Journal of Insect Conservation (2019) 23:635–649
https://doi.org/10.1007/s10841-019-00158-6

ORIGINAL PAPER

Life history and ecology of the endangered Poweshiek skipperling *Oarisma poweshiek* in Michigan prairie fens

Michael W. Belitz[1,3] · Michael J. Monfils[2] · David L. Cuthrell[2] · Anna K. Monfils[3]

Received: 12 December 2018 / Accepted: 29 April 2019 / Published online: 3 May 2019

Abstract
Poweshiek skipperling (*Oarisma poweshiek,* Lepidoptera: Hesperiidae) has experienced a range-wide decline resulting in six reported extant sites. Critical knowledge gaps related to Poweshiek skipperling adult behavior, phenology, habitat structure, and potential larval host plants are limiting the ability to manage this federally endangered species. To address these information needs, we conducted extensive surveys in the last remaining stronghold of four extant prairie fens in Michigan. We used point transect surveys to collect data on plant structure, and Poweshiek skipperling behavior and detection. We estimated Poweshiek skipperling abundance and modeled the influence of local vegetation on Poweshiek skipperling presence/absence. We estimated the abundance of adult Poweshiek skipperling in Michigan prairie fens to be 231 (95% CI 160–332), further highlighting the imperiled status of this species. Presence of Poweshiek skipperling along our transects was negatively associated with obstructive vegetation and positively associated with the availability of the nectar source *Dasiphora fruticosa*. Our observation data indicated females nectared most frequently on *D. fruticosa*, whereas males nectared most often on *Rudbeckia hirta*. Across the field season we observed 7 oviposition events on four plant species (*Muhlenbergia richardsonis*, *Muhlenbergia glomerata*, *Carex sterilis*, and *D. fruticosa*), three of which had no previous documentation as a possible host plant. Results from this study can be used to evaluate management decisions and inform both in situ and ex situ conservation efforts. It is critical to continue monitoring remaining populations, not only to assess conservation efforts, but also to discern the patterns and processes influencing species extinction.

Keywords Butterfly conservation · Distance sampling · Endangered species · Extinction · Hesperiidae · Prairie fen

Introduction

The Poweshiek skipperling (*Oarisma poweshiek,* Lepidoptera: Hesperiidae) is a historically common butterfly formerly found throughout the upper-Midwest in wet-mesic prairie, dry prairie, and prairie fen wetlands (Selby 2005). During surveys conducted in the mid-1990s, Poweshiek skipperling was the prairie specialist butterfly most often detected (Schlicht et al. 2009). Over the past 20 years, there has been a dramatic, range-wide decline in both the number and size of Poweshiek skipperling populations (Swengel et al. 2011; Rosengren and Andow 2016; Pogue et al. 2016). In 2014, the United States and Canada classified the Poweshiek skipperling as Federally Endangered (COSEWIC 2014; USFWS 2014). In 2016, surveyors observed a total of 104 Poweshiek skipperlings across four prairie fen sites in Michigan, USA, two individuals in one site in a wet-mesic prairie in Wisconsin, USA, and five individuals across two sites in the Tallgrass Prairie Preserve in Manitoba, CA (Partnership for Poweshiek skipperling conservation, unpublished data). Factors contributing to the decline remain unknown, but hypotheses include habitat destruction and fragmentation (Selby 2005; Cuthrell and Slaughter 2012), climate change (Landis et al. 2012; Delphey et al. 2016), pathogens (Selby 2005), unsuitable use of prescribed fire (Swengel 1996; Swengel and Swengel 2014), loss of genetic diversity

✉ Michael W. Belitz
mbelitz@ufl.edu

1 Florida Museum of Natural History, University of Florida, Dickinson Hall, Gainesville, FL 32611, USA

2 Michigan Natural Features Inventory, Michigan State University Extension, PO Box 13036, Lansing, MI 48901-3036, USA

3 Institute for Great Lakes Research and Department of Biology, Central Michigan University, 1455 Calumet Court, Biosciences 2401, Mount Pleasant, MI 48859, USA

(Saarinen et al. 2016), and insecticide use (Runquist and Heimpel 2017).

The Poweshiek skipperling is a small bodied (approximately 2.3–3.0 cm), univoltine butterfly that has a short adult flight period lasting from approximately late June to mid-July (Selby 2005). Primary nectar sources noted in the literature include forbs indicative of the tall grass prairie habitat (e.g., *Rudbeckia hirta*, *Solidago ptarmicoides*, and *Echinacea angustifolia*), though reports of nectar use vary across the distribution (Swengel and Swengel 1999; Semmler 2010; Cuthrell and Slaughter 2012). Female Poweshiek skipperlings have been documented to oviposit on a variety of grasses and sedges (e.g., *Sporobolus heterolepsis*, *Muhlenbergia richardsonis*, *Andropogon gerardii*, *Carex* sp.) with larvae and ovipositing females appearing to prefer fine, threadlike structures (McCabe and Post 1977; Borkin 1995; Selby 2005; Cuthrell and Slaughter 2012). However, survival rates of Poweshiek skipperling larvae on different host plants are unknown. The egg stage lasts approximately 9 days, after which larvae emerge and feed until initiating diapause as a fifth instar in the latter part of September. Feeding resumes in late March to early April (McAlpine 1972). Overwintering Poweshiek skipperling do not make shelters like many other skipper species and remain exposed at the base of grasses through winter, potentially leaving Poweshiek skipperling vulnerable to extreme weather conditions, dormant season fire, and other disturbances such as cattle grazing and pesticide drift (Runquist and Heimpel 2017). Poweshiek skipperling conservation efforts has intensified over the last 10 years (Dupont 2011; Delphey et al. 2016; Marquardt et al. 2018), but the numerous knowledge gaps that remain relative to Poweshiek skipperling biology and ecology, limit the potential success of both in situ and ex situ conservation efforts.

Baseline abundance estimates are necessary to study the species effectively through time and monitor management actions. Quantitative abundance estimates do not exist for Poweshiek skipperling. This is true for most of the butterfly species listed as threatened or endangered by the United States Fish and Wildlife Service (Henry and Anderson 2016). Estimating abundance of rare butterflies has numerous challenges including that the methods may injure butterflies, surveys may be too time consuming or cost prohibitive, and strict assumptions and sample size requirements may be difficult to reach (Nowicki et al. 2008; Henry and Anderson 2016; Kral et al. 2018a). Quantitative estimates of Poweshiek skipperling abundance can provide information on detection probability and statistically robust estimates that would inform evidence-based natural resource management.

The relative sex ratios of Poweshiek skipperling across a flight season have not been reported and this can be critical if individuals seeking mates have limited temporal overlap; this phenomenon has been documented in some univoltine butterflies (Calabrese and Fagan 2004). Asynchrony between male and female emergence, unbalanced sex ratios, and low density population numbers all have the potential to decrease reproductive success of butterflies by increasing the likelihood that females die unmated (Calabrese et al. 2008). Information on sex ratios across a flight season can help determine if overlap in males and female emergence is a critical issue for reproductive success, and further inform the timing of ongoing efforts to collect female Poweshiek skipperling for ex situ rearing and conservation.

Poweshiek skipperlings occupy only a small portion of available habitat in a prairie site, but factors contributing to these areas being occupied are poorly understood. Butterflies use a variety of cues to select habitat including physical and vegetative features, the availability and distribution of resources, landscape characteristics such as patch size and spatial arrangement, the visual apparency of host plants, and the microclimate (Wiklund 1984; Fourcade and Öckinger 2017; Szcodronski et al. 2018). Knowledge of Poweshiek skipperling specific habitat requirements within the prairie fen habitats they occupy will inform targeted management actions that encourage beneficial plant community composition and structure.

Although Poweshiek skipperlings have been observed nectaring on a variety of prairie forbs (Selby 2005), information regarding the nectar plant preference relative to nectar plant availability is unknown. In addition, any variation in nectar preferences between male and female Poweshiek skipperling has not been investigated. Sustaining, and effectively managing the preferred nectar resources in Poweshiek skipperling habitat can impact overall reproductive success and population viability of the species (Hill 1992; Boggs and Ross 1993; Schultz and Dlugosch 1999). Maintaining preferred nectar resources can be complex as demonstrated by the endangered Fender's blue butterfly (*Plebejus* [= *Icaricia*] *icarioides fender*), where females selected native nectar species, but males were observed nectaring more frequently on non-native species (Thomas and Schultz 2016). Examining nectar use in comparison to availability and determining nectar preferences of both male and female Poweshiek skipperling can be critical when determining management actions directed towards sustaining nectar resources.

Effort has been made to observe and record larval host plants for Poweshiek skipperling (Borkin 1995; Pointon 2015). Low population numbers and difficulty observing skipper larvae in the field have hindered recent attempts to closely observe this behavior and subsequently determine the degree of host plant dependence/preference or the factors influencing oviposition site selection. Butterfly conservation strategies are most successful when detailed knowledge of the target species' larval resources and microhabitat exist (Thomas et al. 2011). Determining the larval niche breadth of Poweshiek skipperling along a generalist-specialist continuum could directly impact ex situ rearing of larvae and influence in situ habitat management (Marquardt et al. 2018).

To address knowledge gaps in Poweshiek skipperling life history and ecology, we investigated Poweshiek skipperling abundance, prairie fen plant structure, and behavior in four Michigan prairie fens. In 2016, we conducted systematic field surveys of Poweshiek skipperling in all known extant Michigan populations, encompassing the duration of flight season from 10 days pre-emergence through post-flight observance of eggs. We optimized the research design to provide the greatest number and quality of targeted field observations to contribute data on abundance, habitat characteristics, behavior, and life cycle. Information from this study can inform ongoing ex situ and in situ conservation.

