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THE OZARK BALTIMORE CHECKERSPOT, *EUPHYDRYAS PHAETON OZARKAE* (NYMPHALIDAE): LIFE HISTORY IN NORTHERN ARKANSAS

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ABSTRACT. Ecological and geographical differences between eastern and western populations of the Baltimore Checkerspot have led to a division into two subspecies, *E. p. phaeton* and *E. p. ozarkae*. Research concerning *E. p. ozarkae* is sparse, and prior to our work, many aspects of the life history of this subspecies were not known. An accurate assessment of its status has been hindered and confused through the use of data obtained from the eastern subspecies (e.g., mesic habitats and larval food plant) to characterize Ozark populations (e.g., glade habitats and a different larval food plant). From 2011 to 2014 we studied this butterfly in the Ozark Mountains of northern Arkansas. We identified the availability of the primary larval host plant (*Aureolaria flava*) as a potential limiting factor and investigated limitations to the distribution of this plant. We found many similarities concerning the timing of development between the two subspecies but ample evidence to demonstrate the uniqueness of Ozark populations. Our findings provide valuable information for future research, management, and conservation of the Ozark Baltimore Checkerspot.

Additional key words: Specialist, univoltine, metapopulation, species identity, Arkansas

Life histories provide critical insight into the biology and ecology of organisms. Detailed information concerning life stages allows investigators to focus research efforts on prominent issues. Relationships involving food resources, predators, and competitors promote greater understanding of the organism in question, which subsequently leads to better conservation and management efforts to promote sustainable populations.

The Baltimore Checkerspot, *Euphydryas phaeton*, is a nymphalid butterfly that occurs in much of the eastern United States. Ranging from Maine southward along the Appalachians to Georgia and westward to Oklahoma, Kansas, and Texas, the species is divided into two subspecies, *E. p. phaeton* Drury and *E. p. ozarkae* Masters. Both are univoltine and exist in local, isolated populations that are interconnected through adult dispersal. With the majority of their lifetime spent as aggregations of relatively immobile larvae and a flight season of only three weeks, these subpopulations are subject to conditions of the local habitat, sensitive to habitat fluctuations (such as extreme or atypical weather and acute destructive events), and prone to establishment and extirpation on a generational scale, each characteristic of metapopulations (Hanksi & Gilpin 1991, Hanski & Singer 2001).

The subspecies are most readily differentiated by their geographic range and larval host plant. Members of the genus *Euphydryas* specialize on plants containing iridoid glycosides (Bowers 1983), which larvae sequester to render them unpalatable to some vertebrates (Bowers 1980, Belofsky et al. 1989). These compounds are found in relatively large amounts in all chosen host plants (Bowers et al. 1992), but contrasting environmental conditions are present depending upon host plant selection. *E. p. phaeton* are normally associated with White Turtlehead, *Chelone glabra* L. (Plantaginaceae), a wetland species occurring in flooded meadows and stream banks. *C. glabra* has been reported to be in decline due to disappearing wetlands brought about by urbanization (Durkin 2009; wetland urbanization effects highlighted in Johnson et al. 2013). Exotic Ribwort Plantain (*Plantago lanceolata* L., Plantaginaceae) has provided a viable alternative to White Turtlehead (Stamp 1979, Bowers et al. 1992) and occurs in a broader range of habitats, such as meadows, upland grasslands, river banks, and cliffs (Preston et al. 2002), expanding the potential range for *E. p. phaeton*. In contrast, *E. p. ozarkae* uses False Foxglove, *Aureloaria flava* L. and *Aureolaria grandiflora* Bentham (Orobanchaceae) as its primary hosts (Masters 1968, Bauer 1975, Scholtens 1991). These *Aureolaria* spp. occur in dry, upland oak and pine-oak woodlands and are believed to be hemi-parasitic of oak species (Musselman 1996).

Considering different hosts (and habitats), metapopulation dynamics, short flight seasons, geographic distance between, and ecological time separating *E. phaeton* subspecies (>85 generations; Brower 1930), speciation is a possibility. These circumstances have been the basis for subspecies separation and have driven the question of whether *E. phaeton* is a single wide-ranging species or two species. This query arises frequently in studies and references involving *E. p. ozarkae* (e.g., Bauer 1975, Vawter & Wright 1986, Opler & Malikul 1998) and is a topic of interest in our study.

