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Management practices benefit endangered Poweshiek skipperling (*Oarisma poweshiek*) in Manitoba tall grass prairie

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Abstract

Poweshiek skipperling (*Oarisma poweshiek* Parker, 1870) populations have declined precipitously in the past few decades, and their global range is now restricted to two isolated regions, one of which is the managed Manitoba tall grass prairie in Canada. In this paper, we used a decade of survey data from 2010 to 2019 to understand how habitat features, management practices, and extreme weather impact Poweshiek skipperling abundance in Manitoba. The strongest predictor of abundance was the density of black-eyed Susans (*Rudbeckia hirta* L.), a primary nectar plant for adults. Poweshiek skipperling abundance also had a negative relationship with both the number of years since a burn occurred and the number of years since grazing occurred. Cumulative precipitation during their active period (May–June) had a negative relationship with skipperling abundance, whereas warm early springs and cool temperatures during the active period had positive relationships. These results suggest that management actions that maintain tall grass prairie habitat in an early successional stage (burning and grazing) and maintain important nectar sources benefit this population. In contrast, extreme weather events had varying effects on Poweshiek skipperling abundance. Results from this study inform ongoing management practices in the Manitoba tall grass prairie to support this endangered population.

Key words: endangered butterfly, extreme weather, grazing, grassland management, Manitoba tall grass prairie, prescribed burn

Introduction

The Poweshiek skipperling (*Oarisma poweshiek* Parker, 1870) is a small, orange-brown butterfly (Lepidoptera: Hesperiidae) that occurs in isolated populations within its North American range. Historically occurring in eight states and one province, this species is now believed to be restricted to only two jurisdictions: a few isolated prairie fens in Michigan and several areas of tall grass prairie in Manitoba (COSEWIC 2014; Delphey et al. 2016; Belitz et al. 2020). The restricted distribution of Poweshiek skipperling is a result of an alarming decline that has occurred over the past few decades (reviewed in Swengel and Swengel 2014; Belitz et al. 2020), prompting several jurisdictions to protect the species. In Canada, the Poweshiek skipperling is listed as endangered and protected through both federal and provincial species-at-risk legislation (Environment Canada 2012; Government of Manitoba 2020). This population's isolation from natural rescue populations, its small size and ongoing decline, and its restricted distribution make it vulnerable to stochastic events and extirpation (COSEWIC 2014).

Poweshiek skipperling are prairie specialists that rely on native wet-mesic and dry prairie habitat (Catling and Lafontaine 1986; Selby 2005), with adults feeding on forb species primarily associated with dry prairie and larvae feeding on graminoid species primarily associated with wet prairie (Henault and Westwood 2019). They are rarely found in non-native vegetation (Swengel and Swengel 1999; Henault and Westwood 2022; Henault and Westwood 2023). Catling and Lafontaine (1986) first documented the species in Canada in 1985, when they were locally abundant in native tall grass prairies near Vita, Manitoba. Prior to cultivation in the 1800s, there was at least 6000 km^2 of tall grass prairie in Manitoba (Samson and Knopf 1994; Henderson and Koper 2014). Through conversion to annual cropland and urban development, native tall grass prairie is now all but gone from Manitoba, with only a few areas remaining, much of which are within the 44.5 km^2 (as of 2023) Tall Grass Prairie Preserve (TGPP) and surrounding localities in southeastern Manitoba (Fig. 1). Established in 1989 through efforts by the Critical Wildlife Habitat Program (a cooperative initiative involving Nature Manitoba, World Wildlife Fund, Wildlife Habitat Canada, Manitoba Habitat Conservancy (formerly Manitoba Habitat Heritage Corporation), and Manitoba Natural Resources and Northern Development (formerly Manitoba Conservation and Climate), the TGPP encompasses large and contiguous blocks of endangered tall grass prairie (Grantham et al. 2021). The TGPP is part of the larger Tallgrass Aspen Parkland international conservation landscape that extends from near Red Lake Falls, Minnesota to Steinbach, Manitoba, extending over 2,170,000 acres (878,000 ha), an area identified as one of only six "very high conservation priority" sites in the Northern Tallgrass Prairie Ecoregional Plan (Northern Tallgrass Prairie Ecoregional Planning Team 1998). The Canadian population of Poweshiek skipperling is restricted to this area (TGPP and surrounding localities) of tall grass prairie. There has been relatively little habitat loss in the TGPP and surrounding areas in recent decades (COSEWIC 2014), though many regional tall grass prairie patches are declining in size due to woody species encroachment (Koper et al. 2010). It is unknown how local conditions, such as changing climate, may have altered the suitability of the tall grass habitat for the population over this time.

The Poweshiek skipperling has one generation per year (univoltine) and does not migrate (Belitz et al. 2019; Henault and Westwood 2023). The timing of life cycle stages varies across the species' range and between years depending on weather (Selby 2005). In Manitoba, the brief adult flight period occurs from late June to late July, during which time eggs are laid on host plant leaves (Henault and Westwood 2019; Henault and Westwood 2022). Host plants in Manitoba include grasses such as big bluestem (*Andropogon gerardii* Vitman), mat muhly (*Muhlenbergia richardsonis* (Trin.) Rydb), prairie dropseed (*Sporobolus heterolepis* (A. Gray) A. Gray), and little bluestem (*Schizachyrium scoparium* (Michs.) Nash) (Dupont Morozoff 2013; Henault and Westwood 2022). Larvae feed on host plants throughout the remainder of the summer and enter a form of dormancy as larvae in mid-to-late September (K. Eckhardt (personal communication, 24 October 2023)), overwintering at the base of host plant species in or above the litter layer (Borkin 1995; Selby 2005; Henault and Westwood 2022). Larvae emerge from dormancy in May and resume feeding, reaching at least the sixth instar before pupating in mid-to-late June (McAlpine 1973; K. Eckhardt (personal communication, 24 October 2023)). Black-eyed Susan (*Rudbeckia hirta* L.), pale-spiked lobelia (*Lobelia spicata* Lam.), and upland white aster (*Solidago ptarmicoides* (Torr. & A. Gray) B. Boivin) have been the primary nectar plants of adults in Manitoba (Catling and Lafontaine 1986; Semmler 2010; Dupont Morozoff 2013; Westwood et al. 2020), though Poweshiek skipperling have recently been observed nectaring on other species (Henault 2021). Catling and Lafontaine (1986) observed the highest Poweshiek skipperling densities in areas with high pale-spiked lobelia densities, but pale-spiked lobelia was not present during Semmler (2010) and Dupont Morozoff's (2013) studies and was also scarce in Henault's (2021) study. In Michigan, Poweshiek skipperling are more likely to be found in areas with high numbers of their preferred nectar plants (Belitz et al. 2019). Adults have poor dispersal ability, with maximum distances estimated at only 1–1.6 km (Burke et al. 2011) and are unlikely to cross physical barriers such as roads and tall vegetation in their fragmented landscape (Westwood et al. 2012). In Michigan, obstructive vegetation at only 1.5 m tall acted as a barrier, reducing the likelihood of the presence of Poweshiek skipperling in otherwise suitable areas (Belitz et al. 2019). Individuals observed in Manitoba rarely travelled more than 20–30 m beyond the boundaries of occupied sites, even when suitable sites were available nearby (Dupont Morozoff 2013; M. Olynyk (unpublished data)).

