy and Wilcox (1986) found that the number of butterfly species present in riparian habitat "islands" in an arid region was greater where a puddling resource was present. The only other place where *H. ottoe* males were observed in this activity was the gravel boundary road, but this will be only intermittently suitable, following rains.

EFFECTS OF BURNING

The burning experiments provide substantial evidence that when fuel levels are within the low to moderate range typical of the drier prairie at this site, early spring fires will not produce enough mortality in skipper larvae to cause concern. This is consistent with the sublethal temperatures measured 5 mm below the surface during early spring burns in Experiments I and III. Further confirmation comes from the early spring burn of the entire habitat in 1981, which resulted in no marked reduction of skipper population levels compared with 1979 when only a small part was burned.

The high skipper mortality observed in the moderate fuel load plots in Experiment III would appear to conflict with this conclusion. However, the result in this experiment was probably an artifact of special conditions produced by the burning apparatus that would not occur during normal open burning. This mortality occurred in spite of generally sublethal temperature maxima at larval depths. During inspection of these plots immediately after burning I found a number of incinerated larvae on the surface, indicating that they had crawled up out of their shelters and were killed by the intense heat at the surface.

Tashiro et al. (1983) reported that sod dwelling larvae of several Lepidoptera species, including a skipper, crawl upwards from their subsurface shelters when flooded briefly with an irritating detergent solution. A dense, yellowish smoke saturated the fuel matrix within the burning ring used in Experiment III as flames at first spread slowly from the ignition point, and this could have been a similar irritant stimulating upward crawling.

Oxygen starvation is another possible cause of this behavior. In natural grassland fires, convection patterns produce a flow of oxygenated air close to the soil surface into the flame front. Openings in the lower part of the sheetmetal barrier ring meant to allow this air flow were evidently inadequate. A further difference from open burning conditions was the persistence of masses of glowing, carbonized fuel on the soil surface well after visible flame was gone. In open, moving fires these are rapidly dispersed by air currents.

The shallow subsurface temperatures measured in the heavy fuel load plots in Experiment III were high enough that larvae would have perished even if they remained in their shelters. Therefore open burns with this much fuel present probably produce devastating mortality. But, fuel loads this high should be unusual in habitats where larvae of these species occur. High plant mortality in the heavy fuel load plots, especially of *Andropogon scoparius*, indicates that fire intensities exceeded the normal range for the habitat type, which usually produces little mortality in native species.

Unfortunately, these experiments do not shed

satisfactory light on the question of how much the timing of spring burns relative to larval phenology affects the risk of mortality. Only Experiment IV supplied any usable data. The results are consistent with the expectation that late spring burns will produce higher mortality than early ones because of the different locations of immatures at the two times, but the differences were not great enough relative to the variability within treatments (exacerbated in the derived data set) to permit a confident conclusion.

It appears that a late spring burn with fuels equal to the moderate level of this experiment will have a devastating effect, with earlier spring burning possibly affording some amelioration. The "moderate" fuel level of this experiment is slightly greater than the probable equilibrium level for most of the habitat at this site, based on the measurements I made at a nearby undisturbed prairie in conjunction with Experiment III. It is almost equal to that reported for a northern Iowa tallgrass prairie (550 gm^{-2}) (Ehrenreich and Aikman 1963).

In the low fuel level plots, fire intensity was probably lower in the later burn than in the early one, so that greater larval exposure did not result in much increase in mortality. Because of the absence of accumulated litter, new growth constituted a significant fraction of the fuel by the time of the late burn; it was negligible at the early date. This, combined with cooler air temperatures than during the early burn, prevented fire from readily propagating, and I had to make repeated ignitions to burn off the whole area containing the plots. Considerable amounts of unburned material remained in these plots compared with the complete combustion at the early date.

Ordinarily, several years will elapse between prescribed burns, making these very low fuel conditions atypical except possibly for the driest exposures. Obviously, investigation of fuel levels intermediate between the two in this experiment is needed.

The failure of Experiment IV to detect a difference between the two skippers in susceptibility to spring burning has to be regarded cautiously, as the power of this experiment was low to detect any but large effect sizes at the significance level used (Cohen 1969). However, because of the close similarity in larval habits of the two species in the spring, any difference between them in the effects of burning at this time is probably small, too small in fact to be significant for management purposes. Summer fires, when *H. ottoe* larvae are in leaf-blade shelters and those of *H. dacotae* are in subsurface burrows, will undoubtedly cause greater mortality in the former. Although prescribed burning for prairie management is not ordinarily done in midsummer, hay mowing at this time, which is more common, might cause significant mortality in *H. ottoe*.

The effects of fall burning need direct investigation. The subsurface concealment of larval shelters in the

fall is comparable with that in early spring; once feeding has ceased it is identical. However, soil moisture levels are likely to be lower and soil temperatures higher in the fall, providing less buffering of the energy input from a fire.

Fall burning may have an additional impact through increased stress on overwintering larvae deprived of the insulating value of litter and standing dead vegetation, which helps to hold snow cover (Ehrenreich and Aikman 1963). Crawford and Harwood (1964) attribute reduced abundances of sod dwelling Lepidoptera in Washington grass seed fields burned after harvest to such increased winter exposure.

It is possible that the effects of the sudden destruction of food in a late season burn would be serious on larvae that are still feeding. Regrowth of warm season grasses would be negligible and larvae might be forced to initiate diapause prematurely or starve, reducing their chances of successfully overwintering. Late fall burning would avoid this complication. An early spring burn probably has little potential for an adverse effect of this kind because of both the rapid subsequent growth of warm season grasses, and the initially low feeding rate of larvae.