Methods

Study area

Studies were completed in four Michigan, USA prairie fens located in the Jackson Interlobate Regional Landscape Ecosystem (Albert 1995). In Michigan, all known observations of Poweshiek skipperling have occurred within prairie fen systems (Michigan Natural Features Inventory 2014). Prairie fens are calcareous ground water-fed wetland communities that are heterogenous, biodiverse, and distinguished from other fens by their tallgrass prairie components (Kost et al. 2007). Prairie fens are composed of four floristic zones: sedge meadow, inundated flat, calcareous groundwater seep, and wooded fen (Spieles et al. 1999), and Poweshiek skipperling are found only in a subset of sedge meadow regions. We use occupied Michigan prairie fens because they are the current global stronghold of the species, the vegetation and floristic zones have been well characterized, and we have comprehensive occurrence records in the occupied areas that have been georeferenced at high spatial resolution for this species since 2009 (Pogue et al. 2016).

The four prairie fen sites used in this study include all known extant Poweshiek skipperling populations in Michigan and vary in size from 7.75 to 91.72 hectares (Pogue et al. 2016). To protect sensitive Poweshiek skipperling habitat, we refer to specific prairie fens by the letters: A, B, C, and D. Site A has three geographically distinct areas occupied by Poweshiek skipperling (denoted Area 1, 2, 3). This is not necessary in the other three sites where there is a single occupied area within the associated prairie fen system. In Site A, Area 1 and 2 probably function as a meta-population due to their proximity, whereas Area 3 is functioning as a closed population as it occurs about 1 km from Area 2. Sites B, C, and D are closed populations due to the low dispersal capability of Poweshiek skipperling and because the matrix surrounding these sites consist of non-suitable forest, agriculture, and development. All extant sites are formally protected and managed by a local township, non-governmental conservation organization, or the Michigan Department of Natural Resources.

Transect locations

From 2009 to 2018, researchers conducted modified Pollard walks (Pollard and Yates 1993) targeting Poweshiek skipperling in the extant and formerly occupied Michigan sites (Pogue et al. 2016). GPS locations of Poweshiek skipperlings detected using these survey methods from 2009 to 2016 were mapped and a 60-m buffer was mapped around these Poweshiek skipperling observations to define the areas that our study transects would extend to in each occupied area (ArcMap 10.4.1; Esri 2015). We designated a paired set of transects to run lengthwise and crosswise through the occupied areas that consistently support the greatest number of Poweshiek skipperling observations (Fig. 1). A transect method was selected to limit the trampling of sensitive habitat and species. A 60-m buffer around 7 years of Poweshiek skipperling observations allowed us to account for the full extent of the possible population, areas of unoccupied but suitable habitat, and habitat heterogeneity. Placing transects that intersect areas of high Poweshiek skipperling observations increased the likelihood of collecting life history observations. Each transect was extended to the end of the 60-m buffer or to the prairie fen boundary determined using a GIS shapefile provided by the Michigan Natural Features Inventory and updated by Hackett et al. (2016). A total of 12 transects (six paired transects) in six occupied areas were defined and marked at 10-m increments for subsequent observations (Table 1).

Timing of Poweshiek skipperling observations

To determine the start date of our surveys, we examined prior occurrence records that were aggregated from federal agencies (e.g., U.S. Fish and Wildlife Service), natural heritage member programs (e.g., Michigan Natural Features Inventory), state conservation agencies (e.g., Minnesota Department of Natural Resources, South Dakota Game, Fish, and Parks), citizen scientists (e.g., iNaturalist, The Lepidopterists' Society), and natural history collections (Belitz et al. 2018). A total of 2043 records of Poweshiek skipperling occurrence in Michigan were aggregated, spanning from 1893 to the time of this study. Across all Michigan occurrence records, the earliest date an adult Poweshiek skipperling was observed in a season was June 22. The latest date in a season an adult Poweshiek skipperling was observed was July 20 (Belitz et al. 2018). We

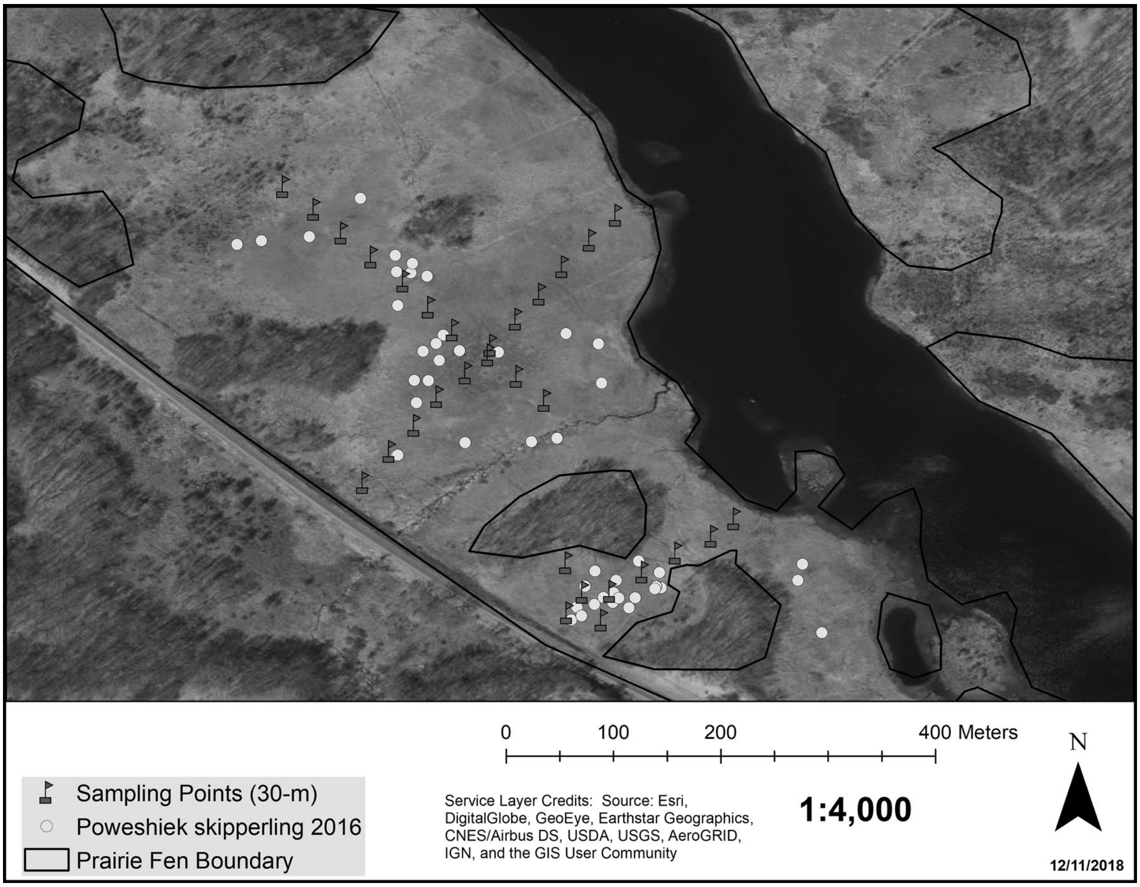

Fig. 1 Poweshiek skipperling prairie fen habitat, 2016 Poweshiek skipperling observations, and survey transects. Points represent 2016 Poweshiek skipperling observations and flags represent 30-m sampling points through the approximate lengthwise and crosswise areas of highest density. This prairie fen (Site A) has three geographically distinct occupied areas of Poweshiek skipperling densities. Here, we display two occupied areas and therefore, two paired transects

Table 1 Description of prairie fen sites in Michigan with extant Poweshiek skipperling populations

Site	Total area (ha)	Occupied area	Size of occupied area (ha)	30-m sampling points	Distance detections	Behavior recordings	First day of *O. poweshiek*	Last day of *O. poweshiek*
A	92.02	1	3.79	21	25	21	29-Jun	18-Jul
		2	1.64	9	35	20	28-Jun	15-Jul
		3	1.01	9	21	17	25-Jun	13-Jul
B	10.25	1	1.86	12	4	1	2-Jul	13-Jul
C	62.21	1	1.25	15	12	11	2-Jul	15-Jul[a]
D	7.76	1	0.75	5	0	3	1-Jul	9-Jul

Total prairie fen area, area of zone occupied by Poweshiek skipperling, and number of 30-m sampling points are listed for each site. The total number of distance detections, behavior recordings, and the first and last day of Poweshiek skipperling observation is listed

[a]A single Poweshiek skipperling was observed on July 22 outside of formal surveys during vegetation structure surveys

began surveys 10 days prior to the earliest Michigan observation of Poweshiek skipperling to ensure that we captured the beginning of the flight period, accounted for possible shifts related to climate fluctuations, and documented nectar plant phenology prior to and during the entire flight period. We conducted daily surveys throughout the flight period and concluded our surveys at each respective paired transect after three consecutive survey days resulted in no Poweshiek skipperling observations.

