Adult activities of endangered *Oarisma poweshiek* butterflies are associated with a soil moisture gradient in tall grass prairie in Manitoba, Canada

Justis Henault[1] · Richard Westwood[1]

Abstract

Endangered in Canada and the United States, the Poweshiek skipperling's (*Oarisma poweshiek* (Parker) (Lepidoptera: Hesperiidae)) recovery likely depends on understanding more about its ecology. The characteristics of locations which facilitate various adult activities, such as oviposition and resting, in Manitoba tall grass prairie are unknown. We followed adults in prairie patches to identify locations associated with various behaviours, and subsequently measure vegetative, structural and microclimatic attributes at these microhabitats. Adult skipperlings were observed 34 times resulting in 24 flight tracks and 56 point interactions being recorded. Skipperlings flew almost exclusively in the prairie plant community, with few flights into wetter communities and none in forests. Tracks tended to be tortuous, typical of occupancy in higher-quality habitats. Adult activities appeared to be distributed along a soil moisture gradient: oviposition was associated with the relatively mesic section, resting and/or basking with the drier section, and nectar feeding generally associated with sections throughout the gradient. Adults nectared from a mixture of species during the flight period, consuming nectar from *Rudbeckia hirta* Linnaeus (Asteraceae) most often. We report previously unknown aspects of *O. poweshiek*'s ecology.

Implications for conservation: Our findings describe how adult skipperlings might use sections of prairie with different soil moistures to lay eggs, rest, bask and consume nectar. We visualise approaches to ensure all sections are disturbed during stewardship activities and evaluate the degree to which all facilitative soil moistures are present in candidate (re)introduction sites, for the successful recovery of *O. poweshiek*.

Keywords Critical habitat · Species-at-risk · Adult behaviour · Moisture gradient · Visualisation

Introduction

Endangered in Canada and the United States as well as critically listed worldwide (Committee on the Status of Endangered Wildlife in Canada [COSEWIC] 2014; United States Fish and Wildlife Service 2015; Canada Gazette 2019; Red List of Threatened Species of the International Union for the Conservation of Nature by Royer 2020), the Poweshiek skipperling's (*Oarisma poweshiek*, (Parker) (Lepidoptera: Hesperiidae) recovery likely depends on understanding more about its ecology. Extant individuals – potentially a

few hundred (COSEWIC 2014; Smith et al. 2016; Grantham et al. 2020) – exist in the 0.1% of remaining tall grass prairie (Samson and Knopf 1994) to which it is endemic (Layberry et al. 1998). Prairie remnants in Manitoba, Canada and Michigan, United States host the known remaining skipperlings following colony disappearances and fewer adults in extant colonies across *O. poweshiek*'s range since approximately the 1980s (McCabe and Post 1977; Catling and Lafontaine 1986; Klassen et al. 1989; COSEWIC 2014; Smith et al. 2016; Belitz et al. 2018; Grantham et al. 2020; P. Klassen and R. Westwood unpublished). However, no mechanisms which may cause this decline are understood (COSEWIC 2014; Smith et al. 2016).

Supportive habitat in Manitoba is contained within the Manitoba Tall Grass Prairie Preserve (MTGPP; Nature Conservancy of Canada interpretive building at approximately 49.153° N, 96.729° W). Irregularly outlined grasslands

✉ Justis Henault
henaultjps@gmail.com

[1] Department of Biology, University of Winnipeg, 515 Portage Avenue, Winnipeg, MB R3B 2E9, Canada

– with *Andropogon gerardi* Vitman and *Solidago rigida* Linnaeus – forests – with *Populus tremuloides* Michaux and *Quercus macrocarpa* Michaux – and permanent and/or ephemeral wetter habitats – with Cyperaceae spp. – comprise the generally wet-mesic tall grass prairie habitat (Catling and Lafontaine 1986; COSEWIC 2014). Sites which support comparatively higher abundances of *O. poweshiek* are relatively less wet (Henault 2017; Grantham et al. 2020), with Poweshiek skipperlings found in most cases at sites within continuous, connected tall grass prairies of approximately 10 km^2 (Westwood et al. 2020).

In Manitoba, adults fly during the end of June to the beginning of August (Semmler 2010; COSEWIC 2014) most often nectaring from *Rudbeckia hirta* Linnaeus, *Solidago ptarmicoides* (Torrey and (A) Gray) (B) Boivin and *Prunella vulgaris* Linnaeus (Semmler 2010; Dupont Morozoff 2013). Females lay eggs during this time on various species, including grasses *A. gerardi* and *Sporobolous heterolepis* (A. Gray) A. Gray and the forb *Hypoxis hirsuta* (Linnaeus) Coville (Dupont Morozoff 2013; Henault and Westwood 2022). Larvae have been observed foraging amongst shoots of several graminoids during summer and fall: *A. gerardi*, *Muhlenbergia richardsonis* (Trinius) Rydberg, *Schizachyrium scoparium* (Michaux) Nash and *S. heterolepis* (Henault and Westwood 2022). In Manitoba and the United States, larvae are then assumed to diapause close to the ground on plants, feed in the spring and pupate in the second half of June (McAlpine 1972; Borkin 1995; Layberry et al. 1998; COSEWIC 2014; Henault and Westwood 2022). Observations of *O. poweshiek* in natural habitat and captive-reared settings in the United States suggests its development there is similar, and may use hosts such as *S. scoparium* and/or various Cyperaceae spp. (Holzman 1972; McAlpine 1972; McCabe and Post 1977; Borkin 1995; Dana 1999 unpublished; Pointon 2015; Smith et al. 2016; Belitz et al. 2019).

The characteristics of locations which facilitate various adult activities of Poweshiek skipperlings, such as oviposition and resting, in Manitoba tall grass prairie are unknown. While a diversity of microhabitats within a site may have the capacity to support a relatively larger suite of species (Kleckova et al. 2014), similarly a diversity of microhabitats might be able to support a larger suite of a butterfly's daily behaviours. By better understanding these behaviour requirements, stewards can manage habitats in ways that may facilitate butterfly behaviours and researchers can incorporate these criteria into reintroduction site assessments, in turn increasing the likelihood of survival and recovery in the species. *Plebejus samuelis* (Nabokov) (Lepidoptera: Lycaenidae) predominantly laid eggs on host plants (lupines) less exposed to sunlight which facilitated quicker larval growth (Grundel et al. 1998). *Carterocephalus palaemon* (Pallas)

(Lepidoptera: Hesperiidae) males searched for mates in locations intermediate between drier and wetter habitat types, with females laying eggs in these transition areas and nectaring in wetter locations (Ravenscroft 1994). Perhaps, *O. poweshiek* also differentially use regions within their habitat. The degree of flight tortuosity/straightness can help to indicate flight in lower-quality (relatively straight flight paths) and higher-quality (relatively tortuous) habitats (Sei 2009; Fernández et al. 2016).

During previous research in the MTGPP, adult Poweshiek skipperlings appeared to be observed most often (since 2015 to study period) in upland prairie patches adjacent to wetlands. Physical slopes may possess a soil nutrient and moisture gradient (Liu et al. 2020) partly causing a succession of plant species (Zalatnai and Körmöczi 2004). We hypothesised that variable soil moisture within prairie patches facilitated specific adult activities (e.g., nectar sources for feeding), and that adults would most often occupy plant communities where activities could be supported. Additionally, that intermediate soil moistures along slopes would simultaneously support a mixture of plant species which prefer drier and wetter soils, which might be most likely to facilitate larval development. Given that local habitat use by adults is not well understood, our objectives were to: (1) determine the plant community(ies) where adults are active within a prairie patch and (2) describe the vegetative, structural and soil moisture attributes of locations which facilitate various adult activities. We also hoped to generate guidelines to facilitate stewardship of habitats and assessment of site candidates for skipperling reintroduction.