Here we provide life history data for *E. p. ozarkae*, the largely under-studied subspecies found primarily in the Ozarks of Arkansas and Missouri. Research on this subspecies has been overshadowed by studies concerning *E. p. phaeton* and therefore lacks focused efforts to understand its status and behavior, which may differ from the nominate subspecies. As such, we compare and contrast the two subspecies when possible.

METHODS

Four persistent (Buckridge, Cozahome, Longbottom, and Tilly) and two ephemeral (Spring Creek and Maumee) populations of Baltimore Checkerspot were located along the Buffalo River and surrounding areas in Arkansas. Sites occupied three counties (Newton, Pope, and Searcy) and were named after prominent nearby landmarks (e.g. land features, roads, and cities). All study areas are dominated by elevated hardwood, oak-hardwood forests of the Ozark subdivisions of the Boston Mountain, Salem, and Springfield Plateaus. Sandstone and shale provide well-drained north-south facing slopes that have been incised into plateaus of elevations upwards of 790 m. Soils are predominantly alluvial, consisting of sandy and/or silt loam. Precipitation averages 48–50 inches and temperatures average 57–59°F (Gentry et al. 2013). Baltimore Checkerspots in these areas use *Aureolaria flava* as their primary host.

Surveys of browsing upon host plants were conducted at all sites in August 2011, excluding Tilly, and July 2013, including Tilly, to estimate the effect of herbivory. Browsing was identified by the removal of the growing tip of any shoot (primary or auxiliary) and exposure to the hollow center of the plants. Because young larvae feed on leaf material, we concluded browsing was due to large herbivores. As such, no corrections or groupings were made to discriminate effects of browsing by herbivores or larvae. Plants housing communal tents, aggregations of *E. p. ozarkae* larvae within structured webbing (also called nests), were categorized as having been browsed or unbrowsed. Data were used to construct a 2×2 contingency table to examine the relationship between browsing and tent presence for both years (SAS 2011; proc freq).

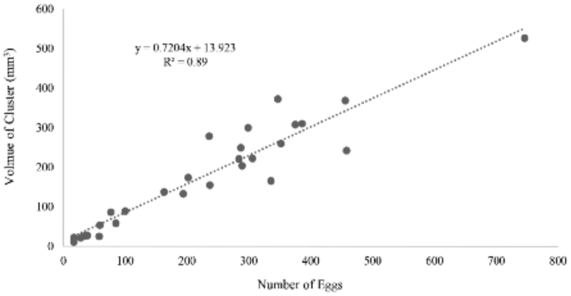

FIG. 1. Regression model generated from volume measures and absolute counts of 29 egg clusters collected in 2013 and 2014.

Observations of *Euphydryas phaeton ozarkae* in our study span the majority of three generations, beginning August 2011 and ending June 2014. Study sites were visited as frequently as every two weeks but no less than once every two months, at which times data concerning behavioral patterns, life cycle stages, morphological characteristics, and biotic and abiotic stressors were collected.

Egg clusters were located in 2012 and their coloration in relation to development recorded. Individual egg counts were obtained by dissecting egg clusters in 2013 and 2014 (n = 29). Using electronic calipers dimensional data (length, width, and height) were obtained from as many clusters as could be located in these years. Egg counts from the collection effort were correlated to

$$x = \frac{(y - b)}{a}$$

volumetric data to generate a predictive model where x is the estimated egg count using the measured volume y, in determining egg numbers (SAS 2011; proc reg; Fig. 1). The model was then used ($r^2 = 0.89$) to determine the approximate number of eggs in each cluster for which measures were taken. Descriptive statistics were calculated for all egg counts (SAS 2011; proc univariate).