During the final two larval stadia, however, when feeding rate is high, larvae might not be able to tolerate the sudden removal of all food. If they begin to migrate in search of live grass they would be highly exposed to predators and parasitoids. In my experiments, the plot enclosures protected them from natural enemies, so that wandering, unless it increased the likelihood of starvation or desiccation, would not have resulted in an increase in mortality. I never saw wandering larvae within the enclosures following late burns, but I did not check them at night. I did not find any larvae that died of starvation or desiccation in these plots.

MANAGEMENT IMPLICATIONS

The similarity between life histories of the two skippers means that management considerations will be largely identical for both. The effects of litter buildup between burns on grass growth and nutritional quality, on microclimate experienced by larvae, and on flowering rates in nectar plants, are probably negative, although no experimental tests confirm this. Division of a site into several management units burned in a rotation that assures at least one unit with no more than three growing seasons since the last burn will reduce the potential for these factors to depress population levels.

Division is also the obvious strategy to minimize the threat of burning itself by assuring that a substantial fraction of the population be unexposed to fire in any prescribed burn. For division to be effective in this, actual skipper habitat within a site has to be determined so that it will be divided among the units.

Rotation should allow sufficient time for numbers to rebuild in the burned area before it becomes the unburned refugium. The minimum interval is a single complete generational cycle, but whether this is enough will depend upon population size and how readily adults will move among the divisions.

For my study site, a good division would be into two units more or less equally sharing the long ridge line between the main valley and the tributary ravine, as *H. dacotae* abundance was clearly greatest along this ridge. These could be burned in alternate years given the large numbers of both species and the free movement of adults along this ridge. With this division, burning alternate units every third year would be the longest rotation satisfying the desideratum that habitat with no more than three growing seasons since the last burn always be available.

No general results emerge from this research regarding what may constitute a barrier to dispersal for either of these skippers. In situations where habitat areas in different proposed burn units are not continuous additional study to determine how much movement occurs between them should be conducted.

Although it can not be concluded from these burning experiments that late spring burning causes higher mortality than early spring burning, the prudent course is to assume that late spring burns are likely to cause very high levels of mortality, and so to burn smaller fractions of the habitat at this time.

A method of determining the proportion of the population likely to be in surface shelters at any point in the spring is needed. Intensive monitoring of post-diapause larvae in the field will be required to develop this. Phenology of selected plants in the habitat provides a more practical index of development than actual degree-day accumulation because of the instrumentation needed for the latter. An additional hazard of late spring burning is that it delays flowering of early and midsummer blooming forbs, even to the point that those that were the most important nectar sources in this study will not begin to bloom until near the close of the flight period of *H. dacotae* (personal observation).

Fall burning may pose a greater risk than burning in spring. An early fall burn (before mid-September at this site) will catch a substantial fraction of the *H. ottoe* population still in elevated shelters, and mortality in this group of larvae would probably be nearly total. Whether burning later in the fall still involves a sufficiently greater risk of mortality to warrant more stringent precautions than are adequate for spring burning will require direct experimental investigation.

If the populations of these skippers decline to persistently lower levels than were present during the study, reintroduction of episodic grazing should be tried on an experimental basis. As the grazing will

probably have to be heavy during the episodes to have the desired effects on vegetation structure, precautions regarding division of the site, with only partial treatment during a single skipper generation, should also be followed in using grazing unless research shows them to be unnecessary.

For sites where fuel loads are typically heavier than in the steeply rolling, thin soil prairie of the study site, greater precautions should be observed in the form of restricting burning to earlier dates in spring or later in fall, and with greater subdivision if possible. Similar precautions are called for where skipper numbers are low, either because of small habitat area or marginal quality. In some situations it may not be practical to use fire in site management without an appreciable risk of skipper elimination.

McCabe (1981) recommends late season mowing as the ideal management for prairies that support *H. dacotae*. This should cause little skipper mortality except possibly when *H. ottoe* larvae are still in elevated shelters. However, mowing is ineffective in reducing the abundance of exotic grasses such as *Poa pratensis*, *Phleum pratense*, etc., and may even facilitate their invasion (Weaver and Fitzpatrick 1934, Conard 1954, Christiansen 1972, Hover and Bragg 1981). There may also be a hay disposal problem, especially in years with good tame hay yields. Finally, topography of many sites, the study site being a good example, make mowing them difficult or impossible.

Despite these drawbacks, mowing may have a useful place along with burning in prairie management. Annual haying, especially if done during the growing season, may improve the quality of mesic and dry-mesic prairie as habitat for these skippers by reducing the vigor of the vegetation and favoring midgrasses relative to tallgrass species (Kucera 1956, Gardner et al. 1957). The effects of such an annual haying may be regarded as somewhat artificial from the perspective of natural area preservation, but less frequent mowing might still be beneficial to the skippers. This mowing might be thought of as providing a partial analogue of the episodic bison grazing that was part of the original natural system.

For smaller sites where moving livestock on and off for a brief period of intensive grazing might be difficult, haying would provide a practical alternative. To be maximally effective, mowing might have to occur before senescence of warm season grasses. This could, however, increase the risk of *H. ottoe* mortality as well as eliminate nectar sources for species of late summer prairie *Hesperia*. Subdivision would again be prudent. Haying after grass senescence provides a low risk alternative to burning for removing accumulated litter and rejuvenating prairie vegetation (although without the exotic-suppressing effects of fire), and thus could be used in combination with burning to maintain a larger proportion of a site in favorable condition for the skippers than would be possible with burning alone.

APPENDIX

THE JOINT RESIDENCE-CATCHABILITY TEST OF TABASHNIK (1980)

This procedure provides a means of evaluating both the equality of catchability and of residence rate between the sexes (or any other pair of subgroups within a population) from the observed recapture proportions.