Survey schedule design

All six paired transects were surveyed daily, which required three surveyors working individually each day. Three combinations of survey blocks with multiple starting times were determined to ensure transects were surveyed evenly across the daily survey period of 9:00 am to 7:00 pm Eastern Time Zone. Schedules of surveyors were systematically shifted to establish even sampling of each transect by the surveyors. Surveys were not conducted if air temperature was below 15 °C, wind speed was above 25 km/h, or if it was raining. Daily surveys have the potential to disturb butterfly populations and their habitat and handling butterflies has been suggested to negatively impact individuals (Singer and Wedlake 1981; Murphy 1988). To minimize potential negative consequences, we did not capture or handle any Poweshiek skipperling during surveys and conducted surveys on only two transect lines per occupied area.

Nectar plant availability and vegetation structure

Surveyors estimated nectar plant availability by counting all potential "nectar units." Nectar units were defined as individual flowers for species with flowers either borne singly on the stem or with one flower open at a time. For plants with a compound inflorescence (e.g., *R. hirta*), a single open and receptive inflorescence was defined as the nectar unit (Thomas and Schultz 2016). For flowering shrubs (e.g., *Dasiphora fruticosa*), we counted each 0.5-m section of flowering plant as one nectar unit if one or more flowers in a 0.5-m section was open. We did not record plants that do not produce nectar (e.g., *Lysimachia quadriflora*).

Relative nectar plant availability within a 5-m semi-circle perpendicular to the transect line were estimated daily along transects at 10-m increments using a DAFOR scale (Rich et al. 2005). To visualize trends in nectar plant availability across the survey period, we also recorded daily absolute nectar plant availability; this was conducted on rotating subsets of transects examined across the field season. Observers recorded all species in flower within a 0.5-m continuous strip paralleling the transect. The 0.5-m continuous strip was located 1-m to the observer's right (Fig. 2). Each paired transect was sampled for absolute nectar plant availability at least once every 3 days and the total number of nectar units counted divided by the number of 30-m sampling points surveyed was calculated for each day. We do not equate nectar plant availability to standing nectar crop, as flowers of the same species may have non-random nectar amounts (Brink 1982) and different species have different nectar volumes and nectar sugar concentrations. Instead our nectar plant availability measures the abundance of flowers that could have nectar resources available and have the potential to serve as a nectar source for butterflies in search of nectar, regardless of if the nectar had been previously consumed by other pollinators.

Vegetation structure variables were measured after the end of the flight period at the starting point of each transect and at every 30-m sampling point thereafter (Fig. 2). End of season vegetation was measured to examine the potential influence of vegetation structure on Poweshiek skipperling within prairie fens. We measured the height of tallest vegetation within a radial distance of 5-m, percent of vegetation greater than 1.5 meters tall within a 30-m semi-circle (hereafter referred to as percent obstructive vegetation), and vertical vegetation density. We adapted a measure of vertical

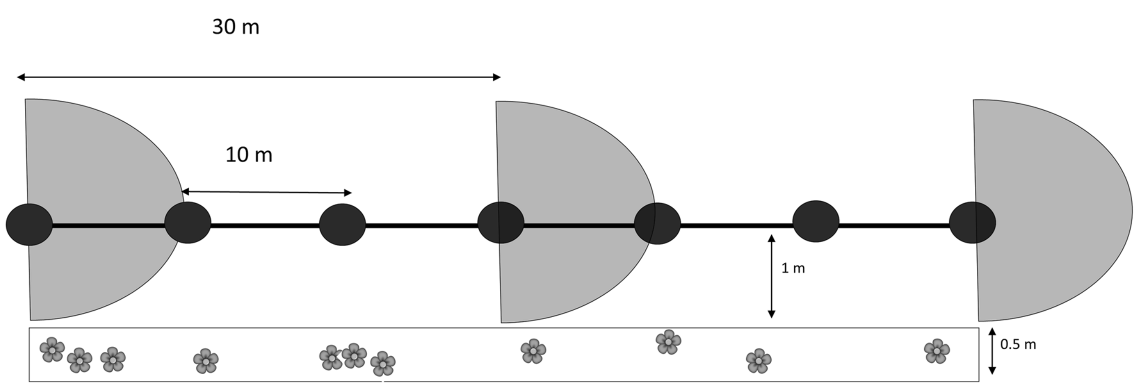

Fig. 2 Sampling methodology for each transect. Ten minute behavior recordings were completed at each sampling point (circle) if a Poweshiek skipperling was detected within 5-m of the observer. At each sampling point, DAFOR rank of nectar availability was also recorded for each plant species within a 5-m semi-circle. At the first sampling point and at every 30-m sampling point, time and wind speed were documented before beginning distance sampling where the distance of all Poweshiek skipperling detected within a semi-circle in front of the surveyor were recorded over a 60-s interval. The number of nectar units falling within a 0.5-m area, 1-m away from the transect was recorded across the entire transect. Vegetation structure variables were measured after the end of the flight period at the starting point of each transect and at every 30-m sampling point thereafter

vegetation density from Henry and Schultz (2013) with one observer holding a meter stick 30-m from the sampling point parallel to the ground at 1-m above the original main sampling point's ground level. A second observer at the original sampling point estimated the percent of the meter stick obscured by vegetation. Sykes et al. (1983) notes that visual percent cover estimates can vary greatly between observers, to address this bias a single observer made all vegetation structure estimates at all survey points.

Behavior surveys

Behavior surveys were conducted at the starting points and at every 10-m sampling point if a Poweshiek skipperling was observed within a 5-m radius. Surveyors remained on the transect and followed an individual Poweshiek skipperling through binoculars, recording behavior and distance moved at 1-min intervals for 10 min or until the individual butterfly was lost. Recorded behavior categories were perch, fly, nectar, mate, and oviposit. Plant species were noted when nectaring behavior was observed.

If we observed an oviposition event at any time while in prairie fens, we tied flagging tape at the base of the plant. Oviposition observations were not common and thus not restricted to transect surveys, during which we observed only two oviposition events. All ovipositing observations were also documented during Pollard walks and incidental field observation. When ovipositioning events were observed, we noted the time, location, and plant species of all oviposition events. We returned to and examined plants daily with Poweshiek skipperling eggs until the egg was no longer visible on the plant or over 30 days had passed.

Distance sampling

We used a point-count distance sampling method to estimate Poweshiek skipperling abundance (Buckland et al. 2001; Henry et al. 2015). Time and windspeed were noted at the starting and at every 30-m sampling point along the transect before beginning distance sampling. Wind speed (m/s) was recorded using a Weather Kestrel 3000 (Nielsen-Kellerman, Boothwyn, Pennsylvania, USA). Observers recorded distance from observer of all Poweshiek skipperling detected during a 60-s time block at the starting and at every 30-m sampling point along the transect (Fig. 2). We restricted distance detections to a semi-circle perpendicular to the observer to allow surveyors to track individual butterflies and reduce the likelihood of double counting individuals. We did not restrict the distance radius of observations to avoid pulling detections into the lowest specified distance and overestimating the number of target species (Simons et al. 2007).

There are three key assumptions to distance sampling (Thomas et al. 2010). The first assumption is that butterflies directly on the survey point must be detected with certainty. The distinctive white outlined veins and overscaling on the ventral wings of Poweshiek skipperling make them easier to detect than other small skippers. The second assumption is that distance measurements are exact. Our survey flags marking points every 10-m along the transect helped calibrate distances for surveyors. The third key assumption is that individuals are detected at their initial locations, with longer point count durations leading to the greater likelihood of individuals moving towards the observer where there is a greater probability of being detected. Our 60-s survey is much shorter than the 5-min survey recommended for birds (Rosenstock et al. 2002), or even the 2- or 3-min surveys recommended for highly active bird species (Cimprich 2009; Peak 2011). Still, 60-s surveys are longer than the 10-s surveys determined to be the optimal for Miami blue butterflies based on an analysis of the rate at which observers accumulated detections (Henry et al. 2015). We recognize that by having a 60-s survey, we may be counting Poweshiek skipperling that have moved towards the observer during the survey. However, density estimates may be less sensitive to count period length than encounter rates, because target species are recorded at greater distances from the recorder as time increases (Lee and Marsden 2008).

Analysis

Chi square independence tests

We used Chi square independence tests to compare independence of frequencies of observations across variables. All behavior events recorded at each minute interval were pooled from individual Poweshiek skipperling for use in analyses. Frequency of butterfly behavior (fly, nectar, perch), frequency of nectaring events per nectar source, and distance moved (binned at ≤ 2 m, 2–10 m, ≥ 10 m) were compared between males and females. We compared frequency of nectaring events per nectar source and sex ratios among three time periods (early, mid, and late) of equal length during the flight, which was based off the first and last day we observed Poweshiek skipperling during the transect surveys. If more than 20% of the contingency cells in any of our Chi square independence tests had expected values of <5, we used Fisher's exact tests. If we were conducting a Chi square independence test in a 2×2 contingency table, we used the Yates' correction to account for the tendency of Chi square tests to bias upwards in 2×2 contingency tables (Yates 1934).

Local habitat modeling

We used logistic regression to model the occurrence of Poweshiek skipperling at 30-m sampling points to determine the influence of local habitat structure on Poweshiek skipperling presence within prairie fens. Presence was defined as detecting at least one Poweshiek skipperling during distance sampling at any time during the flight period. Covariates used in our models were height of tallest vegetation within 5-m, DAFOR rank of black-eyed susan *Rudbeckia hirta*, DAFOR rank of shrubby cinquefoil *Dasiphora fruticosa*, percent obstructive vegetation, and vertical vegetation density. The DAFOR rank of *R. hirta* and *D. fruticosa* availability represents the DAFOR ranking observed on the day with the greatest number of Poweshiek skipperling individuals observed per occupied area and were treated as rank variables. When occupied areas had multiple days with the same greatest count, the earliest day with the high count was used. Percent obstructive vegetation and vertical vegetation density were arcsine square root transformed.