Methods

In 2018, we followed adults in prairie patches within the MTGPP (described in Henault and Westwood 2022). In Henault and Westwood (2022), we reported oviposition and larval feeding components, as well as described vegetative and physical attributes of microhabitats. Here, we report the adult flight behaviour component, and compare characterists of the previous oviposition locations (reported in Henault and Westwood 2022) with those that facilitated nectar feeding, basking, resting and attempted oviposition activities by adults. The inclusion of these previous data is necessary to enable comparisons amongst the activity types. The site is stewarded using prescribed fires, mechanical cutting of vegetation and targeted herbicide application by the Nature Conservancy of Canada (Grantham et al. 2021), or disturbed by stochastic events such as wildfires.

Soil moisture gradient

In 2017, we established transects (n = 8; length: range = 15–25 m) on slopes in prairie patches, from a locally highest elevation to a location with saturated soil (to document the complete moisture gradient within the site). We leveled a string above each transect, and measured the distance to the ground at seven evenly spaced plots (square, 0.25 m²; highest elevation = position 1). We counted the number of shoots of graminoid species and *H. hirsuta* within each plot during 17 through 27 July 2017. During this sampling period, the reproductive structures of plants which mature during a cooler period of the growing season (that is, spring; Kindscher and Wells 1995) were still intact, while the vegetative growth of plants which mature during a warmer period (that is, fall) were well-defined thus increasing the accuracy of plant identification. We verified plant identifications by using the illustrations/pictures and dichotomous keys in Looman and Best (1987) and Leighton and Harms (2014). Nomenclature was matched to Tropicos.org (Missouri Botanical Garden 2021), and common names to the most recent version amongst these three reference publications. *Beckmannia syzigachne* (Steudel) Fernald and *Triglochin* Linnaeus spp. (*T. palustris* Linnaeus and *T. maritima* Linnaeus) were erroneously identified, and counted, as the same species. Therefore, we term corresponding shoots as *B. syg.* /*Tri.* spp.; these taxa all grow almost exclusively in seasonal or permanent wetlands (Lichvar et al. 2012; United States Army Corps of Engineers 2018).

We also estimated the percent cover of graminoids, forbs, shrubs, duff (dead pieces of vegetation, including larger and finer components) and bare soil. The number of blooming *R. hirta* inflorescences (most frequented *O. poweshiek* nectar source in MTGPP; Semmler 2010) within a 3 m radius of each plot's centre were counted, as well as the height of graminoids (~95% of shoots) was measured once in each plot while the depth of duff was randomly measured in three places. We dug two random soil samples (top 15 cm of soil, approximately 7 cm wide at surface) at the start (position 1), middle (position 4 or 5) and end (position 7) along each transect after at least 2 days of no precipitation in July 2017. Samples were maintained in a freezer (approximately −20 °C), air-dried (7 days at 23 °C), homogenised (within each plot) and sieved (2 mm). Then, we used the pipette method (Gee and Bauder 1986) to separate sand, silt and clay portions and determine soil particle size proportions. We also sent approximately one-third of each homogenised sample to Farmers Edge Laboratories in Winnipeg, MB, Canada to analyse soil nutrients. On 9 and 10 May 2019 (after at least 6 days of generally dry conditions; any precipitation that fell did not increase the moisture of the soil surface), a soil probe (Fieldscout TDR 150; Spectrum Technologies,

Incorporated, Aurora, Illinois, United States) was pushed into the ground to 10 cm (beneath soil surface, near roots) at each plot to simultaneously report the soil moisture and electrical conductivity (EC; degree of salinity as in Natural Resources Conservation Services (2012).

Adult activity locations

We conducted daily searches for adults between approximately 10 am and 5 pm, with the exception of days having inclement weather, before the typical adult flight period, during and after to maximise the number of individuals that we could observe. We actively patrolled or stood still and visually scanned prairie patches along established survey paths in three main prairie patches within the site, circulating between patches if we did not observe any adults flying after ~1–3 h. Given the small size of each patch (approximately 0.9 ha, 2.2 ha and 3.9 ha; calculation correction to total patch area of 0.2 km² in Henault and Westwood 2022), we were likely able to observe every individual flying at that time, if they were present. Once an adult was sighted, we began physically walking behind it at a distance of ~2–3 m to be close enough to observe behaviours and movements accurately but far enough away to avoid influencing its behaviours via escape responses. Adults flew consistently about 0.3 m above the vegetation, in a sinusoidal path. Their hindwings were generally held motionless, parallel to the ground, while their forewings were constantly flapped vigorously. When changing direction, adults flapped their hindwings generally once – during which white-silver markings on their hindwings were easily observed – before returning them to parallel. Their flight speed was most often approximate to a comfortable walking pace, while considering undulations in this habitat, for someone approximately 1.8 m tall.

In order to maximise the length of time that adults could be tracked, typically one observer maintained visual contact with butterflies while a second observer followed closely behind placing flags at locations where adults laid eggs, nectared, etc. and providing a second viewpoint if adults were momentarily lost by the first observer. Tracks were recorded while following adults and locations of adult activities were later marked using a GPS unit (Garmin Oregon 700; approximate accuracy 3 m). Protocols for all butterflies were identical (females and males). Adults were observed until lost, or when stationary for 1.5 h. We observed adults from 26 June through 4 July 2018 flying and/or conducting various activities described in Table 1. Basking and resting activities were grouped because adults frequently alternated between these behaviours at the same spot. Although we did not observe mating during this study, we describe mating behaviour in Henault (2021) and Henault and Westwood

Table 1 Typical characteristics adult activities of plant communities. Please refer to Table S1 for plant nomenclature

Adult activity	Attributes
Oviposition	Hovering close to vegetation, sometimes probing, before depositing an egg as in Henault and Westwood (2022)
Attempted oviposition	Searching typically by fluttering and always probing the surface of a leaf blade as observed for "egg laying", but after touching a leaf (usually only once) the female departed and resumed a search at another location.
Resting/Basking	Resting: Positioned stationary on a substrate (living or dead vegetation; no observations on bare soil), with wings closed or opened briefly. Basking: Different in that wings were generally open during the entire observation (forewings 45° angle and hindwings nearly parallel to the ground); may reposition their wings periodically.
Nectar feeding	Landing on a plant (typically directly on an inflorescence) and extending proboscis into flower (s). Adults frequently moved across an inflorescence and probed multiple florets during one visit. While we cannot confirm that nectar feeding occurred while an adult was at a flower, we assume that adults consumed nectar at every visited flower.
Plant community	
Prairie	Open grassland with vegetation less than 0.5 m tall; the most abundant grasses are *Sporobolous heterolepis* and *Andropogon gerardi*; most abundant forbs are *Helianthus maximiliani* and *Dalea purpurea* and most abundant shrub is *Dasiphora fruticosa*; at higher elevation; high light intensity near ground level.
Forest	Stands of trees over 5 m tall; most abundant species is *Populus tremuloides*; low light intensity near ground level.
Tree colony	Forested stand with trees less than 5 m tall; most abundant species is *P. tremuloides*; low light intensity near ground level.
Wetland	Standing water most of the year; perennial vegetation less than 0.5 m tall; most abundant graminoids are *Sporobolus michauxianus*, *B. syg. /Tri.* spp., and *Scirpus* spp.; abundant forbs are *Typha* spp.; at lower elevation; high light intensity near ground level.
Ephemeral wetland	Perennial vegetation less than 0.5 m tall; standing water only a portion of the year; most abundant graminoids include *S. michauxianus* and *B. syg. /Tri.* spp.; high light intensity near ground level.
Shrub wetland	Perennial vegetation more than 0.5 m tall; standing water only a portion of the year; most abundant graminoids include *S. michauxianus* and *B. syg. /Tri.* spp.; most abundant shrubs are *Salix* spp.; intermediate light intensity near ground level.

