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NOVEL OBSERVATIONS OF LARVAL FIRE SURVIVAL, FEEDING BEHAVIOR, AND HOST PLANT USE IN THE REGAL FRITILLARY, *SPEYERIA IDALIA* (DRURY) (NYMPHALIDAE)

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ABSTRACT. *Speyeria idalia* is a prairie specialist that has experienced dramatic population declines throughout its range. *Speyeria idalia* is nearly extirpated from the eastern portion of its former range; however, populations within Kansas are relatively stable. We made several previously undescribed field observations of late-instar larvae and post-diapause female *S. idalia* in northeastern Kansas during 2014–2016. We report finding late-instar larvae at locations that were burned within weeks of detection. The observations of larvae shortly following a burn suggests that *S. idalia* larvae are capable of surviving fire and contradicts our current knowledge of this species. Additionally, we describe a feeding behavior characteristic of late-instar larvae. Larvae observed in the field and lab stripped leaves of host plants leaving only stems. This strip-style feeding behavior provided unique feeding evidence that was valuable to detecting the presence of larvae in the field. Finally, we documented larvae and post-diapause, egg depositing females using *Viola sororia*. The use of this relatively widespread and common plant by *S. idalia* populations in the Central Great Plains has only been implicitly documented but may have important conservation implications. These novel observations further our knowledge of the ecology of this imperiled species and provide timely information that may improve research and conservation management efforts directed toward *S. idalia* populations.

Additional key words: conservation, feeding sign, grasslands, Great Plains, violet

The regal fritillary, *Speyeria idalia* (Drury, 1773) (Nymphalidae), is a large univoltine and non-migratory butterfly. Adult flight begins with the emergence of males in late May and continues through September when females begin to oviposit (Klots 1951, Tilden & Smith 1986, Wagner et al. 1997). *Speyeria idalia* mate shortly after they emerge in late May–early June; however, females postpone oviposition until late August to early September (Scott 1986, Wagner et al. 1997, Zercher et al. 2002). Oviposition site selection appears to be somewhat casual with eggs deposited near, but rarely on host plants (Scott 1986, Kopper et al. 2000, Swengel & Swengel 2001). It is generally suspected that females cue into factors other than the presence of host plants when determining oviposition locations because host plants are senescing when females begin to oviposit eggs (Wagner et al. 1997, Kopper et al. 2000).

Speyeria idalia eggs hatch in ~ 25 days and 1st instar larvae emerge, consume the chorion, and enter a winter diapause. Larval development resumes in early spring with the emergence of host plants and lasts ~ 6–7 weeks. There are six larval instars followed by pupation in late spring and a pupal stage that lasts 2.5 to 4 weeks (Edwards 1879, Hammond 1974, Wagner et al. 1997). *Speyeria idalia* larvae are oligophagous and feed on a variety of violet (*Viola* spp.) host plant species (Klots 1951, Hammond 1974, Ferris & Brown 1981). Local populations are often associated with specific violet species and larvae in the Central Great Plains are reported to preferentially feed on birdfoot, *Viola pedata* (Linnaeus) (Violaceae) or prairie violet, *Viola pedatifida* (G. Don) (Violaceae) (Swengel 1997, Kelly & Debinski 1998, Dole et al. 2004).

The historic range of this once abundant butterfly of N. American prairie communities extended from Oklahoma to the border of Canada and east to the Atlantic coast. Populations have declined by approximately 99%. *Speyeria idalia* is now nearly extirpated from the eastern portion of its former range and western populations have experienced dramatic declines (NatureServe 2016). *Speyeria idalia* was listed as a Category II species under the United States Endangered Species Act (ESA) until this category was removed in 1996 (U.S. Fish and Wildlife Service 1996).

FIG. 1. A late-instar *Speyeria idalia* larva feeding on *Viola pedatifida* leaves in the Flint Hills of northeastern Kansas, USA.

FIG. 2. The characteristic feeding sign exhibited by late-instar *Speyeria idalia* larvae on *Viola pedatifida* in the Flint Hills of northeastern Kansas, USA. On the left is a *V. pedatifida* leaf before being consumed by a larva. On the right are the remnants of a *V. pedatifida* leaf after a late-instar larva strips away the leaflets until only a small portion of leaf and stem remain.

Rapid, range-wide declines continued, prompting the U.S. Fish and Wildlife Service to initiate a status review under the ESA in September 2015. However, some locally abundant populations persist in the west and the species is considered stable in Kansas (Ely et al. 1986, Marrone 2002, Selby 2007).