We used Spearman rank correlation analysis to determine multi-collinearity among potential model input covariates because we had rank variables and Spearman rank correlation allows for non-parametric testing. Variables that were highly correlated ($r \geq 0.60$) were not included in the same model. We found percent obstructive vegetation and tallest vegetation within 5 m to be positively correlated ($r = 0.68$).

We used an iterative modeling approach to examine a limited set of models and used Akaike's Information Criterion corrected for small sample sizes (AIC_c) to rank models (Burnham and Anderson 2002). We report all models considered to be competitive and their associated Akaike weights (w_i). We used delta $AIC_c \leq 2$ to differentiate top models. Models that were a subset of another model examined were not considered competitive if within delta $AIC_c \leq 2$.

Abundance estimates

We estimated density of Poweshiek skipperling incorporating imperfect detection using Program DISTANCE 7.1 to fit a function to our detection data that describes the observed decline in the number of detections as distance from observer increases (Thomas et al. 2010). This detection function is used to estimate detection probability and the effective detection radius at which we miss as many butterflies as we detect (Buckland et al. 2001). With these parameters, we can estimate density of Poweshiek skipperling. We did not detect 40–60 butterflies, the recommended sample size to accurately fit a detection function to the data (Buckland et al. 2001), at any individual occupied area. To overcome the limitation of low densities, we pooled data from all occupied areas on days where we detected a Poweshiek skipperling in the occupied area during distance sampling. Pooling data across space and time can be used if detection probability does not vary across sites or across the flight period (Henry et al. 2015; Henry and Anderson 2016; Kral et al. 2018b). This is a reasonable assumption as the habitat surveyed across these sites are within the sedge meadow floristic zones of prairie fens, all consisting of similar vegetation. To avoid potential biases due to spatial-autocorrelation, we used a random number generator to remove detection data of one of the two 30-m sampling points that occurred closest to where the transects intersected.

We compared three key function and adjustment combinations to determine our best detection function and adjustment combination: half-normal model with cosine adjustment, half-normal model with hermite polynomial adjustment, and hazard rate model with simple polynomial adjustment (Thomas et al. 2010). We used AIC_c to rank models (Burnham and Anderson 2002). After selecting the function and adjustment combination with the lowest AIC_c value, we included the following covariates into our modeling framework: vertical vegetation density, percent obstructive vegetation, wind speed, tallest vegetation within 5-m, time of day, and observer. Each covariate was added to our detection function individually. The model with the lowest AIC_c value was considered the best model.

Our best model was applied to estimate the density and abundance of Poweshiek skipperling in Michigan prairie fens. Program DISTANCE calculates density by dividing the number of detections by the total area surveyed (Thomas et al. 2010). In point transect sampling, where survey points are a full circle, the area surveyed is calculated as $k\pi w^2$, where k is the number of survey points and w is the effective detection radius (Buckland et al. 2001). Our surveys were conducted as semi-circles, and hence, we used a multiplier of two in program DISTANCE to scale our final density estimates (Thomas et al. 2010; Henry et al. 2015). Density per hectare was multiplied by our estimated total area of prairie fen currently occupied by Poweshiek skipperling. Total area of habitat currently occupied by Poweshiek skipperling was estimated by summing the total area of a 30-m buffer around all 2016 Poweshiek skipperling georeferenced observations in Michigan prairie fens.

Results

From June 12 to July 21, 2017 we surveyed a total of 2355 30-m transect sampling points over ~ 474 total person hours. The first day a Poweshiek skipperling was detected occurred on June 25, 2017, and the last day an individual was observed during surveys was July 18, 2017 (Table 1). The most Poweshiek skipperlings were detected across all sites on July 3. The day the first Poweshiek skipperling was observed varied across sites and the length of the flight spanned from 8 (Site D) to 19 days (Site A, Area 1; Table 1). Formal transects were stopped 3 days after the last Poweshiek skipperling was observed per occupied area, but a single female Poweshiek skipperling was observed on July 22 during vegetation structure surveys at Site C. Across all four sites, we detected 97 Poweshiek skipperling individuals during distance sampling and gathered behavior recordings from 73 individual Poweshiek skipperling that resulted in 371 behaviors documented at 1 min intervals. At Site A (Areas 1, 2 and 3), 83.5% of distance detections and 79.4% of behavior recordings were documented, despite only 54.9% of sampling points being at this site (Table 1).

Nectar units

The most abundant potential nectar plant was *D. fruticosa* with 521 nectar units recorded across all sites on the day during the flight period with the greatest nectar unit count (Fig. 3). The plant with the second most recorded nectar units was *Rudbeckia hirta* (103 nectar units). The number of nectar units per 30-m sampling point of *R. hirta* increased from 0.26 to 4.80 across the flight period. The number of nectar units per 30-m sampling point of *D. fruticosa* increased from 5.40 to 19.50 across the flight period (Fig. 4).

Local habitat modeling

Over the 2017 season, we detected Poweshiek skipperling at 34 of the 71 survey points (30-m) during distance sampling. We examined 7 competing logistic regression models. The model with the lowest AIC_c score had 50% percent model weight and included the covariates percent obstructive vegetation and DAFOR ranking of *D. fruticosa* (Table 2). In this model, presence of Poweshiek skipperling within a prairie fen was negatively correlated with the percent of obstructive vegetation and positively correlated with the nectar availability of *D. fruticosa*. Amount of obstructive vegetation was the covariate with highest slope coefficient (Table 3).

Behavior observations

Of the 73 total behavior recordings, 53% percent of the individuals we detected were male, 22% were females, and 25% were not able to be sexed. The proportions of adult behaviors spent perched, nectaring, and flying were not significantly different between males and females ($X_2^2 = 1.7, p = 0.47$), but males moved significantly greater distances than females during 1-min intervals ($X_2^2 = 12.9, p < 0.01$; Fig. 5).

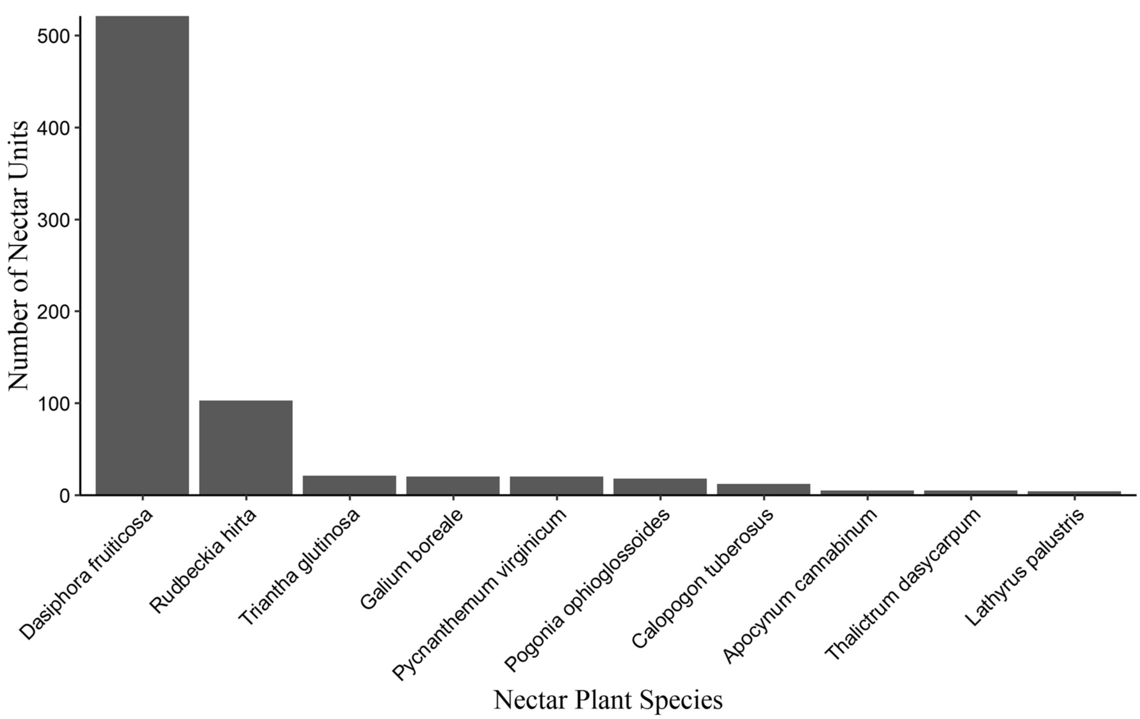

Fig. 3 Maximum number of nectar units observed on a single day across all sites during the flight period (June 25–July 18). Nectar plants with less than 10 nectar units recorded over the flight period are not included in this figure

