Global Ecology and Conservation 19 (2019) e00678

Contents lists available at ScienceDirect

Global Ecology and Conservation

journal homepage: http://www.elsevier.com/locate/gecco

Original Research Article

Strategic mowing of roadside milkweeds increases monarch butterfly oviposition

Samantha M. Knight [a, *], D. Ryan Norris [a], Rachael Derbyshire [a, b], D.T. Tyler Flockhart [a, c]

[a] Department of Integrative Biology, University of Guelph, Guelph, ON, N1G 2W1, Canada
[b] Department of Environmental and Life Science, Trent University, Peterborough, ON, K9J 0G2, Canada
[c] University of Maryland Center for Environmental Science, Appalachian Laboratory, Frostburg, MD, 21532, USA

ARTICLE INFO

Article history:
Received 19 February 2019
Received in revised form 23 May 2019
Accepted 23 May 2019

Keywords:
Asclepias syriaca
Conservation
Danaus plexippus
Linear right-of-way
Management strategies
Species-at-risk

ABSTRACT

The eastern North American migratory population of monarch butterflies (*Danaus plexippus*) has declined precipitously due, in part, to the widespread decline of its obligate host plant, milkweed (*Asclepias* spp.). Linear right-of-ways (e.g. roadsides, power line corridors) are believed to be a significant source of milkweed and represent a valuable target for restoration efforts. Although many current mowing practices in these habitats are detrimental for monarchs because mowing occurs too frequently or is poorly timed, strategic mowing could be beneficial for monarch reproduction if it produces young milkweed at the right time of season. To address this, forty-nine paired experimental and control plots containing common milkweed (*Asclepias syriaca*) were established along habitat adjacent to a two-lane highway in southern Ontario. Experimental plots were mowed once per season and followed one of eight mowing treatments that occurred between mid-June and early August. Milkweed characteristics and the presence of monarchs at all life stages were monitored within plots from late June through September. Overall, mowed plots had higher egg abundance than unmowed controls. Within mowed plots, egg abundance/plant was highest in plots mowed between the 2nd and 3rd weeks of July. At this latitude (43°N), mowing past this window was less effective and would have resulted in high mortality of developing monarchs. Our results suggest that mowing common milkweed once before egg laying peaks could maximize monarch butterfly reproduction in managed landscapes.

1. Introduction

To ensure long-term population viability for threatened species, two frequently adopted management actions are to restore lost habitat or enhance existing habitat quality through specific management practices (Scott et al., 2010). Habitat management practices include maintaining habitat at a particular successional stage, provisioning focal species, controlling invasive species, and minimizing human disturbance (reviewed in Ausden, 2007). In addition to these approaches, the timing, frequency, and extent of management practices will dictate the suitability of a habitat for a given species (reviewed in Ausden,

* Corresponding author.
E-mail address: sknigh04@uoguelph.ca (S.M. Knight).

https://doi.org/10.1016/j.gecco.2019.e00678

2007 and Durant et al., 2008). For example, the timing of grazing in grasslands is important for reducing disturbance during critical life stages for ground-nesting birds (reviewed in Durant et al., 2008).

The eastern North American population of monarch butterflies (*Danaus plexippus*) is well known for its long distance migration. Each autumn, monarchs migrate south to Oyamel fir (*Abies religiosa*) forests in the mountains of central Mexico, where they overwinter in large colonies (Brower, 1995). In spring and summer, successive generations breed and migrate north to recolonize the United States and southern Canada (Brower, 1995; Flockhart et al. 2013, 2019). Milkweed plants (*Asclepias* spp., *Cynanchum laeve*) are the exclusive egg-laying (oviposition) substrate for female monarch butterflies and food source for monarch larvae. Depending on the air temperature, larvae spend approximately 10–20 days growing on milkweed prior to pupating and emerging as adults butterflies (Urquhart, 1960; Zalucki, 1982). The eastern North American population of monarchs has declined precipitously in recent decades (Brower et al., 2012; Vidal and Rendón-Salinas, 2014) and there is concern over the long-term viability of this population (Flockhart et al., 2015; Semmens et al., 2016). Consequently, monarchs are considered as a species-at-risk in Canada (COSEWIC, 2016) and action must be taken for this population to recover.

