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OZARK BALTIMORE CHECKERSPOT *EUPHYDRYAS PHAETON OZARKAE* (NYMPHALIDAE) OVIPOSITION SELECTION FAVORS MORE VIGOROUS HOSTS

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ABSTRACT. Oviposition search behaviors and host-plant selection play a critical role in the individual and population success of phytophagous insects. These characters are particularly important for specialists and metapopulations. The Ozark Baltimore Checkerspot *Euphydryas phaeton ozarkae* (Masters 1968) Nymphalidae specializes on Smooth Yellow False Foxglove *Aureolaria flava* (L. 1753, Farwell 1918) Orobanchaceae and has a metapopulation structure. We examined oviposition search behaviors of *E. p. ozarkae* using many of the same variables from a study on the nominate subspecies, the Baltimore Checkerspot *Euphydryas phaeton phaeton* (Drury 1773). Insight into host selection was obtained by comparing characteristics between plants with and without egg masses. Relationships among habitat conditions (and management therein) and the most selected plant characteristics were also determined. We found *E. p. ozarkae* to be highly selective of oviposition plants, expressing higher values associated with host-plant searching than *E. p. phaeton*. Butterflies consistently oviposited on plants with the greatest height, area, number of stalks, and number of leaves within a given study site. As average plant vigor increased, however, selection of the highest character values converged and became less prominent. In general, important plant characters were greater in habitats with a more open understory and canopy, which were associated with routine fire management. Continued habitat restoration in the Ozark and Boston Mountain regions and perpetual maintenance using prescribed fire (as appropriate seasonally) may positively affect the Ozark Baltimore Checkerspot by improving plant characters selected by these butterflies.

Additional key words: Ozark Baltimore Checkerspot, oviposition host selection, plant vigor, prescribed fire, managing metapopulations

Oviposition search behaviors and host selection criteria (strategies) are among the most important life-history characteristics for phytophagous insects. Most immature herbivorous insects are practically non-motile when compared to winged adult females. Larvae contribute little to host-plant selection and depend largely on the plant the adult female selects for egg deposition (Mackay 1985). Oviposition strategies of phytophagous insects are, by this very nature, strongly correlated with offspring survival and individual fitness (Thompson 1988). Subtle differences among local habitats can nevertheless result in starkly different selection pressures. As a result, strategies by which females search for and accept oviposition sites can vary within species (Thompson & Pellmyr 1991, Renwick & Chew 1994). It is therefore important to examine these strategies from more than one location or subpopulation before drawing population-level conclusions.

Understanding oviposition strategies of butterflies in relation to specific habitat conditions can be an essential factor for proper conservation and management. The insect-resource relationship is complex and varies across an ecological mosaic. Subtle differences in the habitat landscape and relationships with habitat constituents can determine the suitability of resource patches and how these are used (Singer 2004, Henry & Shultz 2013). Appropriate management should begin by understanding how a particular resource is used by butterflies in order to determine what factors contribute to the suitability of locations (Ehrlich & Hanski 2004). As a prime example in Lepidoptera oviposition, Beyer and Schultz (2010) found that the endangered Mardon Skipper *Polites mardon* (Edwards 1881) Hesperiidae was a generalist egg layer in densely vegetated areas in the Cascade Mountains of Washington where the butterfly used 25 different plant species for oviposition. In contrast, Henry and Shultz (2013) found this species to specialize on Roemer's Fescue *Festuca roemeri* (Pavlick 1983) Poaceae in sparsely vegetated areas in the Puget Prairies of Washington. Management strategies applied based on the findings from only one population of Mardon Skipper could have been devastating to the other.