Preliminary definitions are:

- ${}^m\theta_i$ = residence rate for males from day i to $i + 1$
- mP_i = probability for males of capture on day i (catchability)
- ${}^mR_{ij}$ = probability for males of recapture in day j of day i releases
 - = ${}^m\theta_i \times {}^m\theta_{i+1} \times \dots \times {}^m\theta_{j-1} \times {}^mP_j$
 - (${}^f\theta_i, {}^fP_i, {}^fR_{ij}$ are the analogues for females.)
- α_i = relative catchability of males to females on day i
 - = ${}^mP_i / {}^fP_i$
- λ_i = relative residence rate of males to females on day i
 - = ${}^m\theta_i / {}^f\theta_i$

The critical assumptions are that relative catchability and relative residence rate are both constant:

$$\alpha_i = \alpha \text{ and } \lambda_i = \lambda \text{ for all } i$$

Then for any interval $j - i = t$

$${}^mR_{ij} / {}^fR_{ij} = \lambda^t \alpha$$

In a typical MRR study, for most values of t there will be more than one pair of days i and j supplying an observed ratio of recapture proportions after t days. Tabashnik's procedure "collects" all these ratios for each value of t in the expression:

$$\Sigma {}^mR_{ij} / \Sigma {}^fR_{ij} = \lambda^t \alpha$$

where the summations are over all intervals $j - i = t$. Taking logarithms yields the linear expression:

$$\text{Log} (\Sigma {}^mR_{ij} / \Sigma {}^fR_{ij}) = t \text{Log } \lambda + \text{Log } \alpha$$

REFERENCES

- Adler, P. H., and Pearson, D. L. 1982. Why do male butterflies visit mud puddles? *Can. J. Zool.* 60:322-325.
- Alcock, J. 1983. Territoriality by hilltopping males of the great purple hairstreak, *Atides halesus* (Lepidoptera:Lycaenidae): convergent evolution with a pompilid wasp. *Behav. Ecol. Sociobiol.* 13:57-62.
- Alcock, J. 1985. Hilltopping in the nymphalid butterfly *Chlosyne californica* (Lepidoptera). *Am. Midl. Nat.* 113:69-75.
- Anderson, R. C. 1982. An evolutionary model summarizing the roles of fire, climate, and grazing animals in the origin and maintenance of grasslands: an end paper. In: *Grasses and Grasslands: Systematics and Ecology*, eds. J. R. Estes, R. J. Tylr, and J. N. Brunken, 297-308. Norman, OK: University of Oklahoma Press.
- Arms, K., Feeny, P., and Lederhouse, R. 1974. Sodium: stimulus for puddling by tiger swallowtail butterflies, *Papilio glaucus*. *Science* (Washington, DC.) 185:373-374.
- Baker, H. G., and Baker, I. 1973. Amino acids in nectar and their evolutionary significance. *Nature* 241:543-545.
- Baker, H. G., and Baker, I. 1983. A brief historical review of the chemistry of floral nectar. In: *The biology of Nectaries*, eds. B. Bentley and T. Elias, 126-152. New York: Columbia University Press.
- Baker, R. R. 1983. Insect territoriality. *Annu. Rev. Entomol.* 28:65-89.
- Bancroft, T. A. 1968. *Topics in Intermediate Statistical Methods. Vol. I.* Ames, IA: Iowa State University Press. 129 p.
- Barth, R. 1952. Estudos sobre os órgãos odoríferos de alguns Hesperidae Brasileiros. *Mem. Inst. Oswaldo Cruz* 50:423-501, Figs. 1-47.
- Begon, M. 1979. *Investigating Animal Abundance: Capture-recapture for Biologists.* Baltimore: University Park Press. 97 p.
- Bent, A. C. 1942. Life histories of North American flycatchers, larks, swallows and their allies; order Passeriformes. *Smithsonian Institution. U. S. National Museum Bull.* 179. Washington, DC.: Government Printing Office. 555 p.
- Bernays, E. A., and Barbehenn, R. 1987. Nutritional ecology of grass foliage-chewing insects. In: *Nutritional Ecology of Insects, Mites, Spiders, and Related Invertebrates*, eds. F. Slansky, Jr., and J. G. Rodriguez, 147-175. New York: John Wiley and Sons.
- Bigalke, R. C., and Willan, K. 1984. Effects of fire on faunal composition and dynamics. In: *Ecological Effects of Fire in South African Ecosystems*, eds. P. de V. Booysen and N. M. Tainton, 255-271. Berlin and New York: Springer-Verlag.
- Bishop, J. A., and Sheppard, P. M. 1973. An evaluation of two capture-recapture models using the technique of computer simulation. In: *The Mathematical Theory of the Dynamics of Natural Populations*, eds. M. S. Bartlett and R. W. Hiorns, 235-252. New York and London: Academic Press.
- Blower, J. G., Cook, L. M., and Bishop, J. A. 1981. *Estimating the Size of Animal Populations.* London and Boston: George Allen & Unwin. 128 p.
- Boggs, C. L. 1986. Reproductive strategies of female butterflies: variation in and constraints on fecundity. *Ecol. Entomol.* 11:7-15.
- Boggs, C. L., and Gilbert, L. E. 1979. Male contribution to egg production in butterflies: evidence for transfer of nutrients at mating. *Science* (Washington, DC.) 206:83-84.
- Boggs, C. L., and Watt, W. B. 1981. Population structure of pierid butterflies. IV. Genetic and physiological investment in offspring by male *Colias*. *Oecologia* (Berl.) 50:320-324.
- Bragg, T. B. 1971. *Post-settlement Invasion of Woody Species in Kansas Tall-grass Prairie.* M.S. thesis, Kansas State University. 27 p.
- Bragg, T. B., and Hulbert, L. C. 1976. Woody plant invasion of unburned Kansas bluestem prairie. *J. Range Manage.* 29:19-24.
- Brakefield, P. M. 1982. Ecological studies on the butterfly *Maniola jurtina* in Britain. II. Population dynamics: the present position. *J. Anim. Ecol.* 51:727-738.
- Brown, I., and Ehrlich, P. R. 1980. Population biology of the checkerspot butterfly, *Euphydryas chalcedona*. Structure of the Jasper Ridge colony. *Oecologia* (Berl.) 47:239-251.
- Brown, J. L. 1975. *The Evolution of Behavior.* New York: Norton. 761 p.
- Brussard, P. F., and Ehrlich, P. R. 1970a. Adult behavior and population structure in *Erebia epipsodea* (Lepidoptera: Satyrinae). *Ecology* 51:880-885.
- Brussard, P. F., and Ehrlich, P. R. 1970b. The population structure of *Erebia epipsodea* (Lepidoptera: Satyrinae). *Ecology* 51:119-129.
- Buell, M. F., and Buell, H. F. 1959. Aspen invasion of prairie. *Bull. Torrey Bot. Club* 86:264-265.

