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THE DIANA FRITILLARY (*SPEYERIA DIANA*) AND GREAT SPANGLED FRITILLARY (*S. CYBELE*): DEPENDENCE ON FIRE IN THE OUACHITA MOUNTAINS OF ARKANSAS

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ABSTRACT. The Diana fritillary (*Speyeria diana*), a species of conservation concern throughout its range, and the great spangled fritillary (*S. cybele*) both occur in the Ouachita Mountains of west-central Arkansas and eastern Oklahoma. Both species depend on abundant, high quality nectar resources to support populations. Decades of intense fire suppression have greatly altered vegetation structure throughout the Ouachita Mountains resulting in profound ecological changes. In an effort to restore pre-European ecological relationships and biodiversity, managers are restoring shortleaf pine-bluestem communities with the use of frequent prescribed fire. Restored sites support greater abundances of nectar resources and *Speyeria diana* and *S. cybele* than fire suppressed controls.

Additional key words: Interior Highlands, surveys, restoration

INTRODUCTION

The Diana fritillary, *Speyeria diana* (Cramer) is a species of conservation concern throughout its range in the eastern United States. It is currently restricted to the Interior Highlands of Arkansas, Oklahoma, and possibly Missouri, and the Appalachian Mountains from the Virginias to Georgia and Alabama (Hovanitz 1963, Opler & Krizek 1984, Carleton and Nobles 1996, Moran and Baldrige 2002). Historical populations in the Midwest and the Virginia Piedmont were extirpated in the 1800s (but see Shull 1987) and the 1950s (Opler and Krizek 1984), respectively. The cause(s) of these range contractions is unknown; but habitat alteration including loss of forest habitat (Allen 1997), harvest of old-growth forests (Hammond and McCorkle 1983), and loss of nectar plants (Moran and Baldrige 2002) have been proposed.

In the Interior Highlands, Carleton and Nobles (1996) reported records of *S. diana* from 11 counties in Arkansas, Missouri, and Oklahoma since 1980 and an additional 10 counties prior to 1980. Moran and Baldrige (2002) reported recent records for an additional seven counties in Arkansas, and our records add an additional three counties (reported in Moran and Baldrige 2002). Based on these records, *S. diana* remains widespread in the Ouachita Mountains of Arkansas and Oklahoma and perhaps less so in the Ozark Mountains of Arkansas and Missouri.

The great spangled fritillary, *S. cybele* (Fabricius), is widespread in the eastern United States and Canada (Opler and Krizek 1984). It remains relatively common in a variety of habitats throughout most of its extensive range and is common throughout the Ouachita Mountains of Arkansas.

The Ouachita Mountains physiographic region encompasses an area of 3,237,600 ha of east-west oriented ridges and valleys with elevations ranging from 150 to 820 m (Bukenhofer and Hedrick 1997). Historically, much of the region (especially the more xeric south- and west-facing slopes) burned on a regular basis during fires ignited by lightning and Native Americans (Foti and Glenn 1991, Masters *et al.* 1995). These frequently burned forests consisted of open, pine-dominated canopies, sparse midstories, and a diverse understory of grasses and forbs (Featherstonhaugh 1884, du Pratz 1975, Nuttall 1980, Foti and Glenn 1991, Masters *et al.* 1995). In the absence of frequent fire, these forests tend to succeed to an oak (*Quercus* spp.)-hickory (*Carya* spp.) community (Neal and Montague 1991).

Managers of the Ouachita National Forest have been in the process, since 1979, of restoring the fire-maintained shortleaf pine (*Pinus echinata* P. Mill.)-bluestem grass (*Schizachrium* spp.) ecosystem on approximately 48,706 ha primarily on the Poteau Ranger District in west-central Arkansas (Bukenhofer and Hedrick 1997). The primary management tool used to restore shortleaf pine-bluestem habitat is prescribed fire. Restoration is being conducted to restore habitat for the federally endangered red-cockaded woodpecker, *Picoides borealis* (Viellot), and to restore what is thought to be the original forest structure (Foti and Glenn 1991, Bukenhofer and Hedrick 1997). A number of authors have examined the effect of these restoration efforts on a variety of taxa (Masters *et al.* 1998, 2002; Sparks *et al.* 1998, 1999; Thill *et al.* 2004).