While it is suspected that *S. idalia* population declines are caused by habitat loss, fragmentation and land management practices such as heavy grazing, frequent and intensive burning, and haying, the direct causes are unclear (Schultz & Crone 1998, Davies et al. 2005, Ferster & Vulinec 2010). It is estimated that the Great Plains region has lost 70% of its grasslands and only 37% of the historic extent of tallgrass prairie in the Flint Hills of Kansas remains (Samson et al. 2004). Native tallgrass prairie communities have succumbed to anthropogenic land conversion, development, invasive weeds, and plant succession (Samson & Knopf 1996). Historically, unrestricted grazing by herbivores and wildfire played important roles in the maintenance of prairie ecosystems in the Great Plains (Fuhlendorf et al. 2009). However, in the absence of these ecological drivers, remnant tracts of prairie are often maintained by prescribed land management (Shuey 1997, Samson 1999, Toombs 2012). This is crucial to maintaining grassland ecosystems and a lack of management threatens the persistence of remaining prairie remnants (Fuhlendorf and Engle 2004). In particular, prescribed fire can suppress invasive plant species and control woody encroachment, and is considered a primary tool for maintaining the open vegetative structure of grasslands (Fuhlendorf & Engle 2001, Ditomaso et al. 2006).

The effect of fire on prairie insects is contentious. Some studies suggest that prescribed fire benefits prairie specialist butterflies (Selby 2007, Moranz et al. 2014), while others argue that it is harmful (Swengel 1996, 2001, 2004; Swengel & Swengel 2001). In particular, *S. idalia* research often reports that fire reduces or eliminates this species from sites by directly or indirectly killing larvae (Kelly & Debinski 1998, Swengel & Swengel 2001, Powell et al. 2007, among others). Therefore, management recommendations for *S. idalia* populations typically propose prescriptions of mowing, haying, light grazing, rotational burn regimes and the implementation of permanent non-fire refugia (Schlicht & Orwig 1992, Swengel 1996, Schlicht 2001, Panzer 2002, among others).

The uncertainty of the effects of fire on *S. idalia* populations is likely the result of a dearth of autecological information on immature stages. *Speyeria idalia* larvae are inconspicuous, cryptic, and widely dispersed, making them difficult to locate in the field (Scudder 1889, Kopper et al. 2001, TNC 2001). The challenges associated with detecting *S. idalia* larvae have limited field studies on this fundamental life history stage. Consequently, assessments of habitat quality are often conducted by examining relationships between available resources and habitat features and the presence and abundance of adults (Britten & Riley 1994, Smallidge et al. 1996, Grundel et al. 2000, Collinge et al. 2003). However, adult mobility may confound assessments of how the presence and abundance of mature *S. idalia* in an area is affected by management

FIG. 3. A late-instar *Speyeria idalia* larva beginning to feed on the leaves of *Viola sororia* in the Flint Hills of northeastern Kansas, USA.

(Swengel 1996, Ferster & Vulinec 2010, Shuey et al. 2016). Highly vagile adult butterflies can readily move across a landscape to locate resources when conditions change while larvae are generally restricted to the resources and conditions in the area at which they hatched. Thus, habitat features and resources used by adults may not adequately reflect the requirements of the immature stages (Bergman 1999, Lane & Andow 2003, Albanese et al. 2008).

The goal of our study was to investigate the effects of management practices and habitat features on the presence and abundance of *S. idalia* larvae and adults. We made several novel observations of late-instar larvae and post-reproductive diapause female butterflies during this research. Here, we present and discuss the following observations: several late-instar larvae in areas that were recently burned, a distinct and reliable feeding sign exhibited by late-instar larvae, cathemeral larval activity and the use of a less recognized host plant species in our study region by post-reproductive diapause female butterflies and late-instar larvae.

METHODS AND RESULTS

We conducted field and laboratory studies from 2014 through 2016 at the Fort Riley Military Reserve (FRMR) and the Konza Prairie Biological Station (KPBS), in Geary and Riley counties within northeastern Kansas, U.S. These sites are within the Flint Hills, which is characterized by rolling hills, rocky soil, and large tracts of tallgrass prairie (Anderson & Fly 1955, Reichman 1987).

Field surveys for late-instar larvae were conducted in April and May during 2014, 2015, and 2016. Here, we use the term late-instar to describe larvae that were assessed to be in fourth through sixth larval instars when observed. This estimation was based on the period of larval surveys and the relative size of observed larvae. We surveyed ten 2500-m^2 plots for late-instar larvae and the location of surveyed plots were stratified by management regime (i.e., fire, grazing, and haying) and fire-return interval (i.e., low ≥ 10 years, moderate 3–5 years, and high 1–2 years). Six of the plots were located at the FRMR and four were located at the KPBS. Each plot was partitioned into grids of 100-m^2 sub-plots. The 100-m^2 sub-plots included a gradient of violet density. We randomly selected 15 sub-plots within each 2500-m^2 plot for larval surveys each year. Each host plant located within surveyed sub-plots was systematically examined for late-instar larvae and evidence of larval feeding. We also searched the surrounding vegetation, litter, and ground within each sub-plot for larvae.