Oviposition strategies are particularly important for butterflies existing as metapopulations. Animals exhibiting metapopulation structure exist in locally isolated subpopulations connected through individual dispersal (Hanski & Gilpin 1991). Because metapopulations are sensitive to local habitat conditions and experience frequent establishment and extirpation (Hanski & Singer 2001), they rely on the establishment of, often ephemeral, populations that serve to connect habitats (sometimes recolonizing previously occupied areas) that can support source, or more permanent and dense, populations. As such, an integral aspect to the health of butterfly metapopulations is dispersal into suitable, unoccupied habitats. Egg-laying strategies for these butterflies, therefore, serve as critical components for not only the fitness of the individual (and founder effects therein) but also the continued existence of the species. Strategies for such species must necessarily be dynamic to allow for the acceptance of hosts in unfamiliar habitats. This means butterflies must be able to make oviposition decisions in resource landscapes where host usage likely varies from their original habitat in order to ensure larval success. These qualities make oviposition an essential life history characteristic on which to focus when studying the management of butterfly metapopulations.

Euphydryas is an excellent genus in which to study oviposition. Species in this group are typically specialists and very discerning of oviposition plant selection (Ehrlich & Hanski 2004). Where most butterflies deposit one egg before moving on to find another deposition site, *Euphydryas* butterflies are among the few that lay large clusters of eggs during oviposition (Singer 2004). Depositing eggs en masse reduces the amount of time needed to lay entire egg loads, but introduces selective pressures associated with large, aggregate groups (e.g., sibling and intraspecific competition, reduced resource availability, increased predator awareness, etc.). Specialist female butterflies that lay eggs in this manner must be more critical of deposition sites than those that deposit eggs singularly. Herein lies the tradeoff: the time gained by depositing eggs en masse is allocated to host-plant selection, as is suggested by the time-egg load hypothesis (Jaenike 1978). Additionally, *Euphydryas* species are stereotype examples of metapopulations. Changes in local environment and acute destructive events (e.g., fire, storms, land clearing, etc.) can result in the collapse of isolated populations. Broad-ranging habitat deterioration (e.g., climate change, lack of or improper management practices, urbanization, etc.) may cause severe reduction or complete isolation of constituent populations. Checkerspot species such as the Baltimore and the subspecies complex of Edith's *Euphydryas editha* (Boisduval 1852) Nymphalidae are in fact considered endangered or threatened in at least portions of their ranges (NatureServe Explorer 2019). Studying oviposition behaviors of species of *Euphydryas* advances oviposition theory, furthers understanding in metapopulation dynamics, and promotes informed management practices.

Euphydryas phaeton ozarkae is an ideal organism for studying oviposition strategies. This butterfly is endemic to the Ozark and Boston Mountains and utilizes *Aureolaria flava* as its exclusive oviposition and primary larval host plant. Females deposit eggs en masse and exhibit synchronous hatching after development (Fig. 1). The Ozark subspecies expresses classic metapopulation structure, similar to *Euphydryas phaeton phaeton*. The conservation status of *E. p. ozarkae* is unknown and research examining it limited. Populations of *E. p. ozarkae* are far removed from *E. p. phaeton*, both geographically and ecologically. This in combination with differences in habitat have called into question whether these subspecies are distinct and deserving of separate species statuses (e.g., Masters 1968, Vawter and Wright 1986, Opler and Malikul 1998, Robertson and Baltosser 2016). In addition to differences in habitat and host plant, and the geographic isolation between subspecies, Robertson and Baltosser (2016) found *E. p. ozarkae* to have unique predators and parasitoids with which to contend. In theory, adaptation to a new host and environment combined with novel predators and parasitoids could lead to speciation (Johnson et al. 1996, Berlocher & Feder 2002). *Euphydryas phaeton ozarkae* populations have been isolated from the nominate subspecies and potentially diverging for at least 89 generations (univoltine; first mentioned in Ozarks by Brower 1930). Joining these traits with the relatively recent renewal of prescribed fires as a habitat management strategy in areas of Arkansas suitable for subpopulations to exist, the opportunity to examine oviposition in this butterfly was ideal.

The primary goal of this phase of our research (Robertson and Baltosser 2016, 2018) was to describe oviposition strategies of Arkansas populations of the Ozark Baltimore Checkerspot. We examined *E. p. ozarkae* oviposition search behaviors using some of the same variables used by Stamp (1982) in her study of *E. p. phaeton* to detail resident search behaviors and to make comparisons between the subspecies. Multiple subpopulations were followed to describe characteristics of host plants selected for oviposition. We related selected plant-character states with habitat data and management practices to produce a comprehensive assessment of the oviposition strategies of *E. p. ozarkae*. We hope that this information will encourage greater consideration of this butterfly in management decisions and enhance long-term population viability.