Monarch butterflies face multiple threats throughout the annual cycle, including habitat loss on the breeding (Flockhart et al., 2015; Pleasants, 2017) and overwintering grounds (Brower et al., 2002), climate change and extreme weather events (Oberhauser and Peterson, 2003; Batalden et al., 2007), and exposure to pollutants such as pesticides (Pecenka and Lundgren, 2015). There is evidence to suggest that loss of milkweed on the breeding grounds (Flockhart et al., 2015; Pleasants, 2017) is the greatest limitation to monarch butterfly recovery (Pleasants and Oberhauser, 2013; Flockhart et al., 2015; Pleasants et al., 2017). It has been estimated that over one billion milkweed stems have been lost since the 1990s, amounting to an estimated loss of 21–46% of the milkweed on the landscape (Flockhart et al., 2015; Pleasants, 2017). This loss has been attributed to sharp declines of milkweed in agricultural fields (Hartzler, 2010) with the increased use of glyphosate herbicides in conjunction with glyphosate-tolerant crops such as corn and soy (Pleasants and Oberhauser, 2013). Additionally, land use change (conversion to cropland, urban development) reduces milkweed availability (Lark et al., 2015; Pleasants, 2017). While there is a concerted effort to increase the quantity of milkweed on the landscape (Borders and Lee-Mäder, 2014), effective recovery and conservation of monarch butterflies should also incorporate management strategies aimed at increasing milkweed quality.

Understanding female egg-laying preferences is important for developing management strategies aimed at increasing milkweed quality. Previous studies have documented a preference for taller plants (Zalucki and Kitching, 1982) in small (Zalucki and Kitching, 1982; Pitman et al., 2018), low-density (Zalucki and Suzuki, 1987; Pitman et al., 2018) milkweed patches. Monarch butterflies also prefer to lay eggs on what are presumed to be higher quality younger shoots (Zalucki and Kitching, 1982) and, consequently, on regrowth milkweed that has been recently mowed (Fischer et al., 2015; Alcock et al., 2016). Although higher densities of eggs have been observed in agricultural landscapes compared to non-agricultural landscape (Pleasants and Oberhauser, 2013; Pitman et al., 2018), the rapid decline of milkweed in agricultural areas (Hartzler, 2010) has made non-agricultural areas increasingly important habitats for immediate restoration efforts.

In intensively managed non-agricultural landscapes, such as right-of-ways, naturally occurring milkweed is routinely mowed. Right-of-ways include roadsides, power line and utility corridors, and land adjacent to railroads. In the U.S. Midwest, an estimated 60–82% of roadsides in the past decade contained milkweed (Hartzler, 2010; Kasten et al., 2016) and across the monarch breeding range, milkweed on roadsides represents an estimated 10–34% of the currently available milkweed on the landscape (Flockhart et al., 2015; Pleasants, 2017). While there can be lower egg densities on milkweed in roadside habitat compared to other non-agricultural habitats (Kasten et al., 2016; Pitman et al., 2018), roadside right-of-ways cover an estimated 12 million acres of land in the U.S. (Forman et al., 2003) and represent a potentially undervalued conservation resource. However, common management practices for right-of-ways that are used to ensure road safety and aesthetics may be harmful to monarchs because mowing may occur too often or is poorly timed with monarch breeding. Whereas mowing may lead to direct mortality of developing monarchs, appropriately timed mowing can provide monarchs with fresh regrowth milkweed that is preferred for oviposition (Fischer et al., 2015). In addition, mowing temporarily reduces the presence of predators (Haan and Landis, 2019). Linking mowing practices to monarch egg-laying preference is, therefore, important for developing best management practices aimed at improving milkweed quality and understanding the conservation value of right-of-ways for monarchs. Reducing the frequency of mowing also increases species richness of native plants (Entsminger et al., 2017) while maintaining habitat in an early successional stage to benefit other insects that use right-of-ways (Munguira and Thomas, 1992; Berg et al., 2013).

In this paper, we used a paired plot (mowed and unmowed control) experimental design in a linear right-of-way to examine the effects of mowing common milkweed (*Asclepias syriaca*) on monarch butterfly egg-laying preferences. To examine general egg-laying preferences of females, we first tested whether the presence of eggs on milkweed was related to milkweed height, condition (leaf colour and damage), and density. Next, our goal was to determine whether female monarchs showed a preference for a particular age of milkweed. Previous studies have shown that monarchs prefer to lay eggs on young milkweed shoots (Zalucki and Kitching, 1982), including those that have been recently mowed and are regenerating (Fischer et al., 2015; Alcock et al., 2016; Haan and Landis, 2019). In one study, common milkweed that was 15 days of age (i.e. 15 days since mowing) had the highest egg counts following mowing, and egg counts subsequently declined as the milkweed aged (Fischer et al., 2015). We hypothesized that there would be a parabolic relationship between milkweed age and oviposition rates because monarchs prefer to lay eggs on young milkweed, but milkweed is not immediately available after mowing. Given the preferred milkweed age and variation in monarch egg-laying rates throughout the season, we then examined whether there was an optimal time window to mow milkweed to increase monarch egg-laying. We hypothesized that the optimal date to mow milkweed would be the date the peak number of eggs were counted minus the optimal age of milkweed preferred by egg-laying females. We hypothesized that mowing too early would have little effect on egg laying, while mowing too late in the breeding season would result in direct mortality of developing monarchs during peak breeding, in addition to there not being sufficient time for milkweed to regenerate and monarchs to mature. To determine whether mowing could occur more than once during the optimal mowing window, we also estimated developmental time from egg to eclosion, which is temperature-dependent (Zalucki, 1982). A subsequent mowing event should not occur while larvae or pupae, from eggs laid when milkweed was the optimal age following mowing, are still present within the managed area.