As part of extensive studies on the effects of restoration of fire-maintained pine-bluestem habitats on lepidopteran communities, we conducted censuses of butterflies and nectar resources on restored (treatment)

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and unrestored (control) plots (Thill *et al.* 2004). Here we report results for *S. diana* and *S. cybele* and their nectar resources in relation to ecosystem restoration and the prescribed fire regime.

STUDY AREA AND METHODS

This research was conducted on the Poteau District (34°45'N, 94°15'W) of the Ouachita National Forest in west-central Arkansas. The Ouachita Mountains, especially within the Ouachita National Forest, is predominately forested. North-facing slopes are dominated by oaks (*Quercus* spp.), hickories (*Carya* spp.), and a diverse array of additional species, south-facing slopes by shortleaf pine and a varying mixture of angiosperms.

Landscape scale restoration was initiated in 1979, formally incorporated into the Ouachita National Forest Plan in 1996, and currently projects the restoration of 48,706 ha (7.3% of the Forest) to a shortleaf pine-bluestem condition thought to mimic the pre-European forest structure (U. S. Forest Service 1996, Bukenhofer and Hedrick 1997). At the initiation of our studies, approximately 9,071 ha had been restored in a 42,148 ha landscape on the Poteau Ranger District (W. G. Montague pers. com.). Restoration was accomplished by selective thinning of overstory trees, removal of most midstory vegetation, and implementation of a three-year prescribed fire regime. Treatment blocks for restoration are typically 10-45 ha in size, however blocks are combined for purposes of prescribed burning, and individual prescribed fires ranged up to 1,300 ha. We use "restored" in a relative sense and recognize that stands are on a trajectory towards an ecological state thought to mimic pre-European conditions.

We established nine study plots in restored stands and three in control stands. All restored stands had received initial thinning harvests and a minimum of four prescribed fires prior to the initiation of this study. Prescribed fire was applied to restored stands during March and April with few exceptions, all prior to the initiation of this study. During the course of this study prescribed fire was applied to three of the restored stands each year. Consequently, in any given year three restored stands represented first, second, and third growing seasons post-fire. For purposes of analysis, data were grouped by post-fire growing season.

Adult butterflies (Papilionoidea and Hesperioidea) were censused using a time-constrained walking census along a 500-m transect traversing a triangular course within each of the 12 study sites (Pollard 1977, Gall 1985). Individual transects were censused by slowly walking the length of the transect in approximately 20 min. Time required to count butterfly aggregations, net

and identify individuals, and pauses to wait for appropriate wind or sun conditions (see below) was not included in the 20-min census time. All butterflies detected along the census transect during the 20-min census period were counted, regardless of distance from the midline of the transect. Consequently, comparisons across species, especially for species of different sizes or behaviors, are not appropriate. Most individuals (87.2%) were identified to species.

Census counts were conducted four times per year (first week of April, June, August, and October) during 2000 to 2002. Census counts on each site were replicated three times (a different observer on three separate days) during each month surveys were conducted. Individual censuses were conducted between 0900 and 1330 hrs CST on days when temperatures were between 18° and 36° C and wind velocity beneath the canopy was not strong enough to suppress butterfly flight (Beaufort Scale < 4). Census counts were further restricted to periods when sunlight was sufficient to cast discernable shadows. The response of butterflies to temperature, wind, and cloud cover varies seasonally and daily in complex ways. Consequently, observer judgment further constrained censusing to those periods when butterfly flight activity was judged to be substantial.

Nectar resources were quantified during each butterfly sampling month within three 1- x 100-m belt transects located parallel to each butterfly census transect. All nectar resources were counted and recorded by species. For most species, individual flowers or composite heads (capitula) were enumerated. Inflorescences, or portions thereof, were counted for a few species with small and/or dense aggregations of flowers (e.g. *Ceanothus americanus* L., *Allium* sp., *Solidago* spp., Apiaceae). Enumeration decisions were based on the structure that most closely approximated a separate landing site for a typical butterfly.

In addition, throughout our investigations (1999-2004) in the Ouachita Mountains, we recorded observations of nectaring and other feeding activities. Date, resource, and butterfly species were recorded. Voucher specimens of plant species were collected for later identification. Plant nomenclature follows Smith (1994). Plant vouchers will be deposited in the Stephen F. Austin State University Herbarium, Nacogdoches, TX.