Length measurements of larvae were made in 2012 to estimate growth of instars 2–6 at three of the four persistent locations (Buckridge, Coazhome, and Longbottom; throughout the study larval development was consistently two weeks behind at Tilly), with two measurements taken during the fourth instar (late summer and early winter). All sites were visited on three consecutive days during which larvae were assumed to be at specified instars based on coloration, size, date, and presence of recent molted exoskeletons. Measurements,

FIG. 2. Photographs from adult tagging effort in 2013: (left) tagging apparatus with male no. 1 carefully restrained and (right) male no. 2 with tag placed on the venter of the left hindwing.

made from head to anus without respect to time within instars (i.e., early, mid, or late) due to variation in development between tents and individuals, were taken using electronic calipers. Data were compared among sites using ANOVA (SAS 2011; proc GLM) before combining each site into one homogeneous data set. Each data set amassed for instars was analyzed and summarized through descriptive statistics (SAS 2011; proc univariate). Fourth instars were measured twice; during pre-hibernation (late summer) and hibernation (early winter). Fourth-instar data sets were compared by first reducing the pre-hibernation data set (n = 239) using 25 iterations of bootstrap resampling to generate a random sampling equal to the hibernation sample size (n = 32). The resampled data set was then compared to hibernating fourth instars using Student's t-test (SAS 2011; proc ttest).

Anecdotal observations of adults in 2012 were made at Buckridge, Cozahome, and Longbottom. Adults at Tilly, chosen for logistical ease, in 2013 were individually tagged and monitored for life-history characteristics and concurrently studied with ovipositing as the primary focus. Adults were captured, GPS location recorded, and activity described. Tagging was performed using a strip of paper folded into a triangle with circular windows punched out to facilitate marking (Fig. 2). Adults were placed in the paper triangle and secured with a clothespin. Scales were removed from the venter of the left hindwing at the location of the most appropriate window using tape and a gentle scraping motion. Tags were generated using individual identification codes on lightweight printer paper and were fixed to the left hindwing using super glue (Loctite®). Prior to being released unharmed at the site of capture, adults were sexed and forewing lengths measured from the thorax to the wing tip using electronic calipers. Subsequent to release, marked adults were identified through a slow approach and use of binoculars; recaptures were avoided to prevent disrupting ongoing behavior. Forewing lengths were compared between sexes using Student's t-test (SAS 2011; proc ttest).

Communal tents housing larvae were observed during the summer and fall of 2012 (June–October) and 2013 (July–October) to establish larval persistence. Larval dispersal in the spring made it difficult to quantify group size, as counts became highly variable and unreliable. In 2012, tents were tagged for identification using 5 mL Eppendorf tubes containing numbered strips. Larvae were counted during each visit and numbers estimated to categories of 10 (i.e., 1–10, 11–20, 21–30, etc.). Following data collection, categories were reduced to a single average for each group (i.e., 5.5, 15.5, 25.5, etc.). In 2013, tent surveys were made of areas outlined by GPS data. Using a sweep-survey method, all active tents within areas were counted.

During diapause (4th instar) in 2011 a small sample of tents outside the primary area of study were monitored for nest repair and post-damage survival. Nests of pre-hibernating larvae were located and the number of larvae estimated; a 3–6 cm incision was then cut into tents to expose larvae to the external environment. Ten of these incisions were subsequently covered using leaves from the area surrounding the nests to imitate leaf fall and to determine if debris affected repair. Nests were revisited the day following incision and weekly thereafter for a total of three returns across three weeks. Data were recorded as the relative percent of enclosed area (0–4; 0 = no repair, 1 = 25% repaired, etc.) of the incised area with newly formed webbing.

RESULTS

In 2011 and 2013, 79 and 61%, respectively, of all sampled plants without larvae had been browsed. In contrast, only 44 and 43%, respectively, of plants with nests had suffered browsing by the same seasonal period (Table 1). Overall, browsing was more frequently observed on plants without than plants with tents ($X^2 = 11.92$; $p < 0.0001$).

Egg deposition occurred in late spring to early summer with differences as great as four weeks between years and two weeks among some sites (information concerning each stage/instar summarized in Table 2). Variation between years seemed to be correlated with temperature; at a higher elevation, Tilly maintained cooler temperatures throughout larval development. Clusters averaged 271.4 eggs (n = 186, s.d. = 156.4). Eggs took approximately three weeks to develop, following the same color progression each year (bright yellow - red - purple - black - dark grey; in some cases all colors were visible within one cluster, producing a "corn maize" pattern).

Larvae hatched en masse (early June to early July) approximately three weeks after eggs were laid and then proceeded to the growing tip of the stalk on which they hatched. First instars immediately began to construct the first pre-diapause tents, characterized by loosely organized silk, encompassing only the growing tip of the *Aureolaria flava*. Feeding was confined to surficial portions of leaves, creating window-pane injuries.

