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DEER BROWSING INFLUENCES POPULATION DYNAMICS OF THE OZARK BALTIMORE CHECKERSPOT (EUPHYDRYAS PHAETON OZARKAE: NYMPHALIDAE)

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ABSTRACT. White-tailed Deer (*Odocoileus virginianus*) have been shown to be detrimental to a number of Lepidoptera. Potential host plants for specialist butterfly species can be reduced and removed from native areas through deer browsing. The Ozark Baltimore Checkerspot (*Euphydryas phaeton ozarkae*) is a univoltine nymphalid butterfly endemic to the Ozark regions of Arkansas, Kansas, Missouri, and Oklahoma. In the area around the Buffalo River in Arkansas, the larval host for this butterfly is Smooth Yellow False Foxglove (*Aureolaria flava*). We examined the timing and quantified the effect that deer foraging had on *A. flava* in four *E. p. ozarkae* populations. Browsing occurred in late spring and reduced plant availability by as much as 87% over a two-month period. Browsed plants lost an average of 44 cm in height; data show taller plants were more likely to be browsed than shorter ones. Extensive herbivory caused early-fall-active and late-spring-active larvae to contend with reduced host plant availability, which likely resulted in increased mortality. We also found that browsed plants were less likely to be selected for oviposition. The amount of plant loss appeared to be associated with deer abundance and area attributes (i.e., slope, human activity, plant density, etc.). We found that browsing by White-tailed Deer that is too intense or prolonged can have important consequences for the Ozark Baltimore Checkerspot.

Additional Key Words: White-tailed Deer, Smooth Yellow False Foxglove, Aureolaria, herbivore interactions

North American White-tailed Deer (Odocoileus virginianus Zimmermann; Cervidae) populations have increased their range and abundance in recent decades in the absence of predators, increased forage, and alleviation in hunting pressure (Garrot et al. 1993, Côté et al. 2004). Intense browsing by these animals has been shown to cause bottom-up, cascading reductions on forest community complexity and food networks that have negative, potentially long-term, community-level consequences (Nuttle et al. 2011, Bressette et al. 2012, Wheatall et al. 2013, Habeck & Schultz 2015). Deer alter understory plant communities through extensive browsing of herbaceous shrubs and herbs (Rooney & Waller 2003) that are often replaced by resistant plant species, including exotic and invasive species not typical of local communities (Martin et al. 2010). As such, heavy browsing disrupts up-stream community network connectivity, displacing common and native forest fauna, including birds (McShea & Rappole 2000, Martin et al. 2011), small mammals (McShea 2000), large omnivores (Côté 2005), and invertebrates (Stewart 2001, Allombert et al. 2005). Overabundant deer have caused the disappearance of understory plants in areas where hunting has been banned (Horsley et al. 2003), indirectly resulting in the reduction and even extirpation of invertebrate species (Rawinski 2016). This is especially true of Lepidoptera that depend solely on one plant species (Schweitzer et al. 2011). Deer may also directly reduce invertebrate populations through accidental ingestion of larvae and eggs (Schweitzer et al. 2011). Brousseau et al. (2013) showed that unchecked deer populations on Anticosta Island in Quebec have altered invertebrate communities with the greatest effect on Lepidoptera species. In Connecticut and New Jersey, deer are considered among the top three greatest threats to butterflies (Wagner 2007, Schweitzer et al. 2011).