2. Methods

2.1. Study site

This study was conducted in the right-of-ways adjacent to two sections of Hwy 40 in Sarnia, Ontario, Canada (42.973°N, 82.345°W) where common milkweed (*Asclepias syriaca*) naturally occurs. The roadway was a two-lane paved highway with a speed limit of 80 km/h. Roadsides were naturalized grasses and shrub vegetation that was not actively managed for several years prior to the experiment. Plots were established in autumn 2015 and spring 2016, and mowing experiments were conducted during summer 2016 and 2017.

2.2. Experimental set-up

In September 2015 and June 2016, 49 paired plots were established at three different sizes to have variation in milkweed density among plots. There were 16 small (9 m^2), 16 medium (49 m^2), and 17 large (144 m^2) plots established. Plots were established at least 2 m apart in areas with 30–160 naturally occurring common milkweed plants per plot, resulting in milkweed densities ranging from 0.3 plants/m^2 to 6.9 plants/m^2 in the first week of June 2016. The plots were divided in half, with one side randomly assigned to be experimentally mowed once each year according to one of eight mowing treatments between mid-June and early August (Table 1). The other side of the plot was not mowed (control). Flags were used to demarcate all four corners of the plot and divide the two plot sides. Plots were mowed without disturbing the flags using a Briggs & Stratton (Wauwatosa, Wisconsin, USA) push mower with blades at a height of approximately 4 cm off the ground. This is shorter than is typical of mowing practices (15 cm; Zartman et al., 2013) and shorter than is recommended for monarch habitat (>25 cm; Pelton et al., 2018), so milkweed may have regenerated more slowly than usual. Following standard practices of mowing in right-of-ways, vegetation was not removed after mowing.

2.3. Egg and larval surveys

Plots were surveyed weekly from late June through the end of August for milkweed characteristics (see below) and monarch presence (eggs and larvae). At each milkweed plant, we recorded the number of monarch eggs and larvae, the plant height (cm), and condition (measured on a scale of 1–4; 1 = <5%, 2 = 5–40%, 3 = 41–80%, 4 = 81–100% of the plant discoloured or withered). In each instance where an egg or larva was found, we recorded the instar (larvae only; instar 1 through 5) and the height (cm) on the plant stem where the egg/larva was found.

2.4. Temperature data

To determine development rates from egg to eclosion, which depends on ambient temperature (Zalucki, 1982), we installed several thermochron iButtons (Maxim Integrated Products, Sunnyvale, California, USA) to record temperatures in plots throughout the summer of 2016 and 2017. Up to 15 pairs of iButtons were placed 30 cm from the ground in experimental plots (one on the mowed side and one on the control side) to record temperature every 30–60 min. Data were collected bi-

Table 1
Timing of plot mowing and number of replicates for each mowing treatment in 2016 and 2017. The number or replicates for each plot size are listed (L = large, M = medium, S = small). The plots were paired plots, with one half experimentally mowed according to one of the mowing treatments, while the other half was a control.

Mowing treatment	Number of replicates		Total number of replicates
	2016	2017	
June 3rd week	7 (2 L, 2 M, 3 S)	NA	7 (2 L, 2 M, 3 S)
June 4th week	7 (2 L, 3 M, 2 S)	7 (2 L, 2 M, 3 S)	14 (4 L, 5 M, 5 S)
July 1st week	7 (3 L, 2 M, 2 S)	7 (2 L, 3 M, 2 S)	14 (5 L, 5 M, 4 S)
July 2nd week	7 (2 L, 2 M, 3 S)	7 (3 L, 2 M, 2 S)	14 (5 L, 4 M, 5 S)
July 3rd week	7 (2 L, 3 M, 2 S)	7 (2 L, 2 M, 3 S)	14 (4 L, 5 M, 5 S)
July 4th week	7 (3 L, 2 M, 2 S)	7 (2 L, 3 M, 2 S)	14 (5 L, 5 M, 4 S)
August 1st week	7 (3 L, 2 M, 2 S)	7 (3 L, 2 M, 2 S)	14 (6 L, 4 M, 4 S)
August 2nd week	NA	7 (3 L, 2 M, 2 S)	7 (3 L, 2 M, 2 S)

weekly and iButtons reset after each collection. Several iButtons stopped working before the end of the summer, decreasing the number of plots sampled by the end of the season. We calculated mean temperature within plots from the iButton data and used temperature-dependent equations developed by Zalucki (1982) to estimate larval developmental rates.