The cause(s) of the recent rapid Poweshiek skipperling population decline in Manitoba are not well understood. Previous range contractions in the United States have been attributed to inadequate or inappropriate management resulting in unsuitable habitat (Swengel et al. 2011), though there are mixed results on the impacts of management (e.g., prescribed burning and grazing) on Poweshiek skipperling abundance (Royer and Marrone 1992; Swengel 1998; Swengel and Swengel 1999; Dupont-Morozoff et al. 2022). Prior to European colonization, the tall grass prairie was maintained by periodic wildfires and bison (*Bison bison bison* Linnaeus, 1758) grazing that suppressed ecological succession to shrubby habitat and reduced plant litter (Knapp et al. 1999; Allen and Palmer 2011). Therefore, management methods that approximate these natural disturbances, such as prescribed burning, cattle grazing at appropriate intensities, and mechanical brush control, have become important tools for maintaining tall grass prairie. Lack of land management can lead to natural woody encroachment and invasion by non-native plant species, which can reduce host and nectar plant availability (Dornbush 2004). However, these practices may result in direct butterfly mortality, and responses to prescribed burning and grazing vary among butterfly species (Vogel et al. 2007). For prescribed burning, a species' response can be unpredictable, depending on the mortality rate from the burn and the ability of individuals to disperse from adjacent untreated sites to recolonize the burned site (Swengel and Swengel 1999; Swengel and Swengel 2014). For Poweshiek skipperling, there are several limiting factors (e.g., isolated population, limited dispersal ability, a single generation per year) that make them particularly susceptible to excessive prescribed burning (e.g., burning that is too frequent, poorly timed, or too intense) (Swengel et al. 2011) because these factors are associated with slow population recolonization and recovery if the population is reduced (Swengel 1996; Panzer 2002). Altered floral composition within burned areas (Howe 1995; Towne and Kemp 2008) may also result in several years before the floral community is suitable to skipperling again (Swengel 1996; Dupont Morozoff 2013). Previous studies have shown it typically takes 2–5 years for Poweshiek skipperling and other butterflies to recover post-burn (Swengel 1996; Panzer 2002), but some species were not fully recovered after 5 years (Vogel et al. 2010). The sensitivity of Poweshiek skipperling to burns

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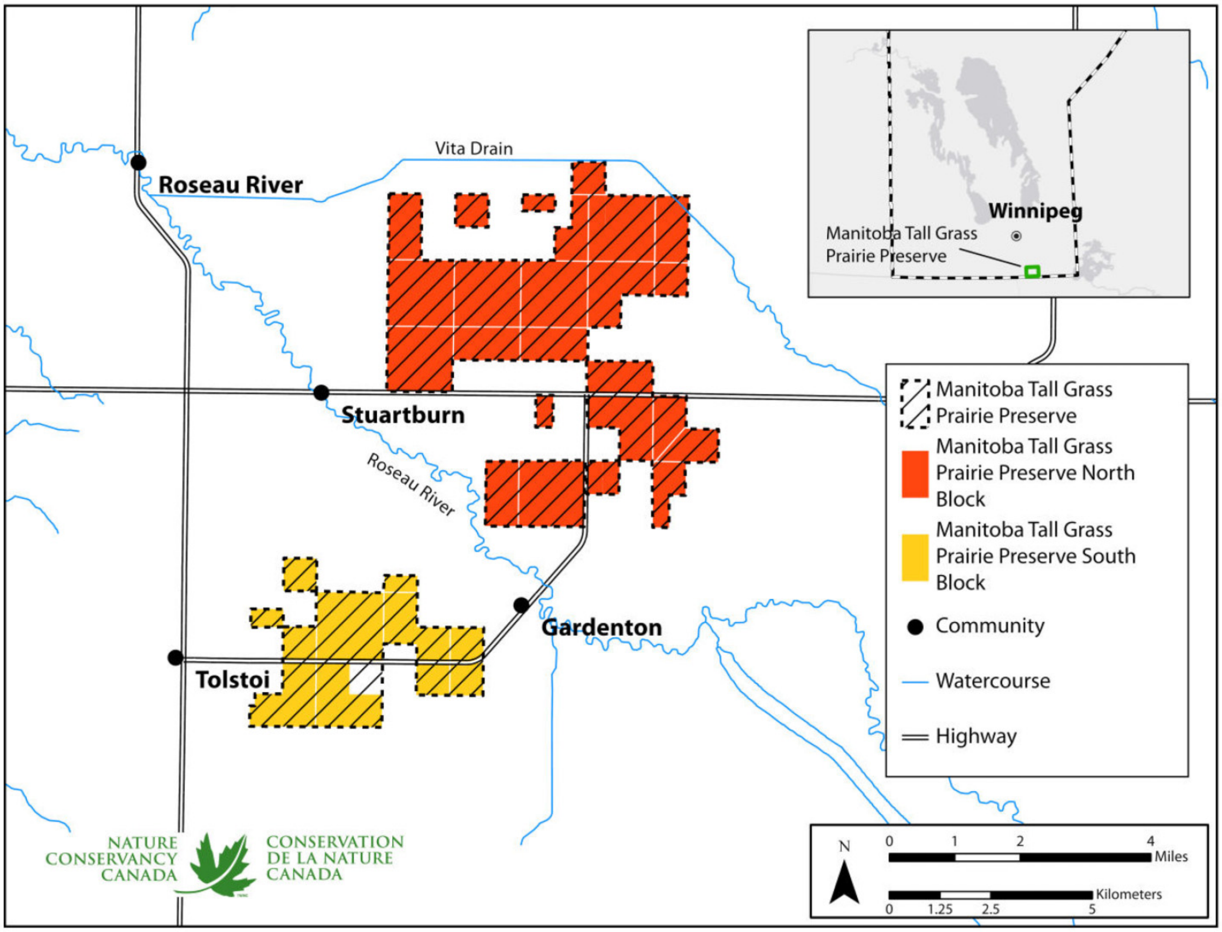
Fig. 1. Map of the Tall Grass Prairie Preserve (TGPP) and surrounding localities in southeastern Manitoba, where the last remaining population of Poweshiek skipperling (*Oarisma poweshiek*) in Canada occurs. The TGPP is divided into two blocks, north (orange) and south (yellow), which are approximately 3 km apart. Each block is divided into parcels (typically quarter sections of land). NCC also owns several parcels of land in the surrounding area, which are not mapped for privacy. Poweshiek skipperling survey sites are located within separate parcels of the TGPP and surrounding area. Basemap sources: Manitoba Land Initiative (2018), Esri, HERE, Garmin, and OpenStreetMap contributors. Map projection: NAD 1983 UTM Zone 14.



(Swengel 1996; Webster 2003) therefore warrants a thoughtful approach. Having a nearby site of core habitat for refuge is necessary (Swengel and Swengel 2007), and burning less than 20% of the occupied area has been recommended for Poweshiek skipperling and other butterflies (Swengel 1996). In this way, burning small patches to create a mosaic of habitat can benefit poor dispersers such as the Poweshiek skipperling, which may have difficulty recolonizing large, burned areas (New et al. 2010).

Another practice that can be used to maintain prairie habitat in its native, early successional state for Poweshiek skipperling is grazing by domestic cattle (*Bos taurus* Linnaeus, 1758). Grazing is generally less disruptive to butterflies than burning because it does not reduce entire stands of vegetation or remove the litter layer in which butterfly larvae reside (Swengel 1996). However, cattle grazing can have different effects on prairie structure than bison grazing, which historically maintained the tall grass prairie (Knapp et al. 1999). For example, bison grazing has been shown to result in higher species richness, higher spatial heterogeneity, higher herbaceous biomass, reduced bare ground, and fewer invasive species than cattle grazing (Towne et al. 2005; Hillenbrand et al. 2019; Ratajczak et al. 2022). These impacts are all important for maintaining ecosystem function; however, cattle grazing is much more practical in most cases, and grazing by either species at low to moderate stocking rates is more beneficial for maintaining prairie habitat and species richness than not grazing at all (Towne et al. 2005; Ratajczak et al. 2022). The risk of trampling or consumption of adults, eggs, and larvae is presumably low unless stocking rates are high (Dupont-Morozoff et al. 2022; as seen for bird nests in Bleho et al. 2014). High stocking rates also result in unselective heavy grazing that removes host and nectar plants and severely diminishes the quality and diversity of tall grass prairie (Howe 1994; Swengel 2008). On the other hand, conservatively grazed prairie may have greater forb cover and species diversity because grazing removes dominant grass cover (Vinton et al. 1993; Towne et al. 2005).