- Burns, J. M. 1968. Mating frequencies in natural populations of skippers and butterflies determined by spermatophore counts. *Proc. Nat. Acad. Sci. U.S.A.* 61:852-859.
- Cancelado, R., and Yonke, T. R. 1970. Effect of prairie burning on insect populations. *J. Kans. Entomol. Soc.* 43:274-281.
- Chew, F. S., and Robbins, R. K. 1984. Egg-laying in butterflies. In: *The Biology of Butterflies: Symposium of the Royal Entomological Society of London*, no. 11. eds. R. I. Vane-Wright, and P. R. Ackery, 65-79. London and Orlando: Academic Press.
- Christiansen, P. A. 1972. Management on Hayden Prairie: past, present, and future. In: *Proceedings of the Second Midwest Prairie Conference*, ed. J. H. Zimmerman, 25-29. Madison and Parkside, WI: University of Wisconsin Press.
- Conard, E. C. 1954. Effect of time of cutting on yield and botanical composition of prairie hay in southeastern Nebraska. *J. Range Manage.* 7:181-182.
- Cook, L. M., Brower, L. P., and Croze, H. J. 1967. The accuracy of a population estimation from multiple recapture data. *J. Anim. Ecol.* 36:57-60.
- Courtney, S. P., and Anderson, K. 1986. Behavior around encounter sites. *Behav. Ecol. Sociobiol.* 19:241-248.
- Crawford, C. S., and Harwood, R. F. 1964. Bionomics and control of insects affecting Washington grass seed fields. *Wash. Agric. Exp. Stn. Tech. Bull.* 44:1-25.
- Dana, R. P. 1981. An unusual oviposition substrate for *Hesperia ottoe* (Hesperiidae) in southwestern Minnesota. *J. Lepid. Soc.* 35:77-78.
- Daubenmire, R. 1968. Ecology of fire in grasslands. *Adv. Ecol. Res.* 5:209-266.
- Davies, N. B. 1978. Ecological questions about territorial behavior. In: *Behavioral Ecology: An Evolutionary Approach*, eds. J. R. Krebs and N. B. Davies, 317-350. Sunderland, MA: Sinauer Associates.
- Dempster, J. P., and Pollard, E. 1981. Fluctuations in resource availability and insect populations. *Oecologia* (Berl.) 50:412-416.
- Dennis, R. L. H., and Williams, W. R. 1987. Mate location behavior of the large skipper butterfly *Ochlodes venata*: flexible strategies and spatial components. *J. Lepid. Soc.* 41:45-64.
- Dix, R. L. 1959. The influence of grazing on the thin-soil prairies of Wisconsin. *Ecology* 40:36-49.
- Douwes, P. 1970. Size of, gain to, and loss from a population of adult *Heodes virgaureae* L. (Lepidoptera: Lycaenidae). *Entomol. Scand.* 1:263-281.
- Drew, W. B. 1947. Floristic composition of grazed and ungrazed prairie vegetation in north central Missouri. *Ecology* 28:26-41.
- Ehrenreich, J. H., and Aikman, J. M. 1963. An ecological study of the effects of certain range management practices on native prairie in Iowa. *Ecol. Monogr.* 33:113-130.
- Ehrlich, A. H., and Ehrlich, P. R. 1978. Reproductive strategies in the butterflies. I. Mating frequency, plugging, and egg number. *J. Kans. Entomol. Soc.* 51:666-697.
- Ehrlich, P. R. 1984. The structure and dynamics of butterfly populations. In: *The Biology of Butterflies: Symposium of the Royal Entomological Society of London*, no. 11. eds. R. I. Vane-Wright, and P. R. Ackery, 25-40. London and Orlando: Academic Press.
- Ehrlich, P. R., and Davidson, S. E. 1960. Techniques for capture-recapture studies of Lepidoptera populations. *J. Lepid. Soc.* 14:227-229.
- Ehrlich, P. R., Launer, A. E., and Murphy, D. D. 1984. Can sex ratio be defined or determined? The case of a population of checkerspot butterflies. *Am. Nat.* 124:527-539.
- Ehrlich, P. R., and Wheye, D. 1986. "Nonadaptive" hilltopping behavior in male checkerspot butterflies (*Euphydryas editha*). *Am. Nat.* 127:477-483.
- Gall, L. F. 1984. Population structure and recommendations for conservation of the narrowly endemic alpine butterfly, *Boloria acrocneuma* (Lepidoptera: Nymphalidae). *Biol. Conserv.* 28:111-138.
- Gardner, C., Jewell, J. A., Dunn, H., and Mahmoud, I. Y. 1957. Effects of mowing a native tallgrass prairie in central Oklahoma. *Proc. Okla. Acad. Sci.* 38:30-31.
- Goodman, D. 1987. How do any species persist? Lessons for conservation biology. *Conserv. Biol.* 1:59-62.
- Great Plains Flora Association. 1986. *Flora of the Great Plains*. Lawrence, KS: University Press of Kansas. 1392 p.
- Grimm, E. C. 1983. Chronology and dynamics of vegetation change in the prairie-woodland region of southern Minnesota, U.S.A. *New Phytol.* 93:311-350.
- Grimm, E. C. 1984. Fire and other factors controlling the Big Woods vegetation of Minnesota in the mid-nineteenth century. *Ecol. Monogr.* 54:291-311.
- Henderson, R. 1982. Vegetation-fire ecology of tallgrass prairie. *Nat. Areas J.* 2(3):17-26.