2.5. Statistical analyses

R version 3.4.4 (R Core Team, 2018) was used for all statistical analyses. To examine the factors that influenced overall egg-laying preference, we used a binomial generalized linear mixed model implemented with the lme4 package (Bates et al., 2015). This model was used to explain whether there were eggs or not on a milkweed plant based on the following fixed effects: milkweed density in the plot, plant height (cm), plant condition, survey date, and year. A quadratic term was included in the model for both plant height and survey date to test for a parabolic relationship. We expected that monarchs would prefer young (short) or tall milkweed (Zalucki and Kitching, 1982). We also expected that egg laying would begin slowly, peak mid-summer, and then taper off at the end of the summer. Plot ID was included as a random effect. The continuous variables (milkweed density, plant height, condition, and survey date) were on vastly different scales, so they were scaled using the base scale function in R (created z-scores).

We compared egg counts following mowing between the mowed and control plot sides, using the glmmTMB package (Brooks et al., 2017) to implement a zero-inflated generalized linear mixed model with a Poisson distribution. The model explained the number of eggs in a plot based on the following fixed effects: plot side (mowed or control), survey date, and year. A quadratic term for survey date was included in the model to test for a parabolic relationship with the number of eggs laid. We also included an interaction between plot side and survey date and an interaction between plot side and survey date^2 to test whether the effect of survey date on the number of eggs laid depended on the plot side. Plot ID was included as a random effect. An offset of the number of milkweeds in the plot side was included in this model so that the response variable (number of eggs) was a per milkweed measure. Survey date was scaled (via z-scores) for model convergence.

To determine an optimal mowing strategy for increasing monarch reproduction, a final egg-laying model was used to explain egg counts in the mowed side of plots based on the following fixed effects: the week the plot was mowed, number of days since mowing, and year. This model was a zero-inflated generalized linear mixed model with a Poisson distribution (glmmTMB package; Brooks et al., 2017). Quadratic ‘mow week’ and ‘days since mow’ terms were included in the model to test for a parabolic relationship between these variables and the number of eggs counted. Plot ID was included as a random effect. An offset of the number of milkweeds in the plot side was also included in this model so that the response variable (number of eggs) was a per milkweed measure.

3. Results

Overall, 2017 was a more productive year for egg laying than 2016 (Tables 2–4). In 2016, a drought year in Southern Ontario, there were only 36 eggs counted throughout the entire season, compared to 437 eggs in 2017. Over both years, 90% of the plants surveyed ($n = 54,278$) were ranked with a condition of 1 (<5% discolouration or withering), 7% were ranked as 2 (5–40%), 1% were ranked as 3 (41–80%), and 1% were ranked as 4 (81–100%).

3.1. General egg-laying preferences

Eggs were preferentially laid on milkweed of better condition (less discolouration/withering; $\beta = -0.47 \pm 0.10$, $z = -4.72$, $p < 0.001$; Table 2). There was a significant parabolic (opening up) relationship between milkweed height and the presence of eggs (milkweed height: $\beta = -0.47 \pm 0.07$, $z = -6.35$, $p < 0.001$ and milkweed height^2: $\beta = 0.29 \pm 0.04$, $z = 7.96$, $p < 0.001$; Table 2), suggesting that eggs were preferentially laid on short (regenerating) and tall milkweed, but not milkweed of

Table 2
Model summary of parameter estimates from a binomial generalized linear mixed model explaining whether there were eggs or not on a milkweed plant based on milkweed density in the plot, milkweed height (cm), milkweed condition (measured on a scale of 1–4, 4 being the worst condition), survey date (Julian), year, and plot ID (random effect). Number of observations = 54,278. Both mowed and unmowed control plots were included in the model.

Parameter	Estimate ±SE	z value	p value	Variance ±SD
Random effect				
Plot ID				0.46 ± 0.68
Fixed Effects				
Intercept	−7.18 ± 0.24	−30.48	<0.001	
Milkweed density	0.01 ± 0.13	0.06	0.95	
Milkweed height	−0.47 ± 0.07	−6.35	<0.001	
Milkweed height^2	0.29 ± 0.04	7.96	<0.001	
Milkweed condition	−0.47 ± 0.10	−4.72	<0.001	
Survey date	0.84 ± 0.10	8.43	<0.001	
Survey date^2	−1.24 ± 0.10	−12.03	<0.001	
Year (2017)	3.24 ± 0.21	15.56	<0.001	

Table 3
Model summary of parameter estimates from a zero-inflated generalized linear mixed model (Poisson) explaining the number of eggs counted following mowing based on the plot side (mowed or control), survey date (Julian), year, interactions between plot side and survey date, and plot ID (random effect). Number of observations = 1141.