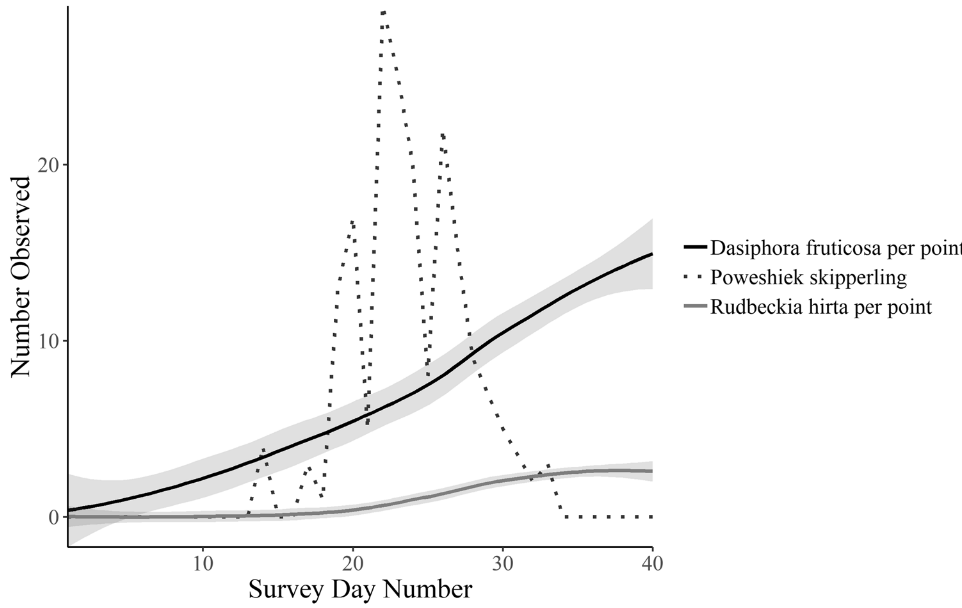

Fig. 4 Nectar units per 30-m sampling point and total number of Poweshiek skipperling observed per day across the survey period for all occupied areas. The first Poweshiek skipperling observation was on June 25 and the final Poweshiek skipperling observation was on July 18, with peak counts occurring on July 3. *Dasiphora fruticosa* and *Rudbeckia hirta* per 30-m distance sampling point were smoothed using LOESS curve fitting (local polynomial regression) with 95% confidence intervals denoted

Table 2 Competing models predicting Poweshiek skipperling presence/absence at sampling points in Michigan prairie fens

Models	# par	AIC$_c$	Δ AIC$_c$	w_i
DAFR + percent obstructive veg	3	96.7	0	0.497
DAFR + tallest veg	3	99.1	2.4	0.147
RUHI + percent obstructive veg	3	99.6	2.9	0.115
RUHI + tallest veg	3	100.2	3.5	0.088
Null	1	100.4	3.7	0.080
DAFR + vertical veg density	3	101.3	4.6	0.050
RUHI + vertical veg density	3	102.9	6.2	0.022

RUHI is an abbreviation for DAFOR rank of nectar availability of *Rudbeckia hirta* on the day with the most Poweshiek skipperling observed per occupied area. DAFR is an abbreviation for DAFOR rank of nectar availability of *Dasiphora fruticosa* on the day with the most Poweshiek skipperling observed per occupied area. Models are ranked based on the difference from the top model in Akaike's Information Criterion corrected for small sample sizes (Δ AIC$_c$) and Akaike weight (w_i)

Table 3 Summary of parameters in the top model (Table 2) for predicting Poweshiek skipperling presence in Michigan prairie fens

Covariate	Coefficient estimate	SE	Pr(> |z|)
(Intercept)	−0.05	0.53	0.93
DAFR	0.60	0.33	0.07
Percent obstructive veg	−2.80	1.34	0.04

DAFR is an abbreviation for DAFOR rank of nectar availability of *Dasiphora fruticosa* on the day with the highest Poweshiek skipperling counts per occupied area

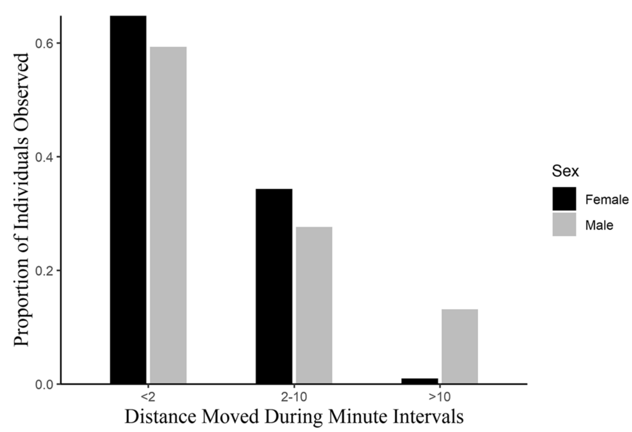

Fig. 5 Distance moved during minute observational intervals for adult Poweshiek skipperling butterflies. Male (n = 221) and female (n = 105) flight distances observed over 1-min intervals differed significantly ($X_2^2 = 12.9, p < 0.01$)

In total, we observed 131 nectaring events from 30 individuals (16 males, 6 females, 8 unknown sex). Of these events, 67% were observed on *R. hirta* and 33% were observed on *D. fruticosa.* Although there were other nectar sources along the transects, *R. hirta* and *D. fruticosa* were the only two species with documented Poweshiek skipperling nectaring during our behavior recordings. We did infrequently observe nectaring on *Triantha glutinosa*, but these observations were not during formal behavior recordings. Males were most frequently observed on *R. hirta* and females on *D. fruticosa* ($X_1^2 = 18.9$ with Yates' correction, $p < 0.01$; Fig. 6). Using pooled nectar events for males, females, and unknown sex butterflies, we found nectar use to be significantly different across the three equal flight periods

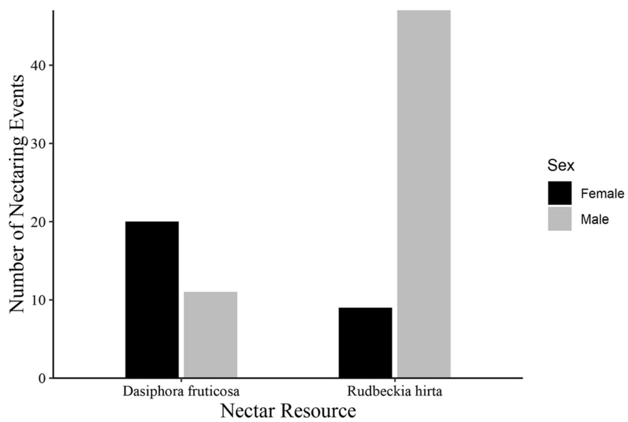

Fig. 6 Number of nectaring events of adult Poweshiek skipperling observed on *Dasiphora fruticosa* and *Rudbeckia hirta.* Males ($n = 58$) and females ($n = 29$) differed significantly in nectar preference ($X_1^2 = 18.9$ with Yates′ correction, $p < 0.01$)

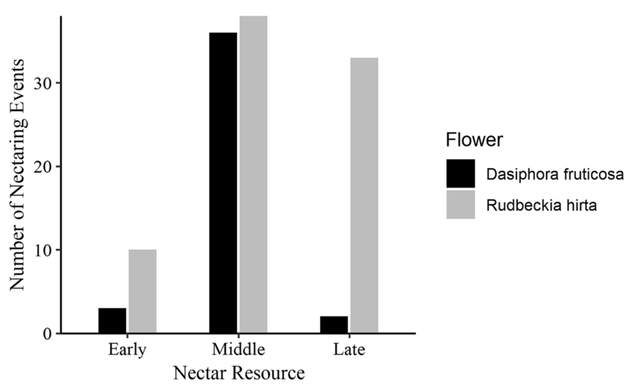

Fig. 7 Number of nectaring events ($n = 117$) of adult Poweshiek skipperling observed on *Dasiphora fruticosa* and *Rudbeckia hirta* across three equal flight periods based off the first and last day Poweshiek skipperling were observed during transect surveys. Poweshiek skipperling use of *D. fruticosa* and *R. hirta* differed significantly across the three time periods ($X_2^2 = 20.3, p < 0.01$), with the highest proportion of nectaring events on *R. hirta* occurring in the late time period coinciding with the time *R. hirta* became available and increased in numbers

($X_2^2 = 20.3, p < 0.01$; Fig. 7), with the greatest proportion of nectar use observations occurring on *R. hirta* in the latest flight period. We did not find a difference in the observed sex ratio over the flight period, with our observed sex ratio consistently remaining around 2 males for every female detected (Fisher′s exact test, $p = 1$).

Oviposition observations

Throughout our 2017 field surveys, Poweshiek skipperling were observed to lay seven eggs on four plant species (*Carex sterilis* [n = 4], *Muhlenbergia glomerata* [n = 1], *Muhlenbergia richardsonis* [n = 1], and *Dasiphora fruticosa* [n = 1]). Oviposition events were observed between the times of 1145 and 1614. Only two of these seven observations occurred during our standardized transect surveys and these eggs were laid on *M. richardsonis* and *C. sterilis*. One oviposition event on *C. sterilis* was observed during Pollard surveys conducted at sites following the methods described in Pogue et al. (2016). The observation of the oviposition event on *D. fruticosa* came from an unmanned camera recording a female that was released after spending 72 h in captivity to collect eggs for an ex situ rearing program spearheaded by the U.S. Fish and Wildlife Service and Minnesota Zoo (DL Cuthrell, personal communication). The remaining three oviposition events were observed directly by DL Cuthrell on *C. sterilis* and *M. glomerata* who noted the events when observing post-release females returned to the field that had also been held in captivity to collect eggs.

Fresh eggs were a pale-yellow green in color and darkened over time. Presence of herbivory was observed on the *M. richardsonis* plant and one of the *C. sterilis* plants that had a Poweshiek skipperling egg. The fate of the egg resulting from the oviposition event documented with a digital video recording was unknown, as the plant was not flagged. The fate of another egg laid on *C. sterilis* is unknown as the flagging on this plant was lost. One egg laid on *C. sterilis* was observed for over a month. This egg, laid on July 1, turned dark brown and was collected on August 7, 2017. We examined the egg under a dissecting scope, where we observed a hole in the egg, a possible sign of a parasitoid. One egg laid on *C. sterilis* was no longer observable after 3 days. A separate egg laid on *M. glomerata* was absent 11 days after the egg was laid.