TABLE 1. Among site browse comparisons for 2011 and 2013.

		Plants without nests		Plants with nests	
Year	Site	Browsed	Unbrowsed	Browsed	Unbrowsed
2011	Buckridge	1244	249	12	9
	Cozahome	331	109	4	21
	Longbottom	48	12	13	10
	Maumee	32	31	4	4
	Spring Creek	174	104	2	1
	Combined	1829	506	34	45
2013	Buckridge	1019	149	64	39
	Cozahome	146	152	20	57
	Longbottom	153	76	30	34
	Tilly	356	691	22	50
	Combined	1674	1068	136	180

Second instar nests grew to encompass the majority of the upper portion of the plant, including most flowering portions of the stalk (typically occurring on secondary stalks near the top of the plant). Individuals continued to feed on leaves but also fed on under- and fully-developed flowers; the latter prevented several plants from reproducing (evidenced by the lack of seed pods).

Third instars constructed larger tents, which often covered the entire plant or lower portions where green leaves remained. Tops of plants were often "browning" and appeared to be dead or in a state of senescence. During this instar it was not uncommon for larvae to

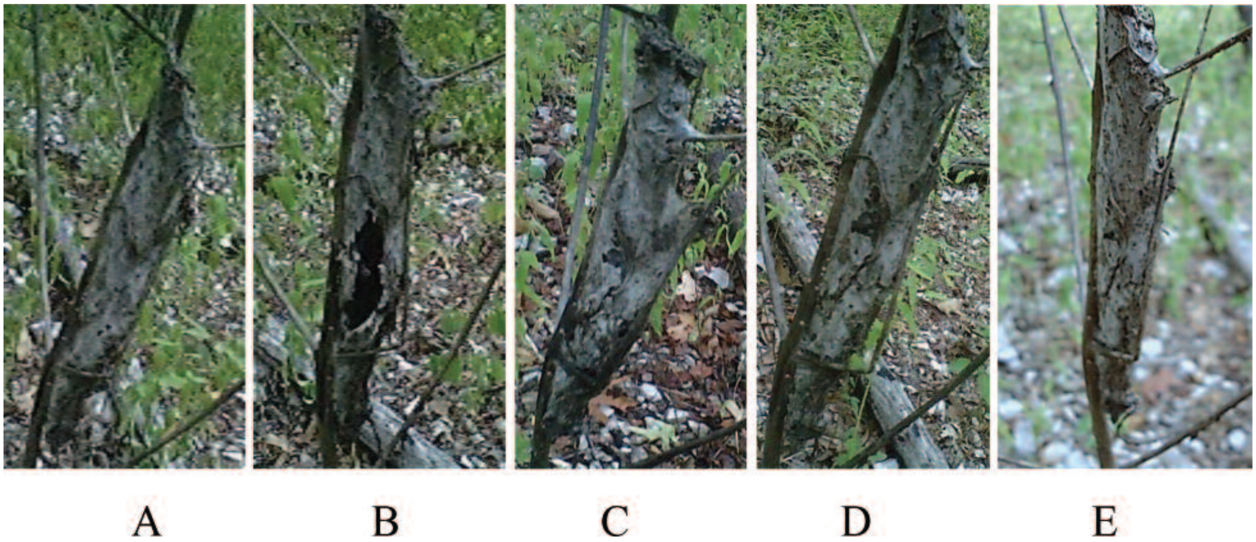

FIG. 3. Sequential photographs of tent repair for nest 20: (**a**) prior to incision, (**b**) incision, (**c**) first revisit, (**d**) second revisit, and (**e**) third revisit.

Table 2. Summarization of results for all butterfly stages; dashes indicate that no data were taken.

