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EFFECTS OF MANAGEMENT ON BUTTERFLY ABUNDANCE IN TALLGRASS PRAIRIE AND PINE BARRENS

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Abstract

In transect surveys during 1987–1995 at 104 tallgrass prairies (and open savannas) in Illinois, Iowa, Minnesota, Missouri, North Dakota and Wisconsin, USA and during 1986–1995 at 141 pine barrens in Wisconsin, 137,402 individuals of 122 butterfly species were counted. Twenty percent of individuals and 15% of species were classified as specialists in such habitats, and 26% and 24%, respectively, as more widely distributed 'grassland species'. Management effects were analyzed as part of stepwise multiple linear regressions for each of 15 specialist and 12 grassland species. Most specialists showed significantly increased numbers associated with less frequent and/or less intrusive managements. However, leaving habitat entirely unmanaged was rarely optimal. Single occasional wildfires were typically more favorable for specialist abundance than regular rotational burning, which often produced very low numbers. Mechanical cutting appeared more favorable than grazing. No management type was clearly favorable for all specialists of a given habitat. The grassland species tended to respond similarly to the specialists except that several favored more frequent and/or more intrusive management and that mechanical cutting was not markedly better for their abundance than grazing, nor wildfire than rotational burning. For conserving specialist butterflies, both consistency of management type within *site and deliberate differences in management type* among *sites of* like *habitat is desirable.*
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Keywords: burning, grassland, grazing, haying, midwest USA, mowing, savanna and wildfire.

INTRODUCTION

The tallgrass prairie of central North America contains vegetation dominated by herbaceous flora. Savanna ('oak savanna' and 'pine barrens'), where trees and brush intersperse with herbaceous patches, occurs along the eastern and northern periphery. Since European contact in North America, >99% of tallgrass prairie and oak savanna have been destroyed primarily because of conversion to agriculture. Fragments of original prairie and savanna remain in preserves, parks, unintensively utilized farmland, and timber reserves (Curtis, 1959; Nuzzo, 1986). Butterflies specialized to these habitats are now rare and primarily restricted to preserves (Opler, 1981; Johnson, 1986; Panzer *et al.*, 1995).

Periodic disturbances or processes are considered necessary for prairies and savannas to persist (Curtis, 1959; Vogl, 1974; Anderson, 1982; Nuzzo, 1986). These processes are disrupted today because of habitat destruction and fragmentation. In unmanaged sites the flora usually alters by invasion of woody species (often called forest succession) and accumulation of plant litter.

Fire (whether set by lightning or native peoples) has been inferred to be the dominant process maintaining the openness of prairie and savanna (Sauer, 1950; Stewart, 1956; Vogl, 1974; Nuzzo, 1986). Butterflies of prairie and savanna (particularly the specialists) are therefore often assumed to be fire-adapted. Even if individuals die as a result of fire, the species are expected to recover and thrive because fire would properly maintain the habitat they require. Without fire, these butterfly populations would be expected to decline and die out because of unsuitable habitat change (Panzer, 1988; Dana, 1991).

Alternative theories assert that climate (Clements, 1916; Transeau, 1935; Borchert, 1950), herbivory (Larson, 1940; England and DeVos, 1969; Moore, 1983), or a combination of these with fire, soil, and/or topography (Anderson, 1982; Nuzzo, 1986; Howe, 1994), maintain the structure of open habitats. Furthermore, some lepidopterists have questioned the assumption that burning benefits rare butterflies (Opler, 1981; Panzer, 1988; Schlicht and Orwig, 1992). Too frequent or too large fires might extirpate rarer butterflies, so that reduced fire and alternative managements would be preferable (McCabe, 1981; Orwig, 1992).

Swengel (1996*a*) presented the effects of conservation management by rotational burning and haying on prairie butterflies. I present, here, the effects of a greater variety of management types on butterflies specialized to live in tallgrass prairie (and savannas) and barrens.

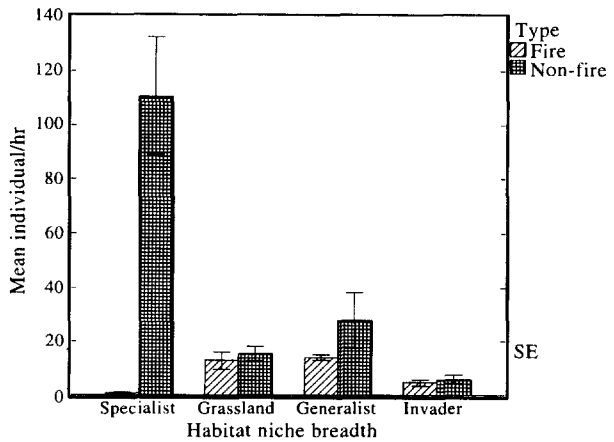


Fig. 1. Mean ± SE of individuals/h for each butterfly group (as defined in this study and Swengel, 1996*a*) on eleven Fourth of July Butterfly Counts in five primarily prairie areas, managed either with fire or non-fire treatments, in southwestern Missouri–northeastern Oklahoma (36·8–38·6° N, 93·3–96·4° W) between 16 June and 4 July 1993–1995 (Opler and Swengel, 1994; Swengel and Opler, 1995; Swengel and Opler, 1996).