Surveys for post-reproductive diapause, egg depositing females were conducted from late August to early October during 2014 and 2015. We surveyed 44 line transects for adult females actively depositing eggs. All line transects were ≥500 m in length and stratified by management regime (i.e., fire, grazing, and haying), violet density and fire-return interval (i.e., low ≥ 10 years, moderate 3–5 years, and high 1–2 years). We conducted surveys when weather conditions were appropriate for adult flight using repeated, modified Pollard walks (Pollard 1977). When a female was detected an observer followed its movements and recorded oviposition locations.

Larvae and Fire. We surveyed a total of 353 100-m^2 sub-plots for late-instar *S. idalia* larvae and feeding evidence during this study. Seventy-six of these sub-plots

FIG. 4. An adult *Speyeria idalia* female dragging her abdomen and probing various substrates in search of oviposition locations in the Flint Hills of northeastern Kansas, USA. The broad-leaf plant in the image is *Viola sororia*.

were located in areas that had been burned during the late winter and spring months preceding a larval survey. We detected late-instar larvae and evidence of larval feeding in 16 (21%) of these sub-plots. A total of 22 late-instar *S. idalia* larvae were detected during this study. Twelve (54%) of the larvae observed were in areas that had been burned ≤61 days prior to detection. Seven of these larvae were observed at the FRMR and five at the KPBS study sites.

Larval Feeding Sign and Behavior. We collected a total of five *S. idalia* larvae from the field. In 2014, we collected two larvae on 19 April and a third on 19 May. In 2015, we collected two larvae on 19 April. Larvae were kept outside in small, clear individual enclosures and we observed each larva's behavior for 18 to 35 days. The larvae were reared on both *V. pedatifida* and *Viola sororia* (Willd) (Violaceae) leaves. All five larvae produced a unique strip-style feeding sign on both host plant species. Larvae defoliated stems by consuming the leaves of host plant species in a "type-writer" fashion, feeding back and forth on a single leaf until all that remained was a small portion of the leaf above the stem (Fig. 1). Larvae were active during both day and night but rested at the base of plants or in the folds of leaf litter provided within enclosures when not foraging.

Late-instar *S. idalia* larvae observed in the field also produced this distinctive feeding sign on host plants and exhibited cathemerality. We observed 19 larvae during daylight, two during twilight and one at night during field surveys. These larvae were actively feeding, foraging and resting when observed. Evidence of late-instar larvae feeding between field and lab larvae was consistent. Late-instar larvae observed in the field also defoliated host plants by stripping away and consuming the leaves until only a small portion of the leaf above the stem remained (Fig. 2). This feeding sign was detected in all of the 100-m^2 sub-plots in which larvae were detected.

***Speyeria idalia* and *Viola sororia*.** Among the ten 2500-m^2 larval survey plots we surveyed for larvae, four contained both *V. pedatifida* and *V. sororia*, and one contained only *V. sororia*. Late-instar *S. idalia* larvae and larval feeding sign was detected on *V. sororia* in three of these plots. The late-instar larvae feeding sign exhibited on *V. sororia* closely resembled the feeding sign we observed on *V. pedatifida* (Fig. 3).

We observed three post-reproductive diapause females oviposit in close proximity (i.e., < 1 m) to *V. sororia* plants during surveys (Fig. 4). All females flew low to the ground and frequently dropped down into vegetation. Upon landing, females maneuvered through vegetation, tasting with their feet and dragging their abdomens while probing various substrates in search of oviposition sites. Females then deposited eggs on the underside of dead vegetation or detritus near *V. sororia* plants. In two of these observations, the only host plant species observed within a 1/4 km of the oviposition location was *V. sororia*.

DISCUSSION

Previous research conducted on *S. idalia* larvae has resulted in relatively small sample sizes of detected larvae (e.g., Barton 1995, n=9; Kopper et al. 2001, n=12; TNC 2000, 2001, n=0), which has limited the application of these data to robust quantitative analysis. However, the identification of a feeding sign distinctive to the larvae of a rare butterfly species can improve larval detection on host plants (Albanese et al. 2007, 2008). The unique feeding sign of late-instar *S. idalia* larvae that we observed was a reliable indication of the presence of larvae and greatly improved our ability to detect this species within host plant patches. Using direct observations of *S. idalia* larvae in conjunction with the feeding sign we describe may improve efforts to conduct field research on this life history stage and ultimately, advance our knowledge of this species' conservation management.