- Herbel, C. H., and K. L. Anderson. 1959. Response of true prairie vegetation on major Flint Hills range sites to grazing treatment. *Ecol. Monogr.* 29:171-186.
- Hover, E. I., and T. B. Bragg. 1981. Effect of season of burning and mowing on an eastern Nebraska *Stipa-Andropogon* prairie. *Am Midl. Nat.* 105:13-18.
- Howe, R. 1984. Wings over the prairie. *Iowa Conserv.* 43(9):5-7.
- Hulbert, L. C. 1969. Fire and litter effects on undisturbed bluestem prairie in Kansas. *Ecology* 50:874-877.
- Hulbert, L. C. 1973. Management of Konza Prairie to approximate pre-white man fire influences. In *Third Midwest Prairie Conference Proceedings*, ed. L. C. Hulbert, 14-17. Manhattan, KS: Division of Biology, Kansas State University.
- Kelting, R. W. 1954. Effects of moderate grazing on the composition and plant production of a native tallgrass prairie in central Oklahoma. *Ecology* 35:200-207.
- Knutson, H., and Campbell, J. B. 1976. Relationships of grasshoppers (Acrididae) to burning, grazing, and range sites of native tallgrass prairie in Kansas. *Proc. Tall Timbers Conf. Ecol. Anim. Control Habitat Manage.* 6:107-120.
- Kucera, C. L. 1956. Grazing effects on the composition of virgin prairie in north central Missouri. *Ecology* 37:389-391.
- Kucera, C. L. 1960. Forest encroachment in native prairie. *Iowa State J. Sci.* 34:635-639.
- Kucera, C. L., and Ehrenreich, J. H. 1962. Some effects of annual burning on central Missouri prairie. *Ecology* 43:334-336.
- Kucera, C. L., Ehrenreich, J. H., and Brown, C. 1963. Some effects of fire on tree species in Missouri prairie. *Iowa State J. Sci.* 38:179-185.
- Kucera, C. L., and Koelling, M. 1964. The influence of fire on composition of central Missouri prairie. *Am. Midl. Nat.* 72:142-147.
- Küchler, A. W. 1964. *Potential Natural Vegetation of the Conterminous United States*. Map. American Geographical Society Special Publication Number 36. New York: American Geographical Society.
- Labine, P. A. 1964. Population biology of the butterfly, *Euphydryas editha*. I. Barriers to multiple inseminations. *Evolution* 18:335-336.
- Leather, S. R. 1984. The effect of adult feeding on the fecundity, weight loss and survival of the pine beauty moth, *Panolis flammea* (D & S.). *Oecologia* (Berl.) 65:70-74.
- Lederhouse, R. C. 1982. Territorial defense and lek behavior of the black swallowtail butterfly, *Papilio polyxenes*. *Behav. Ecol. Sociobiol.* 10:109-118.
- Lederhouse, R. C., Codella, S. G., and Cowell, P. J. 1987. Diurnal predation on roosting butterflies during inclement weather: a substantial source of mortality in the black swallowtail, *Papilio polyxenes* (Lepidoptera: Papilionidae). *J. New York Entomol. Soc.* 95:310-319.
- Lindsey, A. W. 1942. A preliminary revision of *Hesperia*. *J. Sci. Lab. Denison Univ.* 37:1-50.
- MacNeill, C. D. 1964. The skippers of the genus *Hesperia* in western North America, with special reference to California (Lepidoptera: Hesperidae). *Univ. Calif. Publ. Entomol.* 35:1-230.
- MacNeill, C. D. 1975. Family Hesperidae, the skippers. In: *The Butterflies of North America*, coord. ed. W. H. Howe, 423-578. Garden City, NY: Doubleday.
- Magnus, D. B. E. 1963. Sex limited mimicry II—visual selection in the mate choice of butterflies. Translated by D. O. White and edited by L. P. and J. V. Z. Brower. In: *Proceedings, XVI International Congress of Zoology*, vol. 4, ed. J. A. Moore, 179-183. Washington, D.C.: XVI International Congress of Zoology.
- Manly, B. F. J. 1970. A simulation study of animal population estimation using the capture-recapture method. *J. Appl. Ecol.* 7:13-39.
- Matsch, C. L. 1972. Quaternary geology of southwestern Minnesota. In: *Geology of Minnesota: A Centennial Volume in Honor of George M. Schwartz*, eds. P. K. Sims and G. B. Morey, 548-560. St. Paul, MN: Minnesota Geological Survey.
- McCabe, T. L. 1981. The Dakota skipper, *Hesperia dacotae* (Skinner): range and biology, with special reference to North Dakota. *J. Lepid. Soc.* 35:179-193.
- McCabe, T. L., and Post, R. L. 1977. *Skippers (Hesperioidea) of North Dakota: With Additional Records of North Dakota Butterflies and a Butterfly Calendar*. North Dakota Insects, Schaefer-Post Series Publ. No. 11, N.D. Agric. Exp. Stn. Publ. No. 714. Fargo, ND: Department of Entomology and Agricultural Experiment Station, North Dakota State University. 70 p.
- McGuire, W. W. 1982. New oviposition and larval hostplant records for North American *Hesperia* (Rhopalocera: Hesperidae). *Bull. Allyn Mus.* 72:1-6.
- Miller, W. E. 1979. Fire as an insect management tool. *Bull. Entomol. Soc. Am.* 25:137-140.
- Miller, W. E. 1987. Spruce budworm (Lepidoptera: Tortricidae): role of adult imbibing in reproduction. *Environ. Entomol.* 16:1291-1297.