Stage/Instar	Approximate start date	Estimated duration	Size	Appearance	Organization	Typical relative location
Egg	mid-May - mid-June	3 weeks	-	yellow - dark grey	clustered	mid-plant
First instar	early June - early July	1.5 weeks	-	colorless; spineless	aggregated	growing plant tip
Second instar	mid-June - mid-July	2 weeks	4.89 mm ± 1.46 (n = 370)	pale; undeveloped spines	aggregated	upper 2/3 of plant
Third instar	early July - early August	3 weeks	7.66 mm ± 1.20 (n = 316)	orange and metallic-blue; developed spines	aggregated	entire plant; original or adjacent host
Fourth instar1	early - late August	3 months	7.18 mm ± 1.06 (n = 239)	orange and metallic-blue; developed spines	aggregated	mid-plant
Fourth instar2	mid-October - early December	4 months	3.96 mm ± 0.80 (n = 32)	orange and metallic-blue; developed spines	aggregated	leaf litter
Fifth instar	late February - early March	3 weeks	25.24 mm ± 5.85 (n = 180)	orange and metallic-blue; developed spines	loosely aggregated	plant rosettes; wandering
Sixth instar	late March - early April	4 weeks	40.02 mm ± 4.90 (n = 68)	orange and metallic-blue; developed spines	loosely aggregated	growing plants; wandering
Pupa	late April - mid-May	2 weeks	-	mostly white with orange and black markings	dispersed	(see text)
Adult	mid-May - early June	3 weeks	females larger (see text)	mostly orange, black, and white adult butterfly	dispersed	(see text)

[1] Pre-hibernating fourth instar.

[2] Hibernating fourth instar.

leave their original hosts to find new plants, a behavior seemingly dependent on the availability of leaf material on the original host. By some unknown mechanism, new tents on adjacent plants seemed to receive most, if not all, of the individuals from the previous nest and perhaps individuals from other adjacent nests. Larvae at this instar continued to feed on leaf material and were observed feeding on coarser stem material (i.e., not confined to new leaves/shoots).

The fourth instar lasted the longest and extended from late summer to early spring when larvae broke diapause. Once molting took place, larvae constructed pre-hibernation webs that had more compact webbing and were considerably smaller. Pre-hibernation webs seemed to vary in size depending on the number of larvae present. In this state, larvae seldom fed and activity was much reduced, only occasionally exiting the web on excessively warm days or rainy weather. Beginning in October to early December, larvae abandoned pre-hibernation nests and hibernated in leaf material at the base of the host plant. Fourth instars in hibernation were significantly smaller when compared to early fourth instar ($t = 14.55$; $p = < 0.0001$). During hibernation larval activity was seemingly non-existent. In early spring larvae resumed activity, feeding on emerging *A. flava* rosettes.

Larvae gained considerable length during the short period between emergence and the fifth instar. Feeding increased greatly and it was common for emerging larval groups to reduce plant rosettes of the original plant, and those plants in the immediate vicinity, to stubs. Plants subjected to such feeding did not recover until the following year (a phenomenon resulting in the displacement of central location of the following butterfly generation). During this period, larvae continued to specialize on *A. flava*, though two confirmed instances of larvae feeding on Coral Honeysuckle (*Lonicera sempervirens* L., Acanthaceae) were documented.

By the onset of the sixth instar plants had grown enough that foliage was readily available and larvae had noticeably increased in length. As in the fifth instar, sixth instars would move considerable distances to obtain food (one distance measured more than 20 m, but observations suggested even greater distances). Movement by spring-instar larvae often seemed to include full groups (unclear whether they remained in groups or if groups converged). However, it was not uncommon to find larvae alone on plants where no others had previously been. Dispersal during the spring period was widespread and apparently random, seemingly owing to the availability of food plants.

FIG. 4. Anchor Stink Bug (*Stiretrus anchorago* Fabricius) with third instar Baltimore Checkerspot larva.

Pupae were exceptionally difficult to find (n = 9), but were most frequently located less than 25 cm (n = 6) from the ground, attached to any number of items. Substrates included a fallen log (n =1), a branch on a sapling (n = 2), a rock (n = 1), a fallen branch (n = 1), a greenhouse (n = 1), a non-host plant (n = 1), and an axillary shoot of *A. flava* from a previous year (n = 2).