(2022). Classifications of all adult behaviours were determined by the author(s).

At each location where we observed an adult activity we recorded the substrate, such as resting/basking on a graminoid. Where activity flags were placed, we established circular 0.25 m² plots. We then counted the number of shoots (including forb and shrub species) and physical variables using the same methods as for transects, but on 2 through 14, and 26 August 2018 (exception: no soil plug sampling, nutrient analysis). Where oviposition occurred, we placed open-ended plastic bins to observe larval behaviour (0.19 m² instead; see Henault and Westwood 2022). Within plots of all types, soil moisture and EC were sampled on 18 and 30 July 2018 and 17 August 2018, following the same sampling protocol as in 2019.

During observations in the site, we noted typical habitat characteristics and approximate boundaries of plant communities (Table 1), and then used satellite imagery in ArcGIS Pro ("Imagery": Maxar, Microsoft; ESRI Inc. 2021) to finalise boundaries for each community type (Fig. 1).

Lepidopteran nomenclature follow Pohl et al. (2018) to provide taxonomic consistency amongst the species being discussed; for taxa absent from that document, we used nomenclature from GBIF.org (Global Biodiversity Information Facility 2021).

Analyses

Soil moisture gradient

A transect along one slope which initially appeared to have elevation and soil moisture characteristics consistent with other transects, was in fact ridge-shaped and the lowest elevation did not have the wettest recorded soil moisture. Since we could not resample within the same year, we decided to remove this transect from analyses (analysis: seven transects, 49 plots). Elevation along transects differed by a mean 16.3 cm (n = 7; range = 4.0–26.0 cm). Along each transect, we calculated Spearman's rho coefficients of relative elevation with soil moisture and EC separately before calculating a mean of each (RStudio Team 2021); soil moisture (n = 7, mean = 0.648% volumetric water content [VWC], range = 0.312–0.878% VWC) and EC (n = 7, mean = 0.452 mS/cm, range = 0.070–0.796 mS/cm) increased from position 1 to 7. During soil texture analysis, samples with final values where errors during analysis were made were removed (after removals; n = 16).

Although transects in 2017 were established in patches where adult activity had previously been observed, adults in 2018 were only active near four of the seven transects. To address the risk of analysing habitats not used by adults, we first compared the number of shoots of plant species counted at each transect using non-metric multidimensional

Fig. 1 Adult tracks (orange lines; n = 22) and activity locations (convex hulls: attempted oviposition = purple, n = 5; oviposition = red, n = 4; nectar feeding = blue, n = 22; resting/basking = yellow, n = 14) occurring within types of plant communities (as described in Table 1). We display the prairie patch containing most observations

scaling ordination (Kruskal 1964; Mather 1976; McCune and Mefford 2011). Plant composition of the seven transects overlapped substantially which suggested that each area was vegetatively similar even though adults were only observed in four of the seven. Knowing that habitats where all transects were placed were relevant to the study, we continued with the seven transects.

We visually assessed vegetation diversity at positions along transects using non-metric multidimensional scaling (NMDS) (Sorenson distance, orthogonal rotation, no adjustment for tied scores; Kruskal 1964; Mather 1976; McCune and Mefford 2011). The cumulative r^2 of each axis – calculated using the PC-ORD graphing interface – was evaluated, to display the axes which explained the most variation on NMDS 1, then 2 (Peck 2016). We subsequently overlaid physical attributes of locations (un-constrained; lines scaled to 250% for straightforward interpretation) onto the ordination.

Adult activity locations

We did not mark adult skipperlings thus we cannot attribute observed interactions to individuals. Since we observed several combinations of wing wear and sex amongst individuals, we assume that more than a few skipperlings were encountered during this research. Likely, each type of observed interaction was not conducted by every adult during observations, resulting in an unequal sampling distribution (by individuals and interaction types). Therefore, we explore the data while acknowledging limitations to the creation of robust inferences. All attempted ovipositions were conducted by the same adult, and we retain this corresponding data for exploratory comparisons. Despite these biases and limitations, this research can generate biological information which may facilitate an increased likelihood of *O. poweshiek* recovery.

We measured the length of each flight track (excluding those of two adults which moved only one metre over several hours) in QGIS (QGIS Development Team 2022).

Since the GPS unit was erroneously set to "auto", track points were recorded every 13 ± 12 s (n = 346; mean ± SD; range = 1–101 s) and appeared to highlight substantial changes in path directions, instead of at every second regardless of the path changes as intended. To calculate the degree of tortuosity/straightness of tracks, we divided the distance between the start and end of each track by the total length of each track before subtracting this product from 1, to generate a value of tortuosity from 0 (straighter tracks) to 1 (tortuous tracks) (tortuosity = 1 – [net distance from start to end of track/length of track]). This modification to the approach used by Fernández et al. (2016) allows an absolute assessment of tortuosity without comparing relative values of tortuosity from other habitat types. Given that no track started and ended within non-prairie communities, total track distances in non-prairie communities were short (see results), and our limitations with the track recordings, we only calculated tortuosity for the prairie community type. Since track segments do not represent equal units of time, we did not calculate angles or speed of each track segment. We also added convex hulls of locations where adults activities occurred. For Fig. 1, we display only one prairie patch, of the three, where the majority of adult observations occurred (45/56) to see adult activity locations and plant communities at a useful scale. Samples in all prairie patches were used in other analyses.

Depending on the speed that adults flew while we marked activity locations, our ability to navigate the terrain to precisely mark the base of facilitative plants varied. Therefore, we separated locations into high confidence (within approximately 5 cm), where we measured all variables as described earlier, and low (approximately 6–15 cm), where we declined to count the number of shoots which might be disproportionately affected. While all oviposition and attempted oviposition locations were marked with high confidence, a total of 5/14 resting and/or basking locations and 23/31 nectar feeding locations were similarly marked.

During analyses, we used all plant species which were counted in at least one adult sample location, to identify any species which might be important to *O. poweshiek*. We standardised the number of shoots counted at all activity locations to 0.19 m² to maintain consistency between oviposition locations and other activity locations.

Associating activity types with positions along the moisture gradient

For each focus (moisture gradient and adult activities), the following multivariate analyses were conducted using PC-ORD (McCune and Mefford 2011) with groups as positions along the gradient (positions 1–7) and types of interactions of adults (oviposition, attempted oviposition, resting/

basking, and nectar feeding): We used indicator species analysis (ISA) to determine if individual plant species were associated with a specific group(s) (incorporates abundance of species amongst groups; Dufrêne and Legendre 1997; McCune and Mefford 2011). Prior to analysis, the number of shoots of each species in sample plots were divided into the maximum number of respective shoots counted amongst plots in all groups (McCune and Mefford 2011).