METHODS

Search Behavior

Search behavior was documented during the 2013 flight season at a site located west of Tilly in Pope County Arkansas. The segment of the property used in our study is routinely managed with fire (every other year) by the owners to restore and maintain ~40% canopy cover (pers. comm. with owner). As such, the Tilly site provided a small, open area with a high density

FIG. 1. Photograph taken 28 June 2014 showing typical egg mass (top) and photograph taken 29 June 2014 showing synchronous hatching (bottom).

of Smooth Yellow False Foxglove and Ozark Baltimore Checkerspots, which increased the potential for successful monitoring.

Tilly was visited on most sunny days from 27 May through 18 June 2013 by as many as six people. Female butterflies were net captured with global position, time, and activity at time of capture recorded. Butterflies were restrained in a triangular-paper envelope having circular holes (windows) for tagging. Scales within the tagging window were removed using a rolled piece of clear tape to expose the wing membrane. Animals were tagged by gluing (Loctite®) number- or letter-labeled 1-cm diameter paper discs to the ventral surface of the left hind wing (see Robertson and Baltosser 2016).

Tagged animals were released at the capture site immediately after glue dried. To avoid disruption in search behavior (either searching or laying), females were captured and tagged following egg laying.

Focus shifted from tagging to monitoring search behavior once the first oviposition event was observed. During the hours of 1000 and 1700 on observation days, investigators positioned themselves in areas of the study site with the greatest density of host plants. Frequent patrols were made to locate female checkerspots. Those females suspected of searching were identified by host circling, a noticeably slowed flight, and frequent alights; laying of eggs verified the intent of the observed behavior. Searching females were followed no less than two meters away, with data recorded for search time, plant groups visited, stalks visited, leaves touched, leaves examined (as determined by dipping or scratching of leaf surface with foretarsi), turns on top surface of leaves (recorded as 180° turns), times abdomen tucked under leaves, and times returned to top surface of leaves. The time and duration of oviposition laying events were also recorded. Observations, search behaviors, and oviposition parameters (time and duration) were used to profile behavior analytically or anecdotally when statistical analyses were not possible. All analyses, including those in the following section, were performed with SAS 9.3 (2011).

Plant Acceptance

Four locations in Arkansas were used in 2013 and 2014 to compare host plants with and without egg clusters. These sites were Buckridge (Newton County), Cozahome (Searcy County), Longbottom (Searcy County), and Tilly (described above). Sites were visited in close succession prior to the majority of egg hatching (June–early July) and were surveyed for *A. flava*. Plants with egg clusters were chosen based on the presence of egg clusters (preferred) or first instar caterpillars with the cluster(s) still intact enough for measurements. The number of clusters on each plant were counted and the height of clusters above ground measured. Plants without egg clusters were sampled randomly. Global position of and canopy cover above (as measured with a densitometer) sampled plants were recorded. We counted the number of stalks and leaves and measured all stalk heights (from the ground to the growing tip) and stalk widths (tip to tip perpendicular to the stalk of the widest leaves or lateral shoots). Plant area was derived using the summation of stalk heights multiplied by their respective stalk widths.

Plant data were separated by site for analyses after finding significant differences for various plant characters among sites (analyses not reported). Data were first analyzed with Principal Component Analyses to identify the four most informative variables differentiating plants with and without egg clusters. Identified variables were then used to compare plants with and without egg clusters within sites using Student's t-tests adjusted via Bonferroni procedures (corrected $\alpha = 0.0125$).

The number of eggs in clusters was estimated using the cluster volume in a linear regression model verified in a previous study (Robertson and Baltosser 2016). We explored egg-count data for trends that might help better understand the egg-laying behaviors of this subspecies. To determine if annual conditions affected the numbers of eggs laid, we combined site data and compared numbers of eggs between years (Student's t-test). To determine if the conditions at each site affected egg counts, we combined year data and compared numbers of eggs among sites (ANOVA). We examined among-site differences of egg counts within years to look for consistency between years. Relationships from these analyses were determined using the Tukey method. Combined results were interpreted broadly for the influence of regional and local factors on egg counts. Within-site egg counts and number of clusters were examined for significant correlations with each other, number of stalks, plant height, plant width, plant area, and number of leaves in an effort to further describe oviposition behaviors.