The establishment and spread of invasive plant species is not always detrimental to Lepidoptera populations. For example, both the larvae of wild indigo duskywing, *Erynnis baptisiae* (Forbes, 1936) (Hesperiidae) and Baltimore checkerspot, *Euphydryas phaeton* (Drury, 1773) (Nymphalidae) have adapted to feed on nonnative, invasive plant species (i.e., crown vetch, *Securigera varia* (Linnaeus) (Fabaceae) and English plantain, *Plantago lanceolata* (Linnaeus) (Plantaginaceae), respectively) as alternatives to their native host plants, which have relatively restricted distributions. Subsequently, both butterfly species have increased in abundance (Bowers 1992, Opler and Malikul 1992, Ferge 2008). *Viola sororia* is arguably the most common and widespread *Viola* species in N. America and often considered an invasive weed (Solbrig et al. 1980). Although it is known that *S. idalia* larvae are able to feed on different *Viola* species, direct field observations of larvae feeding on *V. sororia* have not been well documented especially within our study region. Moreover, the selection of oviposition sites by adult females near *V. sororia* further indicates the potential importance of this alternative host plant to *S. idalia* ecology and conservation management. Research suggests that predicted global climate and land use change will continue to facilitate increases in the distribution and abundance of adaptive, generalist species and negatively impact populations of specialist plant and insect species (Sparks 2000, Menendez et al. 2008, Betzholtz et al. 2012). More widespread use of *V.*

sororia by *S. idalia* populations as an alternative to *Viola* restricted to native grasslands (i.e., *V. pedatifida*) may represent an important adaptation toward the reestablishment and range expansion of this imperiled butterfly species particularly in light of predictions of climate and land use change.

Based on our observations of *S. idalia* larvae at recently burned sites, we hypothesize that *S. idalia* larvae have adaptive physiological and/or behavioral mechanisms that facilitate survival of low to moderate intensity surface fires. Previous research has suggested adult *S. idalia* populations are negatively affected by fire (Swengel 1996, Powell et al. 2007) or has presumed that fire is fatal to larvae (Moffat & McPhillips 1993, Kelly & Debinski 1998, Swengel 1998, Huebschman & Bragg 2000, among others) leading to recommendations against prescribed fire as a conservation management tool for this species. However, the response of many species to fire, particularly invertebrates, is complex, inconsistent and driven by a number of different factors. For example, fire increases ant-tending of Fender's blue butterfly, *Icaricia icarioides fendri* (Macy, 1931) (Lycaenidae) larvae and this mutualistic relationship actually increased larval survival the following year (Warchola et al. 2015). Further, some butterfly species evade fire by being semi-fossorial. Immature atala hairstreak, *Eumaeus atala* (Poey, 1832) (Lycaenidae) and frosted elfin, *Callophrys irus* (Godart, 1824) (Lycaenidae) survived fire when pupae were > 1.75 cm below the ground surface (Thom et al. 2015). We observed several larvae resting in dense litter and even underneath rocks at recently burned sites and hypothesize that *S. idalia* larvae use heat as a cue to seek refuge under structures or possibly even underground during fires.

To understand and conserve populations of *S. idalia* and other rare Lepidoptera, we must investigate the ecology of all life history stages. Our observations represent the first time, to our knowledge, that *S. idalia* larvae have been reported in recently burned areas. *Speyeria idalia* populations in the Central Great Plains have evolved with fire for millennia. This species' and its primary host plants' specialization to fire-dependent systems further suggests that *S. idalia* larvae may have adaptations to survive fire and its relationship with fire may be more complex than previously suggested. Our observations highlight the need for additional research investigating the relationship between fire and this species' immature life history stages.

Moreover, adapting to increased use of the more common, generalist *V. sororia* as a host over the prairie restricted *V. pedatifida* may be advantageous to *S. idalia* populations, especially in light of predictions of climate change and the continued loss of prairie communities. Considering the potentially positive implications of host range expansion to conservation efforts, we recommend the documentation and study of the host plant species' used by *S. idalia* larvae across its geographic distribution. The distinctive feeding sign exhibited by late-instar *S. idalia* larvae that we observed may provide a unique tool toward facilitating further field research on this rare species' cryptic immature stages. Given current conservation concerns for *S. idalia* populations, the timely information we provide offers knowledge of this species ecology that can enhance further research and conservation management efforts directed towards this imperiled butterfly.

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