Their responses may shed light on prehistoric ecosystem function and on designing habitat conservation and management programs to conserve biodiversity today.

METHODS

Study sites

Sites were deliberately selected for conservation interest, i.e. those known or thought to have specialist butterflies. Of the 104 prairie (and open savanna) sites in six states (Appendix 1; cf. Figure 1 in Swengel, 1996*a*), all but 13 were conservation lands in private or government ownership. Most conservation sites were managed primarily with cool-season fire typically in a rotation of 2–5 years, with some mowing or haying also at 21 sites. In Missouri, 25 sites were hayed in summer typically in a rotation of 1–2 years, with two also lightly grazed by cattle on occasion. In five sites or parts of sites, no active management had occurred for many years. The non-conservation prairies included two hay prairies in Minnesota next to preserves, one currently grazed and one long fallow grazed site in Wisconsin, and nine sampling areas in Sheyenne National Grassland (North Dakota) with grazing for both ecological and economic purposes. The 141 pine barrens in central and northwestern Wisconsin included conservation lands, forest reserves (some burned by wildfire and/or used for off-road vehicle trails), military reservation and rights-of-way for highways and powerlines.

The sites were grouped into three regions: (1) Missouri; (2) Western Upper Midwest (North Dakota–Minnesota–western Iowa west of 94°W); and (3) Eastern Upper Midwest (Wisconsin–Illinois–Iowa east of 94°W). The Eastern Upper Midwest contained both prairie (south of central Wisconsin) and pine barrens (central and northern Wisconsin). The herbaceous flora of pine barrens is similar to sand prairies ('sand barrens' in Curtis, 1959) and the butterfly distribution from prairie to barrens appears clinal.

Butterfly transect surveys

My research assistant and I conducted transect butterfly surveys along similar routes each year (Swengel, 1996*a*). A new sampling unit was designated when the vegetation along the route changed by type, quality, canopy, and/or management. Phenological dates were calculated by adjusting that year's survey dates within a region ahead or behind based on plant development. The dataset spans 1986–1995, but most surveys occurred during 1990–1995. It was never possible to visit all sites within a region each year, but most sites were visited more than once both within a year and among years.

This study focused on 'specialists' (within study region, restricted or nearly so to prairie, savanna, and/or barrens; sensitive to vegetative quality) (Appendix 1, giving all English and scientific names). Specialists were further subdivided by biotope narrowness and tolerance for habitat degradation as highly restricted, moderately restricted, or less restricted (see Table 1). One specialist, the Persius duskywing, was identified as a species complex because field identification was not adequately reliable. Survey timing varied by region (Appendix 1), especially to target frosted elfin and Karner blue in pine barrens, and regal fritillary, Poweshiek skipperling, Dakota and Ottoe skippers in tallgrass prairie.

'Grassland' species (inhabiting open non-forested habitat, both native and degraded, without strong sensitivity to vegetative quality) (Appendix 1) were also analyzed as a comparison to the specialists. For the 'range-restricted' gray copper and Aphrodite fritillary, central North American open habitats comprise their primary range. The remaining grassland species were analyzed if >200 were observed within the region. The monarch, a regular summer breeder in the study area, was also included because of conservation concern over its migratory phenomenon (Brower and Malcolm, 1991).

Statistical analysis

Stepwise multiple linear regression was done for each species by region with ABstat 7·20 software (1994 Anderson-Bell Corp., Parker, CO). The dependent variable (unweighted observation rates of individuals/h in each unit) was natural log-transformed: $\ln(1 + \text{rate})$.

The first regression included 21 independent variables in eight categories: (1) geography (latitude, longitude); (2) survey (*n* surveyors—usually two, but occasionally one, beginning time, calendar and phenological date); (3) site (patch size, togographical diversity or uniformity, whether prairie or barrens); (4) unit (vegetative type, quality, canopy category); (5) weather (% sunshine, average temperature, average wind speed); (6) flight period (nearness to midpoint of flight period in calendar

and phenological dates, spring or summer brood if multivoltine); (7) year (calendar, ranking of annual abundance by mean unweighted rate per year if >2 units); and (8) management ('intrusiveness'). Patch size (a variable in category 3) was available for prairie and for wild lupine *Lupinus perennis* (larval host for several barrens species) but not for barrens. Types of management (category 8) were ordered along the following sequence of increasing intrusiveness with consecutive numbering of each testable type (>10 units) in that region: (1) Nothing; (2) Grazing; (3) Grazing and Haying; (4) Cutting (brush- and/or hand-cutting); (5) Mowing (leaving clippings); (6) Haying (removing clippings); (7) Timber (tree cutting and/or planting); (8) Wildfire; (9) Wildfire and Other (tree planting, vehicle trails); (10) Mowing and Burning in rotation (i.e. regular treatments occurring successively around units of the site); (11) Haying and Burning in rotation; (12) Burning in rotation.