- Milliken, G. A., and Johnson, D. E. 1984. *Analysis of Messy Data. Vol. I: Ddesigned Experiments*. Belmont, CA: Lifetime Learning Publications. 473 p.
- Moore, C. T. 1972. *Man and Fire in the Central North American Grassland 1535-1890: A Documentary Historical Geography*. Ph.D. diss., University of California, Los Angeles. 155 p.
- Morrison, D. F. 1976. *Multivariate Statistical Methods*. 2nd ed. New York: McGraw-Hill Book Co. 415 p.
- Morton, A. C. 1984. The effects of marking and handling on recapture frequencies of butterflies. In: *The Biology of Butterflies: Symposium of the Royal Entomological Society of London, no. 11*. eds. R. I. Vane-Wright, and P. R. Ackery, 55-58. London and Orlando: Academic Press.
- Murphy, D. D., Launer, A. E., and Ehrlich, P. R. 1983. The role of adult feeding in egg production and population dynamics of the checkerspot butterfly *Euphydryas editha*. *Oecologia* (Berl.) 56:257-263.
- Murphy, D. D., and Wilcox, B. A. 1986. Butterfly diversity in natural habitat fragments: a test of the validity of vertebrate-based management. In: *Wildlife 2000: Modeling Habitat Relationships of Terrestrial Vertebrates*, eds. J. Verner, M. L. Morrison, and C. J. Ralph, 287-292. Madison, WI: University of Wisconsin Press.
- Nagel, H. G. 1973. Effect of spring prairie burning on herbivorous and non-herbivorous arthropod populations. *J. Kans. Entomol. Soc.* 46:485-496.
- Nielsen, M. C. 1958. Observations of *Hesperia pawnee* in Michigan. *Lepidopterists' News* 12:37-40. (Corrected to *H. ottoo* in Nielsen (1960)).
- Nielsen, M. C. 1960. A correction on *Hesperia pawnee* in Michigan. *J. Lepid. Soc.* 14:57.
- Norris, M. J. 1935. A feeding experiment on the adults of *Pieris rapae*. *Entomologist* 68:125-127.
- Norton, B. E., and McGarity, J. W. 1965. The effect of burning of native pasture on soil temperature in northern New South Wales. *J. Br. Grassl. Soc.* 20:101-105.
- Ode, D. J., Tieszen, L. L., and Lerman, J. C. 1980. The seasonal contribution of C₃ and C₄ plant species to primary production in a mixed prairie. *Ecology* 30:322-332.
- Old, S. M. 1969. Microclimates, fire, and plant production on an Illinois prairie. *Ecol. Monogr.* 39:355-384.
- Opler, P. A. 1981. Management of prairie habitats for insect conservation. *J. Nat. Areas Assoc.* 1(4):3-6.
- Peterson, A. 1948. *Larvae of Insects: An Introduction to Nearctic Species*. Pt. I. Lepidoptera and plant infesting Hymenoptera. Columbus, OH: by the author. 315 p.
- Pitelka, F. A. 1959. Numbers, breeding schedule, and territoriality in pectoral sandpipers of northern Alaska. *Condor* 61:233-264.
- Porter, K. 1982. Basking behavior in larvae of the butterfly *Euphydryas aurinia*. *Oikos* 38:308-312.
- Redmann, R. E. 1975. Production ecology of grassland plant communities in western North Dakota. *Ecol. Monogr.* 45:83-106.
- Reichert, S. E., and Reeder, W. G. 1972. Effects of fire on spider distribution in southwestern Wisconsin prairies. In: *Proceedings of the Second Midwest Prairie Conference*, ed. J. H. Zimmerman, 73-90. Madison and Parkside, WI: University of Wisconsin Press.
- Rice, L. A. 1932. Effect of fire on the prairie animal communities. *Ecology* 13:392-401.
- Risser, P. G., Birney, E. C., Blocker, H. D., May, S. W., Parton, W. J., and Wiens, J. A. 1981. *The True Prairie Ecosystem*. Stroudsburg, PA: Hutchinson Ross Publishing Co. 557 p.
- Roff, D. A. 1973. On the accuracy of some mark-recapture estimators. *Oecologia* (Berl.) 12:15-34.
- Rutowski, R. L. 1984. Production and use of secretions passed by males at copulation in *Pieris protodice* (Lepidoptera: Pieridae). *Psyche* 91:141-152.
- Rutowski, R. L., and Gilchrist, G. W. 1986. Copulation in *Colias eurytheme* (Lepidoptera: Pieridae): patterns and frequency. *J. Zool.* 207:115-124.
- Rutowski, R. L., Long, C. E., Marshall, L. D., and Vetter, R. S. 1978. Courtship solicitation by *Colias* females (Lepidoptera: Pieridae). *Am. Midl. Nat.* 105:334-340.
- Savage, M. J. 1980. The effect of fire on the grassland microclimate. *Herb. Abstr.* 50:589-603.
- Schoener, T. W. 1968. Sizes of feeding territories among birds. *Ecology* 49:123-141.
- Scott, J. A. 1973a. Adult behavior and population biology of two skippers (Hesperiidae) mating in contrasting topographic sites. *J. Res. Lepid.* 12:181-196.
- Scott, J. A. 1973b. Convergence of population biology and adult behavior in two sympatric butterflies, *Neominois ridingsii* (Papilionoidea: Nymphalidae) and *Amblyscirtes simius* (Hesperioidea: Hesperidae). *J. Anim. Ecol.* 42:663-672.
- Scott, J. A. 1973c. Lifespan of butterflies. *J. Res. Lepid.* 12:225-230.
- Scott, J. A. 1974a. Adult behavior and population biology of *Poladryas minuta* and the relationship of the Texas and Colorado populations (Lepidoptera: Nymphalidae). *Pan-Pacific Entomol.* 50:9-22.
- Scott, J. A. 1974b. Mate-locating behavior of butterflies. *Am. Midl. Nat.* 91:103-117.