The Ozark Baltimore Checkerspot (Euphydryas phaeton ozarkae Masters; Nymphalidae) is a univoltine butterfly that specializes on perennial Smooth Yellow False Foxglove (Aureolaria flava L.; Orobanchaceae) in the region near the Buffalo River in Arkansas. Eggs are laid on the underside of leaves in large clusters in late spring (May-June) and larvae hatch en masse approximately three weeks later (Robertson & Baltosser 2016). All developing larvae depend on this natal host plant (and, in some circumstances, those in close proximity) for shelter and nutrients. The host plant (usually completely defoliated by larval feeding) senesces in late summer, at which time larvae enter diapause and do not feed until they emerge the following spring (Robertson & Baltosser 2016). Such a long period without feeding demands large resource reserves for subsistence. A. flava is among the first plants to sprout in spring and the timing corresponds with the initiation of larval activity. Starting as purple and red anthocyanin-filled rosettes, plants grow quickly and are often browsed by herbivores (Fig. 1). Perhaps due to its relative early emergence or its nutritive qualities, deer forage heavily on A. flava in early to late spring. Plants respond by producing alternate, viable stalks if browsing occurs early (March-April; pers. obs.)



FIG. 1. Photographs taken 20 April 2014 showing the difference between unbrowsed (top) and browsed (bottom) *Aureolaria flava*.

and undergo early senescence if browsing occurs late (mid-April–August; pers. obs.). As a result, availability and suitability of host plants can be dramatically reduced for all life stages of *E. p. ozarkae*, including females searching for suitable oviposition locations (Robertson 2015). This reduction is of particular interest given the patchwork distribution of this plant and, by extension, the Ozark Balitmore Checkerspot. Durkin (2009) documented a similar threat to the eastern subspecies, *E. p. phaeton*, stating that White-tailed Deer have contributed to its threatened status in Maryland.

Most studies have considered the effect of overabundant deer populations on entire forest ecosystems and arthropod communities. While this approach is extremely valuable in maintaining forest habitat and infrastructure, it does not inform land managers and conservation biologists about the effects deer have on specific species of invertebrates. Whitetailed Deer, even in areas of intense management, can have a large effect on certain plant species, with serious implications for specialist insect herbivores that feed on one or few select plant species during development.

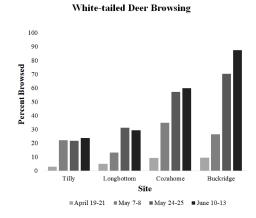


FIG. 2. Comparisons of White-tailed Deer browsing made at 15-day intervals among study sites.

Here we examine the timing and impact of deer browsing on A. *flava* and how this might relate to the status of E. p. ozarkae in Northern Arkansas. While not regarded as threatened, little is known about the distribution and current status of this butterfly. Ozark populations differ significantly from populations elsewhere throughout the range of the species (Robertson 2015, Robertson & Baltosser 2016), leading some researchers (e.g., Masters 1968, Vawter & Wright 1986, and Opler & Malikul 1998) to speculate that the Ozark Baltimore Checkerspot may be worthy of specieslevel status. This butterfly (and other checkerspots) survives in metapopulations, where colonies are prone to collapse and re-establishment within local habitats (Hanski & Singer 2001). Our goal within this communication is to document the effects of deer browsing upon Yellow False Foxglove and, in turn, gauge the potential for negative consequences to the Ozark Baltimore Checkerspot. Additionally, we believe our findings are potentially relevant to populations that exhibit boom-bust cycles (e.g., Himes Boor et al. 2017, Crone 2018).

Methods

Data were collected from four widely separated *E. p.* ozarkae populations in Arkansas: Buckridge (within the Gene Rush Wildlife Management Area in Newton County; 35.99 N, -92.95 E), Cozahome (southeast of the town for which it is named in Searcy County; 36.02 N, -92.46 E), Longbottom (south of Gilbert in Searcy County; 35.97 N, -92.72 E), and Tilly (west of Tilly in Pope County; 35.72 N, -92.85 E). In 2014 sites were visited on consecutive days every two-and-a-half weeks from 19 April through 13 June, for a total of four visits to each site. Sites were surveyed for A. flava having been browsed or left unbrowsed. Percentages of browsed plants were calculated for each visit and plotted (Fig. 2) to visualize timing and extent of foliage loss. Ratios of browsed to unbrowsed plants from each site were analyzed with 2×2 contingency tables between each successive week and over the entirety of the four visits.