The second regression added another management variable, 'age class'. This was coded as 0 years since last management (i.e. treatment since last summer), 1, 2, etc. This information was unavailable for some units, thus reducing sample size for this regression. Rotational burning age classes >4 years were lumped as 5+. Wildfire age classes ranged from 4 to 18 years. No Mowing or Haying unit exceeded 3 years, and Grazing was 0 since grazing occurred each year in those units. 'Nothing' was coded as 5+ years in prairie, but 20+ in barrens. For types combining several management types, the most recent treatment was used to code age class. Since relatively few species in barrens had significant management effects, third and fourth regressions were run, corresponding to the first and second but excluding units that had 'Nothing' for management.

RESULTS

Altogether, we counted 137,402 individuals of 122 species. Of these, 27,938 (20%) of individuals and 18 (15%) of species were specialists and 35,855 (26%) and 29 (24%), respectively, were grassland species (Appendix 1). Within each regression, all variables produced a significant effect in at least one species, demonstrating the need for including non-management variables in analyses of management effects on butterfly abundance. Summary data on the regressions are in Appendix 2; results apart from management effects are beyond the scope of this paper.

Specialists

Regions

In Missouri, two of three specialists had significant management effects (Table 1); the arogos skipper and regal fritillary both favored less intrusive management (Haying/Grazing).

In the Western Upper Midwest, all five testable specialists showed significant management effects (Table 1), favoring either less intrusive management or higher age classes. Their peak numbers occurred either in Haying or Nothing, with Grazing intermediate to low. Haying also produced poor numbers for some species, but Burning (management type 12) never had relatively high numbers and most often produced the lowest abundance index.

In the Eastern Upper Midwest, eight of 11 testable specialists showed significant management effects (Table 1). Many (particularly cobweb skipper, regal fritillary, gorgone checkerspot, and Leonard's skipper) seemed rather intolerant of management type (producing relatively low numbers in all but a few types) and of more intrusive/frequent management, particularly Burning. By contrast, the Ottoe and dusted skippers produced peak numbers in Burning, but the regressions did not support a simple interpretation that Burning favored higher abundances. The Ottoe skipper significantly correlated with higher age classes (independent of management type), but not with greater intrusiveness, and declined considerably in abundance during the study, which raises questions about the viability of those populations. The dusted skipper significantly favored more intrusive management only in the first of the four regressions, which included Nothing. This skipper more strongly favored higher age classes in both regressions that included this variable. Likewise, the olympia marble showed a significant positive effect from more intrusive management in the second regression (including Nothing) but a non-significant negative effect in the fourth regression (excluding Nothing) (Table 1). It also much more strongly favored higher age classes in both those regressions and had highest indices after Wildfire (types 8 and 9). These complex results suggest that moderate management is favorable, with both no management and too frequent/intrusive management unfavorable.

Except for the Karner blue, all specialists had rather low numbers in Nothing (Table 1). The small sample from Timber also usually produced low numbers (Table 1). Areas burned by a single Wildfire (4–18 years ago) produced results strongly contrasting with and much more favorable than Burning for the frosted elfin, cobweb skipper, gorgone checkerspot, and Leonard's skipper in addition to the olympia marble (Table 1).

Within species among regions

Three specialists were testable in more than one region (Table 1). The arogos skipper significantly favored less intrusive management in both Missouri and the Western Upper Midwest, with very low numbers in Burning, especially in the latter region. It was relatively more abundant in Haying, and Grazing and Haying, in Missouri (conservation managements), but virtually absent in the sample of farm Haying in the Western Upper Midwest, where it peaked in Nothing (a type not sam-

Table 1. Butterfly abundance indices (individuals observed per survey hour within the flight period) in each of 12 management types, and regression results for management intrusiveness (int) and management age class (age)

If management variable(s) showed significant effect(s) in regression, the highest rate is boldfaced and the lowest italicized. Types: (1), Nothing; (2), Grazing; (3), Grazing and Haying; (4), Cutting (brush- and/or hand-cutting); (5), Mowing; (6), Haying; (7), Timber (tree cutting and/or planting); (8), Wildfire; (9), Wildfire and Other (tree planting, vehicle trails); (10), Mowing and Burning in rotation; (11) Haying and Burning in rotation; (12) Burning in rotation. For regression results, the sign indicates the direction of correlation. # for $p \geq 0.1$; (+) or (−) for $p < 0.1$; + or − for $p < 0.05$; + + or − − for $p < 0.01$; + + + or − − − for $p < 0.001$; + + + + or − − − − for $p < 0.0001$.