Adult males eclosed approximately 5–7 days prior to females. Females were significantly larger than males, with male wings averaging 30.4 mm and female wings averaging 36.4 mm (males: n = 57, s.d. = 1.4; females: n = 45, s.d. = 1.8; t = 18.91, $p < 0.0001$). Adults spent much of early morning basking on leaves in the understory. By 1000 (until late afternoon), males most frequently perched at the top of plants, with occasional patrols of surrounding areas. Females could be found searching for oviposition plants, ovipositing, or simply flying during this time. When two *E. p. ozarkae* came into contact, they often flew straight upward, circling one another. Females were less likely to be seen following tagging, with few secondary observations and only one tagged female observed laying twice within the study area. Both sexes were heavy nectar feeders, with multiple cases of adults spending greater than 45 minutes on a single flowering plant. Nectaring plants varied, but included Purple Milkweed (*Asclepias purpurascens* L.), Butterfly Milkweed (*Asclepias tuberosa* L.), Pale Purple Coneflower (*Echinacea pallida* Nutt.), and Wild Quinine (*Parthenium integrifolium* L.). Puddling was seen infrequently. Adult females mated shortly after emerging and copulation was maintained for as long as three hours; polyandry was not observed. Two tagged females were observed laying their first mass of eggs within 24 hours of mating. Egg deposition averaged 88.2 min (n = 28, s.d. = 38.2 min), but on three occasions was interrupted due to harassment by a paper wasp (Vespidae sp.; n = 1) and high-wind events (n = 2). With secondary observations of males declining dramatically after approximately two weeks of first captures, and females similarly disappearing one week later, adult lifespan was estimated to be about two weeks with a flight season of about three weeks; females persisted later than males.

The number of larvae in 2012 dropped by 76% prior to hibernation. Buckridge experienced the most dramatic reduction, with 88% of individuals perishing, missing, or otherwise absent from original tents. Cozahome and Longbottom persistence was reduced by 81 and 64%, respectively. The majority of disappearances during 2012 occurred prior to July, with 35, 56, and 34% of individuals being unaccountable for Buckridge, Cozahome, and Longbottom, respectively. Nests remained active but individual disappearance was high during this period. Nests experienced the greatest decline in August, with losses of 47, 57, and 50% for Buckridge, Cozahome, and Longbottom, respectively. Similarly, the number of nests in 2013 was dramatically reduced in August. Buckridge, Cozahome, Longbottom,

FIG. 5. Photographs showing interactions between chalcid wasp (superfamily Chalcidoidea) and *E. p. ozarkae*: wasp attacking a sixth-instar (top), a healthy chrysalis (lower left), and a parasitized chrysalis (lower right).

and Tilly experienced reductions of 46, 40, 64, and 49% (respectively) during this month. The overall decline of nests within these sites during the study period was 62, 48, 78, and 58%, respectively; total loss among all sites was 61%.

Repair was observed in 18 of the 20 pre-hibernation tents damaged artificially (Fig. 3). All larvae died in unmended tents by the end of the experimental period, as did those in three additional partially mended tents. Furthermore, three of the five nests where all larvae died contained only 1–10 individuals at the beginning of the experiment.

Predation and parasitism were common throughout all life stages, though the constituents changed over the lifespan of larvae. Few marked egg clusters were removed, but if they were, a slight imprint on the leaf was the only evidence that remained. These disappearances were attributed to an unidentified neuropteran larva and an ant species (actual feeding not observed), each found in close proximity to multiple clusters. Early instars were eaten by Araneae, specifically jumping spiders (Salticidae) and Hentz's Orbweaver (*Neoscona crucifera* Lucas). One instance of attack by a paper wasp (Vespidae) was observed during an early instar (2–3). Early instars (1–3) suffered massive losses to the Anchor Stink Bug (*Stiretrus anchorago* Fabricius, Fig. 4). The stink bug, which often remained close to tents until all individuals had been consumed, patrolled the outer surface of pre-diapause tents inserting its proboscis through the webbing to attack larvae. Larvae ceased feeding and aggregated behind layers of loose webbing at the center of nests when this predator was present. Late instars (5–6) were attacked by a parasitoid wasp (superfamily Chalcidoidea). A single attack on a sixth instar by this parasitoid was observed (Fig. 5). The wasp maintained a distance of about 15–20 mm from its prey. The larva was noticeably agitated in the presence of this parasitoid, thrashing defensively with either the front or rear portions of its body when perturbed. This larva had seemingly punctured itself with its spines, but eventually killed the attacker with this defense. Other larvae were observed that lacked many of their rear spines and it was presumed these spines were lost in similar interactions. Chrysalides formed by larvae infected by this wasp were formed prior to healthy counterparts and developed a darker exoskeleton. The parasitoid is believed to be polyembryonic, with one collected chrysalis containing 137 wasp pupae. Adult wasps emerged soon after healthy adult butterflies eclosed, as shown by the presence of hollow, darkened chrysalides with obvious exit holes.