RESULTS

Search Behavior

Oviposition was first observed on 6 June, 11 days following the first observation of adult butterflies (27 May—two males). Searching females often flew directly towards *A. flava*, circling the host plant before alighting. Non-searching females did not display an interest towards *A. flava* and instead spent long periods basking on random plants or flew quickly through monitored areas. In periods between examining potential hosts, searching females periodically basked on plants near potential hosts (but rarely on actual hosts), immediately resuming their search following basking. We recorded 28 oviposition-search events during the monitoring period. Most searching females were recorded between the hours of 1100 and 1400 ($n = 26$); only two females were observed searching later in the day. Females were observed for as little as one minute ($n = 3$) and for as long as 99 minutes ($n = 1$), with an average of 17.0 minutes (s.d. = 19.0). Most females were observed searching for less than 30 minutes ($n = 19$) before they began to lay eggs. Owing to our positioning within the habitat, the majority of females are believed to have been detected shortly after, or the moment, searching began. Further, it is possible that females continue searches from the previous day, as suggested by the early morning juxtaposition of females to host plants. These females frequently displayed search behavior immediately following morning basking.

After selecting an oviposition site, females invert themselves using their mid-legs for support while laying egg clusters in tight rows and off-set columns. Oviposition took an average of 88.3 minutes (s.d. = 38.2), and only rarely (n = 3) did they become dislodged or disrupted. Wind blew two females off the leaves on which they were depositing eggs. One immediately began searching again but did not return to the previously chosen plant; the other was lost after the wind gust. A third female was disrupted by an aggressive wasp; she did not return to searching but instead quickly and directly flew towards a heavily wooded area.

Tagged females totaled 45 individuals but search behavior was recorded for only 18 of these individuals. Of the 18, three were tagged prior to search behavior and only one was documented to have laid eggs twice within the study area. Ten females for which egg laying was recorded could not be captured once egg laying had ceased.

Plant Acceptance

Within-site Principal Component Analyses identified tallest stalk, plant area, number of leaves, and number of stalks as the most informative variables across all sites. Widest stalk was also identified, though excluded from further analyses because of a strong correlation with plant area, large and inconsistent variance within groups, and lack of observed effect in the field. Egg clusters were found at an average height of 52.7 cm (n = 199, s.d. = 18.43) with 75% of observations being above 39.0 cm. ANOVAs concerning these variables showed inconsistent relationships, with none taking precedence. Plants bearing egg clusters at Buckridge were significantly taller with greater area than plants without egg clusters (Table 1) but were not significantly different concerning number of leaves and number of stalks. However, the average number of leaves for plants with egg clusters was more than double that of randomly selected plants without egg clusters. Plants with egg clusters at Cozahome and Tilly had taller stalks, greater plant area and number of leaves, but did not differ significantly in number of stalks. Accepted plants at Longbottom maintained significantly greater means across all four variables.

Significantly fewer eggs per cluster were laid on plants in 2014 ($p = 0.0355$); mean = 250.6, s.d. = 142.4, n = 109 vs. mean = 299.5, s.d. = 170.3, n = 76 for 2013. Among year comparisons of egg counts ($F_{13} = 5.45$, $p = 0.0020$; $F_{14} = 5.39$, $p = 0.0017$) revealed similar relationships, placing Buckridge between Tilly and the other sites. Interestingly, when data were combined for both years, Tilly maintained the highest average number of eggs per cluster ($F = 11.54$, $p < 0.0001$; Table 2). No consistent relationships were found between egg counts or number of clusters and any input variable among all sites. Buckridge had significant correlations between egg count and number of stalks and between number of clusters and plant width and plant area. Results for Cozahome were consistent and statistically significant for relationships between egg count and number of clusters, and between number of clusters and number of stalks. Longbottom showed significant relationships between number of clusters and plant height, plant width, and plant area. There was only one significant relationship at Tilly, which was between egg count and number of leaves.