RESULTS

In the Ouachita Mountains, male *S. diana* emerge in late May to early June and *S. cybele* emerge in mid- to late May. Females of both species emerge approximately 7-10 days later in each species. Adult

males are generally dead by early July, although very worn males are occasionally noted as late as early October. Females are less obvious until late September-early October when numerous individuals, still in fairly good condition, are frequently observed.

Nectaring observations for *S. diana* (n = 307) and *S. cybele* (n = 607) were obtained during 1999-2004 (Table 1). Both species used a small subset of the total nectar species available and used by the total butterfly fauna throughout the flight period. More than 95% of *S. diana* nectaring records were from only eight plant species and more than 88% of *S. cybele* records were from only 11 species. Nectaring by *S. diana* was recorded on 11 additional species and by *S. cybele* on 26 additional species. These numbers were summed over the entire flight period, however the pattern was even more extreme within individual months. All but one of the heavily used species (*Carduus nutans* L.) and most of the rarely used species were native, herbaceous perennials. *Allium canadense* L. was the only monocot used by both species.

The availability and use of nectar resources varied considerably across months (Table 1). During the main flight period of males of both *Speyeria* species (late May and June), the primary nectar resources used were *Asclepias tuberosa* L., *Monarda fistulosa* Sims, *Cirsium carolinianum* (Walt.) Fern. & Schub., *Echinacea purpurea* (L.), *E. pallida* (Nutt.), and *Pycnanthemum tenuifolium* Schrad. Male *S. cybele* also used *Carduus nutans* and *Liatris squarrosa* (L.) Michx. Females tended to use the same species during this period. However, due to the slightly later emergence of females, the rapidly declining availability of *A. tuberosa*, *Cirsium carolinianum* and *E. pallida* flowers early in June reduced use of these species by females, especially the later emerging *S. diana*. Nectaring records were infrequent during July and August; as most males were dead and females were infrequently observed. *Pycnanthemum albescens* Torr. & Gray dominated the few nectaring records of both species during this period. Females became much more obvious during September and October and nectaring was primarily on *Cirsium discolor* (Muhl. ex. Wild.) Spreng.

Males of *S. diana* were frequently (n = 118) observed imbibing from non-nectar, apparently electrolyte rich resources (Smedley and Eisner 1995) including feces of a wide variety of vertebrates, carrion, wads of grass vomitus from coyotes, human sweat, damp soil, and dusty surfaces (i.e. roads, vehicles, etc.) (Table 1). This behavior was observed exclusively in newly eclosed males, possibly during their first two days, as judged by fresh appearance and absence in previous days. This behavior was less frequently (n = 67) observed in *S.*

cybele, presumably because our June survey period was several days after most males of the earlier emerging *S. cybele* had discontinued this ephemeral behavior.

A consequence of the above behavior for male *S. diana*, and presumably for the earlier emerging *S. cybele*, was frequent vehicle-related mortality. Imbibing from feces, carrion, etc. was most frequent in the morning shortly after individuals first began flying, and occurred most frequently on unpaved roads where feces and carrion were common. Aggregations of up to 16 male *S. diana* were often present at a single site and they were generally reluctant to take flight. Consequently, multiple mortalities were not uncommon.

A total of 73 *S. diana* and 201 *S. cybele* were detected during a total of 324 census transects during 2000, 2001, and 2002 (Table 2). Equal numbers of transects (n = 36) were conducted in early June, early August, and early October of each year. Most detections were during the June surveys immediately following emergence of adults, with reduced numbers, primarily females, in August and October. Significant differences across treatments were detected for total numbers of both *S. diana* ($\chi^2 = 39.6$, df = 3, P < 0.001) and *S. cybele* ($\chi^2 = 166.6$, df = 3, P < 0.001). The overwhelming majority of detections of *S. diana* (71 of 73, 97.3%) and *S. cybele* (197 of 201, 98.0%) were from the restored treatments. Among the restored treatments, abundances for both species were highest during the second growing season post-fire.