Parameter	Estimate ±SE	z value	p value	Variance ±SD
Random effect				
Plot ID				1.10 ± 1.05
Conditional model				
Intercept	-6.63 ± 0.38	-17.59	<0.001	
Plot side (mowed)	1.67 ± 0.26	6.45	<0.001	
Survey date	-0.23 ± 0.19	-1.24	0.22	
Survey date^2	0.04 ± 0.18	0.22	0.82	
Year (2017)	2.85 ± 0.27	10.64	<0.001	
Plot side (mowed): Survey date	-0.99 ± 0.27	-3.61	<0.001	
Plot side (mowed): Survey date^2	-0.55 ± 0.25	-2.23	0.03	
Zero-inflated model				
Intercept	0.37 ± 0.19	1.92	0.05	

Table 4
Model summary of parameter estimates from a zero-inflated generalized linear mixed model (Poisson) explaining the number of eggs in mowed plot sides based on the week of mowing (Table 1), number of days since the plot was mowed, year, and plot ID (random effect). Number of observations = 515.

Parameter	Estimate ±SE	z value	p value	Variance ±SD
Random effect				
Plot ID				0.48 ± 0.69
Conditional model				
Intercept	-6.18 ± 1.16	-5.34	<0.001	
Mow week	0.70 ± 0.57	1.23	0.22	
Mow week^2	-0.10 ± 0.07	-1.37	0.17	
Days since mow	0.06 ± 0.04	1.49	0.14	
Days since mow^2	-0.002 ± 0.001	-3.15	<0.01	
Year (2017)	3.11 ± 0.42	7.39	<0.001	
Zero-inflated model				
Intercept	0.04 ± 0.29	0.13	0.90	

intermediate heights. There was also a significant parabolic (opening down) relationship between the date a plot was surveyed and the probability of eggs being present (survey date: $\beta = 0.84 \pm 0.10$, $z = 8.43$, $p < 0.001$ and survey date^2: $\beta = -1.24 \pm 0.10$, $z = -12.03$, $p < 0.001$; Table 2). The highest total number of eggs across all plots were counted at the end of July. There was no significant effect of milkweed density on eggs being present or absent ($\beta = -0.01 \pm 0.13$, $z = 0.06$, $p = 0.95$; Table 2).

3.2. *Effects of mowing on egg laying*

Mowing had a positive effect on the number of eggs laid in a plot following mowing ($\beta = 1.67 \pm 0.26$, $z = 6.45$, $p < 0.001$; Table 3; Fig. 1a). In this model, there was no significant effect of survey date on the number of eggs laid (survey date: $\beta = -0.23 \pm 0.19$, $z = -1.24$, $p = 0.22$ and survey date^2: $\beta = 0.04 \pm 0.18$, $z = 0.22$, $p = 0.82$; Table 3), but there were significant interactions between the plot side and survey date (mowed plot side*survey date: $\beta = -0.99 \pm 0.27$, $z = -3.61$, $p < 0.001$ and mowed plot side*survey date^2: $\beta = -0.55 \pm 0.25$, $z = -2.23$, $p = 0.03$; Table 3). These interactions indicate that in mowed plot sides, there was a more negative effect of survey date on the number of eggs laid than in control plots. On average, 0.033 ± 0.128 (SD) eggs were laid per plant in mowed plots following mowing compared to 0.007 ± 0.061 eggs/plant in control plots.

3.3. *Timing of mowing and preferred milkweed age*

Among mowed plots, there was no significant effect of the week a plot was mowed on the number off eggs counted in a plot following mowing, though the parameter estimates showed a trend toward a parabolic (opening down) relationship (mow week: $\beta = 0.70 \pm 0.57$, $z = 1.23$, $p = 0.22$ and mow week^2: $\beta = -0.10 \pm 0.07$, $z = -1.37$, $p = 0.17$; Table 4; Fig. 2). The most eggs laid per plant following mowing were in plots mowed between the 2nd and 3rd weeks of July (Table 5; Fig. 1a). There were no eggs laid in plots that were mowed in the 3rd week of June or 2nd week of August. There was a trend toward a parabolic (opening down) relationship between the days since a plot was mowed (milkweed age) and the number of eggs counted in a plot following mowing (Fig. 2), but only the quadratic term was significant (days since mow: $\beta = 0.06 \pm 0.04$, $z = 1.49$, $p = 0.14$ and days since mow^2: $\beta = -0.002 \pm 0.001$, $z = -3.15$, $p < 0.01$; Table 4). Eggs were counted on regrowth