DISCUSSION

The use of an alternate host plant (irreversible?) between subspecies, and to which Ozark populations have become dependent, is fundamental to understanding the basic biology and continued evolution of the Baltimore Checkerspot. *E. p. phaeton* is reported to persist in areas where *Chelone glabra*, *Aureolaria flava*, and *Plantago lanceolata* are its primary hosts (Shapiro 1974, Stamp 1979, Scholtens 1991, Bowers et al. 1992). Masters (1968) and Scholtens (1991) noted populations of *Chelone glabra* in Ozark sites occupied by *E. p. ozarkae*, but neither found the butterfly associated with this plant. Bauer (1975) found *E. p. ozarkae* to be intolerant to changes in original larval food plant when switched from either *Lonicera* (a reported alternate primary host to *Aureolaria* for *E. p. ozarkae*; unconfirmed in this study) or *Chelone* to the other. Vawter and Wright (1986) report that *E. p. ozarkae* performs significantly better on *Aureolaria*, while *E. p. phaeton* performs equally well on both *Aureolaria* and *Chelone*. Scott (1986) notes that after hibernation, larvae of *Euphydryas* spp. are more tolerant and occasionally may forage on plants that are botanically very different. A recent plant atlas for Arkansas (Gentry et al. 2013) shows *Plantago lanceolata* to be found in all counties within which our study occurred, but *E. p. ozarkae* was never found with this plant. Further, no records of *E. p. ozarkae* exist from north-eastern areas of Arkansas, where *C. glabra* is reported to grow.

Herbivore browsing may represent an important threat to populations of *E. p. ozarkae*. *A. flava* in all areas was heavily browsed. The majority of browsing was attributed to populations of White-tailed Deer (*Odocoileus virginianus* Zimmermann). Study sites are largely secluded from human populations and deer were frequently seen within study areas, except Tilly (private homestead with free-ranging dogs). Heavy herbivory of host plants by deer is a common threat to butterfly species (Schweitzer et al. 2011). Large populations are known to alter plant communities in forest understories (Côté et al. 2004), reducing available hosts for many specialized invertebrate herbivores. Schweitzer et al. (2011) suggest herbivory by large populations of deer is a primary cause of decline and imperilment for as many as 15 rare butterfly species. *Chelone glabra* in Maryland, where the Baltimore Checkerspot is state-listed (S-3), is also reported to suffer heavy losses to deer herbivory (Durkin 2009). The importance of herbivory during key periods of the present study is supported by the fact that more larval nests/tents were on unbrowsed plants, which may suggest a preference for unbrowsed plants that are generally not in great abundance.

Larval persistence on hosts in late-summer and early-fall seemed dependent on food availability and predation. Individuals in 2012 experienced the greatest loss within one month of hatching, the same period that the presence of *Stiretrus anchorago* was noticed. Many nests remained active with much fewer individuals into August, the period when nests most frequently deteriorate and when *A. flava* begins to senesce and larvae enter diapause. Food consumed by this point must provide enough of a reserve to carry larvae through winter. In 2012 an increase in larval numbers was recorded during this period. It is possible that larvae at this time aggregate in larger groups, perhaps because there may be energetic or defensive benefits to this behavior.

Comparisons between the two subspecies reveal a number of similarities but there are major differences. Behavior and life-stage characteristics seem similar between the two subspecies (Bowers 1978). Larval group size within communal tents appears to be smaller in *E. p. ozarkae* (present study) than reports for *E. p. phaeton* (Stamp 1982b), though precise data were not taken. An interesting difference in behavior regarding conditions for exiting pre-hibernation tents was noted. More animals were observed outside of nest webbing immediately following rain, perhaps owing to the dryer conditions of the habitat, and on atypically warm days, likely due to the increase of temperatures in aggregate groups. In winter, all larvae aggregated at the base of the host plant, in contrast to observations by Scholtens (1991) concerning *E. p. phaeton* in the Great Lakes region. Feeding behavior in spring larvae was similar between subspecies. Both exhibited broader diets and both aggressively feed on available resources, even to the point of detriment to later life stages (Bowers & Schmitt 2013). The adult flight season is believed to be shorter in *E. p. ozarkae* (Masters 1968) than that of *E. p. phaeton*, which persist up to four weeks. Our results are similar to Masters (1968) in that adult *E. p. ozarkae* persisted for three weeks, with an estimated lifespan of only two weeks for individuals. Wing lengths reported for males and females by Masters (1968) were of similar magnitude in our study, with females being significantly larger than males. It has been reported that *E. p. ozarkae* is larger and darker than the nominate subspecies (Heitzman & Heitzman 1996), but we have not yet made these comparisons.