DISCUSSION

Search Behavior

The search behavior documented for *E. p. ozarkae* in our study is typical for members of *Euphydryas* (see Ehrlich & Hanski 2004). These butterflies are considered highly selective, often visiting multiple plants before selecting one for oviposition. However, there are key differences when compared with a similar study that examined *E. p. phaeton* (Stamp 1982). In most cases, estimates for *E. p. ozarkae* were greater than were recorded for its counterpart (Table 3). Search parameter estimates for *E. p. ozarkae* are believed to be somewhat low, as at least a few females were not observed at the exact moment searching began. Assuming data accurately assesses *E. p. ozarkae* behavior, data describe an animal that is more scrupulous in its choice of oviposition plant, spending longer periods of time searching for plants and physically interacting with more plant groups, stalks, and leaves.

Adult female *E. p. ozarkae* appear prone to dispersal. The tagging effort is believed to have been successful, with 45 of the potential total of 55 being tagged (unable to capture 10 following oviposition). However, only 18 search-pattern observations came from tagged females. In fact, 25 of the 45 tagged females were never located following tagging, especially in the case of the earliest females to emerge. Known to disperse considerable distances (12 km; Brussard & Vawter 1975), it is believed that these females left the study area. Males were more readily located and observed following tagging. This difference suggests females readily vacate areas from which they originate, which follows metapopulation theory that suggests colonies should be

TABLE 1. Student's t-tests results for all measures at each site; values for plants with eggs are above those for plants without eggs.

Site	Measure	Mean	S.D.	t-value	p-value
Buckridge	Tallest stalk	107.3	37.5	5.49	< 0.0001
With Eggs (n = 48)		62.8	42.8		
Without Eggs (n = 51)	Plant area	7598.0	9007.3	3.20	0.0023
		3221.5	3079.2		
	Number of leaves	247.6	384.6	2.34	0.0232
		113.6	101.6		
	Number of stalks	4.6	3.8	1.93	0.0571
		3.3	3.0		
Cozahome	Tallest stalk	101.1	34.6	8.54	< 0.0001
With Eggs (n = 52)		52.6	23.3		
Without Eggs (n = 59)	Plant area	4740.9	3273.5	5.36	< 0.0001
		2009.5	1781.5		
	Number of leaves	128.0	108.8	4.71	< 0.0001
		47.5	61.8		
	Number of stalks	2.2	1.1	-0.50	0.6208
		2.4	1.8		
Longbottom	Tallest stalk	87.6	27.1	10.11	< 0.0001
With Eggs (n = 54)		38.8	22.9		
Without Eggs (n = 54)	Plant area	5121.5	4216.4	5.59	< 0.0001
		1602.0	1902.9		
	Number of leaves	146.1	136.5	5.29	< 0.0001
		41.6	49.0		
	Number of stalks	3.4	2.1	3.55	0.0006
		2.1	1.7		
Tilly	Tallest stalk	84.5	19.5	3.31	0.0014
With Eggs (n = 51)		65.6	35.6		
Without Eggs (n = 51)	Plant area	7794.9	4992.9	4.76	< 0.0001
		3570.0	3913.4		
	Number of leaves	638.9	434.7	3.61	0.0005
		326.6	437.7		
	Number of stalks	5.9	3.4	1.43	0.1555
		4.6	5.5		

founded by dispersing females and that subsequent generations will carry this dispersal trait (Hanski & Singer 2001).