- Scott, J. A. 1975a. Flight patterns among eleven species of diurnal Lepidoptera. *Ecology* 56:1367-1377.
- Scott, J. A. 1975b. Mate-locating behavior of western North American butterflies. *J. Res. Lepid.* 14:1-40.
- Scott, J. A. 1982. Mate-locating behavior of western North American butterflies. II. New observations and morphological adaptations. *J. Res. Lepid.* 21:177-187.
- Scott, J. A. 1986. *The Butterflies of North America: A Natural History and Field Guide*. Stanford: Stanford University Press. 583 p.
- Scriber, J. M., and Lederhouse, R. C. 1983. Temperature as a factor in the development and feeding ecology of tiger swallowtail caterpillars, *Papilio glaucus* (Lepidoptera). *Oikos* 40:95-102.
- Seastedt, T. R. 1984. Microarthropods of burned and unburned tallgrass prairie. *J. Kans. Entomol. Soc.* 57:468-476.
- Seber, G. A. F. 1973. *The Estimation of Animal Abundance, and Related Parameters*. London: Griffen Co. 506 p.
- Sellier, R. 1972. Etude ultrastructurale en microscopie électronique à balayage et essai d'interprétation du mode de fonctionnement des poils androconiaux alaires chez les Hesperiidæ (Lepidoptera Rhopalocera). *C. R. Hebd. Seances Acad. Sci. Ser. D. Sci. Nat.* 275:2239-2242.
- Sevastopulo, D. G. 1974. Lepidoptera feeding at puddle-margins, dung and carrion. *J. Lepid. Soc.* 28:167-168.
- Shapiro, I. 1975. Courtship and mating behavior of the fiery skipper *Hylephila phylæus* (Hesperiidæ). *J. Res. Lepid.* 14:125-141.
- Sheldon, E. P. 1910. Notes on the alpine characteristics of the Minnesota crest flora of the Coteau des Prairies. *Bull. Minn. Acad. Nat. Sci.* 4:60-63.
- Shields, O. 1967. Hilltopping. *J. Res. Lepid.* 6:69-178.
- Shreeve, T. G. 1984. Habitat selection, mate location, and microclimatic constraints on the activity of the speckled wood butterfly, *Pararge aegeria*. *Oikos* 42:371-377.
- Shreeve, T. G. 1986. Egg-laying by the speckled wood butterfly (*Pararge aegeria*): the role of female behavior, host plant abundance, and temperature. *Ecol. Entomol.* 11:229-236.
- Smith, C. C. 1940. The effect of overgrazing and erosion upon the biota of a mixed-grass prairie of Oklahoma. *Ecology* 21:381-397.
- Smith, E. F., and Young, V. A. 1959. The effect of burning on the chemical composition of little bluestem. *J. Range Manage.* 12:139-140.
- Sokal, R. R., and Rohlf, F. J. 1969. *Biometry: The Principles and Practice of Statistics in Biological Research*. San Francisco: W. H. Freeman and Co. 776 p.
- Steel, R. G. D., and Torrie, J. H. 1980. *Principles and Procedures of Statistics: A Biometrical Approach*. 2nd ed. New York: McGraw-Hill Book Co. 633 p.
- Stern, V. M., and Smith, R. F. 1960. Factors affecting egg production and oviposition in populations of *Colias philodice eurytheme* (Boisduval) (Lepidoptera: Pieridae). *Hilgardia* 29:411-454.
- Stinson, K. J., and Wright, H. A. 1969. Temperature of headfires in the southern mixed prairie of Texas. *J. Range Manage.* 22:169-174.
- Stringer, I. A. N., Giebultowicz, J. M., and Riddiford, L. M. 1985. Role of the bursa copulatrix in egg maturation and reproductive behavior of the tobacco hawk moth, *Manduca sexta*. *Int. J. Invertebr. Reprod. Dev.* 8:83-91.
- Sugawara, T. 1979. Stretch reception in the bursa copulatrix of the butterfly, *Pieris rapae crucivora*, and its role in behavior. *J. Comp. Physiol.* 130:191-199.
- Suzuki, Y. 1976. So-called territorial behavior of the small copper, *Lycaena phlaeas dalmio* Seitz (Lepidoptera: Lycaenidae). *Kontyu* 44:193-204.
- Suzuki, Y., and Zalucki, M. P. 1986. The influence of sex ratio on female dispersal in *Danaus plexippus* (L.) (Lepidoptera: Danaidae). *J. Aust. Entomol. Soc.* 25:31-35.
- Svärd, L. 1985. Parental investment in a monandrous butterfly, *Pararge aegeria*. *Oikos* 45:66-70.
- Svärd, L., and Wicklund, C. 1986. Different ejaculate strategies in first versus subsequent matings in the swallowtail butterfly *Papilio machaon* L. *Behav. Ecol. Sociobiol.* 18:325-330.
- Tabashnik, B. 1980. Population structure of pierid butterflies. III. Pest populations of *Colias philodice eriphyle*. *Oecologia* (Berl.) 47:175-183.
- Tainton, N. M., and Mentis, M. T. 1984. Fire in grassland. In: *Ecological Effects of Fire in South African Ecosystems*, eds. P. de V. Booysen and N. M. Tainton, 115-147. Berlin and New York: Springer-Verlag.
- Tashiro, H., Murdoch, C. L., and Mitchell, C. W. 1983. Development of a survey technique for larvae of the grass webworm and other lepidopterous species in turfgrass. *Environ. Entomol.* 12:1428-1432.
- Taylor, M. F. J., and Sands, D. P. A. 1986. Effects of ageing and nutrition on the reproductive system of *Samea multiplicalis* Guenee (Lepidoptera: Pyralidae). *Bull. Entomol. Res.* 76:513-517.