	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)	Int[a]	Age[b]
Missouri														
Specialist: highly restricted														
Arogos skipper			**3·63**			3·33					2·22	*1·85*	(−),−	#
Byssus skipper			0·00			0·28					0·86	0·00	#	#
Specialist: moderately restricted														
Regal fritillary			68·68			**89·04**					31·03	*13·06*	− − − −	#
Grassland: range-restricted														
Gray copper			*0·25*			0·63					**2·06**	1·96	+ +	#
Grassland: other														
Black swallowtail			3·51			2·46					2·83	1·19	#	#
Eastern tailed-blue			1·93			2·36					2·36	2·62	#	#
Tawny-edged skipper			**4·38**			4·29					4·30	*0·55*	−	#
Crossline skipper			**4·91**			3·33					2·33	*0·56*	− − −	#
Delaware skipper			1·09			2·17					3·37	1·05	#	(−)
Migrant														
Monarch			**7·71**			*5·27*					6·59	7·61	#	#
Western Upper Midwest														
Specialist: highly restricted														
Dakota skipper	7·02					**34·46**						*3·73*	−	#
Arogos skipper	**6·09**					*0·00*						0·48	− − − −	#
Specialist: moderately restricted														
Regal fritillary	41·39	22·00				**57·24**						*21·06*	#	+ + +
Poweshiek sk.	**43·53**					*5·13*						26·38	#	+ + + +
Pawnee skipper		16·09				**46·41**						*3·51*	− − − −	#
Grassland: range-restricted														
Gray copper	**2·10**					*0·00*						0·18	− − − −	#
Grassland: other														
Aphrodite frit.	9·90	9·89				**17·19**						*7·84*	#	+ +
Black swallowtail	0·76					1·08						1·58	#	#
Melissa blue	14·28	1·09				1·84						1·39	#	#
Silver-bord. fr.	*0·00*					*0·00*						**3·29**	#	+
Meadow frit.	1·25	**31·08**				24·64						*5·08*	−	+
C. ringlet	**16·21**	*0·48*				0·75						2·60	#	+ +
C. wood-nymph	40·39	*2·95*				**117·47**						65·28	+ +	+ + +
Long dash	3·79	**4·80**				*2·99*						3·43	#	+ +
Migrant														
Monarch	8·65	*4·51*				13·36						**135·24**	#	− −

Table 1—*contd*

	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)	Int[a]	Age[b]	Int[c]
Eastern Upper Midwest															
Specialist: highly restricted															
Frosted elfin[B]	0·67			0·08	1·87		0·61	2·27	2·48			0·32	#	#	#,(−)
Mottled dusk.[B]	0·00			1·45	0·46		0·00	0·36	0·73	1·12		1·54	#	#	#
spring	0·00			1·66	0·14		0·00	0·36	0·73	1·85		1·91			
summer				0·00	1·02		0·00			0·86		1·31			
Persius comp.[B]	1·35			2·06	**3·12**		*0·24*	1·16	1·64	1·33		1·03	−−−−	#	−−−−
Ottoe skipper [P]	1·32	0·25								*0·00*		**7·77**	#	+ +	
1990–1992	3·24	0·39								0·00		10·91			
1993–1995	0·33	0·18								0·00		3·61			
Cobweb skipper	*0·00*			**3·04**	*0·00*		*0·00*	1·80	*0·00*			*0·00*	#	#	−
Specialist: moderately restricted															
Regal fritillary [P]	7·25	**17·52**								8·56		*3·46*	−−−−	#	
Gorgone check.	*0·00*	17·94		2·45	0·65		*0·00*	**56·95**	2·05	2·46		3·38	#	#	−−−
spring	0·00			2·99	0·52		0·00	56·40	2·05	2·60		0·76			
summer	0·00	17·94		0·38	40·00			67·93		2·12		5·32			
Leonard's sk.	8·99	0·75		4·65	24·23			**32·35**	7·57	*0·00*		3·36	#	+	#
Dusted skipper	3·06			1·21	*0·66*		6·00	6·09	4·13	13·86		**16·50**	+ +	#	#
Specialist: less restricted															
Olympia marble	5·32			*3·39*	6·64		4·34	18·23	**23·77**	4·50		12·15	#,+	+ +	#,(−)
Karner blue[B]	68·13			45·77	45·53		11·22	49·70	51·21	12·40		64·56	#	#	#
spring	93·21			29·69	37·32		0·00	43·25	14·76	14·30		95·81			
summer	46·46			57·64	53·45		15·63	57·05	61·29	11·98		54·01			
Grassland: other															
Aphrodite frit.	13·41	22·64		*5·01*	9·89		18·75	**39·26**	5·52	19·81		8·69	#	+ + +	#
Black swallowtail[P]	*0·69*	**5·73**			1·14					3·09		1·14	#,−	−−−	
American cop.	3·25			12·49	1·72		0·00	0·68	1·47	0·08		4·51	(−)	#	#
E. tailed-blue	1·18	0·28		0·61	0·98		*0·00*	0·52	0·46	0·91		**2·79**	#	(−)	+ +
Meadow frit.	**3·56**	*0·00*		0·58	1·80		1·71	1·10	0·48	0·29		0·93	#	#	#
C. wood-nymph	21·46	6·27		18·73	13·61		13·13	23·31	*5·42*	**41·30**		31·29	#	+	#
Tawny-edged sk.	*0·58*	4·30		0·79	4·03			**5·95**		0·36		1·37	#	#	−−
Crossline sk.	1·27	3·07		1·54	0·26		**5·36**	1·68	1·80	*0·00*		2·01	−	#	−
Delaware sk.	1·93	2·43		0·78	0·38		**3·60**	0·60	*0·00*	1·48		0·88	−−−−	#	#
Migrant															
Monarch	8·75	4·70		3·29	0·90		2·11	0·79	*0·50*	6·20		**11·10**	#	−−−−	#,(+)

[a]From first regression; if a second result is provided, it is from the second regression (that also included age class).
[b]From second regression; if a second result is provided, it is from the fourth regression (that excluded 'Nothing').
[c]From third regression (that excluded 'Nothing'); if a second result is provided, it is from the fourth regression.
[B]Sample only from barrens.
[P]Sample only from prairie.

pled in Missouri). The Pawnee skipper significantly decreased with greater intrusiveness in the Western Upper Midwest, but this was not significant for the conspecific Leonard's skipper in the Eastern Upper Midwest, where it significantly increased with higher age class. The regal fritillary significantly decreased with greater intrusiveness in both Missouri and the Eastern Upper Midwest, but not in the Western Upper Midwest, where it significantly correlated with increasing age class. Despite variation within species among regions, these species tended to increase with less frequent and/or less intrusive management.