The degree of plant species dissimilarity/similarity (composition and abundance; all species and host species) amongst groups was assessed using multi-response permutation procedures (MRPP) (Berry et al. 1983; Mielke 1984; Mielke and Berry 2001; McCune and Mefford 2011), using Sorenson (Bray-Curtis) distances to weigh each species equally (Bray and Curtis 1957; McCune and Mefford 2011). MRPP is suitable for datasets, such as ours, which contain unequal samples in groups and numerous zeroes (Magurran 1988; McCune and Mefford 2011). Host species were absent from some plots, prohibiting the software from completing the analysis. Thus, to enable MRPP analysis we removed those samples (all part of moisture gradient: position 6, one sample; position 7, two samples). We calculated summary statistics and Spearman's rho in RStudio (RStudio Team 2021; R version 4.1.2 by R Development Core Team (2021), using packages accompanied by helpful vignettes: "ggforce" (Pedersen 2021; "super-ellipse" by Kindt (2020), "ggplot2" (Wickham et al. 2020; "convex hull points" by Chizinski (2014) and "svglite" (Wickham et al. 2021). We conducted the NMDS analysis in PC-ORD, exported scores to create plots in RStudio, then imported plots into Adobe Illustrator (Adobe Inc 2023) to improve the resolution.

Results

Soil moisture gradient

In the NMDS ordination of transect data (3 axes, mean stress = 15.0, p = 0.012; Fig. 2), positions along the transects appear to follow the soil moisture gradient. Species composition appeared to transition from low to high ends of the transects. *B. syg.* /*Tri.* spp., *Eleocharis* spp. and *Juncaceae* spp. were most associated with the lower end of the transects; greater graminoid height and soil EC were positively associated with the lower end of the transects (approximately equal direction and magnitude; EC not displayed), greater graminoid percent cover and density of *R. hirta* inflorescences with the higher end and deeper duff weakly associated with the intermediate to higher sections.

Evaluating trends, the host species *S. heterolepis* was associated with the dry section (Table 2: Stem counts, Table 3: ISA, Fig. 2: NMDS), with stem counts declining
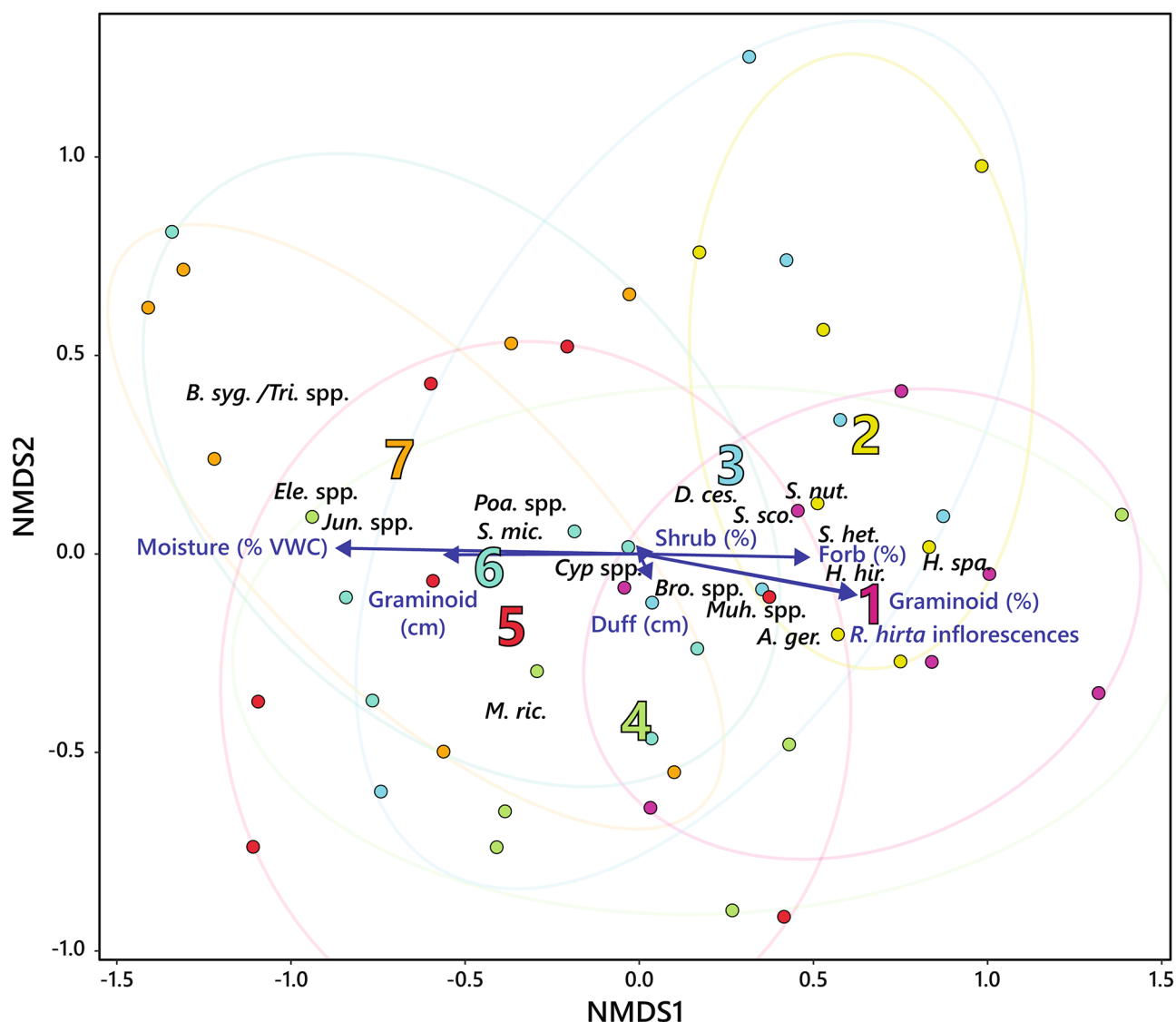
Fig. 2 An NMDS ordination of plant species enumerated and environmental attributes measured (blue font; scaled to 250%) at transect positions along the slopes (labels at centroids; accompanied by respective convex ellipses in corresponding colours). Species names abbreviated

along the transect through the wettest section. *Muhlenbergia richardsonis* was situated near position 5 in the NMDS, with highest stem counts in the mesic section but lower at both the dry and wet ends. *Schizachyrium scoparium* ordinated closest to the driest end of the moisture gradient accompanied by consistent stem counts through to the mesic section before dropping off in the wettest section. *Andropogon gerardi* was associated with the dry section (NMDS) and its stem counts indicate its presence was consistent throughout most of the transect. *Hypoxis hirsuta* was associated with the driest positions in all analyses. Soil nutrients and texture in gradient positions 1 (top), 4 (middle) or 7 (bottom) along transects were not significantly different (Table S2).

The MRPP analysis showed that the transect positions contained different abundances of shoots of all plant species enumerated (n=49, T = -3.785, A=0.067, p=0.001) and of only species consumed by larvae (n=46, T = -2.240, A=0.057, p=0.024) (unadjusted numerical values in Table S3).