- Taylor, O. R. 1968. Relationship of multiple mating to fertility in *Atteva punctella* (Lepidoptera: Yponomeutidae). *Ann. Entomol. Soc. Am.* 60:583-590.
- Thomas, J. A. 1984. The conservation of butterflies in temperate countries: past efforts and lessons for the future. In: *The Biology of Butterflies: Symposium of the Royal Entomological Society of London, no. 11*. eds. R. I. Vane-Wright and P. R. Ackery, 333-353. London and Orlando: Academic Press.
- Thornhill, R., and Alcock, J. 1983. *The Evolution of Insect Mating Systems*. Cambridge, MA: Harvard University Press. 547 p.
- Thornthwaite, C. W., in cooperation with Division of Climate and Crop Weather, U.S. Weather Bureau. 1941. *Atlas of Climatic Types in the United States, 1900-1939*. U. S. Dept. of Agriculture Misc. Publ. 421. Washington, D.C.: U.S. Government Printing Office. 7 p. + 96 maps.
- U.S. Department of Agriculture, Soil Conservation Service Staff, in cooperation with University of Minn. Agricultural Experiment Station. 1970. *Soil Survey of Lincoln County, Minnesota*. Washington D.C.: U.S. Government Printing Office. 84 p. + 90 maps.
- U.S. Department of Commerce, National Oceanic and Atmospheric Administration. 1982a. *Climatography of the United States. No. 60. Climate of South Dakota*. Asheville, NC: Environmental Data and Information Service, National Climatic Center. 17 p.
- U.S. Department of Commerce, National Oceanic and Atmospheric Administration. 1982b. *Climatography of the United States. No. 81. Monthly Normals of Temperature, Precipitation, and Heating and Cooling Degree Days 1951-1980. South Dakota*. Asheville, NC: Environmental Data and Information Service, National Climatic Center. Unpaged.
- U.S. Department of the Interior, Fish and Wildlife Service. 1978. Proposed endangered or threatened status or critical habitat for 10 butterflies or moths. *Federal Register* 43(128):28938-28945.
- U.S. Department of the Interior, Fish and Wildlife Service. 1980. Notice of withdrawal of expired proposals for listing eight arthropod species. *Federal Register* 45(171):58171.
- U.S. Department of the Interior, Fish and Wildlife Service. 1984. Review of invertebrate wildlife for listing as endangered or threatened species. *Federal Register* 49(100):21664-21675.
- Voight, J. W., and Weaver, J. E. 1951. Range condition classes of native midwestern pasture: an ecological analysis. *Ecol. Monogr.* 21:39-60.
- Watt, W. B., Chew, F. S., Snyder, L. R. G., Watt, A. G., and Rothschild, D. E. 1977. Population structure of pierid butterflies. I. Numbers and movements of some montane *Colias* species. *Oecologia* (Berl.) 27:1-22.
- Watt, W. B., Hoch, P. C., and Mills, S. G. 1974. Nectar resource use by *Colias* butterflies. Chemical and visual aspects. *Oecologia* (Berl.) 14:353-374.
- Weaver, J. E. 1954. *North American Prairie*. Lincoln, NE: Johnsen Publishing Co. 384 p.
- Weaver, J. E., and Fitzpatrick, T. J. 1934. The prairie. *Ecol. Monogr.* 4:108-295.
- Wells, P. V. 1970. Vegetational history of the Great Plains: a post-glacial record of coniferous woodland in southeastern Wyoming. In: *Pleistocene and Recent Environments of the Central Great Plains*, eds. W. Dort, Jr., and J. K. Jones, Jr., 185-202. Lawrence, KS: University Press of Kansas.
- Wells, S. M., Pyle, R. M., and Collins, N. M., compilers. 1983. *The IUCN Invertebrate Red Data Book*. Gland, Switzerland: IUCN. 632 p.
- Whitman, W. C. 1950. Productivity of natural prairie vegetation. N.D. Agricultural Experiment annual report, 1949. *N.D. Agric. Exp. Stn. Bull.* 356:29-30.
- Wickman, P.-O. 1985. The influence of temperature on the territorial and mate locating behavior of the small heath butterfly, *Coenonympha pamphilus* (L.) (Lepidoptera: Satyridae). *Behav. Ecol. Sociobiol.* 16:233-238.
- Wickman, P.-O., and Wiklund, C. 1983. Territorial defense and its seasonal decline in the speckled wood butterfly (*Pararge aegeria*). *Anim. Behav.* 31:1206-1216.
- Wiklund, C. 1984. Egg-laying patterns in butterflies in relation to their phenology and the visual apparency and abundance of their host plants: *Oecologia* (Berl.) 63:23-29.
- Willers, J. L., Schneider, J. C., and Ramaswamy, S. B. 1987. Fecundity, longevity, and caloric patterns in female *Heliothis virescens*: changes in age due to flight and supplemental carbohydrates. *J. Insect Physiol.* 33:803-808.
- Wright, H. A., and Bailey, A. W. 1982. *Fire ecology, United State and Southern Canada*. New York: Wiley. 501 p.