Restrictedness

The highly restricted specialists generally had such low numbers as to preclude significant management effects, but were the only species absent in Burning (byssus and cobweb skippers, and frosted elfin except for three individuals at one site 4 years since the last fire, Swengel, 1996*b*). With higher numbers observed, the moderately restricted specialists showed the most significant aversion to more intrusive or frequent management. Of the two less restricted specialists, the olympia marble was consistent with the other specialists' responses while the Karner blue showed no statistical pattern despite its large samples and considerable variability (Table 1).

Summary

Most specialists showed significant effects from management, typically favoring less frequent and/or less intrusive management but producing low numbers in Nothing. Wildfire was often more favorable for specialist abundance than Burning, which generally produced very low numbers. Haying or Mowing appeared more favorable than Grazing. No particular management type was optimal for all specialists.

Grassland and migrant species

Of the two range-restricted grassland species, the gray copper significantly increased with more intrusiveness in Missouri, peaking in Haying and Burning (Table 1). By contrast, in the Western Upper Midwest it significantly increased with less intrusiveness, peaking in Nothing (Table 1). In both regions its numbers were low, suggesting that highly favorable management for this species was not observed in this study. The Aphrodite fritillary significantly favored higher age classes and peaked in Haying or Wildfire (Table 1).

The other grassland species tended to respond similarly to the specialists (Table 1). Less intrusiveness and/or higher age classes were more favorable and peak numbers occurred among the less intrusive managements. But the eastern tailed-blue had the opposite pattern in the Eastern Upper Midwest, with a peak in Burning. Three species (black swallowtail, meadow fritillary, common wood-nymph) had mixed patterns of management effects. Unlike the specialists, grassland species were as likely to have higher numbers in Grazing than Haying/Mowing as vice versa, and their numbers in Wildfire were often lower than in Burning. The migrant monarch favored lower age classes and peaked in Burning in two regions.

DISCUSSION

The mobility of adult butterflies may obscure how management affects a species' abundance. Adults may move away from areas where immature stages are concentrated, yet suitable resources and conditions for both immatures and adults are necessary to maintain butterfly populations. Systematic data on immatures of the species in this study are unavailable except for the Karner blue, whose larval and adult numbers correlated strongly within site (Swengel, 1995). The effects of adult mobility seem more problematic for more adaptable and mobile species (rather than specialized and less mobile species), and for barrens species (rather than prairie species), as the prairie sites were more isolated and generally managed in relatively large, uniform, and consistent treatments. These results therefore remain preliminary and of more use for suggesting general patterns of management effects than for establishing a particular species' response to a specific type.

Narrowness of management tolerance

Many rare butterflies require vegetation management for their populations to be maintained effectively (e.g. BUTT, 1986; New, 1991, 1993; Oates, 1995; Robertson *et al.*, 1995). The habitats in this study are widely considered to require management (see Introduction), and most specialist butterflies showed significant management effects. Only two peaked in Nothing.

Rare butterflies may also exhibit narrow tolerances for management type, more so than the flora they depend on (New *et al.*, 1995). In this study, less intrusive management types generally produced more favorable responses than rotational burning types (Table 1). Results from the Fourth of July Butterfly Counts also indicate that prairie management primarily with rotational burning is less favorable for butterfly abundance, particularly specialists, than non-fire managements (primarily haying) (Fig. 1). Likewise, McCabe (1981) advocated late-season mowing rather than burning for Dakota skippers.

The tendency for specialists in this study to respond more favorably to mechanical cutting types than grazing contrasts with Morris (1975, 1981) regarding leafhoppers and Oates (1995) regarding butterflies that grazing was more favorable because it can be relatively gradual and unintrusive, while mowing/haying is catastrophic. Burning is even more catastrophic and to be avoided, while haying could, with attention to timing and rotation, effectively substitute for grazing (Morris, 1975, 1981; BUTT, 1986; Kirby, 1992; Oates, 1995). The grazing studied here was either combined with other

management or applied in whole or in part for non-conservation purposes. Grazing (like other non-conservation managements studied here) specifically designed for conservation might produce more favorable results.