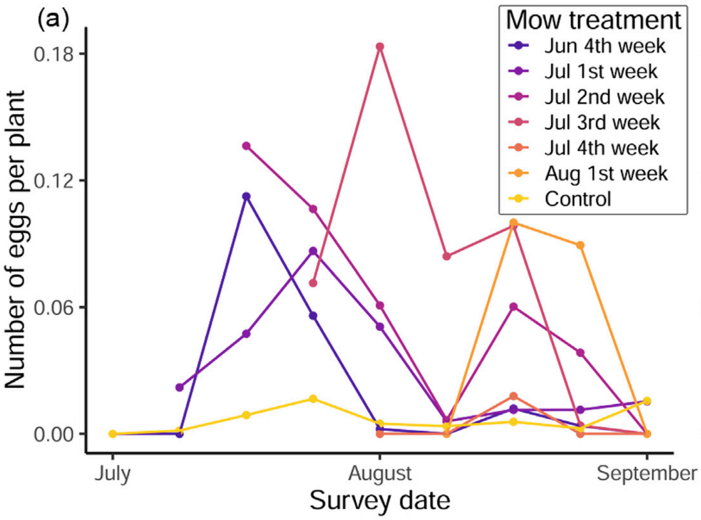

Fig. 1. (a) Number of eggs counted per plant over two survey seasons averaged across all plots by mow treatment. There were no eggs counted on plots mowed in in the 3rd week of June or the 2nd week of August, so these treatments are not displayed. Error bars were large, with extensive overlap, and not included to simplify the figure. (b) Number of eggs counted per plant in mowed plots based on the number of weeks since the plot was mowed (milkweed age). The sample size decreases as the number of weeks since mow increases because plots were not surveyed past the first week of September.

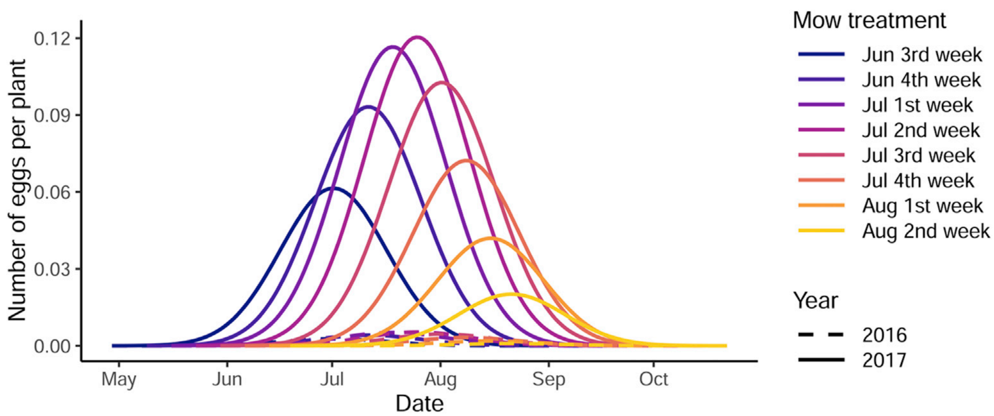

Fig. 2. Predicted number of eggs per milkweed plant given the date of mowing (colours) based on a zero-inflated generalized linear mixed model (Poisson; Table 4). There were more eggs counted in 2017 (solid) compared to 2016 (dashed). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 5
Mean number of eggs laid per plant (±SD) based on mowing treatment in 2016, 2017, and total.

Mow treatment	Number of eggs/plant (mean ± SD)		Total number of eggs/plant (mean ± SD)
	2016	2017	
June 3rd week	0	NA	0
June 4th week	0.003 ± 0.016	0.044 ± 0.138	0.022 ± 0.097
July 1st week	0.001 ± 0.008	0.060 ± 0.108	0.032 ± 0.083
July 2nd week	0.031 ± 0.115	0.082 ± 0.200	0.058 ± 0.166
July 3rd week	0	0.140 ± 0.280	0.074 ± 0.213
July 4th week	0	0.006 ± 0.030	0.004 ± 0.023
August 1st week	0	0.095 ± 0.281	0.049 ± 0.205
August 2nd week	NA	0	0
Control	0.001 ± 0.009	0.015 ± 0.089	0.007 ± 0.061

milkweed as early as 7 days following mowing, though plots were not revisited sooner than 6 days following mowing. The maximum number of eggs/plant counted in mowed plots occurred 1–3 weeks after the plot was mowed (Fig. 1a and b).