To estimate the affect deer browsing has on availability of *A. flava*, 30 browsed and 30 unbrowsed plants were measured for height and stalk width on the final visit. Heights were measured from base of plants to point of browsing (browsed) or growing tips (unbrowsed). Stalk widths were measured within 1 cm of the soil using electronic calipers. Stalk heights of unbrowsed plants were regressed against corresponding stalk widths. Regression plots were made for each site to account for potential phenotypic differences in plants at different sites (Fig. 3). Regression models for each location were then used to estimate potential height of

TABLE 1. Comparisons of browse ratios between weeks (° significant ratio increase) and cumulative examination showing a significant pattern of increase over the duration of the study for each area.

Site	Weeks	χ² Value	p-value
Tilly	1 vs 2*	89.87	< 0.0001
	2 vs 3	0.01	0.9301
	3 vs 4	0.52	0.4700
	1 vs 4*	112.92	< 0.0001
Longbottom	1 vs 2*	5.83	0.0157
	2 vs 3*	18.23	< 0.0001
	3 vs 4	0.09	0.7689
	1 vs 4*	31.43	< 0.0001
Cozahome	1 vs 2*	22.88	< 0.0001
	2 vs 3*	13.31	0.0003
	3 vs 4	0.10	0.7491
	1 vs 4*	67.63	< 0.0001
Buckridge	1 vs 2*	101.35	< 0.0001
	2 vs 3*	409.43	< 0.0001
	3 vs 4*	94.15	< 0.0001
	1 vs 4*	1287.88	< 0.0001

browsed plants within sites using stalk widths. Differences between actual and model-estimated heights were used to generate descriptive data. Stalk widths (and therefore heights) of unbrowsed and browsed plants were further compared using a Student's t-test to determine if there was differential utilization between the two categories.

Stalk height was the most predictive variable in the selection of plants for oviposition (Robertson 2015). To determine how deer browsing affects stalk height, 40 plants at each site (20 browsed, 20 unbrowsed), except Longbottom, which offered only 30 plants (15/15), were randomly selected. Plants were flagged near the ground prior to oviposition (early May) and revisited to detect the presence or absence of egg masses. Data were analyzed using a 2×2 contingency table.

Results

Browsing was heaviest at Buckridge (87.4%, n = 1098) and Cozahome (59.8%, n = 117), whereas Longbottom and Tilly suffered the least amount of herbivory 29.3% (n = 167) and 23.8% (n = 424), respectively. Chi-square analyses for all comparisons made for Buckridge, Cozahome, Longbottom, and Tilly colonies are shown in Table 1. The greatest increase in ratios varied among sites, with only Buckridge having consistently significant increases in browsing ratios between weeks.

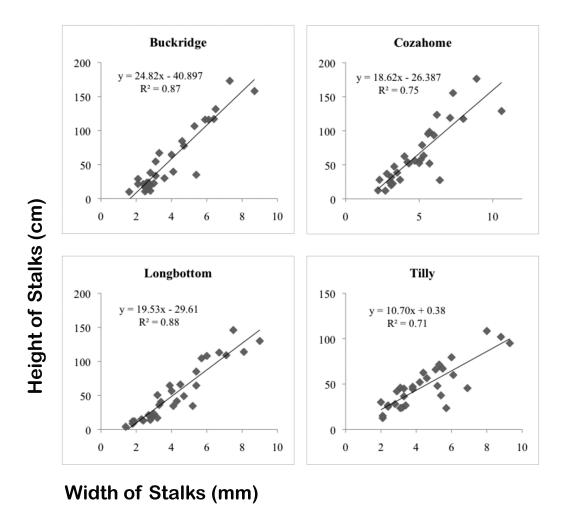


FIG. 3. Regression analyses showing the relationship between height versus width of browsed Aureolaria flava stalks among study sites.