Wildfire and rotational burning

Many species in this study responded more favorably to a single occasional wildfire, even if very large (up to *c.* 7000 ha), than to rotational burning. New's (1993) compendium on Lycaenidae butterflies contained 11 species accounts mentioning fire as a general threat, including three of four accounts asserting a role for fire in maintaining the species' habitat prehistorically (as in the regions in this study; see Introduction). The few examples in New (1993) of fires benefiting a butterfly were typically *infrequent* burns that *create* new habitat patches to be occupied by the butterflies afterward during long fire-free intervals, rather than *repeated* fires that *maintain* existing habitat already occupied by the butterfly. These more favorable fires occurred in a context of unburned habitat also occupied by the butterfly. Likewise, Shapiro (1965) reported that the cobweb skipper occupied 'fire-scar grasslands' but only after the second year postfire. Williams (1988) found that many sites naturally occupied by Gillette's checkerspot *Euphydryas gillettii* had been burned by wildfire. However, natural colonization of apparently suitable wildfire-burned habitat may take many years, as no natural colonizations were verified at multiple sites through at least 1993 within a large region of wildfires in 1988 (Williams, 1995). Hessel (1954) attributed some apparent absences of Papaipema moth larvae from extensive host patches to burning up to 15–20 years previously.

Furthermore, in those cases where fire resulted in suitable habitat occupied by a rare butterfly, other managements could also maintain suitable occupied habitat (Williams, 1988; Kirby, 1992; New, 1993; Webb and Thomas, 1994). Nor might fire be the most favorable way of maintaining habitat occupied by the species, even in places where burning traditionally occurred. Thomas and Harrison (1992) found that the silver-studded blue *Plebejus argus* occurred in both grazed and burned heaths, but with higher persistence in grazed than burned heaths. In the present study, not only was burning not necessary for long-term maintenance of specialist butterflies, but non-fire alternatives, whether in conservation application or not but in place for at least as many years as rotational fire, produced significantly more favorable results for many species (Table 1).

Optimal management

Even with these general patterns of specialist management responses, these species vary in their particular responses to specific management types and frequencies (Table 1). Certain management types were more favorable for more species than others, but no one type was favorable, much less optimal, for all. Consistent with this, the habitat preferences of chalk grassland butterflies form a continuum of turf heights mediated by management (BUTT, 1986) and the frequency and type of woodland management determines which butterflies benefit or decline (Robertson *et al.*, 1995).

Applications to ecosystem function

Because of the specialists' diverse responses to management, it is unclear how much of an understanding of the natural maintenance of prairie and barrens can be inferred from their responses (or those of other species). In this study, the less fire, typically the more favorable the specialists' responses, yet these species must be adapted to events essential for their habitat's existence. Thus, fire might be assumed to have occurred in the past sufficiently infrequently to be consistent with the widespread recent occurrence of these fire-averse specialists at extant habitat fragments. Nonetheless, past events in natural habitats need not have optimized rare butterfly abundance and distribution, nor could they have occurred in an optimal way in a given place for all specialist butterflies at once.

It is also unclear whether the most relevant conservation issue for maintaining diverse natural communities (including the appropriate specialists) in today's landscape is to infer and replicate past natural processes. These events might cause local extirpation, followed by natural recolonization (as evident after wildfire today). But where habitat fragmentation now disfavors recolonization, such events might result in an unnaturally high rate of permanent local extirpations. Thus, conservation management should not focus merely on replicating past natural processes, but might also seek to modify them or ameliorate their effects on rare species.

Applications to site management

As recommended in Kirby (1992), consistency of management type *within* a site is a favorable strategy, given the narrow management tolerances of many rare species. Sequential use of different management types may successively eliminate rare species sensitive to each type. Equally useful is deliberate diversity in management type *among* sites of *like* habitat because the various rare species differ as to favorable and adverse management types, even among specialists of the same habitat.

Consistency within site and differences among sites can be furthered by continuing the management used at the site before conservation, modified as necessary to reduce undesirable effects (e.g. reducing frequency or intensity if previously overmanaged). In this study, the non-conserved prairies and barrens varied in current and historical management types. But relatively few of these management activities were continued after site conservation, although many types (e.g. Grazing, Mowing, Haying, even Nothing for a long period) appeared favorable for some specialist butterflies

(Table 1). Studying these and other managements (such as localized ('spot') brushing and carefully targetted herbiciding) in deliberate conservation application would be valuable, as this might improve their effects on rare species.

If fire is used for management, it should not be the only or primary management at most conserved sites of a given habitat within a region. Furthermore, for specialist butterfly conservation, burning in rotation over most or all of a habitat patch appears less favorable than burning that mimics wildfires (i.e. their infrequency, occurrence in *un*occupied patches, and context of unburned and alternatively managed occupied habitat).

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APPENDIX 1

Summary statistics on study sites, survey effort, and total numbers of specialist, grassland, and migrant butterflies observed by region

Scientific and English nomenclature follows NABA (1995). Major European alternates to English names shown in parentheses follow Higgins (1983). *, Identifications were based on phenotype and range, but these were not adequate for reliable field identification of all individuals at the species level. Location abbreviations: IA, Iowa; IL, Illinois; MN, Minnesota; MO, Missouri; N, northern; ND, North Dakota; NE, northeastern; NW, northwestern; S, southern; SE, southeastern; SW, southwestern; W, western; WI, Wisconsin. Abbreviations for habitat niche breadth (defined in Methods): s, specialist; g, grassland; m, migrant.