Extreme weather is another factor that may have influenced Manitoba Poweshiek skipperling abundance, especially because small populations are more vulnerable to stochastic weather events. Extreme weather relative to species' tolerances predicts species abundance and local extinction risk in insects and terrestrial vertebrates (Kerr 2020; Soroye et al. 2020; Williams and Newbold 2021). For butterflies specifically, weather has been shown to be a strong determinant of population dynamics (Roy et al. 2001; Woods et al. 2014). Univoltine butterflies in the United Kingdom are most vulnerable to extreme heat during the winter, extreme cold during the adult life stage, and extreme precipitation as pupae (McDermott Long et al. 2017). These effects were more significant for habitat generalists than for habitat specialists. For species overwintering in cold climates, the ground temperature is moderated from extreme temperature fluctuations by the consistent snowpack (Geiger 1965; Sharratt et al. 1992), but extreme heat in the winter can melt this snowpack and make overwintering butterflies vulnerable to fluctuating temperatures, reducing their survival (Scriber et al. 2012). In addition, butterflies have appeared in spring significantly earlier over the past several decades due to warmer spring weather (Roy and Sparks 2000; Forister and Shapiro 2003). This may be concerning if it results in a timing mismatch with a population's obligate host plant(s), such as that occurred in Indiana when larvae of the endangered Karner blue butterfly (*Lycaeides melissa samuelis* Nabokov, 1944) hatched early and before its host plant, wild blue lupine (*Lupinus perennis* L.), became available, resulting in low larval survival (Patterson et al. 2020). Poweshiek skipperling may also be vulnerable to extreme weather outside of their physiological tolerances that has been exacerbated by climate change, such as loss of snow cover in the winter or a cool, wet spring (Selby 2005). Because the Manitoba tall grass prairie is susceptible to flooding due to naturally poor drainage and a high water table in the area (Westwood et al. 2020), increased precipitation may negatively impact this population. In their analysis of wide-range Poweshiek skipperling populations over time, Belitz et al. (2020) concluded that weather drove presence prior to the steep population declines that began in the early 2000s, but since these steep declines, presence has been driven primarily by land cover (a positive effect of natural land cover and a negative effect of fragmentation). Even so, increased temperatures were negatively correlated with the probability of Poweshiek skipperling presence during the recent declines (Belitz et al. 2020). Precipitation extremes did not appear to be an important factor explaining the probability of presence during the declines. Understanding the effects of extreme weather specifically on the Poweshiek skipperling population in Manitoba since its steep decline began may enable land managers to predict population fluctuations and adjust management activities accordingly.

At the northern edge of the Poweshiek skipperling range, in the tall grass prairie of Manitoba, there is still much to learn about the population dynamics of this endangered species. The Nature Conservancy of Canada (NCC) has comanaged the TGPP, where these butterflies are found, with several partners since the 1990s and annual Poweshiek skipperling inventory and monitoring have consistently occurred since 2009. Using a decade of survey data, our objectives were to assess how various habitat characteristics, land management practices, and extreme weather affected the Poweshiek skipperling population in Manitoba. Specifically, we were interested in (1) which habitat characteristics (black-eyed Susan density and distance to the nearest occupied site) were associated with higher Poweshiek skipperling abundance, (2) whether the timing since broad-scale management practices (prescribed burning and grazing) last occurred correlated with higher Poweshiek skipperling abundance, and (3) the relationship between extreme weather (temperature or precipitation) during winter–spring (larvae–pupae) and Poweshiek skipperling abundance (adult butterflies) in the summer.

Methods

Study area

The only known Canadian population of Poweshiek skipperling is located within the 44.5 km^2 (4,450-hectare) TGPP and surrounding areas of tall grass prairie near Tolstoi, Stuartburn, and Gardenton, Manitoba (49°04′28″N, 96°48′40″W; Fig. 1). The local landscape is a mixture of natural habitats, gravel and paved roads, agricultural lands, homesteads, and small communities. Natural habitats in the area are a dynamic mosaic of wet prairies, shrubby wetlands, upland prairies, savannahs, and deciduous woodlands. Most land in the TGPP is owned by NCC and its partners and is jointly managed by a management committee that includes Manitoba Agriculture and Resource Development, Environment and Climate Change Canada, Nature Manitoba, and the Manitoba Habitat Heritage Corporation. The TGPP is divided into two blocks, north and south, separated by approximately 3 km. Each block is divided into parcels (typically quarter sections of land). Within a given parcel, Poweshiek skipperling occupy an irregularly shaped area that is henceforth defined as a "site". There are sometimes multiple sites within one parcel, and those that are under a different management regime were treated as separate sites in this analysis. Distances between occupied sites within blocks range from several meters to 3 km, as measured between site boundaries (rather than parcel boundaries) using a geographic information system (GIS), though we do not have a good understanding of the connectedness or extent of Poweshiek skipperling movement among sites. It is possible that Poweshiek individuals are capable of traversing between sites when they are relatively close together (within 1–2 km of one another) and the intervening areas are composed of grasslands, open shrublands, or wetlands as opposed to dense forest stands. However, we have not observed any Poweshiek adults in these intervening areas to date.

Data collection

Numerous sites in the TGPP and surrounding areas have been surveyed for the presence of skipperling since 2009. Data included in this analysis spans from 2010–2019 and across eighteen sites, which ranged in size from 5.4 to 32.1 ha (Table 1). Survey sites were delineated based on the geographic location of previous Poweshiek skipperling observations and refined using GIS, interpretation of aerial imagery (2012 digital ortho photos of the TGPP and surrounding area

Table 1. Site details.

Site	Area (ha)	No. analysis years	No. analysis years POSK observed	Years grazed by cattle	Years burned
3	13.4	10	8	2008	2007, 2009, 2011
4/5	17.6	9	5	Pre-1995	2006, 2011[§]
8	22.6	10	10	Pre-1995	2002, 2009, 2011
9	8.5	8	6	2007	2005
10	10.9	9	0	Pre-1995	2008*, 2009, 2011
11	25.6	6	3	Pre-1995	2006, 2011*, 2014*
12	13.0	8	3	Pre-1995	2006
15	8.6	7	2	2008, 2014–2016, 2018	2002, 2012
21	13.7	9	4	Pre-1995	2006, 2011
22	18.2	9	5	Pre-1995	2006, 2011
23	7.7	6	2	Pre-1995	2006, 2011
24	5.4	9	3	Pre-1995	Pre-1995, 2011
25	8.6	9	7	Pre-1995	2007, 2009, 2011
26	6.8	5	3	2008	2007, 2009, 2011
27	11.9	8	0	2008	2008*
J42	9.8	6	0	2008	Pre-1995, 2014*
J67	7.7	6	5	2006, 2012–2016, 2018–2019	2008, 2011*
JB4	32.1	8	0	2008, 2019	2007, 2009, 2011

Note: Details about the 18 sites included in the analysis of how habitat features, management practices, and extreme weather events impacted Poweshiek skipperling (*Oarisma poweshiek*) abundance between 2010 and 2019 in Manitoba. All sites are located within the Manitoba Tall Grass Prairie Preserve and surrounding area. Sites are irregularly shaped areas (measured in hectares) that Poweshiek skipperling occupy within distinct land management parcels (typically quarter sections). There were sometimes multiple sites within one parcel, and those that were under a different management regime were treated as separate sites in this analysis. For each site, we list the number of years it was surveyed with a consistent measure of survey effort (the number of analysis years), the number of years Poweshiek skipperling (POSK) were observed at each site, the years cattle grazing occurred, and the years a burn occurred (prescribed burn or wildfire).

*Indicates a spring burn, otherwise burn occurred in fall.

§The east and west sides of this site have different burn histories. There was a burn on the west side in 2000 and a burn on the east side in 2006. The entire site was burned in 2011, so prior to this, we considered 2006 to be the year of the last burn for the site as a whole because there was butterfly movement observed between the burned and unburned sides.

retrieved from the Manitoba Land Initiative), vegetation classification mapped on the ground by the NCC to determine the extent of habitat available to support this species, and additional information collected from site visits. Vegetation classification data for the TGPP and the surrounding area was compiled by the NCC. Classification is typically completed once for a given area, then may be repeated at a set time interval (e.g., every 10 years) if ecosystems are particularly dynamic (e.g., increasing moisture in the tall grass prairie). All vegetation communities fall into a "Community Category" adapted from the IUCN Habitat Categories (IUCN 2023). Standard classification systems and/or naming conventions have been identified or developed for all the communities found within these categories. The sites generally encompassed a native tall grass prairie meadow, bounded on all sides by unsuitable habitat (e.g., forest, wetland, roadway).