Adult activities

Movement and habitat use. Adults were observed 34 times (at least 13 females 9 males; unable to determine sex of other adults); a butterfly with the same scratch on its hindwing was observed on 26 June and 28 June 2018 thus was likely the same individual (male). During the 34 observations of

Table 2 Number of graminoid shoots counted (0.25 m^2) at positions along transects (mean (range); each position: n = 7). The fonts of taxa which were used during oviposition activities and larval foraging behaviours are bolded

Position	*A. gerardi*	*B. syz. /Tri.* spp.	*Bromus* spp.	Cyperaceae spp.	*D. cespitosa*	*Eleocharis* spp.	*H. hirsuta*	*H. spartea*
1	**105.1 (0 to 214)**	0.0 (0 to 0)	1.0 (0 to 6)	64.0 (5 to 158)	5.0 (0 to 17)	0.1 (0 to 1)	**0.6 (0 to 2)**	0.9 (0 to 4)
2	**56.7 (17 to 120)**	0.0 (0 to 0)	0.0 (0 to 0)	59.7 (14 to 130)	25.0 (0 to 139)	0.0 (0 to 0)	**0.0 (0 to 0)**	1.0 (0 to 7)
3	**61.9 (17 to 111)**	0.0 (0 to 0)	0.0 (0 to 0)	63.7 (10 to 136)	44.3 (0 to 207)	2.7 (0 to 18)	**0.0 (0 to 0)**	0.3 (0 to 2)
4	**56.7 (3 to 132)**	0.0 (0 to 0)	0.1 (0 to 1)	60.9 (8 to 133)	4.3 (0 to 28)	4.4 (0 to 17)	**0.0 (0 to 0)**	0.0 (0 to 0)
5	**59.4 (3 to 247)**	0.0 (0 to 0)	0.0 (0 to 0)	65.4 (6 to 126)	6.1 (0 to 13)	15.7 (0 to 71)	**0.0 (0 to 0)**	0.0 (0 to 0)
6	**78.7 (0 to 194)**	0.6 (0 to 4)	0.1 (0 to 1)	55.7 (13 to 84)	4.6 (0 to 20)	26.7 (0 to 87)	**0.0 (0 to 0)**	0.0 (0 to 0)
7	**28.9 (0 to 96)**	5.0 (0 to 20)	0.0 (0 to 0)	57.7 (29 to 91)	5.0 (0 to 18)	63.9 (0 to 144)	**0.0 (0 to 0)**	0.0 (0 to 0)

Position	Juncaceae spp.	*M. richardsonis*	*Muhly* spp.	Poaceae spp.	*S. heterolepis*	*S. michauxianus*	*S. nutans*	*S. scoparium*
1	0.0 (0 to 0)	**33.9 (0 to 104)**	7.7 (0 to 24)	0.0 (0 to 0)	**64.0 (20 to 145)**	0.0 (0 to 0)	22.4 (0 to 122)	**20.0 (0 to 65)**
2	0.0 (0 to 0)	**23.6 (1 to 59)**	10.3 (0 to 27)	0.0 (0 to 0)	**63.9 (4 to 136)**	0.0 (0 to 0)	16.4 (0 to 69)	**17.0 (0 to 82)**
3	24.6 (0 to 148)	**86.3 (0 to 408)**	8.6 (0 to 13)	0.0 (0 to 0)	**36.0 (5 to 113)**	0.4 (0 to 3)	12.4 (0 to 49)	**13.0 (0 to 40)**
4	14.1 (0 to 91)	**98.7 (0 to 231)**	11.7 (0 to 70)	0.1 (0 to 1)	**20.3 (0 to 100)**	4.9 (0 to 34)	11.6 (0 to 46)	**18.9 (0 to 125)**
5	43.9 (0 to 93)	**146.7 (27 to 457)**	1.9 (0 to 13)	0.0 (0 to 0)	**10.9 (0 to 42)**	5.3 (0 to 16)	1.6 (0 to 11)	**3.9 (0 to 23)**
6	55.4 (0 to 116)	**72.4 (0 to 129)**	1.4 (0 to 6)	0.0 (0 to 0)	**11.3 (0 to 31)**	4.6 (0 to 20)	0.0 (0 to 0)	**2.4 (0 to 14)**
7	42.3 (0 to 97)	**50.4 (0 to 157)**	1.6 (0 to 6)	0.3 (0 to 1)	**3.4 (0 to 14)**	21.9 (0 to 62)	0.0 (0 to 0)	**0.7 (0 to 5)**

Table 3 Indicator species of moisture gradient positions (position 1 = driest) and of adult activity locations. Indicator value, generated during ISA, is abbreviated as "IV". Transects: all positions, n = 7; adult activities: attempted oviposition, n = 5 (all one adult); oviposition, n = 6; nectar feeding, n = 23; resting/basking, n = 5

Moisture gradient positions			Adult activity locations		
1	*S. heterolepis*	IV = 30.5, p = 0.046	Resting/Basking	*Rosa* spp.	IV = 40.0, p = 0.031
	H. hirsuta	IV = 42.9, p = 0.012			
7	*S. michauxianus*	IV = 50.6, p = 0.003	Attempted oviposition	*M. richardsonis*	IV = 75.1, p = 0.002
	Eleocharis spp.	IV = 40.2, p = 0.012		*Eleocharis* spp.	IV = 37.6, p = 0.037
				Cyperaceae spp.	IV = 38.0, p = 0.029

adults, 24 flights were tracked. Adults were observed flying almost exclusively in prairie plant communities (Fig. 1), rarely in shrub or ephemeral wetland communities and never in wetland or forest communities (communities as described in Table 1). The mean distance we followed an adult was 86.5 ± 65.4 m (n = 22; mean ± SD; range = 2.1 to 228.0), and in total 1.9 km (1696.7 m in the prairie plant community, 166.2 m in shrub wetland, and 39.1 m in ephemeral wetland). The mean tortuosity of adult tracks was 0.57 ± 0.30 (n = 22; mean ± SD; range = 0.04 to 0.94). Of the individuals we could identify, the tortuosity of female tracks was 0.56 ± 0.32 (n = 4; mean ± SD; range = 0.19 to 0.84) and of male tracks was 0.66 ± 0.23 (n = 6; mean ± SD; range = 0.34 to 0.90).

During the 34 observations of adults, six adults flew without conducting an observable activity, thus 28 adults created 56 activity events (attempted oviposition: n = 5, oviposition: n = 6, nectar feeding: n = 31, resting/basking: n = 14; focal patch in Fig. 1). In the focal prairie patch, attempted oviposition locations were concentrated at a relatively lower elevation and egg locations were generally adjacent to the wetland with one laid at a higher elevation (oviposition of 6 eggs by up to 5 adults). Nectar feeding locations ranged through most elevations, and resting/basking locations appeared to be relatively concentrated, and at the highest

relative elevation. Including locations from all patches, 49 were within the prairie plant community, 3 bordered in-between the prairie and shrub wetland communities (1 oviposition, 2 resting/basking) and 4 were within the shrub wetland community (all nectar feeding).

Nectar feeding and activity substrates. Amongst all prairie patches, adults used various plant substrates for most types of activities (Table 4; nomenclature in Table S1). Resting/basking on plants typically occurred at the top of the vegetative canopy.

Nectar feeding was observed 26 June through 3 July 2018, during which adults consumed proportions of nectar from different species, using *R. hirta* most often (Fig. S4). When considering only dates where nectar feeding was reported more than once, the mixed diet at the beginning of the flight period transitioned to one dominated by *R. hirta* at the end.

Microhabitat attributes. The highest relative shoot abundances of individual larval food species were not consistently recorded at locations associated with oviposition or attempted oviposition (Table 5). The majority (81%) of *R. hirta* shoots were counted at locations where adults consumed nectar.