A broadly similar pattern existed for the nectar resources (Table 3). With minor exceptions, nectar resources were more abundant in restored treatments than in controls, and more abundant during growing seasons most proximal to prescribed fires. Significant differences existed for many of these patterns. In most comparisons, significantly more nectar resources were detected in 1st and 2nd years post-burn than in the corresponding controls. Exceptions were the April 1st year post-burn sites in 2000 and 2001 when plants had not had sufficient time to recover from the very recent prescribed fires, and the 1st year post-burn sites in April 2002 when prescribed-burning was delayed until after the scheduled surveys. The only other exception was the 2nd year post-burn sites for April 2002. The prescribed fires during 2001 in each of the three replicates for this treatment were unusually intense, with substantial canopy mortality. The recovery rate of herbaceous plants was tremendous, and the anomalously low counts of nectar resources in April 2002 may have been a result of shading by the very high residual herbaceous biomass remaining from the 2001 growing season.

TABLE 1. Feeding records (1999-2005) of Diana fritillary (*Speyeria diana*) male/female and great spangled fritillary (*Speyeria cybele*) male/female/unknown in the Ouachita Mountains of western Arkansas by month.

Source	Species	May	Jun.	Jul.	Aug.	Sept.	Oct.	Total
Major Nectar Species								
<i>Asclepias tuberosa</i> L.	<i>S. diana</i>	0	18/0	0	0	0	0	18
	<i>S. cybele</i>	0/0/1	41/25/56	0	0	0	0	123
<i>Echinacea purpurea</i> (L.)	<i>S. diana</i>	0	11/2	0/1	0	0	0	14
	<i>S. cybele</i>	0	6/14/4	0/0/8	0	0	0	32
<i>Echinacea pallida</i> Nutt.	<i>S. diana</i>	3/0	0	0	0	0	0	3
	<i>S. cybele</i>	0/0/9	0/0/8	0	0	0	0	17
<i>Cirsium carolinianum</i> (Walt.) Fern. & Schub.	<i>S. diana</i>	0	23/1	0	0	0	0	24
	<i>S. cybele</i>	0/0/9	21/23/31	0	0	0	0	83
<i>Cirsium discolor</i> (Muhl.) Spreng.	<i>S. diana</i>	0	0	0	0	1/147	0/23	171
	<i>S. cybele</i>	0	0	0	3	0/43/24	0/0/12	82
<i>Carduus nutans</i> L.	<i>S. diana</i>	0	0	0	0	0	0	0
	<i>S. cybele</i>	0/0/11	0/0/9	0	0	0	0	20
<i>Liatris elegans</i> (Walt.) Michx.	<i>S. diana</i>	0	0	0	0	0	0/11	11
	<i>S. cybele</i>	0	0	0	0	0	0/5/0	5
<i>Liatris squarrosa</i> (L.) Michx.	<i>S. diana</i>	0	0	0	0	0	0	0
	<i>S. cybele</i>	0	2/4/20	0	0	0	0	26
<i>Monarda fistulosa</i> L.	<i>S. diana</i>	0	21/13	0	0	0	0	34
	<i>S. cybele</i>	0	9/11/93	0/0/5	0	0	0	118
<i>Porteranthus stipulatus</i> (Muhl.) Baill.	<i>S. diana</i>	0	1/0	0	0	0	0	1
	<i>S. cybele</i>	0	0/0/18	0	0	0	0	18
<i>Pycnanthemum albescens</i> Torr. & Gray	<i>S. diana</i>	0	0	0	0/8	0	0	8
	<i>S. cybele</i>	0	0	0	0/8/2	0	0	10
<i>Pycnanthemum tenuifolium</i> Schrad.	<i>S. diana</i>	0	5/7	0	0	0	0	12
	<i>S. cybele</i>	0	1/2/6	0/0/5	0	0	0	14
Secondary Nectar Species								
<i>Cephalanthus occidentalis</i> L.	<i>S. cybele</i>	0/0/4	0	0	0	0	0	4
<i>Rhexia</i> sp.	<i>S. diana</i>	0	0	0	0/1	0	0	1
<i>Scutellaria ovata</i> Hill	<i>S. diana</i>	0	1/0	0	0	0	0	1
	<i>S. cybele</i>	0	0/0/1	0	0	0	0	1
<i>Erigeron strigosus</i> Willd.	<i>S. diana</i>	0	1/1	0	0	0	0	2
	<i>S. cybele</i>	0	1/0/1	0	0	0	0	2
<i>Bidens aristosa</i> (Michx.) Britt.	<i>S. diana</i>	0	0	0	0	0/1	0	1
<i>Eupatorium fistulosum</i> Barr.	<i>S. diana</i>	0	0	0	0/1	0	0	1
<i>Solidago rugosa</i> (Small) Fern.	<i>S. diana</i>	0	0	0	0	0	0/1	1
<i>Helianthus divaricatus</i> L.	<i>S. diana</i>	0	1/0	0	0	0	0	1
	<i>S. cybele</i>	0	0/0/2	0/0/2	1/0/0	0	0	5
<i>Vernonia gigantea</i> (Watt.) Trel.	<i>S. diana</i>	0	0	0	0	0/1	0	1
	<i>S. cybele</i>	0	0	0	0	0/1/0	0/1/0	2
<i>Vernonia baldwinii</i> Torr.	<i>S. diana</i>	0	2/0	0	0	0	0	2
	<i>S. cybele</i>	0	0	0/0/1	0/0/2	0	0	3