Surveys were conducted during the adult flight period from late June or early July to mid/late July each year. The earliest survey date was 22 June, and the latest date was 29 July, with each site being surveyed one to nine times during each flight period (mean = three times). A meandering walk transect (Royer et al. 1998; Hamel et al. 2013) was used to survey the sites for Poweshiek skipperling for varying lengths of time (range = 15–360 min) by at least one surveyor depending on the length of the survey and difficulty of the terrain. Daily surveys were conducted between 09:00 and 18:00 h. Surveys were generally conducted on days with no to partial cloud cover, no precipitation, low wind speeds (<20 km/h), and temperatures exceeding 20 °C, though there were a few instances of light localized rain and moderate winds. To develop a standardized measure of Poweshiek skipperling abundance (the number of individuals observed per hour of survey effort), we selected the highest total number of individuals observed among all timed survey rounds within each site for each year. Each of those highest total numbers of observed individuals per site was divided by the number of survey hours for the associated survey round at each site for each year.

Past visual observations suggested there may be a correlation between the presence of black-eyed Susan, one of the primary nectar plants of Poweshiek skipperling (Dupont Morozoff 2013), and the density of Poweshiek skipperling in the TGPP and surrounding areas. However, analysis of the black-eyed Susan count data from 2007 to 2009 found no correlation between plant and skipperling density (Dupont-Morozoff et al. 2022). Beginning in 2010, the density of black-eyed Susan was visually estimated at most sites during the adult skipperling surveys. Density was ranked as none (no flowering stems), low (<1 flowering stem/3 m^2), moderate (1–2 flowering stems/3 m^2), or high (>2 flowering stems/3 m^2).

Land management information

Management activities in the TGPP include cattle grazing and prescribed burning to remove encroaching woody vegetation and maintain the broad-scale integrity of the tall grass prairie. Land management planning is guided by landscape-scale conservation principles, and management decisions are made within a multi-species context, addressing the need for land management for species with varying ecological needs (Grantham et al. 2021). Land management information was compiled from pasture assessment, fire prescriptions, annual monitoring reports, and annual staff report records maintained by NCC and TGPP staff.

Burn events included both prescribed burns and wildfires because the source of the burn was not consistently recorded historically. Prescribed burns are defined as the application of fire under controlled conditions in a manner designed to generate a prescribed habitat effect (typically reduction in woody encroachment into prairies, meadows, and savannahs) and to ensure the continued maintenance of biodiversity (Grantham et al. 2021). Prescribed burns must be conducted according to a written approved Prescribed Burn Unit Plan and under a Burning Permit from rural municipalities. In contrast, wildfires are defined as unplanned ignitions caused by lightning or unauthorized or accidental human actions (National Wildfire Coordinating Group 2010). In this study, the specific causes of wildfires were not recorded or incorporated into analyses. Most prescribed burns occurred in the fall in the TGPP, but some occurred in the spring. At the start of the study, some survey sites had been burned as recently as the previous year and others more than 10 years prior. One site was burned twice between 2010 and 2019, fourteen sites were burned once, and three sites were not burned (Table 1). Before 2010, the extent of burns was mapped only at the land parcel scale. It was assumed in analyses that survey sites within burned parcels were burned, although this could not be confirmed.

Grazing by cattle has been used for management in the TGPP since 1995 on a portion of the land parcels. The TGPP grazing system is designed in collaboration with the Preserve's management committee to produce a prescribed habitat condition. A prescription (stocking rates and cattle movement) is set to allow the interaction of cattle with a given parcel's plant communities in a way that ensures the continued maintenance of biodiversity (Grantham et al. 2021). Cattle movement through paddocks is managed, and pasture health assessments and direct measures of biodiversity are regularly conducted to ensure that the desired habitat condition is being achieved. Grazing has generally been a three-paddock, twice-over rotational system (Sedivec and Barker 1991), with paddocks grazed for 15 days on the first rotation and 30 days on the second rotation. A single-rotation system is also used, with each paddock grazed for 30–40 days, depending on its carrying capacity (Grantham et al. 2021). Grazing occurred between June and October, and stocking rates are considered low for the local area (see Dupont-Morozoff et al. 2022). One site was grazed once, two sites were grazed several times, and the remaining fifteen survey sites were not grazed by cattle between 2010 and 2019 (Table 1).

Weather data

Historical weather data (daily minimum temperature, maximum temperature, and total precipitation) were obtained from Environment and Climate Change Canada (https://climate.weather.gc.ca/index_e.html). Data were primarily collected from the Emerson station (49° N, 97.24° W), which is located approximately 37 km southwest of the study area. For 85 days between 2010 and 2019, daily temperature data were missing when a few hours of data were missing from the hourly dataset. In this case, we estimated the minimum and maximum temperature for the missing days using the hourly data available from the Emerson station ($n = 11/2153$ days). When the station was missing data for too many hours in a day to get reliable minimum and maximum temperature estimates, we supplemented these data with data from the Gretna station (49.03° N, 97.56° W), which is located approximately 63 km southwest of the study area and directly west of the Emerson station ($n = 74/2153$ days). Total precipitation could not be calculated from the hourly Emerson data and was sometimes missing from the Gretna data, so we did not include precipitation estimates for 41/2153 (2%) days. This would result in underestimates of total precipitation during some time periods. We also note that temperatures estimated from weather stations several meters above the ground tend to be slightly lower than measurements taken at the soil surface where developing Poweshiek skipperling are located (Dearborn and Westwood 2014). In addition, temperatures under the winter snowpack may differ dramatically from the air above the snowpack. For example, paired data loggers from one of the land parcels simultaneously recorded mean temperatures in January below the snowpack at around −7 °C and above the snowpack at around −16 °C (NCC, unpublished data).

To understand the effect of extreme weather on Poweshiek skippering abundance each year across sites, we calculated various metrics of temperature and precipitation over three time periods:

1) Active period (larvae–adults; May–June)
2) Pre-active period (larvae; March–April)
3) Previous winter (inactive) period (larvae; December–February)

The timing and duration of life stages were approximated from several sources (McAlpine 1973; COSEWIC 2014; Belitz et al. 2020). We excluded July from this active period to facilitate interannual comparisons, as the end dates of surveys varied among years. The first metric used was lower threshold degree days, which are a count of the daily minimum degrees below an estimated threshold for development. For Poweshiek skipperling, the lower developmental threshold has been estimated at 6 °C for Manitoba (Dearborn and Westwood 2014), and we calculated lower threshold degree days using this threshold for the active period. Conversely, we calculated the daily maximum temperatures above the lower threshold of 6 °C during the pre-active period (degree days above the lower threshold). Thaw degree days are a count of the daily maximum degrees above zero calculated over the previous winter period and are used as a proxy for melting snowpack that can make overwintering butterflies vulnerable to fluctuating temperatures. Over the same winter months in Manitoba, Westwood and Blair (2010) measured a warming temperature trend between 1971 and 2004. Last, cumulative precipitation was calculated for the active period.

Data analysis

To determine the trend in the Poweshiek skipperling population over time and understand the effects of several habitat, management, and extreme weather predictor variables on Poweshiek skipperling abundance, we used a zero-inflated generalized linear mixed-effects model with a Poisson distribution using R version 3.6.1 (glmmTMB package; Brooks et al. 2017). This was used to model the count data while independently modelling the excess observations of zeros (compared to a traditional Poisson probability distribution). We confirmed that distributional assumptions and homogeneity of variance were met and confirmed by simulating model residuals using the DHARMa package (Harting 2020). Conditional model-fixed effects included year, distance to the nearest occupied site, black-eyed Susan density, years since the last burn (measured as 0–10+), years since the last graze (measured as 0–10+), thaw degree days in the previous winter, degree days above the lower threshold during the pre-active period, lower threshold degree days during the active period, and cumulative precipitation during the active period. The site was included as a random effect. All fixed effects in the conditional model were included in the zero-inflated model. All numerical predictor variables were scaled to *Z*-scores for modelling. The sample size for all models was $n = 147$. We also checked for correlations among all predictor variables and found only low–moderate correlations (range = −0.52 to 0.59), so we retained all variables in the final model. In our early data exploration, we also tested several reduced models. All models included year as a predictor variable, but otherwise, they were subsets of the variables included in the full model. There was (1) a model with the management variables (burning and grazing), (2) a model with the four extreme weather variables, and (3) a model with distance to the nearest occupied site and black-eyed Susan density, and several models with all possible combinations of these three simple models (e.g., management and extreme weather). However, most reduced models did not meet distributional assumptions and homogeneity of variance, so we did not consider them. For the two models that did meet these assumptions, we reviewed the AIC (Akaike information criterion) scores relative to the full model described above. The AIC scores were full model = 986.8, management variables (burning and grazing) + year model = 1216.3, and extreme weather variables (thaw degree days in the previous winter, degree days above the lower threshold during the pre-active period, lower threshold degree days during the active period, and cumulative precipitation during the active period) + year model = 1121.1.