The ISA generated four species to indicate activity locations (Table 3). Additionally, *H. hirsuta* was nearly indicative

Table 4 Proportion of substrates used during adult activity types (% (number of observations))

Attempted oviposition		Oviposition		Nectar feeding		Resting/Basking	
Graminoid	100% (n = 5)	*A. gerardi*	67% (n = 4)	*R. hirta*	58% (n = 18)	Graminoid	43% (n = 6)
		H. hirsuta	17% (n = 1)	*Packera* spp.	19% (n = 6)	*G. lepidota*	36% (n = 5)
		S. heterolepis	17% (n = 1)	*G. lepidota*	13% (n = 4)	*Packera* spp.	14% (n = 2)
				Apocynum spp.	3% (n = 1)	*A. canescens*	7% (n = 1)
				D. fruticosa	3% (n = 1)		
				Unidentified	3% (n = 1)		

Table 5 The number of shoots of host plants and the most frequently used nectar species – *R. hirta* (mean (range)) in locations where adults conducted various activities. For all species: attempted oviposition, n = 5 (all one adult); oviposition, n = 6; nectar feeding, n = 23 and resting/basking, n = 5

Plant species	Attempted oviposition	Oviposition	Nectar feeding	Resting/ Basking
A. gerardi	31.6 (6.1 to 65.4)	43.2 (16.0 to 76.0)	21.3 (0.0 to 76.0)	27.5 (22.0 to 44.1)
M. richardsonis	129.0 (28.1 to 305.5)	17.0 (0.0 to 45.0)	18.5 (0.0 to 147.4)	7.3 (0.0 to 30.4)
S. heterolepis	55.9 (10.6 to 107.2)	57.3 (4.0 to 133.0)	42.8 (0.0 to 106.4)	44.5 (9.1 to 66.9)
S. scoparium	10.9 (3.0 to 25.1)	5.0 (0.0 to 23.0)	18.7 (0.0 to 66.1)	17.9 (0.8 to 47.1)
R. hirta	0.2 (0.0 to 0.8)	0.7 (0.0 to 4.0)	1.0 (0.0 to 3.0)	0.2 (0.0 to 0.8)

Table 6 The environmental characteristics associated with various adult activities (mean (range)). For characteristics: attempted oviposition, n = 5 (all one adult); oviposition, n = 6; nectar feeding, n = 31 (duff (cm) and graminoid (cm): n = 30); resting/basking, n = 14

Environmental characteristic	Attempted oviposition	Oviposition	Nectar feeding	Resting/ Basking
Soil moisture (% VWC)	29.5 (22.5 to 41.7)	28.5 (16.5 to 41.4)	20.8 (9.0 to 38.3)	21.2 (12.7 to 30.8)
Soil EC (mS/cm)	0.17 (0.10 to 0.30)	0.15 (0.06 to 0.25)	0.09 (0.00 to 0.24)	0.10 (0.04 to 0.18)
Graminoid (cm)	40.6 (38.5 to 42.5)	31.7 (24.7 to 35.3)	34.0 (17.0 to 53.4)	28.9 (13.4 to 41.5)
Duff (cm)	6.33 (5.2 to 7.6)	4.0 (2.5 to 4.9)	4.9 (2.4 to 8.4)	4.1 (2.2 to 7.6)
Shrub (%)	0.8 (0.0 to 2.0)	0.3 (0.0 to 1.1)	4.4 (0.0 to 28.5)	3.9 (0.0 to 25.0)
Forb (%)	7.4 (3.0 to 15.0)	7.8 (3.0 to 15.8)	9.2 (2.0 to 20.0)	8.2 (1.9 to 14.0)
Graminoid (%)	59.2 (55.0 to 62.0)	60.8 (50.0 to 70.0)	55.6 (42.0 to 75.0)	57.4 (40.0 to 80.0)
Duff (%)	31.6 (28.0 to 36.0)	29.8 (19.0 to 37.5)	29.3 (20.0 to 39.0)	29.1 (15.0 to 38.0)
Bare soil (%)	1.0 (1.0 to 1.0)	1.3 (1.0 to 2.5)	1.6 (1.0 to 4.0)	1.4 (1.0 to 3.0)
Number of *R. hirta* flowers	2.0 (1.0 to 4.0)	3.2 (0.0 to 9.0)	2.7 (0.0. to 7.0)	1.9 (0.0 to 4.0)

of oviposition locations (IV = 38.0, p = 0.052). Species composition and abundance were dissimilar amongst locations in which various adult activities were supported (MRPP: all plant species: n = 39, T = -3.132, A = 0.041, p = 0.005; host food species: n = 39, T = -2.476, A = 0.046, p = 0.017; uncorrected scores for analysis of pairwise comparisons in Table S3). The wetland species *B. syz* and/or *Tri* spp. was not found in any adult activity plot.

The varied magnitudes of microhabitat characteristics amongst activity types are shown in Table 6. Soil moisture was relatively the highest in locations where oviposition and attempted oviposition were observed. Graminoids were tallest, and duff was deepest, in locations where attempted oviposition was observed. Locations associated with oviposition and attempted oviposition had lower average and

maximum shrub covers compared to locations associated with resting/basking and nectar feeding (albeit still only up to ~25% coverage). The density of *R. hirta* inflorescences was relatively highest at locations where oviposition or nectar feeding were observed.

Discussion

Adult flight

Adults flew most often in the prairie plant community, where various activities were also supported; forested and relatively wet communities were generally avoided (Fig. 1 and track lengths in plant communities). Tracks of individual adults

overlapped each other with a few adults flying in both main sections of prairie within the focal patch, suggesting some degree of affinity by adults for the prairie community type (as in male *C. palaemon* in Ravenscroft 1994; female *Maculinea rebeli* (Hirschke) (Lepidoptera: Lycaenidae) in Kőrösi et al. 2008). Adult tracks within prairie community types tended towards the tortuous side, typical of adult movements in higher-quality habitats containing required resources (Sei 2009; Fernández et al. 2016; Henault 2021; Henault and Westwood 2022), and likely in prairies elsewhere with similar habitat attributes. Specifically regarding oviposition, prairies may support relatively robust host plants which confer survival benefits to foraging larvae (Grundel et al. 1998).

Slopes in prairie patches

We found that physical slopes in prairie patches had a moisture gradient (theoretically consistent with Liu et al. 2020), and that as soil moisture increased the plant species also changed (Zalatnai and Körmöczi 2004). Our findings about soil moisture and texture attributes of a typical tall grass prairie patch in Manitoba, build on general wet-mesic tall grass prairie knowledge by Catling and Lafontaine (1986).

Interactions along a soil moisture gradient

Analysed vegetative and physical characteristics measured along transects and at locations which facilitated adult

activities, collectively suggest that adult habitat interactions are associated along a soil moisture gradient in Manitoba, summarised in Fig. 3. Given the limitations of our data, these are tentative conclusions open to further investigations.

The dissimilar plant composition amongst the various activities, as indicated by summary statistics, ISA and MRPP analyses, appears to be expressed gradually among the activity types. The varied magnitudes of vegetative and physical factors, suggest that specific combinations stimulate adults to conduct various activities in prairie communities. The relatively wet soil, close proximity to wetlands, tall graminoid height, low density of *R. hirta*, and differential associations with *Eleocharis* R. Brown spp. and *S. michauxianus* suggests that attempted oviposition occurs in a relatively wet section, mediated by its association with the mesic indicator *M. richardsonis* (at least for this female). The adult appears to have been initially attracted to this area, but was inadequately stimulated upon arrival to oviposit (Singer 1971; Rabasa 2005; Lund et al. 2019). The absence of wetland *B. syzigachne* and/or *Triglochin* spp. from all activity locations suggest that adults avoid wettest areas.