TABLE 1. Continued

Source	Species	May	Jun.	Jul.	Aug.	Sep.	Oct.	Total
<i>Achillea millefolium</i> L.	<i>S. cybele</i>	1/0/0	0	0	0	0	0	1
<i>Coreopsis palmata</i> Nutt.	<i>S. cybele</i>	0/0/1	0	0	0	0	0	1
<i>Coreopsis grandiflora</i> Sweet	<i>S. cybele</i>	0	0/0/2	0	0	0	0	2
<i>Coreopsis tripteris</i> L.	<i>S. cybele</i>	0	0	0/0/1	0	0	0	1
<i>Rudbeckia hirta</i> L.	<i>S. cybele</i>	0	0/0/2	0	0	0	0	2
<i>Verbesina helianthoides</i> Michx.	<i>S. cybele</i>	0	2/0/7	0/0/3	0	0	0	12
<i>Silphium integrifolium</i> Michx.	<i>S. cybele</i>	0	0	0/0/1	0	0	0	1
<i>Parthenium integrifolium</i> L.	<i>S. cybele</i>	0	0/0/2	0	0	0	0	2
<i>Aster ericoides</i> L.	<i>S. cybele</i>	1/0/0	0	0	0	0	0	1
<i>Trifolium pratense</i> L.	<i>S. cybele</i>	1/0/0	1/0/0	0	0	0	0	2
<i>Cornus drummondii</i> C. A. Mey.	<i>S. cybele</i>	0	0/0/2	0	0	0	0	2
<i>Daucus carota</i> L.	<i>S. cybele</i>	0	0/0/1	0	0	0	0	1
<i>Phlox glaberrima</i> L.	<i>S. cybele</i>	0	0/0/1	0	0	0	0	1
<i>Prunella vulgaris</i> L.	<i>S. cybele</i>	0/0/1	0	0	0	0	0	1
<i>Strophostyles leiosperma</i> (Torr. & Gray) Piper	<i>S. cybele</i>	0	0	0	0/0/2	0	0	2
<i>Aralia spinosa</i> L.	<i>S. cybele</i>	0	0	0	0/0/2	0	0	2
<i>Lonicera japonica</i> Thunb.	<i>S. cybele</i>	0	2	0	0	0	0	2
<i>Ligustrum vulgare</i> L.	<i>S. cybele</i>	0/0/2	0	0	0	0	0	2
<i>Ruellia</i> sp.	<i>S. cybele</i>	0	0/0/1	0	0	0	0	1
<i>Allium canadense</i> L.	<i>S. cybele</i>	0/0/4	0	0	0	0	0	4
Carrion	<i>S. diana</i>	0	5/0	0	0	0	0	5
	<i>S. cybele</i>	5/0/0	1/0/0	0	0	0	0	6
Feces	<i>S. diana</i>	0	83/0	0	0	0	0	83
	<i>S. cybele</i>	36/0/01	18/0/0	0	0	0	0	54
Vomit ¹	<i>S. diana</i>	0	5/0	0	0	0	0	5
Sweat (human)	<i>S. diana</i>	0	5/0	0	0	0	0	5
Wet Soil	<i>S. diana</i>	0	18/0	0	0	0	0	18
	<i>S. cybele</i>	0	7/0/0	0	0	0	0	7
Dust	<i>S. diana</i>	0	5/0	0	0	0	0	5

¹ Regurgitated plant material, primarily grass, presumably from Canids

TABLE 2. Total number of *Speyeria diana* and *S. cybele*, summer across years, detected on restored sites and control sites (n = 3 plots/treatment) on the Ouachita National Forest during 2000-2002.