Results

Poweshiek skipperling abundance among sites decreased over time (Table 2 and Fig. 2A). Poweshiek skipperling abundance was higher at sites that were closer to another occupied site (Table 2) and increased as black-eyed Susan density increased (Fig. 2B). The 2 years with the highest black-eyed Susan densities were the first 2 years of the study (median = "moderate" density compared to median = "low" density in the last 8 years of the study). Conversely, abundance decreased with both the number of years since the last burn (Fig. 2C) and the number of years since the last graze (Fig. 2D). Poweshiek skipperling abundance was also influenced by extreme temperature and precipitation; abundance was higher when there were more degree days above the lower threshold during the pre-active period, higher when there were more lower threshold degree days during the active period, and lower when there was higher cumulative precipitation during the active period (Table 2). There was no significant effect of thaw degree days in the previous winter on Poweshiek skipperling abundance. Black-eyed Susan density, degree days above the lower threshold during the pre-active period, and lower threshold degree days during the active period were the variables with the largest standardized back-transformed effect sizes (incidence rate ratios = 1.55, 1.34, and 1.22, respectively).

Discussion

The endangered Poweshiek skipperling has experienced precipitous declines in Manitoba over the past two decades. Understanding the factors that influenced their abundance over ten of these years is essential for land managers to effectively support the recovery and long-term persistence of this population through thoughtful land management practices. We found that black-eyed Susan density was the variable with the largest effect on Poweshiek skipperling abundance, being positively correlated (Table 2). Furthermore, Poweshiek skipperling were never present in sites with no black-eyed Susans (Fig. 2B). This plant appears to be an important nectar source for adult Poweshiek skipperling in Manitoba, though they will also visit other species if in bloom during the adult flight period (Semmler 2010; Dupont Morozoff 2013; Henault and Westwood 2023). As nectar is the adult Poweshiek skipperling's only food source, it follows that management actions ensuring black-eyed Susan and other primary nectar plants are present in high densities are important for maintaining high Poweshiek skipperling abundances within sites. These results contrast with a recent analysis of data from the TGPP spanning 2008–2009, which found no correlation between black-eyed Susan density and Poweshiek skipperling density (Dupont-Morozoff et al. 2022). These different results may be explained by the increased precision in the 2008–2009 black-eyed Susan measurements, where actual counts were made per unit area versus visual estimates of density. On the other hand, there were only 11 sites in this 2-year analysis, and black-eyed Susan density was relatively high in all sites.

Habitat configuration at the landscape scale was also important for Poweshiek skipperling, as indicated by their increased abundance when closer to another occupied site. This is not surprising given that these butterflies are considered poor dispersers (Burke et al. 2011). Ongoing habitat loss and fragmentation in this area may threaten this species, as we found that 17% of the nearest occupied sites were further than 1.6 km, the maximum estimated dispersal distance for Poweshiek skipperling (Burke et al. 2011). In fact, Dupont

Table 2. Model results.

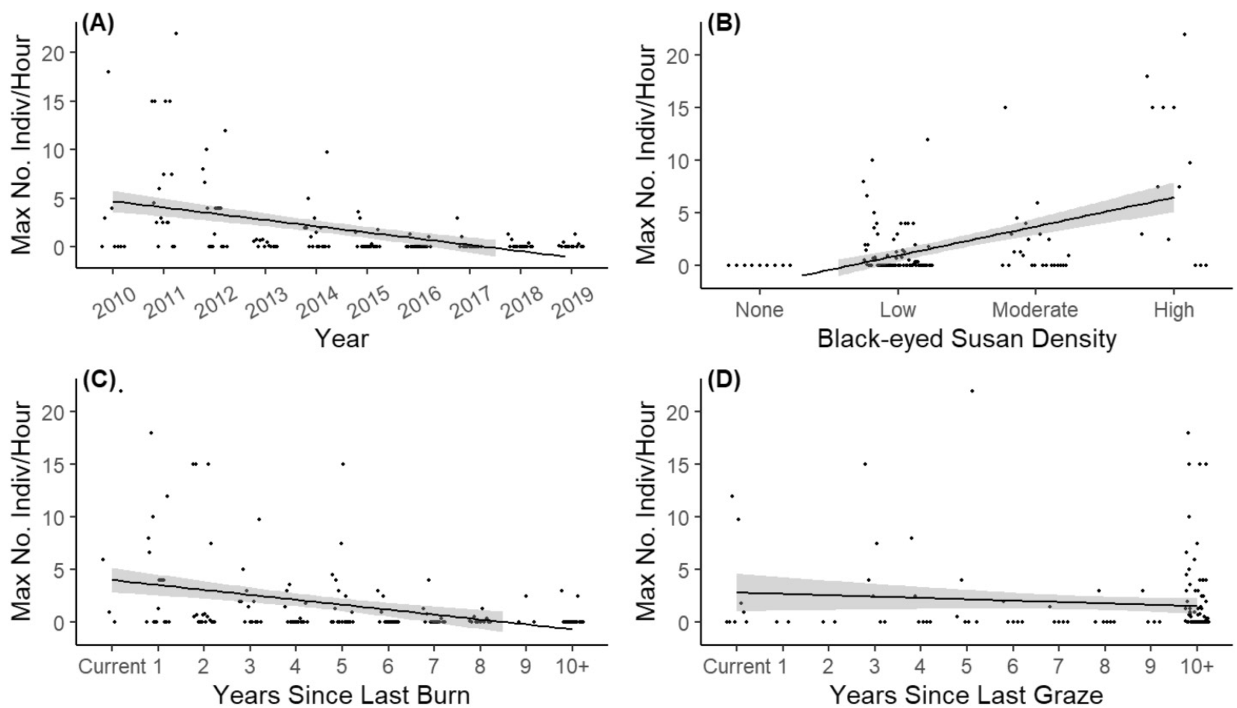
Predictors	Log-mean	Incidence rate ratio	Std. error	Statistic	*p*
Conditional model					
(Intercept)	1.43	4.17	0.59	2.44	*0.015*
Year	− 0.64	0.53	0.07	− 9.03	*<0.001*
Distance to the nearest occupied site	− 0.10	0.91	0.04	− 2.76	*0.006*
Black-eyed Susan density	0.44	1.55	0.04	10.37	*<0.001*
Last burn	− 0.21	0.81	0.07	− 3.16	*0.002*
Last graze	− 0.20	0.82	0.06	− 3.38	*0.001*
Thaw degree days (previous winter)	0.04	1.04	0.06	0.59	0.558
Degree days above the lower threshold (pre-active)	0.29	1.34	0.05	6.08	*<0.001*
Lower threshold degree days (active period)	0.20	1.22	0.07	3.01	*0.003*
Cumulative precipitation (active period)	− 0.19	0.83	0.04	− 4.46	*<0.001*
Zero-inflated model					
(Intercept)	− 0.34	0.71	0.29	− 1.17	0.240
Year	1.73	5.62	0.59	2.93	*0.003*
Distance to the nearest occupied site	− 0.08	0.93	0.24	− 0.32	0.749
Black-eyed Susan density	− 1.31	0.27	0.46	− 2.87	*0.004*
Last burn	0.36	1.43	0.39	0.92	0.357
Last graze	− 0.15	0.86	0.28	− 0.53	0.593
Thaw degree days (previous winter)	0.07	1.07	0.37	0.18	0.856
Degree days above the lower threshold (pre-active)	0.28	1.32	0.32	0.87	0.386
Lower threshold degree days (active period)	− 0.89	0.41	0.38	− 2.32	*0.020*
Cumulative precipitation (active period)	1.04	2.84	0.40	2.61	*0.009*
Random effects					
σ^2	0.81				
Variance $_{\text{Site}}$	5.47				
N_{Site}	18				
Observations	142				
Marginal R^2/conditional R^2	0.142/0.890				

Note: Zero-inflated generalized linear mixed-effects model (Poisson) predicting Poweshiek skipperling (*Oarisma poweshiek*) abundance between 2010 and 2019 ($n = 142$). Conditional model-fixed effects included year, distance to the nearest occupied site, black-eyed Susan (*Rudbeckia hirta L.*) density (ranked on a scale from 0 to 3 representing none: no flowering stems, low: <1 flowering stem/3 m^2, moderate: 1–2 flowering stems/3 m^2, or high: >2 flowering stems/3 m^2), years since the last burn, years since the last graze, thaw degree days in the previous winter (larvae; December–February), degree days above the lower threshold during the pre-active period (larvae; March–April), lower threshold degree days during the active period (larvae–adults; May–June), and cumulative precipitation during the active period. These variables were also included in the zero-inflated model. The site was included as a random effect.