Plant Acceptance

Females consistently selected plants that were more vigorous within study locations. While what defined relative vigor varied among sites, values from plants with egg clusters were nearly double those of plants that had none. The difference seems best explained by the plant vigor hypothesis (Price 1991). This hypothesis suggests that plant vigor, most closely associated with plant size and age, is the most important predictor for herbivorous larval insect performance and is the most prominent selective force. This model has received a great amount of experimental support (Price et al. 1987, Preszler & Price 1995, Woods et al. 1996, Inbar et al. 2001, Santos et al. 2006) and accounts for findings in the present system. Our results may, however, be more aligned with the optimal oviposition theory, which suggests plants most suitable for fitness will be preferentially chosen for oviposition (Jaenike 1978). This theory is broad, with constituents of "suitability" being all biotic and abiotic factors that contribute to larval development at habitat and microhabitat levels. The breadth of factors in this theory allows for a robust categorization of oviposition strategy (i.e., "if the females CHOSE it, it must be the best") but limits explanatory ability: ideal when strategies seemingly vary between sites. In support of this conclusion, Tilly and Buckridge maintained the most vigorous plants overall while also having the smallest difference between hosts with and without egg clusters. In other words, at sites where a higher average plant vigor is maintained, plant vigor appears less important for female host choice for oviposition; we speculate much of the preference in host choice for *E. p. ozarkae* is dependent on plant variability within sites.

Management that promotes an increase in light availability and an open understory appears to enhance the health and overall density of *A. flava*, the primary host plant for *E. p. ozarkae*. *Aureolaria flava* is a hemiparasite of tree roots (Yatskievych 2013), particularly oak, and occurs most frequently in open woodlands where oak trees are common. In the areas studied, *A. flava* is particularly abundant along roadways, forest edges, and in more open woodland where light is plentiful. The plant is less common and presumably easily excluded or lost from locations in which fire or other factors have not reduced woody plant encroachment. Buckridge and Tilly are routinely managed with fire in two or three-year rotations, reducing overstory and understory densities. Among other less obvious and untested beneficial consequences (e.g., promoting periodic exposure of soil on which plants can establish), routine prescribed fire allows more light to reach the ground. Buckridge and Tilly had the lowest mean overstory densities (75.9 and 47.4%, respectively). Overstory density at Buckridge was inconsistent, however, with some areas having an overstory density as low as 29.0%. Areas with the lowest overstory densities within sites seemed most likely to contain stands of *A. flava* with taller stalks, larger areas, and greater numbers of leaves and stalks, the four most important components for oviposition selection, when compared to areas with above average canopy cover. Though the relationships were not significantly different, Buckridge maintained averages that were intermediate between Tilly (greatest) and the other, less-managed sites. Cumulatively, data suggests that *A. flava* grows best in open woodlands and historical disturbance regimes may have been a key component in the establishment and persistence of *E. p. ozarkae* in the region.

TABLE 2. Means and Tukey-Kramer test results (in parentheses) for eggs per cluster and plant characteristics among sites.

Site	Eggs/Cluster	Tallest stalk	Plant area	Number of leaves	Number of stalks
	$F = 11.54$ $p < 0.0001$	$F = 11.93$ $p < 0.0001$	$F = 16.78$ $p < 0.0001$	$F = 76.64$ $p < 0.0001$	$F = 31.83$ $p < 0.0001$
Buckridge	271.2 (A)	83.0 (B)	5246.4 (B)	150.6 (A)	3.9 (B)
Cozahome	201.5 (A)	73.5 (B)	3002.5 (A)	80.7 (A)	2.3 (A)
Longbottom	227.9 (A)	58.0 (A)	2723.5 (A)	75.5 (A)	2.5 (A)
Tilly	358.3 (B)	76.1 (B)	6839.5 (B)	524.2 (B)	5.5 (C)

It was not uncommon for multiple females to select the same plant to deposit eggs, with 25.4% (52/205) of plants chosen for oviposition in 2013 and 2014 receiving more than one cluster. Twelve of the plants with multiple depositions had three or four clusters ($n_3 = 9$, $n_4 = 3$) and only once did a plant have more than four clusters (LB_{1407} had 8 clusters). This is far fewer than were reported by Stamp (1982) for *E. p. phaeton*, perhaps owing to differences between host plants. The prevalence of multiple depositions on a single plant likely varies considerably between sites and years, depending on the plant landscape. This conclusion is supported by the fact that only Longbottom, the smallest and most host-limited study site, had plants receiving four or more clusters and maintained more than a third of all plants with multiple clusters.