Abundance estimate

After removing spatially autocorrelated distance observations, we were left with 81 detections. The detection function with the lowest AIC_c was the hazard-rate model with a

Table 4 Model ranking of Poweshiek skipperling detection functions

Model	# par	AIC_c	Δ AIC_c	w_i
Observer	5	519.3	0	0.952
Null	2	525.5	6.20	0.043
Wind speed	3	532.8	13.54	0.001
Tall vegetation	3	532.8	13.54	0.001
Vertical vegetation density	3	532.9	13.56	0.001
Percent obstructive vegetation	3	533.0	13.68	0.001
Time	3	533.1	13.85	0.001

Models are ranked based on the difference from the top model in Akaike's Information Criterion corrected for small sample sizes (Δ AIC_c) and Akaike weight (w_i)

simple polynomial adjustment. Wind speed, time of survey, or vegetation structure covariates did not improve our detection function models. The detection function model with the lowest AIC_c value included observer as a covariate, indicating detection differences among observers (Table 4). Using this best model, we estimated density to be 22.4 (95% CI 15.5–32.2) Poweshiek skipperling per hectare. We estimated detection probability to be 40.7% and the effective detection radius to be 7.9 m (95% CI 7.0–8.9 m). We calculated a total of 10.3 hectares of suitable habitat. Given this total area, we estimated the abundance of adult Poweshiek skipperling in Michigan during 2017 to be 231 (95% CI 160–332).

Discussion

We determined an abundance estimate of 231 adult Poweshiek skipperlings present in Michigan prairie fens, the last remaining stronghold for this species. This estimate confirms the imperiled status of this butterfly and further highlights the need for federal protections. When the data used in abundance estimates are parsed by prairie fen, it is notable that over 80% of distance detections were from a single site (A). Sites B, C, and D have critically low numbers of observed Poweshiek skipperlings (see Table 1). Four Poweshiek skipperlings were detected during distance sampling at Site B, 12 were detected at Site C, and zero were detected at Site D. Sites B, C, and D are highly vulnerable to extirpation. Within these sites, Poweshiek skipperlings currently occupy only small areas of these prairie fens. Efforts to maintain all four sites must remain a management priority for the survival of this species. Sustaining multiple occupied areas can increase the probability of persistence by spreading risk of stochastic events to multiple independent sites (Schultz and Crone 2015). Management and monitoring efforts at all sites need to be assessed annually to determine areas of highest need and prioritize urgent management measures to address critically low numbers. With such low numbers, management success evaluated in terms of total observed Poweshiek annually may not provide the sensitivity needed to evaluate management actions, requiring proxies for ecological integrity of the sites and extensive, consistent monitoring. Focused monitoring pre- and post-management would assist in detangling the influence of management, annual weather fluctuations, and population size effects on population dynamics.

During our behavior observations, we detected over twice as many males as females. This sex ratio was consistent across the 2017 season, suggesting synchrony between male and female emergence. Male biased sex ratios are commonly reported in studies of butterflies (Vlasanek et al. 2009; Seixas et al. 2017). Behavioral differences have been suggested as one reason for why male biased sex ratios are observed in the field (Ehrlich and Gilbert 1973; Seixas et al. 2017). Our results are consistent with these studies as male Poweshiek skipperling were observed flying greater distances than females and were frequently observed patrolling habitat (likely for females). This male specific behavior likely influenced our sex ratio by making these males more likely to be detected.

Our logistic regression models indicate that adult Poweshiek skipperling are less likely to be present in areas with vegetation stands greater than 1.5 m tall (obstructive vegetation). The models also indicate Poweshiek skipperling are more likely to be present in areas with high numbers of flowering *Dasiphora fruticosa*. *Dasiphora fruticosa*, is a low-lying shrubby plant that serves as an indicator species for prairie fens and the wet meadow floristic zones Poweshiek skipperlings occupy. This native plant is also the preferred nectaring plant for female Poweshiek skipperlings. These results are consistent with previous studies that suggest that flower density influences abundance of *Lycaena virgaurea* and *Maniola jurtina* (Schneider et al. 2003) and presence of *Lycaena hermes* (Marschalek and Deutschmann 2008).

In the prairie fens surveyed, obstructive vegetation was primarily composed of invasive woody plants (e.g., *Frangula alnus*) or cattails (*Typha* spp.), both of which occur in degraded prairie fens, tend to form monocultures, and threaten native plant biodiversity (Landis et al. 2012). Woody encroachment and invasive obstructive vegetation threaten the native prairie fen flora and can reduce the quantity and quality of Poweshiek skipperling habitat. In addition, the obstructive vegetation has the potential to act as intra-fen barriers to Poweshiek skipperling dispersal. Poweshiek skipperlings have low flight heights and specific habitat requirements, so individuals are unlikely to traverse areas with tall vegetation. If unchecked, obstructive vegetation can fragment the occupied areas of the prairie fen and result in progressively smaller and more isolated populated patches. Habitat deterioration is suggested as the driver of range retraction in the calcareous fen specialist butterfly, *Coenonympha tullia* (Weking et al. 2013). Encroachment by woody species is widely recognized as a conservation concern to grassland ecosystems and their specialized flora and fauna (WallisDeVries et al. 2002; Schultz et al. 2011). Management for native non-invasive species and removal of invasive obstructive vegetation can lead to higher quality suitable habitat and maintain open micro-habitat structure, potentially leading to higher Poweshiek skipperling densities (Brückmann et al. 2010). In Michigan prairie fens, prescribed fire and hand cutting followed by herbicide application are the common techniques used to control invasive shrubs. Swengel (1996) and Swengel and Swengel (2014) note concerns with potentially negative effects of fire on Poweshiek skipperling. More study is needed to understand the costs and benefits of prescribed fire and cutting to plant communities and Poweshiek skipperling populations in prairie fen ecosystems.

Maintaining nectar resources is important to endangered butterfly conservation, because nectar shortages may reduce adult longevity, decrease fecundity and increase emigration from breeding sites (Jervis et al. 2005). Throughout the range, Poweshiek skipperling have been documented nectaring on a variety of prairie forbs (Swengel and Swengel 1999; Selby 2005; Cuthrell and Slaughter 2012). During our study, Poweshiek skipperling were observed nectaring on the two most frequently encountered plants with available nectar (*D. fruticosa* and *R. hirta*). Females were observed nectaring more frequently on *D. fruticosa*, whereas males were observed nectaring more frequently on *R. hirta*. Differences in butterfly foraging between male and female butterflies has been documented in a variety of species (Rusterholz Rusterholtz and Erhardt 2000; Severns et al. 2006; Bakowski et al. 2010; Thomas and Schultz 2016). Suggested explanations for sex-specific feeding include differences in foraging behavior (Rusterholtz and Erhardt 2000) and differential nutritional needs (Boggs 1997). For example, males may select for higher sugar nectar to support greater flight activity, while females may select for nectar higher in amino acid concentration for egg production (Ehl et al. 2018). Structurally, *R. hirta* and *D. fruticosa* differ in prairie fens. *R. hirta* flowers emerge above associated small graminoid species, potentially providing a perch for males to observe competing males and receptive females when nectaring. Conversely, *D. fruticosa* flowers sprawl low among graminoid species and can provide some coverage for nectaring females close to their potential oviposition plants. Similar observations have been made in *Parnassius apollo* where males flying in search of females seek flowers on top of long stems, while females select for flowers near the ground (Baz 2002).

Natural habitat succession and invasion of exotic species can diminish both larval and adult butterfly resources (Severns and Warren 2008). For example, Mardon skippers (*Polites mardon*) in the Puget prairies of Washington state selected oviposition sites in sparsely vegetated areas of the prairie (Henry and Schultz 2013). In Michigan prairie fens, successional changes in plant communities may have led to decline of nectar species abundance and even local extinctions of a previously documented nectar source. In 1970, Poweshiek skipperling were observed preferentially nectaring on *Lobelia spicata* and secondarily on *R. hirta* (Holzman 1972). We did not detect *Lobelia spicata* along our transects and it was not detected during intensive vegetation surveys conducted across 29 Michigan prairie fens in the Jackson Interlobate Regional Landscape Ecoregion and adjacent Ann Arbor Moraine Ecoregion (Hackett et al. 2016). This regional survey included surveys conducted across the growing season in the same prairie fen where Holzman's observations were initially made.

Poweshiek skipperlings have been observed ovipositing on a variety of plant species and researchers have proposed that larvae may display generalist feeding ecology (Selby 2005; Saarinen et al. 2016). In Michigan, a total of only seven oviposition events are documented, one on *Eleocharis elliptica* (Holzman 1972) and six on *Muhlenbergia richardsonis* (Pointon 2015). In the 2017 field season, we recorded seven oviposition events on four plant species, three of which (*Muhlenbergia glomerata*, *Carex sterilis*, and *D. fruticosa*) were not previously suggested as possible host plants. All four of these plants are wetland specific plants (Reznicek et al. 2011), further suggesting that Poweshiek skipperling populations are restricted to prairie fens in Michigan. Our oviposition observations on the *C. sterilis*, *M. glomerata*, and *M. richardsonis* are consistent with prior suggestions that Poweshiek skipperling prefer feeding on very fine, threadlike structures (Selby 2005). In butterflies, conservation of declining species often hinges on understanding the optimum larval resources and microhabitat (Thomas et al. 2009, 2011; Henry and Schultz 2013). A female's oviposition decision can have vital consequences for her reproductive fitness, by affecting the embryo survival, juvenile performance and offspring phenotype (Refsnider and Janzen 2010). Continued focused observations of oviposition are needed to determine the drivers of female oviposition selection and the microhabitat requirements of larvae.