3.4. Larval development rate

Larval development from egg to eclosion was estimated at on average 22 days (range: 20.5–23.6 days).

4. Discussion

Our results suggest that mowing can have a positive effect on monarch egg laying depending on the time of year habitats are mowed in relation to peak egg laying rates and milkweed age preference. At our site in southern Ontario, we showed that the optimal time to mow (2nd–3rd week of July; Table 5) corresponded to seasonal peak egg-laying (end of July) minus the preferred age of milkweed by female monarchs (1–3 weeks since mow; Fig. 1a and b). This preferred age of milkweed corresponds to the amount of time it took predators to recolonize mowed milkweed in a previous study (2–4 weeks; Haan and Landis, 2019). In addition to a preference for regenerating milkweed, we found that monarchs preferred to lay eggs on the tallest milkweed plants and milkweed plants in good condition. There was no preference for oviposition in low-density milkweed patches, unlike in previous studies (Zalucki and Suzuki, 1987; Pitman et al., 2018). This may be because maximum milkweed densities in this study were low (11 milkweeds/m^2) compared to previous studies (29 milkweeds/m^2; Zalucki and Suzuki, 1987, 58 milkweeds/m^2; Pitman et al., 2018).

The timing of mowing did not have a statistically significant effect on egg laying, but mowing mid-July resulted in the largest number of eggs laid per plant at our study sites in southern Ontario, in the north-central part of the monarch breeding range (Table 5, Fig. 2). The effect of mowing prior to July at this latitude is unclear because few eggs were laid before July, but the survival of these eggs may be particularly important since they are produced by the first generation of monarchs. Mowing late July through mid-August would have resulted in higher mortality due to mowing during seasonal peak egg laying. In this study, plots were not mowed more than once in a season, yet considering the frequency of mowing would be important for allowing eggs that are laid following mowing to develop into adults prior to a second mowing event. Developmental time was estimated at 22 days from egg to adult and, further, peak egg laying occurred up to three weeks after a plot was mowed (Fig. 1a). This means that subsequent mowing could not have occurred sooner than 43 days after the previous mowing event if a majority of the eggs laid on mowed milkweed were to safely reach the adult stage. Lastly, when developing management plans for a large area of habitat, the extent of mowing within the habitat should be considered. Egg laying may not resume immediately after mowing as milkweed regrows, so a number of milkweeds should be left for monarchs to lay eggs while mowed milkweed is unavailable. Given these constraints, summer mowing of common milkweed in managed landscapes should not occur more than once around mid-July at this latitude (43°N), ideally leaving a few patches of mature milkweed behind.

Given that eastern North American monarch butterflies breed across a wide geographic area, optimal mowing regimes will no doubt differ by geographic location (particularly latitude) and local plant phenology. Furthermore, monarchs use at least 27 different species of milkweed across their range (Malcolm and Brower, 1986) and optimal strategies will likely differ depending on the target milkweed species. Since common milkweed is dominant in mid-west roadsides (Kasten et al., 2016), results from our study will be widely applicable. Similar to our results, in upstate New York (~42°N), the timing of mowing common milkweed differentially influenced the number of eggs laid on mowed plants (Fischer et al., 2015). There was increased egg-laying on plants that were mowed up until July 24 (a few days later than our study), but milkweeds that were mowed in August did not regrow with sufficient time left in the breeding season to allow for oviposition. The breeding season was also extended by 2 weeks as a result of mowing in July at this latitude. Similarly, mowing common milkweed in Virginia (~39°N) resulted in a three-week extension of the breeding season (Alcock et al., 2016), yet, unlike in upstate New York or southern Ontario, mowing was able to occur until mid-August at this latitude. In contrast to the studies in New York and Virginia, we found no evidence that the breeding season was extended in response to mowing, though we did not survey past the first week of September. While uncertainty remains about mowing regimes across the monarch breeding range and depending on the species of milkweed involved, these three studies (current study, Fischer et al., 2015; Alcock et al., 2016) show that mowing milkweed to benefit breeding monarchs can occur later in the season with decreasing latitude. Between 43°N and 39°N, mowing was beneficial for approximately one additional week into the summer with each degree of latitude south. However, mowing frequency is still an essential consideration and should not occur more frequently than every 43 days based on monarch developmental time at this latitude, though developmental time varies geographically by temperature (Urquhart, 1960; Zalucki, 1982).