Morozoff (2013) observed that individuals in Manitoba rarely travelled more than 20 m beyond the boundaries of inhabited sites, even when suitable sites were available nearby, suggesting that even small amounts of habitat fragmentation might threaten this species. Skipperling also actively avoid treed areas adjacent to tall grass prairie sites (Dupont Morozoff 2013; Henault and Westwood 2023), suggesting that succession towards forest habitats in this region leads to poor landscape permeability. Forested areas have been observed to act as barriers to movement of other prairie butterfly species (Stasek et al. 2008); in Michigan, 1.5 m tall vegetation acted as a barrier and reduced the likelihood of Poweshiek skipperling presence in otherwise suitable areas (Belitz et al. 2019). These results suggest that Poweshiek skipperling in Manitoba may have difficulty recolonizing sites once locally extirpated.

Three of the four extreme weather variables (degree days above the lower threshold during the pre-active period, lower threshold degree days during the active period, and cumulative precipitation during the active period) were statistically significant predictors of adult Poweshiek skipperling abundance. Degree days above the lower threshold during the pre-active period had the largest effect on Poweshiek skipperling, being positively correlated with adult abundance. During this period (March–April in Manitoba), Poweshiek skipperling larvae do not experience climate conditions to support resumption of development from dormancy, which most likely starts again in May (K. Eckhardt (personal communication, 24 October 2023)). This positive effect could indicate that warmer spring days were beneficial, possibly because these larvae were able to emerge earlier (Selby 2005), allowing them more time to feed on host plants and grow before pupating or experiencing less harsh environmental conditions while waiting for new host plant tissue to emerge. There was also a large positive effect of lower threshold degree days (i.e., cool weather) during the active period (May–June, when skipperling are larvae or pupae) on adult Poweshiek skipperling abundance. This was surprising, as cool weather below the Poweshiek skipperling's developmental threshold

Fig. 2. Scatterplots showing the Manitoba Poweshiek skipperling (*Oarisma poweshiek*) population abundance (maximum number of individuals observed per hour) in all Tall Grass Prairie Preserve sites surveyed (A) between 2010 and 2019, (B) in relation to black-eyed Susan (a primary nectar plant of this butterfly) density (ranked on a scale from 0 to 3 and labelled as none: no flowering stems, low: <1 flowering stem/3 m^2, moderate: 1–2 flowering stems/3 m^2, or high: >2 flowering stems/3 m^2), (C) in relation to the number of years since a site last burned ("Current" indicates a spring burn that occurred prior to the July surveys, otherwise a site burned the previous fall has been 1 year since last burn), and (D) in relation to the number of years since a site was last grazed by cattle. The points are "dodged" to show points that would otherwise overlap. All plots show a line of best fit with a 95% confidence interval.



was expected to have the opposite, negative effect on adult abundance. Consistent with predictions from the literature (Selby 2005; McDermott Long et al. 2017), there was a negative effect of precipitation during the active period on adult abundance. Given the Manitoba tall grass prairie is susceptible to flooding (Westwood et al. 2020), high precipitation may have led to direct mortality of Poweshiek skipperling larvae and pupae by drowning or indirect mortality of larvae by starvation from limited access to host plants. Inconsistent with the literature (Selby 2005; McDermott Long et al. 2017), there was no observed effect of thaw degree days on overwintering larvae. This may have been because the thaws were not warm or long enough to actually melt the snowpack.

Two common management practices for maintaining tall grass prairies are prescribed burning and cattle grazing. We found a negative effect of both years since the last burn and years since the last graze on Poweshiek skipperling abundance, indicating that these practices can be beneficial to the Poweshiek skipperling population in Manitoba. The highest Poweshiek skipperling abundances were recorded at sites that had been burned 5 or fewer years prior (Fig. 2C). This is consistent with results from Dupont-Morozoff et al. (2022), who found that sites that were burned more than 15 years prior had the fewest Poweshiek skipperling compared to more recent burns (1–6 years). For grazing, there were high skipperling abundances recorded at sites that were grazed 5 or fewer years prior, but also at many sites that were grazed ten or more years prior (Fig. 2D). As has been suggested in previous studies on this species and others (Swengel 1996; Panzer 2002; Vogel et al. 2010; Dupont-Morozoff et al. 2022), approximately 5-year burn and grazing cycles appear to be optimal, though Poweshiek skipperling were relatively abundant even 1–2 years after a burn (Figs. 2C and 2D). Despite these results, caution should still be taken when burning and grazing are implemented by land managers. Burning of small patches (a few hectares or less), interspersed with refuge habitat, may be the best way to ensure the persistence of locally restricted populations that are poor dispersers (New et al. 2010), such as the Poweshiek skipperling (Swengel and Swengel 2007). As for reestablishment to occur, burned sites must be within dispersing distance of other occupied sites (Swengel et al. 2011). As for grazing, cattle stocking rates should be kept low to minimize the risk of trampling and consumption of skipperling or their food plants by cattle. Other mechanisms of habitat disturbance, such as haying and mowing, may be a viable alternative to burning or grazing but have not been studied for Poweshiek skipperling. Haying and mowing have been beneficial for the Dakota skipper (*Hesperia dacotae*) in central Manitoba (Webster 2003; Rigney 2013).

Conclusion

The results presented in this paper provide further evidence that Poweshiek skipperling abundance has declined in Manitoba in the past decade. Our results demonstrate the importance of maintaining high densities of primary nectar plants for Poweshiek skipperling and the importance of functional connectivity among discrete areas of suitable habitat. Restoration that links suitable habitat or reduces dispersal distance would be beneficial for these skipperling. A rearing program that is currently underway at the Assiniboine Park Zoo in Winnipeg, Manitoba (Assiniboine Park Conservancy 2022) is also planning to return Poweshiek skipperling to unoccupied sites on the landscape that may help bridge the gaps among sites and facilitate further dispersal and increase population stability. The first reintroduction of skipperling to an unoccupied site occurred in summer 2023 (L. Burns (personal communication, 30 October 2023)). We also show that burning and grazing cycles of approximately 5 years can increase population abundance, but we agree with previous studies that suggest maintaining nearby refugia during these management actions is essential for recolonization. Continued active vegetation management of the Manitoba TGPP and surrounding area through prescribed burning and conservative cattle grazing, coupled with the captive breeding program, will give the Poweshiek skipperling population a chance at recovering and persisting into the future. The greatest uncertainty is caused by extreme weather events, which had varying effects on this population and may be exacerbated by climate change.

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Poweshiek skipperling occurrence data analyzed during this study are not available due to the endangered status of this species. Management data analyzed during this study are available from the corresponding author on reasonable request.

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References

Allen, M.S., and Palmer, M.W. 2011. Fire history of a prairie/forest boundary: More than 250 years of frequent fire in a North American tallgrass prairie. Journal of Vegetation Science, **22**(3): 436–444. doi:10.1111/j.1654-1103.2011.01278.x.

Assiniboine Park Conservancy Inc. 2022. 2022 Annual report. Available from https://www.assiniboinepark.ca/uploads/public/documents/2022_AnnualReport.pdf.

Belitz, M.W., Monfils, M.J., Cuthrell, D.L., and Monfils, A.K. 2019. Life history and ecology of the endangered Poweshiek skipperling *Oarisma poweshiek* in Michigan prairie fens. Journal of Insect Conservation, **23**(3): 635–649. doi:10.1007/s10841-019-00158-6.

Belitz, M.W., Monfils, M.J., Cuthrell, D.L., and Monfils, A.K. 2020. Landscape-level environmental stressors contributing to the decline of Poweshiek skipperling (*Oarisma poweshiek*). Insect Conservation and Diversity, **13**(2): 187–200. doi:10.1111/icad.12399.