Species	B-1 ^a	B-2	B-3	Control
<i>S. diana</i>	19	39	13	2
<i>S. cybele</i>	41	126	30	4

^a B-1, B-2, and B-3 correspond to 1st, 2nd, and 3rd growing seasons post-burn.

TABLE 3. Response of nectar resources to shortleaf pine-bluestem restoration on the Ouachita National Forest during 2000–2002. Mean numbers of nectar resources per 300 m² plots in restored and control stands (*n* = 3 plots/treatment). Letters represent significantly different means in a 1-way ANOVA with REGWQ at *P* < 0.1 (SAS Inst. Inc. 1988:598). Because abundance values varied greatly within treatments, data were rank transformed prior to analysis.

Year	Month	B-1		B-2		B-3		Control		P
		x	SE	x	SE	x	SE	x	SE	
2000	April	84.7A	45.5	960.0B	532.1	154.7A	62.3	150.7A	12.4	0.0278
	June	1018.3A	364.0	420.3A	134.9	399.3A	172.3	49.7B	15.4	0.0191
	August	417.7A	157.3	583.0A	312.6	56.3B	41.4	3.7B	0.7	0.0011
	October	746.3A	66.4	84.3B	45.9	59.3B	21.9	7.3C	5.0	0.0010
2001	April	0.0A	0.0	1234.3B	415.3	661.3B	391.2	117.7C	42.7	0.0003
	June	1492.7A	859.8	462.7A	320.9	215.3A	82.7	26.7B	8.1	0.0088
	August	1735.7A	669.6	588.7B	127.5	483.0B	218.5	24.3C	8.8	0.0011
	October	2745.0A	604.9	3219.0A	1605.5	515.3B	106.2	183.7B	130.4	0.0047
2002	April	241.0A ¹	77.1	17.0A	15.0	270.3A	41.7	197.0A	187.1	0.2593
	June	1067.7A	601.2	1316.7A	417.1	721.3A	99.3	49.7B	20.3	0.0595
	August	768.3A	102.2	702.7A	137.9	156.0B	57.3	9.0B	2.1	0.0011
	October	4587.3A	2987.2	1746.7A	689.1	719.3AB	355.0	35.0B	8.3	0.0181

¹ Plots scheduled to be burned prior to April 2002 surveys were not burned until after the April surveys were complete and thus represent the fourth growing season post-fire.

Within the restored treatments the 1st year post-burn sites generally supported the most nectar resources and the 3rd year post-burn treatments the least, in all months and years (Table 3). Many significant differences support this overall pattern (Table 3). The only exceptions were those noted above and three of 12 instances when the abundance of nectar resources on the 2nd year post-burn sites exceeded those on the corresponding 1st year post-burn sites.

Viola spp., the only larval host of *Speyeria* spp. (Opler and Krizek 1984), were abundant in the restored treatments and uncommon in the controls. *Viola pedata* L. (bird's foot violet) was the predominant species, although *Viola sagittata* Ait. (arrow-leaved violet) was also present in more mesic sites. These and additional species were also present in adjacent habitats. Based on the nectar resource surveys, *Viola* flowers were more abundant on treatment transects (Table 4) than on control transects, and significant differences existed across treatments ($\chi^2 = 71.0$, *df* = 3, *P* < 0.001).

TABLE 4. Mean number of *Viola* spp. flowers (flowers/300 m²) detected during June surveys on restored sites and control sites (*n* = 3 plots/treatment) on the Ouachita National Forest during 2000–2002.

Year	B-1	B-2	B-3	Control
2000	79.7	52.2	2.92	6.2

DISCUSSION

Restoration treatments effectively altered forest structure to more closely resemble the inferred pre-European structure (Sparks *et al.* 1999, Thill *et al.* 2004). The primary changes were reduced canopy cover, elimination of most midstory vegetation, and the restoration of a dense herbaceous ground cover (Thill *et al.* 2004). In addition, the reintroduction of frequent prescribed fire reduced the litter layer, removed dead herbaceous vegetation, and stimulated flowering of a diverse array of herbaceous angiosperms (Sparks *et al.* 1998).