	Tallgrass prairie and oak savanna								Pine barrens	
	SW MO	SE ND	W MN	NW IA	NE IA	N IL	S WI	S WI	N WI	N WI
Survey information										
First year	1992	1994	1988	1991	1991	1991	1987	1988	1988	1986
Last year	1995	1995	1995	1995	1993	1995	1995	1995	1995	1995
Earliest date	14 Jn	3 Jl	18 Jn	28 Jn	1 Jl	27 Jn	26 Ap	27 Jn	2 My	14 Jn
Latest date	24 Jn	17 Ag	20 Ag	21 Ag	21 Ag	1 Sp	23 My	13 Sp	24 Jn	14 Sp
Kilometers	178·2	13·7	336·4	15·1	9·9	60·9	26·2	261·4	369·6	309·0
Hours	95·9	7·2	200·4	9·3	5·2	29·4	15·2	151·4	191·7	162·3
Units	339	33	628	35	20	155	79	856	633	455
Number of sites	42	9	22	4	3	6	6	18	129	90
Minimum prairie size (ha)	6	259	16	13	2	3	1	1		
Maximum prairie size (ha)	571	2024	445	65	97	162	324	324		
Family Papilionidae										
g Black swallowtail *Papilio polyxenes*	235		241	27	3	32	1	193	3	3
Family Pieridae										
g Checkered white *Pontia protodice*	17		15			13		2		2
s Olympia marble *Euchloe olympia*						121		1103		
Family Lycaenidae										
g American (small) copper *Lycaena phlaeas*	4					30	134	347	448	930
g Gray copper *Lycaena dione*	91		34							1
g Bronze copper *Lycaena hyllus*		8	17		1	1		2		1
g Purplish copper *Lycaena helloides*										4
s Frosted elfin *Callophrys irus*									139	
s Henry's elfin *Callophrys henrici*									14	
g Eastern tailed-blue *Everes comyntas*	228		30	31	25	151	2	171	109	219
g Western tailed-blue *Everes amyntula*									56	
g Silvery blue *Glaucopsyche lygdamus*									56	
g Melissa blue *Lycaeides melissa melissa*		11	396							
s Karner blue *Lycaeides melissa samuelis*									3702	6262
Family Nymphalidae										
g Aphrodite fritillary *Speyeria aphrodite*		43	1538	86	7	584		1180		2096
s Regal fritillary *Speyeria idalia*	5779	100	3590	141	1	90		779		
g Silver-bordered (small pearl-bordered) fritillary *Boloria selene*			538		2				19	42
g Meadow fritillary *Boloria bellona*		164	1100		1	18		105	310	97
g Fritillary *Boloria* sp·			52						9	8
s Gorgone checkerspot *Chlosyne gorgone*			1	6		25	1	92	1177	75

g Tawny crescent *Phyciodes batesii*										*5
g Baltimore checkerspot *Euphydryas phaeton*					1					1
g Eyed brown *Satyrodes eurydice*			124	4				9		59
g Common ringlet (large heath) *Coenonympha tullia*		1	269							
g Common wood-nymph *Cercyonis pegala*	20	52	12585	200	35	655		4452		2656
s Chryxus arctic *Oeneis chryxus*									7	
m Monarch *Danaus plexippus*	600	29	25630	265	68	614		1581	46	409
Family Hesperiidae										
g Southern cloudywing *Thorybes bathyllus*	3					1		5		
s Mottled duskywing *Erynnis martialis*	1								28	27
g Wild indigo duskywing *E. baptisiae*	60					*7		*8	*13	*1
s Persius duskywing *Erynnis persius*									*291	
g Common sootywing *Pholisora catullus*	1					47	5	20	3	4
g Least skipper *Ancyloxypha numitor*			1						2	7
s Poweshiek skipperling *Oarisma poweshiek*			2043	24						
g European (Essex) skipper *Thymelicus lineola*						37		75		64
s Common branded (silver-spotted) sk. *H. comma*		1								
s Ottoe skipper *Hesperia ottoe*			14			1		462		
s Leonard's skipper *Hesperia leonardus leonardus*						1		113		324
s Pawnee skipper *Hesperia leonardus pawnee*		70	220							
s Cobweb skipper *Hesperia metea*							5		87	
s Dakota skipper *Hesperia dacotae*			300							
g Indian skipper *Hesperia sassacus*								71		
g Peck's skipper *Polites peckius*	1	1	7			3				14
g Tawny-edged sk. *Polites themistocles*	372	5	40	5		29		165		20
g Crossline skipper *Polites origenes*	264	1	25	4		16		223		34
g Long dash *Polites mystic*		12	259					1	1	10
s Arogos skipper *Atrytone arogos*	268		79							
g Delaware skipper *Anatrytone logan*	221		34	8		8		123		63
s Byssus skipper *Problema byssus*	21							1		
s Dusted skipper *Atrytonopsis hianna*							132		220	

APPENDIX 2

Summary statistics on regressions (all had $p < 0.002$): *n*, units in sample; *r*, multiple correlation coefficient; St, number of significant ($p < 0.05$) steps; Int, step number for management intrusiveness; Age, step number for age class