In Henault and Westwood (2022), locations where eggs were laid were differentiated by a combination of vegetative and physical attributes from under-stimulating locations (duff and graminoid heights, duff and shrub covers, humidity; host foods present at all types); we similarly observed relatively shallower duff and taller graminoids.
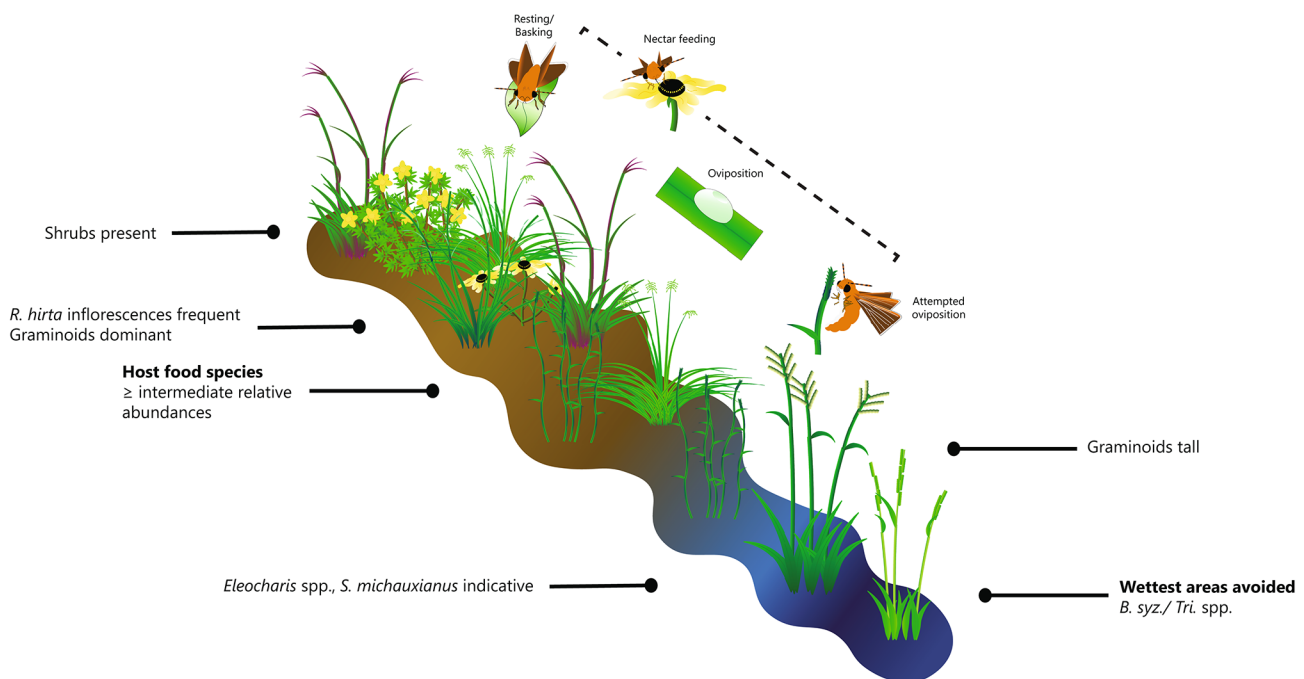

Fig. 3 Tentative conclusions about locations of adult activities along the soil moisture gradient (elevation declines to the right). We illustrate species typical of positions along the gradient, and note evaluative attributes between both foci of the study (dotted line adjacent to the nectaring illustration represents the range of the gradient used for this activity)

The fact that host food plants were not at their relatively highest abundance at oviposition locations (Table 5), further suggests an additional larval need for abiotic components in microhabitats. Oviposition occurred where relative counts of *M. richardsonis* were low, *S. heterolepis* were high, *S. scoparium* were low, and *A. gerardi* were high. The presence of all hosts at at least intermediate abundances from positions 1 to 5 (Table 2), and relatively wet soil, close proximity to wetlands, low graminoid height, high density of *R. hirta* inflorescences, and high graminoid cover suggests that mesic sections of the gradient most likely facilitate immature development. Oviposition likely occurs wherever suitable components of a microhabitat exist, whether physically at the midpoint along a slope or in shallow depressions/mounds amongst level areas at relatively high/low elevations.

The concentration of resting/basking activities at higher elevations, with relatively dry soil, low graminoid height, and high graminoid cover suggests that these activities occur at drier elevations, mediated by a low density of *R. hirta*. Adults which were resting/basking might have concentrated at the highest elevation to take advantage of optimal conditions. Perhaps, the funnelling of adults navigating between the two prairie lobes of this patch increased the concentration of adults, thus becoming a better vantage point to locate potential mates (instead of using elevated grassland ridges by several Hesperiidae; McCabe 1981; Scott 1986). Previous mating observations contrastingly occurred in visually mesic locations (Henault 2021; Henault and Westwood 2022).

Nectar feeding locations had characteristics representative of positions throughout the gradient, weighted slightly to the drier end: high variation in elevation and plant composition (including host plants), relatively dry soil and shrubs present, intermediate density of *R. hirta* and height of graminoids, and relatively low graminoid cover. During their flight period, adults initially nectared from several species and then used one species most often (*R. hirta*) midway through the end (*R. hirta* also most often used in Semmler 2010). In contrast to Semmler (2010) and Dupont Morozoff (2013), adults nectared from *Dasiphora fruticosa* (Linnaeus) Rydberg but not *S. ptarmicoides* or *P. vulgaris*. Mature *S. ptarmicoides* inflorescences were not prevalent until after the flight period of our study. We think that *O. poweshiek* feed opportunistically (e.g., *Packera* Linnaeus spp., *Glycyrrhiza lepidota* Pursh) based on phenological timing, use *R. hirta* during the majority of the flight period and if they fly later may use *S. ptarmicoides*. If *Lobelia* Linnaeus spp. – reported as a source in the general area by Catling and Lafontaine (1986) – was present where we observed *O. poweshiek*, we assume it would have been used if synchronised. *Parnassius mnemosyne* (Linnaeus) (Lepidoptera: Papilionidae) also feeds on nectar species available during its flight period, even though it prefers relatively few species (Szigeti et al. 2018). Butterflies may also respond to droughts by diversifying their nectar sources among those still in bloom (Depisch and Fiedler 2023). Although climate-induced asynchronization between butterfly emergence and nectar availability may lead to butterfly mortality (Hindle et al. 2015; Donoso et al. 2016; Patterson et al. 2020), *O. poweshiek*'s opportunistic feeding patterns appear to make it more resilient to this threat.

We explored the relative elevations, and inferred soil moisture, where each nectar species was used: *R. hirta*, *G. lepidota* and *D. fruticosa* were nectar sources at the relatively high elevation/dry section; *R. hirta*, *Packera* spp. and *Apocynum* Linnaeus spp. at intermediate/mesic section and only *Packera* spp. at low/wet section. Given the range of moisture gradient sections and nectar species associated with nectar feeding, adults likely take advantage of diverse sources while they fly in prairie communities. However, we cannot reject a hypothesis where adults preferentially fly to specific sections to feed from certain species.

Carterocephalus palaemon laid eggs, mated and nectared at different soil moistures along a slope (Ravenscroft 1994), similarly to how we suggest Poweshiek skipperling use habitat. Whereas ovipositing *C. palaemon* in mesic areas were possibly trying to avoid male harassment, *O. poweshiek* were likely influenced by a fitness benefit to larvae (the low density of *O. poweshiek* makes conspecific dispersal mechanisms unlikely, but at least possible if populations were historically dense). Relatively steep prairie slopes might cause the same moisture spectrum to occur over a shorter distance (e.g., slope 15 m vs. 100 m), enabling adults to conduct activities across the moisture spectrum more efficiently (e.g., moving from a resting/basking location to an oviposition location), perhaps facilitating an increased fitness. Additionally, host species which require different soil moistures would likely grow in closer proximity, causing larval foraging amongst shoots of various species to be less costly in terms of energy and predation (perhaps also produce unique microclimates; Henault and Westwood 2022).