We were able to establish a baseline abundance estimate for Poweshiek skipperling, which is a critical first step in evaluating the population status and establishing and evaluating conservation goals. Results from this study inform our understanding of Poweshiek skipperling habitat requirements and contribute towards a better understanding of their ecology. Measuring success of management will involve tracking population estimates over time, and our study demonstrates a need to control for observer differences through survey design, observer training, and modeling approaches. Data from this study, and research at extant sites, is important and timely for evaluating potential drivers of extinction, informing ex situ and in situ conservation efforts by filling gaps in our understanding of the Poweshiek skipperling life cycle, providing baseline habitat and population metrics to develop range-wide conservation strategies, and establishing protocols and measurable management outcomes that can be used in developing and implementing an effective management framework.

Acknowledgements T Gehring provided valuable editorial suggestions and G Forthaus assisted with data curation. We thank our reviewers for comments that improved the manuscript. We thank B Cahill, R Hackett, C Pogue, L Hendrick, K Finch, M Schott, and M Parr for conducting field surveys. Additionally, we thank the landowners, including the Michigan Nature Association, Oakland County, Springfield Township, Michigan Department of Natural Resources, and private landowners, for allowing us access to their properties for survey activities. Finally, we are grateful to the members of the Partnership for Poweshiek skipperling Conservation for their continued long-term dedication to this species. Research funding was provided by the Great Lakes Restoration Initiative through the U.S. Fish and Wildlife Service's Endangered Species Program, Central Michigan University—College of Science and Engineering's Dean's Research Assistantship, and Central Michigan University Biology Department—Marion Whitney Summer Graduate Scholarship. The findings and conclusions in this project are those of the authors and do not necessarily represent the views of the U.S. Fish and Wildlife Service or the U.S. Environmental Protection Agency. Funding also came from the National Science Foundation award DBI-1730526 to develop educational materials for biodiversity data literacy (https://www.biodiversityliteracy.com/poweshiek-skipperling). This paper is contribution number 125 of the Central Michigan University Institute for Great Lakes Research.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Informed consent This article does not contain any studies with human participants.

Research involving human participants and/or animals This article does not contain any studies where animals were manipulated. All data were collected by observations and researchers did not handle animals. We had an incidental take permit through the U.S. Fish and Wildlife service, which outlined how we would minimize and mitigate authorized incidental take of *Oarisma poweshiek*.

References

Albert DA (1995) Regional landscape ecosystems of Michigan, Minnesota, and Wisconsin: a working map and classification. In: Gen. Tech. Rep. NC-178 U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station, Northern Prairie Wildlife Research Center Online, St. Paul; Jamestown

Bakowski M, Filipiak A, Fric Z (2010) Foraging behaviour and nectar use in adult large copper butterflies, *Lycaena dispar* (Lepidoptera: Lycaenidae). Entomol Fennica 21:49–57

Baz A (2002) Nectar plant sources for threatened Apollo butterfly (*Parnassius apollo* L. 1758) in population of central Spain. Biol Conserv 103:277

Belitz MW, Hendrick LK, Monfils MJ, Cuthrell DL, Marshall CJ, Kawahara AY, Cobb NS, Zaspel JM, Horton AM, Huber SL, Warren AD, Forthaus GA, Monfils AK (2018) Aggregated occurrence records of the federally endangered Poweshiek skipperling (*Oarisma poweshiek*). Biodivers Data J 6:e29081

Boggs CL (1997) Reproductive allocation from reserves and income in butterfly species with differing adult diets. Ecology 78:181–191

Boggs CL, Ross CL (1993) The effect of adult food limitation on life history traits in *Speyeria Mormonia* (Lepidoptera: Nymphalidae). Ecology 74:433–441

Borkin SS (1995) 1994 Ecological studies of the Poweshiek skipper (*Oarisma poweshiek*) in Wisconsin. Milwaukee Public Museum, Milwaukee, Wisconsin. http://www.fwspubs.org/doi/suppl/10.3996/052015-JFWM-049/suppl_file/052015-jfwm-049.s1.pdf?code=ufws-site. Accessed 23 May 2018

Brink D (1982) A bonanza-blank pollinator reward schedule in *Delphinium nelsonii* (Ranunculaceae). Oecologia 52:292–294

Brückmann SV, Krauss J, Steffan-Dewenter I (2010) Butterfly and plant specialists suffer from reduced connectivity in fragmented landscapes. J Appl Ecol 47:799–809

Buckland ST, Anderson DR, Burnham KP, Laake JL, Borchers DL, Thomas L (2001) Introduction to distance sampling: estimating abundance of biological populations. Oxford University Press, Oxford

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. Springer, New York

Calabrese JM, Fagan WF (2004) Lost in time, lonely, and single: reproductive asynchrony and the Allee effect. Am Nat 164:25–37

Calabrese JM, Ries L, Stephen F, Debinski DM, Auckland JN, Roland J, William F (2008) Reproductive asynchrony in natural butterfly populations and its consequences for female matelessness. J Anim Ecol 77:746–756

Cimprich DA (2009) Effect of count duration on abundance estimates of black-capped Vireos. J Field Ornithol 80:94–100

COSEWIC (2014) Assessment and the status report on the Poweshiek skipperling *Oarisma poweshiek* in Canada. https://www.registrelep-sararegistry.gc.ca/virtual_sara/files/cosewic/sr_Poweshiek%20Skipperling_2014_e.pdf. Accessed 23 May 2018

Cuthrell DL, Slaughter SL (2012) Special animal abstract for *Oarisma poweshiek* (Poweshiek skipperling). Michigan natural features inventory, Lansing. https://mnfi.anr.msu.edu/abstracts/zoology/Oarisma_poweshiek.pdf. Accessed 6 Mar 2018

Delphey P, Runquist E, Harris T, Nordmeyer C, Smith T, Traylor-Hozer K, Miller PS (2016) Poweshiek skipperling and Dakota skipper: Ex situ feasibility assessment and planning workshop. IUCN/SSC Conservation Breeding Specialist Group, Apple Valley. https://portals.iucn.org/library/sites/library/files/documents/Rep-2016-004.pdf. Accessed 23 May 2018

Dupont J (2011) Minutes from the Poweshiek skipperling workshop, March 24 and 25, Winnipeg. http://www.fwspubs.org/doi/suppl/10.3996/052015-JFWM-049/suppl_file/052015-jfwm-049.s6.pdf. Accessed 23 May 2018

Ehl S, Hostert K, Korsch J, Gros P, Schmitt T (2018) Sexual dimorphism in the alpine butterflies *Boloria pales* and *Boloria napaea*: differences in movement and foraging behavior (Lepidoptera: Nymphalidae). Insect Sci 25:1089–1101

Ehrlich PR, Gilbert LE (1973) Population structure and dynamics of the tropical butterfly *Heliconius ethilla*. Biotropica 5:69–82

Fourcade Y, Öckinger E (2017) Host plant density and patch isolation drive occupancy and abundance at a butterfly's northern range margin. Ecol Evol 7:331–345

Hackett RA, Monfils MJ, Monfils AK (2016) Evaluating a sampling protocol for assessing plant diversity in prairie fens. Wetl Ecol Manage 24:609–622

Henry EH, Anderson CT (2016) Abundance estimates to inform butterfly management: double-observer versus distance sampling. J Insect Conserv 20:505–514

Henry EH, Schultz CB (2013) A first step towards successful conservation: understanding local oviposition site selection of an imperiled butterfly, mardon skipper. J Insect Conserv 17:183–194

Henry EH, Haddad NM, Wilson J, Hughes P, Gardner B (2015) Point-count methods to monitor butterfly populations when traditional methods fail: a case study with Miami blue butterfly. J Insect Conserv 19:519–529

Hill C (1992) Temporal changes in abundance of two Lycaenid butterflies (Lycaenidae) in relation to adult food resources. J Lepidopterist's Soc 46:173–181

Holzman RW (1972) Eastern range extension for *Oarisma powesheik* Parker (Lepidoptera: Hesperiidae). Great Lakes Entomol 5:111–114

Jervis MA, Boggs CL, Ferns PN (2005) Egg maturation strategy and its associated trade-offs: a synthesis focusing on Lepidoptera. Ecol Entomol 30:359–375

Kost MA, Albert DA, Cohen JG, Slaughter BS, Schillo RK, Weber CR, Chapman KA (2007) Natural communities of Michigan: classification and description. Michigan Natural Features Inventory, Report No. 2007-21, Lansing. https://mnfi.anr.msu.edu/reports/2007-21_Natural_Communites_of_Michigan_Classification_and_Description.pdf. Accessed 6 Mar 2018

Kral KC, Harmon JP, Limb RR, Hovick TJ (2018a) Improving our science: the evolution of butterfly sampling and surveying methods over time. J Insect Conserv 22:1–14

Kral KC, Hovick TJ, Limb RF, Harmon JP (2018b) Multi-scale considerations for grassland butterfly conservation in agroecosystems. Biol Conserv 226:196–204

Landis DA, Fiedler AK, Hamm CA, Cuthrell DL, Schools EH, Pearsall DR, Herbert ME, Doran PJ (2012) Insect conservation in Michigan prairie fen: addressing the challenge of global change. J Insect Conserv 16:131–142