Step number is shown in parentheses if non-significant ($0.05 < p < 0.1$). Each regression was set for $p < 0.1$; 0–2 non-significant steps occurred per regression, occasionally intermixed in sequence of significant steps

	Missouri									Western Upper Midwest								
	First				Second					First				Second				
	n	*r*	St	Int	*n*	*r*	St	Int	Age	*n*	*r*	St	Int	*n*	*r*	St	Int	Age
Dakota skipper										325	0·650	8	6	214	0·644	5	(6)	—
Arogos skipper	337	0·445	6	(2)	290	0·445	8	2	—	233	0·553	5	1	148	0·587	4	1	—
Byssus skipper	199	0·258	2	—	188	0·281	2	—	—									
Regal fritillary	337	0·667	9	1	290	0·669	6	1	—	512	0·512	8	—	337	0·572	8	—	4
Poweshiek skipperling										370	0·654	11	—	252	0·690	7	—	2
Pawnee skipper										101	0·837	6	5	77	0·840	5	3	—
Gray copper	337	0·301	4	1	290	0·265	3	1	—	302	0·477	6	1	198	0·506	5	1	—
Aphrodite fritillary										621	0·513	6	—	404	0·555	8	—	4
Black swallowtail	342	0·245	2	—	295	0·235	2	—	—	517	0·484	5	—	339	0·499	5	—	—
Eastern tailed—blue	342	0·376	2	—	295	0·402	3	—	—									
Melissa blue										646	0·506	7	—	455	0·515	6	—	—
Silver-bordered fritillary										493	0·503	3	—	322	0·534	5	—	4
Meadow fritillary										575	0·527	8	6	378	0·551	9	—	6
Common ringlet										263	0·715	4	—	199	0·777	4	—	1
Common wood-nymph										655	0·665	14	6	453	0·651	11	7	8
Tawny-edged skipper	342	0·471	6	3	295	0·444	3	(6)	—									
Crossline skipper	335	0·441	5	1	289	0·458	4	1	—									
Long dash										270	0·583	5	—	205	0·580	4	—	3
Delaware skipper	335	0·450	5	—	289	0·409	5	—	(6)									
Monarch	342	0·354	5	—	295	0·378	5	—	5	674	0·673	10	—	468	0·671	10	—	9

	Eastern Upper Midwest																	
	First				Second					Third				Fourth				
	n	*r*	St	Int	*n*	*r*	St	Int	Age	*n*	*r*	St	Int	*n*	*r*	St	Int	Age
Frosted elfin	287	0·359	5	—	154	0·436	4	—	—	271	0·357	5	—	138	0·404	2	(4)	—
Mottled duskywing	280	0·302	3	—	235	0·277	2	—	—	275	0·300	3	—	230	0·275	2	—	—
Persius complex	500	0·326	5	3	248	0·277	4	2	—	471	0·305	5	3	260	0·240	2	1	—
Ottoe skipper	597	0·530	8	—	531	0·550	9	—	8	—				—				
Cobweb skipper	192	0·439	4	—	119	0·533	4	—	—	184	0·485	5	5	111	0·611	6	1	—
Regal fritillary	902	0·348	10	2	806	0·359	9	2	—	—				—				
Gorgone checkerspot	433	0·479	5		330	0·548	6			397	0·523	7	5	315	0·615	8	4	—

Leonard's skipper	267	0·622	6	—	218	0·647	6	—	4	241	0·647	4	—	131	0·414	2	—	2
Dusted skipper	282	0·629	5	4	192	0·623	4	—	—	268	0·629	6	—	178	0·637	6	—	5
Olympia marble	488	0·657	10	—	273	0·747	11	11	10	453	0·655	9	—	257	0·741	11	(12)	—
Karner blue	617	0·586	12	—	400	0·685	13	—	—	588	0·583	12	—	371	0·684	12	—	—
Aphrodite fritillary	1339	0·521	10	—	1104	0·531	10	—	9	1173	0·530	8	—	963	0·540	9	—	6
Black swallowtail	730	0·279	7	—	657	0·344	7	6	3	617	0·380	5	1	544	0·417	5	1	—
American copper	1294	0·427	8	(9)	931	0·490	8	—	—	1202	0·430	8	—	839	0·500	8	—	—
Eastern tailed-blue	1670	0·364	13	—	1253	0·346	11	—	(8)	1528	0·389	11	8	1111	0·385	10	9	10
Meadow fritillary	1363	0·441	8	—	1005	0·474	7	—	—	1193	0·241	6	—	855	0·302	8	—	5
Common wood-nymph	1314	0·510	12	—	1104	0·544	15	—	15	1165	0·507	13	—	955	0·543	14	—	9
Tawny-edged skipper	684	0·367	6	—	606	0·357	5	—	—	588	0·373	7	5	510	0·362	6	3	—
Crossline skipper	749	0·416	9	9	668	0·446	9	9	—	638	0·417	7	(8)	557	0·459	11	9	—
Delaware skipper	802	0·340	6	2	700	0·320	5	2	—	710	0·311	7	—	608	0·272	4	—	—
Monarch	1647	0·563	10	—	1320	0·563	9	—	7	1473	0·573	10	—	1146	0·575	9	(10)	7