Bleho, B.I., Koper, N., and Machtans, C.S. 2014. Direct effects of cattle on grassland birds in Canada. Conservation Biology, **28**(3): 724–734. doi:10.1111/cobi.12259. PMID: 24617945.

Borkin, S.S. 1995. Ecological studies of the Poweshiek Skipper (*Oarisma poweshiek*) in Wisconsin. Bureau of Endangered Resources, Wisconsin Department of Natural Resources. Madison, WI. 13p.

Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., et al. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. The R Journal, **9**: 378–400. doi:10.32614/RJ-2017-066.

Burke, R.J., Fitzsimmons, J.M., and Kerr, J.T. 2011. A mobility index for Canadian butterfly species based on naturalists' knowledge. Biodiversity and Conservation, **20**(10): 2273–2295. doi:10.1007/s10531-011-0088-y.

Catling, P.M., and Lafontaine, J.D. 1986. First documented record of *Oarisma powesheik* (Lepidoptera, Hesperiidae) in Canada. The Great Lakes Entomologists, **19**: 63–66.

COSEWIC. 2014. COSEWIC assessment and status report on the Poweshiek skipperling Oarisma poweshiek in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa. xi + 43pp.

Dearborn, K., and Westwood, R. 2014. Predicting adult emergence of Dakota skipper and Poweshiek skipperling (Lepidoptera: Hesperiidae) in Canada. Journal of Insect Conservation, **18**, 875–884. doi:10.1007/s10841-014-9695-8.

Delphey, P., Runquist, E., Harris, T., Nordmeyer, C., Smith, T., Traylor-Hozer, K., and Miller, P.S. 2016. Poweshiek skipperling and Dakota skipper: Ex situ feasibility assessment and planning workshop. IUCN/SSC Conservation Breeding Specialist Group, Apple Valley, Minnesota.

Dornbush, M.E. 2004. Plant community change following fifty-years of management at Kalsow Prairie Preserve, Iowa, USA. The American Midland Naturalist, **151**(2): 241–250. doi:10.1674/0003-0031(2004)151%5b0241:PCCFFO%5d2.0.CO;2.

Dupont Morozoff, J.M. 2013. Determination of key habitat and best management practices for the conservation of Poweshiek skipperling, *Oarisma poweshiek*, in Manitoba. M.Sc. thesis, University of Winnipeg.

Dupont-Morozoff, J., Westwood, R., and Henault, J. 2022. An assessment of prairie management practices for maintaining habitat quality for the endangered Poweshiek skipperling butterfly in Canada. The American Midland Naturalist, **188**(1): 74–101. doi:10.1674/0003-0031-188.1.74.

Environment Canada. 2012. Recovery strategy for the Poweshiek skipperling (*Oarisma poweshiek*) in Canada. Species at Risk Act Recovery Strategy Series, Ottawa. iv + 22 pp + Appendices.

Forister, M.L., and Shapiro, A.M. 2003. Climatic trends and advancing spring flight of butterflies in lowland California. Global Change Biology, **9**(7): 1130–1135. doi:10.1046/j.1365-2486.2003.00643.x.

Geiger, R. 1965. The climate near the ground. Harvard University Press, Cambridge. 611p.

Government of Manitoba 2020. Species listed under The Endangered Species and Ecosystems Act. Wildlife and Fisheries Branch, Government of Manitoba. Available from https://www.gov.mb.ca/sd/environment_and_biodiversity/species_ecosystems/index.html [accessed 21 July 2020].

Grantham, M., Pelc, J., Neufeld, R., Greaves, L., Anderson, S., and Hamel, C. 2021. Land management in the tall grass prairie natural area. The Nature Conservancy of Canada, Winnipeg, MB. 12p.

Hamel, C., Becker, J., and Westwood, R. 2013. Poweshiek skipperling, *Oarisma poweshiek*, population trends in south eastern Manitoba Report on 2012 field surveys, habitat preferences and land management. Nature Conservancy of Canada, Winnipeg, MB.

Harting, F. 2020. DHARMa: residual diagnostics for hierarchical (Multi-Level/Mixed) regression models. R package version 0.3.1.

Henault, J. 2021. Endangered *Oarisma poweshiek* butterfly larval foraging and adult habitat interactions in Manitoba, Canada. M.Sc. thesis, University of Winnipeg, Winnipeg, Manitoba, Canada. doi:10.36939/ir.202112221602.

Henault, J., and Westwood, R. (2019, February 12). Adult oviposition and nectar feeding in critical habitat of the endangered Poweshiek Skipperling (*Oarisma poweshiek*) in Manitoba. [Webinar Presentation]. International Poweshiek Skipperling Partnership: 2019 Science Series.

Henault, J., and Westwood, R. 2022. Endangered *Oarisma poweshiek* larvae vary their graminoid forage in Manitoba, Canada. Canadian Entomolgist, **154**(1): e49. doi:10.4039/tce.2022.34.

Henault, J., and Westwood, R. 2023. Adult activities of endangered *Oarisma poweshiek* butterflies are associated with a soil moisture gradient in tall grass prairie in Manitoba, Canada. Journal of Insect Conservation, 1–15. PMID: 37360646.

Henderson, D.C., and Koper, N. 2014. Historic distribution and ecology of tall-grass prairie in Western Canada. In Proceedings of the 23rd North American Prairie Conference. Vol. **23**. pp. 40–49.

Hillenbrand, M., Thompson, R., Wang, F., Apfelbaum, S., and Teague, R. 2019. Impacts of holistic planned grazing with bison compared to continuous grazing with cattle in South Dakota shortgrass prairie. Agriculture, Ecosystems & Environment, **279**: 156–168.

Howe, H.F. 1994. Managing species diversity in tallgrass prairie: assumptions and implications. Conservation Biology, **8**: 691–704. doi:10.1046/j.1523-1739.1994.08030691.x.

Howe, H.F. 1995. Succession and fire season in experimental prairie plantings. Ecology, **76**: 1917–1925. doi:10.2307/1940723.

IUCN. 2023. Habitats classification scheme (Version 3.1). International Union for Conservation of Nature. Available from https://www.iucnredlist.org/resources/habitat-classification-scheme.

Kerr, J.T. 2020. Racing against change: understanding dispersal and persistence to improve species' conservation prospects. Proceedings of the Royal Society B: Biological Sciences, **287**(1939): 20202061. doi:10.1098/rspb.2020.2061.

Knapp, A.K., Blair, J.M., Briggs, J.M., Collins, S.L., Hartnett, D.C., Johnson, L.C., and Towne, E.G. 1999. The keystone role of bison in North American tallgrass prairie: bison increase habitat heterogeneity and alter a broad array of plant, community, and ecosystem processes. Bioscience, **49**(1): 39–50. doi:10.2307/1313492.

Koper, N., Mozel, K.E., and Henderson, D.C. 2010. Recent declines in northern tall-grass prairies and effects of patch structure on community persistence. Biological Conservation, **143**(1): 220–229. doi:10.1016/j.biocon.2009.10.006.

Manitoba Land Initiative. 2018. Core maps—data warehouse. Available from https://mli.gov.mb.ca/mli_data/.

McAlpine, W.S. 1973. Observations on life history of *Oarisma Poweshiek* (Parker) 1870. Journal of Research on the Lepidoptera, **11**: 83–93. doi:10.5962/p.333611.

McDermott Long, O., Warren, R., Price, J., Brereton, T.M., Botham, M.S., and Franco, A.M.A. 2017. Sensitivity of UK butterflies to local climatic extremes: which life stages are most at risk? Journal of Animal Ecology, **86**(1): 108–116. doi:10.1111/1365-2656.12594.

National Wildfire Coordinating Group, Fire Policy Committee. 2010. Terminology updates resulting from release of the Guidance for the Implementation of Federal Wildland Fire Management Policy 2009. NWCG#024-2010 Memorandum. National Wildfire Coordinating Group. Boise, ID. 3p. (+ Attachment A: Terminology updates list April 30, 2010; 8 p.). [82133].

New, T.R., Yen, A.L., Sands, D.P.A., Greenslade, P., Neville, P., York, A., and Collett, N. 2010. Planned fires and invertebrate conservation in south east Australia. Journal of Insect Conservation, **14**: 567–574. doi:10.1007/s10841-010-9284-4.