Ample food resources during development probably leads to greater female fecundity in adulthood; by far Tilly had the most vigorous plants. The number of eggs per cluster was also significantly greater. Although a precise relationship between number of eggs per cluster and measured plant variables could not be established, there is likely biological importance to this finding. Food resources seemed to be a highly limiting factor at all sites except Tilly. Plants were in fall defoliated and quickly reduced to the ground in spring, often leaving relatively long, energetically expensive, and risky treks for caterpillars to reach new resources. Further, White-tailed Deer Odocoileus virginianus (Zimmerman 1780) Cervidae in all areas were competitors for available A. flava in spring (Robertson & Baltosser 2018). Both stressors were greatly reduced at Tilly due to high host abundance and vigor that provided ample, proximal resources for developing larvae, and dogs that harassed and prevented deer from intense browsing seen at other study locations. It is possible that the greater abundance of food during larval development in combination with reduced stressors at Tilly allowed for more eggs to be produced by adult females.

CONCLUSION

The magnitude of search variables were generally greater for *E. p. ozarkae* than for *E. p. phaeton*. This likely is due to differences in host plant and may be influenced by variation in plant availability. However, data indicate a predisposition to locate plants meeting very specific criteria (some tested, some not) regardless of greater expended time and energy. Perhaps conditions available in the Ozarks are less optimal, requiring a stricter approach to maintain fitness.

As the first detailed examination of oviposition selection strategies for *E. p. ozarke*, our research provides informative and critical data for the conservation and management of this subspecies. It is obvious that these animals utilize the *A. flava* plants with greater resource potential no matter what each environment offers. Their choice suggests other factors, such as predation and parasitism, are not limiting within these areas. The relationships between plant data and sites were not always significant towards routinely managed (Tilly and Buckridge) or lightly managed (Cozahome and Longbottom) sites, though there is a beneficial trend towards plant characteristics that represented the greatest variances between plants with

TABLE 3. Comparisons of oviposition search related variables recorded for *E. p. phaeton* (Stamp 1982) and *E. p. ozarkae* (present study).

Search Behavior	Mean per female based on total observations (+S.E.)	
	E. p. phaeton	*E. p. ozarke*
	n = 21	n = 28
Minutes observed	11.4 (± 1.4)	17.0 (± 3.6)
Plant groups visited	1.6 (± 0.2)	6.6 (± 1.1)
Stalks visited	8.1 (± 0.9)	9.0 (± 1.4)
Leaves touched	7.5 (± 1.0)	16.5 (± 2.7)
Leaves examined	2.1 (± 0.3)	5.1 (± 1.1)
Turns on top surface of leaves	4.9 (± 0.8)	6.3 (± 1.0)
Times abdomen placed under leaves	9.2 (± 1.7)	8.2 (± 1.5)
Times returned to top surface of leaves	8.1 (± 1.6)	7.2 (± 1.5)

and without eggs. Forest management that aids in the production of more vigorous plants for oviposition produces habitats that are also attractive to deer, which on occasion places deer and checkerspots into competition (Robertson & Baltosser 2018).

Our study provides a basis for understanding the factors that influence the persistence of this butterfly within the Ozark regions. Returning periodic fire to these areas through prescribed burns is likely a key item. Although losses of occupant populations are inevitable, recolonization occurs rápidly (Robertson 2015) and the benefits to habitat favor the health of the greater population. However, the timing of this management is an important factor. All study sites exposed to prescribed fires were treated in early spring. In early spring, caterpillars remain under leaf litter near their original host (Robertson & Baltosser 2016). Although the exact mechanism is unknown, many early-spring caterpillars survived prescribed burns during this period (unpublished data). The effect of a fall burn is unknown but considering the stage in development and the differences in mobility of spring and fall caterpillars, we speculate fall burns, when caterpillars are in diapause nests above ground level, would be highly detrimental. Burning should be limited to late winter/very early spring and interspersed with burn-free refugia.

Our complete work on *E. p. ozarkae* (Robertson and Baltosser 2016, 2018, and current manuscript) has provided the most comprehensive life history information to date. We spotlight an animal sensitive to habitat conditions, having a complex and dynamic relationship with its host plant, and subject to the vagaries of most metapopulations. Our findings can be used to guide land management towards conserving *E. p. ozarkae* in its endemic habitats and offers direction for future research into this and similar species.

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