In fire-maintained pine forests in eastern Texas (Rudolph and Ely 2000), the complete data set for Arkansas (Thill *et al.* 2004), and migrating monarchs in Arkansas (Rudolph *et al.* 2006) butterfly abundance was significantly greater in sites with a frequent fire regime compared to fire-suppressed sites. Furthermore, butterfly abundance was greatest in the first growing season following late winter-early spring prescribed fires and declined markedly in successive growing seasons, at least through the first few years (Rudolph *et al.* unpub. data). These changes in butterfly abundance were correlated with similar abundance patterns for the nectar resources (Thill *et al.* 2004, Rudolph *et al.*, unpub. data). A similar pattern was detected in fire-maintained pine forests in Texas (Rudolph and Ely 2000). In a ponderosa pine ecosystem in Arizona, also a

fire-maintained system, Waltz and Covington (1999) found parallel responses of butterflies and nectar plants following thinning and prescribed fire.

Both species of *Speyeria* and their primary nectar resources were essentially absent from control treatments, but more abundant on the restored treatments for at least three years post-fire. We suggest that the increased abundance of both *Speyeria* was due to the significantly increased availability of nectar resources in the restored treatments. The increased abundance of *Speyeria*, especially *S. diana*, is consistent with observations of *S. diana* throughout the Interior Highlands. *Speyeria diana* was characterized by Carleton and Nobles (1996) as rare and local, and by Moran and Baldrige (2002) as widespread and local in the Interior Highlands. They associated occupied sites with disturbance, including fire, and Moran and Baldrige further noted their association with high quality nectar resources. We observed similar patterns during 5 years of field work in the Ouachita Mountains. In addition, our observations, and those reported by Carlton and Nobles (1996) and Moran and Baldrige (2002), beyond the restoration landscape are primarily of one or a few individuals. In marked contrast, we have observed, on several occasions, up to 12-16 males on a single black bear (*Ursus americanus* Pallas) or coyote (*Canis latrans* Say) fecal deposit, and 4-6 females on a single thistle (*Cirsium discolor*) plant with multiple inflorescences, within the restored shortleaf pine/bluestem landscape. The more general occurrence of nectar resources across the landscape, including those most frequently utilized by *Speyeria*, following restoration and prescribed fire is consistent with these observations. Without restoration, abundant nectar resources of the frequently used species are generally restricted to disturbed sites including road verges, recently disturbed logging sites, and utility rights-of-way (Rudolph *et al.* pers. obs.).

Unlike the pattern for all butterflies, the abundance of both species of *Speyeria* was greatest in the second growing season post-fire. Several hypotheses, not necessarily mutually exclusive, are available that may explain this pattern. First, *Speyeria* may require more than one growing season to fully re-colonize a site. If substantial mortality of immature stages occurs during fire events, re-colonization by volant adults may not be complete within the first flight period following fires. Second, and related to the first, adult *Speyeria* abundance may be a consequence of enhanced on-site reproduction due to the abundance and/or vigor of the larval host, *Viola* spp., following fires. Third, the preferred nectar resources used by both *Speyeria* peak following the first growing season post-fire, and

Speyeria abundance is simply tracking nectar resources. Fourth, the majority of the increase in *Speyeria* abundance in the second growing season post-fire compared to the first was found in 2002. It is possible that the abundance of *Speyeria* in the first year post-fire plots in 2002 was depressed due to a landscape effect resulting from the somewhat peripheral location of the first year post-fire sites in the overall restoration area in 2002.