Sites supporting relatively high adult abundances (from 2007 to 2016) appeared to contain a wider range of the local moisture gradient, as indicated by plant communities, compared to those supporting lower abundances (Henault 2017, 2021; Grantham et al. 2020). Agricultural activities and climate change could conceivably change local hydrology, causing a loss/gain of moisture sections used by adults (e.g., drying removes wet through mesic moisture sections). We assume adults would continue to conduct activities (e.g., oviposition), but possibly at lower quality locations. Would this decrease fitness, and partly explain recent population declines?
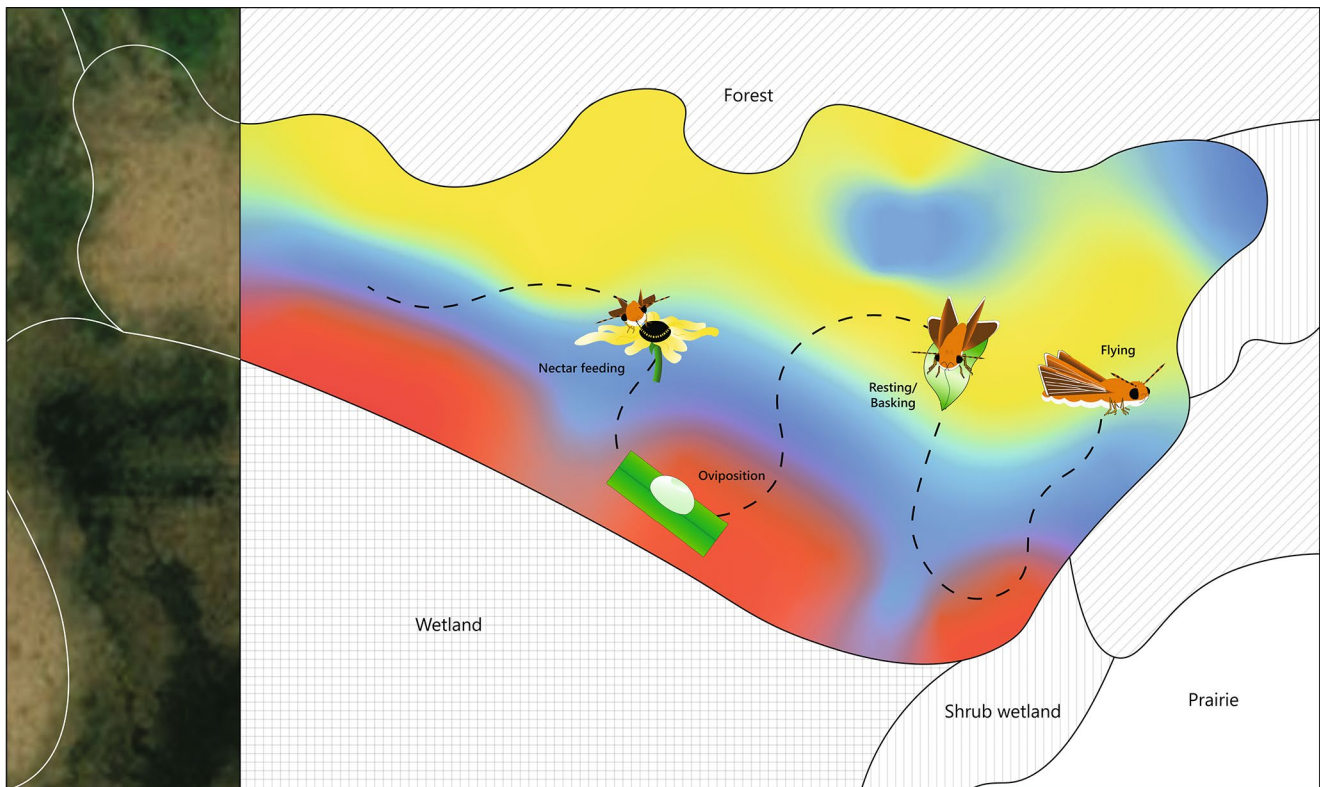
Fig. 4 A theoretical sequence in which an *O. poweshiek* might interact with a prairie patch. We used our findings and satellite imagery ("Imagery" by Maxar, Microsoft in ESRI Inc. (2021)) to outline plant communities, and estimate regions where each adult activity may occur along the soil moisture gradient (resting/basking=yellow, oviposition=red, nectar feeding=blue)

Future research

Given the limitations of our research, we encourage further studies to confirm or revise our tentative conclusions about associations of adult activities along a moisture gradient. Specifically, do particular soil moistures facilitate mating, are hill-topping or patrolling behaviours (Scott 1986) employed by Poweshiek skipperling and do changes in adult diet determine fitness and subsequent population size during the following year? How might localised environmental effects of adjacent habitats (trees/shrubs influencing temperature, moisture, snow accumulation, wind flow) and emigration-immigration processes amongst habitat patches influence adult within-patch habitat use? How might other Lepidopteran and neighbouring species in tall grass prairies interact along these gradients? To provide a focused research strategy, we suggest manipulation of the moisture gradient in a patch, subsequent comparisons of adult responses and documentation of population dynamics. Such research might generate strategies to remediate degraded habitats and respond to future changes which ensure supportive habitats for Poweshiek skipperling.

Implications for conservation

Visualising habitat interactions

We report the flight tendencies of Poweshiek skipperlings in relation to vegetative community types in Manitoba, Canada for the first time. Despite the scarcity of Poweshiek skipperlings during extensive survey efforts, we suggest a reasonable concept of how adults interact along a soil moisture gradient in prairie patches (Fig. 4). If our conclusions are confirmed with further research, then a combination of GIS techniques and field sampling could be used to map the soil moisture gradient in a site, before modelling facilitative regions for various behaviours (similar to Vanreusel and van Dyck 2007). This ecological understanding might prompt research of previously unconsidered aspects of *O. poweshiek* biology.

Applications for stewardship and reintroduction

Disturbances to maintain habitat using haying (Swengel 1996) and fire (Dupont-Morozoff et al. 2022) can be compatible with *O. poweshiek* survival, while the effects of grazing are unclear (Swengel 1998; Dupont-Morozoff

et al. 2022). The implementation of refugia may help to avoid destruction of individuals (Swengel and Swengel 2007, 2015). Using mapped Poweshiek skipperling habitat patches, a habitat steward might improve the effectiveness of disturbances by ensuring that portions of all facilitative regions are adequately disturbed, while rotating the location of refugia. Whether applying disturbances in the fall (when larval proximity to the ground might reduce chance of displacement; Henault and Westwood 2022) or near the flight period (depending on needs of other species-at-risk), this strategy might enable continued adult/immature activity followed by recolonisation (within year, or next). Additionally, we are unaware of techniques that act at the microhabitat-scale examined in our study, but we assume that stewardship strategies which use a variety of techniques (e.g., haying, burning, and/or other strategies conducted at varying spatial scales, intensities and frequencies) will be most likely to generate suitable habitat for *O. poweshiek* and other species-at-risk.

Additionally, organisations can evaluate the capacity of a candidate (re)introduction site to support all skipperling activities to possibly increase the likelihood that butterflies will survive for the long-term in Manitoba (incorporating new knowledge as needed).

Our research improves the understanding of adult habitat interactions, and is applicable during habitat stewardship and butterfly reintroductions. We hope that our research will help to fuel recovery of *Oarisma poweshiek*, as well as additional species-at-risk.

Declarations

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