Northern Tallgrass Prairie Ecoregional Planning Team. 1998. Ecoregional planning in the Northern Tallgrass Prairie ecoregion. The Nature Conservancy, Midwest Regional Office, Minneapolis, MN. 208 pp. + appendices.

Panzer, R. 2002. Compatibility of prescribed burning with the conservation of insects in small, isolated prairie reserves. Conservation Biology, **16**(5): 1296–1307. doi:10.1046/j.1523-1739.2002.01077.x.

Patterson, T.A., Grundel, R., Dzurisin, J.D., Knutson, R.L., and Hellmann, J.J. 2020. Evidence of an extreme weather-induced phenological mismatch and a local extirpation of the endangered Karner blue butterfly. Conservation Science and Practice, **2**(1): e147. doi:10.1111/csp2.147.

Ratajczak, Z., Collins, S.L., Blair, J.M., Koerner, S.E., Louthan, A.M., Smith, M.D., et al. 2022. Reintroducing bison results in long-running and resilient increases in grassland diversity. Proceedings of the National Academy of Sciences of the United States of America, **119**(36): e2210433119. doi:10.1073/pnas.2210433119.

Rigney, C.L. 2013. Habitat characterization and biology of the threatened Dakota Skipper (*Hesperia dacotae*) in Manitoba. M.Sc. thesis. University of Winnipeg, Winnipeg, MB.

Roy, D.B., and Sparks, T.H. 2000. Phenology of British butterflies and climate change. Global Change Biology, **6**(4): 407–416. doi:10.1046/j.1365-2486.2000.00322.x.

Roy, D.B., Rothery, P., Moss, D., Pollard, E., and Thomas, J.A. 2001. Butterfly numbers and weather: predicting historical trends in abundance and the future effects of climate change. Journal of Animal Ecology, **70**(2): 201–217. doi:10.1111/j.1365-2656.2001.00480.x.

Royer, R., Austin, J.E., and Newton, W.E. 1998. Checklist and "Pollard Walk" butterfly survey methods on public lands. The American Midland Naturalist, **140**: 358–371. doi:10.1674/0003-0031(1998)140%5b0358:CAPWBS%5d2.0.CO;2.

Royer, R.A., and Marrone, G.M. 1992. Conservation status of the Poweshiek skipper (*Oarisma poweshiek*) in North and South Dakota. Unpublished report. U.S. Fish and Wildlife Service, Denver, CO. 31p.

Samson, F., and Knopf, F. 1994. Prairie conservation in North America. Bioscience, **44**(6): 418–421. doi:10.2307/1312365.

Scriber, J.M., Maher, E., and Aardema, M.L. 2012. Differential effects of short term winter thermal stress on diapausing tiger swallowtail butterflies (*Papilio* spp.). Insect Science, **19**(3): 277–285. doi:10.1111/j.1744-7917.2011.01477.x.

Sedivec, K.K., and Barker, W.T. 1991. Design and characteristics of the twice-over rotation grazing system. NDSU Libraries.

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, MN. 53p.

Semmler, S.J. 2010. The nectar sources and flower preferences of the Poweshiek Skipperling (*Oarisma poweshiek*) in Manitoba. Honours thesis, University of Winnipeg.

Sharratt, B.S., Baker, D.G., Wall, D.B., Skaggs, R.H., and Ruschy, D.L. 1992. Snow depth required for near steady-state soil temperatures. Agricultural and Forest Meteorology, **57**: 243–251. doi:10.1016/0168-1923(92)90121-J.

Soroye, P., Newbold, T., and Kerr, J. 2020. Climate change contributes to widespread declines among bumble bees across continents. Science, **367**(6478): 685–688. doi:10.1126/science.aax8591.

Stasek, D.J., Bean, C., and Crist, T.O. 2008. Butterfly abundance and movements among prairie patches: the roles of habitat quality, edge, and forest matrix permeability. Environmental entomology, **37(4)**: 897–906. doi:10.1093/ee/37.4.897.

Swengel, A.B. 2008. Poweshiek paradise lost. American Butterflies **16**: 16–32.

Swengel, A.B. 1996. Effects of fire and hay management on abundance of prairie butterflies. Biological Conservation, **76**(1): 73–85. doi:10.1016/0006-3207(95)00085-2.

Swengel, A.B. 1998. Effects of management on butterfly abundance in tallgrass prairie and pine barrens. Biological Conservation, **83**: 77–89. doi:10.1016/S0006-3207(96)00129-2.

Swengel, A.B., and Swengel, S.R. 1999. Observations of Prairie skippers (*Oarisma poweshiek*, *Hesperia dacotae*, *H. Ottoe*,*H.* l*eonardus Pawnee*, and *Atrytone arogos* Iowa) [(Lepidoptera: Hesperiidae] in Iowa, Minnesota, and North Dakota During 1988–1997. The Great Lakes Entomologist, **32**(4): 5.

Swengel, A.B., and Swengel, S.R. 2007. Benefit of permanent non-fire refugia for Lepidoptera conservation in fire-managed sites. Journal of Insect Conservation, **11**: 263–279. doi:10.1007/s10841-006-9042-9.

Swengel, A.B., and Swengel, S.R. 2014. Paradoxes of Poweshiek skipperling (*Oarisma poweshiek*) (Lepidoptera: Hesperiidae): abundance patterns and management of a highly imperiled prairie species. Entomology, **2014**: 1–10.

Swengel, S.R., Schlicht, D., Olsen, F., and Swengel, A.B. 2011. Declines of prairie butterflies in the midwestern USA. Journal of Insect Conservation, **15**: 327–339. doi:10.1007/s10841-010-9323-1.

Towne, E.G., and Kemp, K.E. 2008. Long-term response patterns of tallgrass prairie to frequent summer burning. Rangeland Ecology & Management, **61**: 509–520. doi:10.2111/08-043.1.

Towne, E.G., Hartnett, D.C., and Cochran, R.C. 2005. Vegetation trends in tallgrass prairie from bison and cattle grazing. Ecological Applications, **15**: 1550–1559. doi:10.1890/04-1958.

Vinton, M.A., Hartnett, D.C., Finck, E.J., and Briggs, J.M. 1993. Interactive effects of fire, bison (*Bison bison*) grazing and plant community composition in tallgrass prairie. American Midland Naturalist, **129**: 10–18. doi:10.2307/2426430.

Vogel, J.A., Debinski, D.M., Koford, R.R., and Miller, J.R. 2007. Butterfly responses to prairie restoration through fire and grazing. Biological Conservation, **140**(1–2): 78–90. doi:10.1016/j.biocon.2007.07.027.

Vogel, J.A., Koford, R.R., and Debinski, D.M. 2010. Direct and indirect responses of tallgrass prairie butterflies to prescribed burning. Journal of Insect Conservation, **14**, 663–677. doi:10.1007/s10841-010-9295-1.

Webster, R.P. 2003. 2002 survey of the Dakota skipper, *Hesperia dacotae* (Skinner) in Canada. Unpublished report prepared for the Committee on the Status of Endangered Wildlife in Canada. 14 p.

Westwood, A.R., and Blair, D. 2010. Effect of regional climate warming on the phenology of butterflies in boreal forests in Manitoba, Canada. Environmental entomology, **39(4)**: 1122–1133. doi:10.1603/EN09143.

Westwood, R., Dupont, J., and Hamel, C. 2012. Surveys for Poweshiek skipperling, *Oarisma poweshiek*, in the region of the Tall Grass Prairie Preserve in south eastern Manitoba—report on the 2011 field activities of the University of Winnipeg and Nature Conservancy of Canada. Nature Conservancy of Canada, Winnipeg, MB. 29p.

Westwood, R., Westwood, A.R., Hooshmandi, M., Pearson, K., LaFrance, K., and Murray, C. 2020. A field-validated species distribution model to support management of the critically endangered Poweshiek skipperling (*Oarisma poweshiek*) butterfly in Canada. Conservation Science and Practice, **2**(3): 1–15. doi:10.1111/csp2.163.

Williams, J.J., and Newbold, T. 2021. Vertebrate responses to human land use are influenced by their proximity to climatic tolerance limits. Diversity and Distributions, **27**(7): 1308–1323. doi:10.1111/ddi.13282.

Woods, J.N., Wilson, J., and Runkle, J.R. 2014. Influence of climate on butterfly community and population dynamics in western Ohio. Environmental Entomology, **37**(3): 696–706. doi:10.1093/ee/37.3.696.