E. p. ozarkae exhibited a much greater variance in the number of eggs per cluster by comparison to *E. p. phaeton*. Eggs were laid in similar quantities per cluster between subspecies (*E. p. phaeton*: 273.8, Stamp 1982a; *E. p. ozarkae*: 271.4). However, the standard deviation of 156.4 for *E. p. ozarkae* as compared to 23.1 for *E. p. phaeton* represents a nearly seven-fold difference. The magnitude of this difference is largely the result of differences in host relationships among our study sites. Tilly, which maintains much larger plants (more abundant, shorter stalks with greater numbers of leaves) and experiences less browsing (free-ranging dogs) by large herbivores, had the highest within site average for eggs per cluster (Robertson 2015).

Both subspecies are able to break diapause for nest repair (Bowers 1978, present study). Our findings concerning the number of individuals and persistence may point to a potential benefit of larger group size. Tent damage was observed frequently, mostly as circular holes. These holes appeared to have been caused by organisms residing within the protective webbing, particularly katydids (Tettigoniidae).

E. p. ozarkae had a different suite of predators and parasitoids than reported for the nominate subspecies and exhibits behavior that suggest adaptation over an extended period of association. Eggs were likely preyed upon by an unidentified ant species and a chrysopid larvae, both reported by Stamp (1982b) to occupy early instar communal tents. While vespids have not been reported as predators for the eastern subspecies, these insects are generalists and likely do impact *E. p. phaeton*. Predation by *Stiretrus anchorago* (unreported as a predator of *E. p. phaeton*) was common and observed at all sites. Larvae behaved differently when pre-diapause webs were being patrolled by this predator, which may suggest recognition and predator-specific behavioral responses. The impact of this predator was noticeable, with multiple nests lost to its appetite. Parasitism by a chalcidoid wasp is also unrecorded for *E. p. phaeton* and changes in behavior were noted during this interaction; the timing of the attacks (April) seemed specific to the 6th instar of *E. p. ozarkae*.

CONCLUSION

We have shown through the study of life-history traits that there are important differences between Ozark populations and those of the nominate subspecies of the Baltimore Checkerspot. Given the nature of this butterfly (univoltine, short-adult flight period, etc.) and the fact that Ozark populations have received very little study, our findings are noteworthy. The importance of shifts in host plant and differences in ecological environments among populations of phytophagous insects has been shown to lead to speciation (Matsubayashi et al. 2010). Ozark populations of this checkerspot have thrived on different host plants than its more eastern counterpart for at least 85 generations [first report of *E. p. ozarkae* by Bower (1930)]. Throughout this period, which has to have been much greater in duration, the Ozark subspecies has experienced distinctly different habitat conditions and been affected by different predators than the nominate subspecies. The extent to which these differences are sufficient to raise each of the two subspecies to the level of full species has been of interest for many years (e.g., Bauer 1975, Vawter & Wright 1986, Opler & Malikul 1998). Vawter and Wright (1986) found little genetic evidence among 25 allozyme loci to suggest species separation. In comparing mtDNA (COI) between subspecies (4 Arkansas specimens vs 1 Maryland specimen), we too found little genetic difference (0.25 to 0.38%, unpublished data). However, differences in habitat and behavior between the two may supersede lack of genetic evidence (Vawter & Wright 1986, present study). Whether full species or subspecies, there should be no denying that *E. p. ozarkae* populations constitute butterflies that, from a conservation and management perspective, should receive greater consideration. Continuing to treat *E. p. ozarkae* populations of the Baltimore Checkerspot as extensions of the nominate subspecies is not justified and management activities should take this into account.

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