Lee DC, Marsden SJ (2008) Adjusting count period strategies to improve the accuracy of forest bird abundance estimates from point transect distance sampling surveys. Ibis 150:315–325

Marquardt SR, Annis M, Drum RG, Hummel SL, Mosby DE, Smith T (2018) On the cutting edge of research to conserve at-risk species: maximizing impact through partnerships. Integr Comp Biol 58:1–10

Marschalek DA, Deutschmann DH (2008) Hermes copper (Lycaena [Hermelycaena] hermes: Lycaenidae): life history and population estimation of a rare butterfly. J Insect Conserv 12:97–105

McAlpine WS (1972) Observations on life history of *Oarisma poweshiek*. J Res Lepidoptera 11:83–93

McCabe TL, Post RL (1977) Skippers (Hesperioidea) of North Dakota. North Dakota insects publication no. 11. Department of Entomology and Agricultural Experiment Station, North Dakota State University, Fargo

Michigan Natural Features Inventory (2014) Biotics 5—Michigan's natural heritage database. Lansing

Murphy D (1988) Are we studying our endangered butterflies to death? J Res Lepid 26:236–239

Nowicki P, Settele J, Henry P, Woyciechowski M (2008) Butterfly monitoring methods: the ideal and the real world. Isreal J Ecol Evol 54:69–88

Peak RG (2011) A field test of the distance sampling method using golden-cheeked Warblers. J Field Ornithol 82:311–319

Pogue CD, Monfils MJ, Cuthrell DL, Heumann BW, Monfils AK (2016) Habitat suitability modeling of the federally endangered Poweshiek skipperling in Michigan. J Fish Wildl Manag 7:359–368

Pointon H (2015) Larval host plant selection and daily behavior of Poweshiek skipperling (*Oarisma poweshiek*) in Michigan. Undergraduate Thesis, Kalamazoo College

Pollard E, Yates TJ (1993) Monitoring butterflies for ecology and conservation. Chapman and Hall, London

Refsnider JM, Janzen FJ (2010) Putting eggs in one basket: ecological and evolutionary hypotheses for variation in oviposition-site choice. Annu Rev Ecol Evol Syst 41:39–57

Reznicek AA, Voss EG, Walters BS (2011) Michigan Flora online. In: University of Michigan. Web. https://michiganflora.net. Accessed 22 Mar 2019

Rich T, Rabane M, Fasham M, McMeechan F, Dobson D (2005) Ground and shrub vegetation. In: Hill D, Fasham M, Tucker G, Shewry M, Shaw P (eds) Handbook of biodiversity methods—survey, evaluation and monitoring. Cambridge University Press, Cambridge, pp 201–221

Rosengren EC, Andow DA (2016) Spatiotemporal patterns of population decline in *Oarisma poweshiek* (Hesperiidae) in Michigan and Minnesota between 1990 and 2013. Great Lakes Entomol 49:27–35

Rosenstock SS, Anderson DR, Giesen KM et al (2002) Landbird counting techniques: current practices and an alternative. Auk 119:46–53

Runquist E, Heimpel GE (2017) Potential causes of declines in Minnesota's prairie butterflies with a focus on insecticidal control of the soybean aphid. Prepared for College of Food, Agricultural and Natural Resource Sciences—University of Minnesota. https://mitppc.dl.umn.edu/sites/g/files/pua746/f/media/mitppc_soybean.final_.pdf Accessed 22 Apr 2018

Rusterholtz H, Erhardt A (2000) Can nectar properties explain sex-specific flower preferences in the Adonis Blue butterfly Lysandra bellargus? Ecol Entomol 25:81–90

Saarinen EV, Reilly PF, Austin JD, Packer L (2016) Conservation genetics of an endangered grassland butterfly (*Oarisma poweshiek*) reveals historically high gene flow despite recent and rapid range loss. Insect Conserv Divers 9:517–528

Schlicht D, Swengel A, Swengel S (2009) Meta-analysis of survey data to assess trends of prairie butterflies in Minnesota, USA during 1979–2005. J Insect Conserv 13:429–447

Schneider C, Dover J, Fry GLA (2003) Movement of two grassland butterflies in the same habitat network: the role of adult resources and size of the study area. Ecol Entomol 28:219–227

Schultz CB, Crone EE (2015) Using ecological theory to develop recovery criteria for an endangered butterfly. J Appl Ecol 52:1111–1115

Schultz CB, Dlugosch KM (1999) Nectar and hostplant scarcity limit populations of an endangered Oregon butterfly. Oecologia 119:231–238

Schultz CB, Henry E, Carleton A, Hicks T, Thomas R, Potter A, Collins M, Linders M, Fimbel C, Black SH, Anderson H, Diehl G, Hamman S, Gilbert R, Foster J, Hays D, Page N, Heron J, Kroeker N, Webb C, Reader B (2011) Conservation of prairie-oak butterflies in Oregon, Washington, and British Columbia. Northwest Sci 85:361–388

Seixas RR, Santos SE, Okada Y, Freitas AVL (2017) Population biology of the sand forest specialist butterfly *Heliconius hermathena*. J Lepid Soc 71:133–140

Selby G (2005) Status assessment and conservation guidelines: Poweshiek skipperling (*Oarisma poweshiek* (Parker) (Lepidoptera: Hesperiidae). Prepared for Twin Cities Field Office, U.S. Fish and Wildlife Service, Bloomington. http://dx.doi.org/10.3996/052015-JFWM-049.S8. Accessed 24 May 2018

Semmler SJ (2010) The nectar sources and flower preferences of the Poweshiek Skipperling (*Oarisma poweshiek*) in Manitoba. Honours Thesis, University of Winnipeg. http://ion.uwinnipeg.ca/~moodie/Theses/Semmler2010.pdf. Accessed 27 Apr 2018

Severns PM, Warren AD (2008) Selectively eliminating and conserving exotic plants to save an endangered butterfly from local extinction. Anim Conserv 11:476–483

Severns PM, Boldt L, Villegas S (2006) Conserving a wetland butterfly: quantifying early lifestage survival through seasonal flooding, adult nectar, and habitat preference. J Insect Conserv 10:361–370

Simons TR, Alldredge MW, Pollock KH et al (2007) Experimental analysis of the auditory detection process on avian point counts. Auk 124:986–999

Singer MC, Wedlake P (1981) Capture does affect probability of recapture in a butterfly species. Ecol Entomol 6:215–216

Spieles JB, Comer PJ, Albert DA, Kost MA (1999) Natural community abstract for prairie fen. Michigan Natural Features Inventory, Lansing

Swengel AB (1996) Effects of fire and hay management on abundance of prairie butterflies. Biol Conserv 76:73–85

Swengel AB, Swengel SR (1999) Observations of prairie skippers (*Oarisma poweshiek*, *Hesperia dacotae*, *H. ottoe*, *H. leonardus* *pawnee*, and *Antrytone arogos iowa*) [Lepidoptera: Hesperiidae] in Iowa, Minnesota, and North Dakota during 1988-1997. Great Lakes Entomol 32:267–292

Swengel AB, Swengel SR (2014) Paradoxes of Poweshiek skipperling (*Oarisma poweshiek*) (Lepidoptera: Hesperiidae): abundance patterns and management of a highly imperiled prairie species. ISRN Entomology. https://doi.org/10.1155/2014/216427

Swengel SR, Schlicht D, Olsen F, Swengel AB (2011) Declines of prairie butterflies in the midwestern USA. J Insect Conserv 15:327–339

Sykes JM, Horrill AD, Mountford MD (1983) Use of visual cover assessments as quantitative estimators of some British woodland taxa. Ecology 71:437–450

Szcodronski KE, Debinski DM, Klaver RW (2018) Occupancy modeling of *Parnassius clodius* butterfly populations in Grand Teton National Park, Wyoming. J Insect Conserv 22:267–276

Thomas RC, Schultz CB (2016) Resource selection in an endangered butterfly: females select native nectar species. J Wildl Manag 80:171–180

Thomas JA, Simcox DJ, Clarke RT (2009) Successful conservation of a threatened *Maculinea* butterfly. Science 325:80–84

Thomas L, Buckland ST, Rexstad EA et al (2010) Distance software: design and analysis of distance sampling surveys for estimating population size. J Appl Ecol 47:5–14

Thomas JA, Simcox DJ, Hovestadt T (2011) Evidence based conservation of butterflies. J Insect Conserv 15:241–258

U.S. Fish and Wildlife Service (USFWS) (2014) Endangered and threatened wildlife and plants; threatened species status for dakota skipper and endangered Species status for poweshiek skipperling. Federal Register 79 FR 63671

Vlasanek P, Hauck D, Konvicka M (2009) Adult sex ratio in the *Parnassius mnemosyne* butterfly: effects of survival, migration, and weather. Israel J Ecol Evol 55:233–252

WallisDeVries MF, Poschlod P, Willems JH (2002) Challenges for the conservation of calcareous grasslands in northwestern Europe: integrating the requirements of flora and fauna. Biol Conserv 104:265–273

Weking S, Hermann G, Fartmann T (2013) Effects of mire type, land use and climate on a strongly declining wetland butterfly. J Insect Conserv 17:1081–1091

Wiklund C (1984) Egg-laying patterns in butterflies in relation to their phenology and the visual apparency and abundance of their host plants. Oecologia 63:23–29

Yates F (1934) Contingency tables involving small numbers and the $\chi 2$ test. J R Stat Soc 1:217–235