Browsing was directed towards taller plants. Modeling plant height using stalk width produced R² values of 0.868, 0.746, 0.881, and 0.709 for Buckridge, Cozahome, Longbottom, and Tilly, respectively. Browsing reduced plant heights by an average of 44.0 cm (n = 122, s.d. = 40.5). Browsed stalks were significantly wider than unbrowsed stalks (t = 6.05, p < 0.0001), with browsed-stalk widths averaging 5.92 mm (n = 122, s.d. = 1.97) and unbrowsed-stalk widths averaging 4.39 mm (n = 120, s.d. = 1.96). Browsed plants were selected for egg deposition less frequently than unbrowsed plants (n = 150, χ^2 = 11.55, p = 0.0007). Habitat quality and host plant availability for the Ozark Baltimore Checkerspot were thus diminished by deer browsing.

DISCUSSION

The greatest impact of White-tailed Deer browsing of *A. flava* occurred in May. At this time *A. flava* had reached approximately half its full height and was easily observed and differentiated from a landscape of otherwise short undergrowth. The nutritive properties of this plant to White-tailed Deer are unknown, but given the relatively barren understory, we believe its availability at this time explains much of the observed utilization.

Site conditions and management regimes affected browsing in some interesting ways. Browsing was most extensive at Buckridge over the study period. This location is a wildlife management area and has an abundance of deer. This location is routinely managed with fire, a management regime designed to maintain historic conditions and is known to promote Whitetailed Deer populations by supporting open, earlysuccessional habitats (Masters et al. 1993). On every visit in 2014 deer were observed within the study area. Tilly was browsed the least, perhaps owing to conditions of private ownership. While this site is also routinely managed with fire, deer in the area are harvested by the landowner and *A. flava* are in close proximity to the homestead where multiple dogs are frequently outdoors.

White-tailed Deer compete with *E. p. ozarkae* by consuming the host plant. Browsing of taller plants can greatly reduce available resources for spring larvae, ovipositioning females, and summer larvae. Fall larvae on heavily browsed plants (estimated half of plant resources or more) did not survive to spring emergence (unpublished data). Diminished food availability has a myriad of consequences, each of which could be studied in detail, but within the context of a larger study (Robertson & Baltosser 2016), this was not feasible. However, we were able to note that heavy browsing coincided with larvae having to make relatively long treks in search of additional hostplants across food-reduced to food-barren landscapes.

Oviposition was documented more often on unbrowsed plants, but the effect may be even greater than our data suggest with respect to overall habitat suitability. Most browsed plants that received egg clusters were browsed only slightly, leaving much of the vegetation intact. If *E. p. ozarkae* chooses oviposition hosts based on *A. flava* density (untested), browsing by deer in spring may reduce host acceptance in an otherwise high-quality resource patch. Our data and observations demonstrate that deer can play a role in the population dynamics of Ozark Baltimore Checkerspots.

Managing for the effect of White-tailed Deer browsing requires further, long-term studies having much greater breadth and depth. Using fire to open the understory and remove successional effects allows A. *flava* to thrive but also attracts deer (Masters et al. 1993). Providing more abundant resources may concentrate butterflies and deer. Areas that support dense stands of A. *flava* in the summer may increase the likelihood that a female accepts such areas for oviposition, while also increasing deer browsing the following spring. This creates a dichotomy between present (during oviposition) and future (spring larval feeding period) landscapes depending upon time of year. Considering the typical rise and fall of subpopulations in metapopulations, this may not produce a negative effect overall. Deer browsing only wounded plants for the year, but because A. flava is

perennial, this allowed plants browsed by deer to return the following year. Heavy *E. p. ozarkae* feeding in spring resulted in the demise of the plant (Robertson & Baltosser 2016), reducing future resources within areas. Rather than being totally detrimental, it may be possible that deer browsing can result in a population equilibrium among each of the three constituents (False Foxglove, White-tailed Deer, and Baltimore Checkerspot) by limiting present resources and maintaining future resources. Whatever long-term effects may occur in response to this relationship, our research establishes that the consumption of *A. flava* in the Ozark regions of Arkansas by White-tailed Deer can have important consequences for the Ozark Baltimore Checkerspot.

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