Speyeria used a limited subset of the nectar resources potentially available or used by the overall butterfly fauna. More than 88% of nectaring observations for *S. cybele* were from 11 species, and more than 95% of observations for *S. diana* were from only 8 nectar plant species. These numbers represent a small minority of the 154 species of nectar plants used as nectar sources by the entire butterfly fauna during the flight period of *S. cybele* and *S. diana* (Rudolph *et al.* unpub. data). Moran and Baldrige (2002) reported similar results. These data suggest that *Speyeria* populations in the Interior Highlands, and especially *S. diana*, may be dependent on the availability of a limited number of plant species that provide high quality nectar resources. In the absence of frequent fire, suitable nectar resources are rare and fragmented, and may be able to support only localized and small populations of *S. diana*. Moran and Baldrige (2002) recorded the greatest abundances of *S. diana* in remnant prairie habitat with abundant floral resources, and wetlands with abundant *Cephalanthus occidentalis* L., a preferred nectar resource for *Speyeria* in areas peripheral to the core of the Ouachita Mountains. These habitats are infrequent in our study area. *Speyeria cybele*, perhaps due to its smaller size, may be less specialized with regard to high quality nectar resources and consequently is considerably more abundant in fire-maintained pine habitats (this study) as well as in fire-suppressed habitats throughout the Ouachita Mountains (Rudolph *et al.* pers. obs.).

It is important to realize that this discussion is based entirely on observations of adult *Speyeria*. Despite considerable effort, we have been unable to identify the larval hosts or habitats of either species in the Ouachita Mountains. *Viola* spp., the only known host of larval *Speyeria* spp., are abundant in diverse habitats in the Ouachita Mountains. *Viola pedata* is abundant in the fire-maintained pine community, less so in fire-suppressed sites, and several other species are common to abundant in more mesic sites on north-facing slopes and along drainages (pers. obs.) Whether *Speyeria* spp. use *Viola* spp. in fire-maintained communities or adjacent habitats remains an important question. Several females were observed exhibiting possible

ovipositing behavior (Harris 1972) in fire-maintained pine habitat in the vicinity of *V. pedata*, but actual egg laying could not be verified.

Based on these data and observations, we agree with Moran and Baldrige (2002), that loss of high quality nectar resources may be the primary cause of population declines and range contractions in *S. diana*, and further suggests that similar considerations may apply to *S. cybele*, at least in the Ouachita Mountains. Lepidoptera exhibit two strategies in relation to the nutritional reserves used to mature eggs (Tammeru and Haukioja 1996). At one extreme (capital breeders) reserves accumulated during the larval stage are used; at the other extreme (income breeders) reserves acquired by adult foraging are used. Increased fecundity and longevity are dependent on adult food intake in income breeders (Gilbert 1972, Fischer and Fielder 2001). *Speyeria*, at least the longer lived species, are best characterized as income breeders with increased fecundity dependent on adult feeding (Boggs and Ross 1993, Boggs 1997).

We suggest that reduced fecundity due to reduced nectar abundance and quality is the proximate cause of the observed low populations of *Speyeria*, especially *S. diana*, throughout most of the Interior Highlands. We further suggest that the Interior Highlands, much of which remains forested, have experienced a massive decline in nectar resources since the arrival of Europeans, due primarily to changes in vegetation structure resulting from alteration of the pre-European fire regime. The resulting suppression of the herbaceous flora within the original fire-maintained pine communities has had negative effects on the overall butterfly fauna (Thill *et al.* 2004). A prescribed fire regime that restores a fire-maintained pine/bluestem community on a landscape scale in the Ouachita Mountains has been demonstrated to result in at least a local increase in *Speyeria* spp., including *S. diana*, a species of conservation concern. Additional research addressing competition between the two *Speyeria* species, larval biology especially in relation to host plants, mimicry relationships with the Pipevine Swallowtail, *Battus philenor* (L.), and effects of landscape parameters would provide additional insight into the abundance and ecology of *Speyeria* in the Interior Highlands.

Fire, including prescribed fire, has profound effects on the composition and structure of plant communities, and consequently on butterfly faunas. The effects on butterfly faunas are a complex interplay of effects on host plants (Kwilosz and Knutson 1999), nectar resources (Shuey 1997, Rudolph and Ely 2000), mortality of immature stages (Dana 1991, Swengel

1995, 2001), microclimate (Rudolph and Ely 2000), and other interactions. Often, these effects are beneficial, at least in maintaining populations of species that have declined due to habitat alteration in the absence of fire (Williams 1995, Shuey 1997). In the increasingly fragmented landscapes that characterize much of the planet, fire can affect entire habitat patches with negative results. This is often the case in small prairie remnants in North America (Dennis and Eales 1997). However, the landscape scale restoration of a frequent fire regime on the Ouachita National Forest appears to increase populations of most butterfly species (Thill *et al.* 2004, Rudolph *et al.* 2006) including *S. diana* and *S. cybele*.

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