Results from this study suggest habitat management may increase habitat quality for monarchs along roadsides. While there have been lower egg densities reported in roadside habitat compared to other habitats (Kasten et al., 2016; Pitman et al., 2018), roadsides could still represent an undervalued conservation resource owing to the reduction of milkweed in agricultural landscapes (Hartzler, 2010) and high incidence of milkweed in roadside habitats (Hartzler, 2010; Kasten et al., 2016, Grant et al., 2018). In addition, maintaining breeding habitat in linear right-of-ways ensures landscape connectivity (Ries et al., 2001), which could increase monarch oviposition rates (Zalucki et al., 2016). However, there is the potential that improving habitat quality for monarchs in roadsides could act as an ecological trap. Uptake of road salt run-off or contaminants from cars by milkweeds have the potential to negatively affect feeding monarchs. In one study, larval survival rates were lower on roadside-collected milkweed compared to prairie-collected milkweed, though it is unclear whether this was due to the elevated sodium levels in roadside milkweed or another factor (Snell-Rood et al., 2014). Monarchs are sodium-limited, and though extreme levels are dangerous, access to sodium has been shown to benefit developing monarchs (Snell-Rood et al., 2014). In addition, monarchs risk fatal collisions with vehicles (McKenna et al., 2001; Keilsohn et al., 2018; Kantola et al., 2019) and developing larvae that are exposed to traffic noise could perceive it as a stressor (Davis et al., 2018). Reducing the negative impact of traffic will be essential to maximizing the conservation potential of roadsides. Mowing may increase dispersal as individuals are forced to find new habitat, so reducing the frequency of mowing and mowing only a portion of roadside habitat can reduce road mortality (Skórka et al., 2013). In addition, estimating larval survival rates (a challenge with unmarked individuals), both among habitats and depending on different management practices, is an important next step toward understanding the conservation potential of roadsides.

Management strategies identified in this study are broadly applicable, both to other managed landscapes, such as power line corridors and urban parks, and because they may benefit other species that rely on landscapes in an early successional stage. For example, power line corridors are another undervalued conservation resource, where optimal timing and frequency of mowing of selected areas in the corridor could benefit not only monarchs, but also a variety of other butterflies (Lensu et al., 2011; Berg et al., 2013). Further, a single mowing event in summer would renew nectar resources for numerous insects when plants re-flower later in the summer (Noordijk et al., 2009), while reducing the frequency of mowing may increase native plant species richness (Entsminger et al., 2017). Management across various landscapes would also boost habitat connectivity for monarchs and other early successional-reliant species (Ries et al., 2001). However, avoiding mowing in certain areas remains important because it ensures habitat is available while mowed areas regenerate. It also preserves sections with taller vegetation (e.g. shrubs) to avoid completely altering habitat structure in these landscapes, considering that other organisms are reliant on this habitat. While mowing may make habitat attractive to some ground-nesting birds, mowing prior to August may not allow enough time for fledging and result in high nestling mortality (Patterson et al., 1996; Dale et al., 1997). Thus, the optimal mow date may need to shift to balance the needs of multiple species. Lack of optimal mowing practices in these habitats could either lead to ecological succession (i.e. avoiding mowing) or infrequent vegetation availability and high mortality of young (i.e. mowing too often).

Recovery and conservation of migratory eastern North American monarch butterflies, a population that has declined precipitously (Brower et al., 2012; Vidal and Rendón-Salinas, 2014), relies heavily on mitigating the drastic loss of milkweed on the landscape in the past few decades (Flockhart et al., 2015; Pleasants, 2017). Whereas increasing the quantity of milkweed should be a priority, monarchs can also benefit from improving the quality of existing milkweed on the landscape. We show that adhering to an optimal mowing regime in managed landscapes, such as right-of-ways, increases monarch oviposition. Management that considers the timing, frequency, and extent of mowing is optimal for breeding monarchs. We recommend that if mowing is to occur in the summer, it should occur before the seasonal breeding peak (timing), no more than once during this period (frequency), and some milkweed patches must not be mowed to ensure there remains oviposition substrate while mowed milkweed regenerates (extent). Further, rapid action is required if we are to reverse declines and aid in the recovery of this iconic species.

Role of the funding source

Funding was provided by the Ministry of Transportation Ontario (MTO) Highway Infrastructure Innovation Funding Program (D.R.N., D.T.T.F.), ECCC Habitat Stewardship Program (D.R.N.), Syngenta Canada, and the Liber Ero Fellowship (D.T.T.F.). The MTO provided us access to the study site, but the funding sponsors were not involved in the study design, data collection, analysis, interpretation, or writing of the manuscript.

Conflicts of interest

The authors declare no competing interests.

Acknowledgements

We thank Alex Kelly, Mark Bosco, Madison MacKinnon, Michelle Polley, and Sanjana Tarranum for conducting fieldwork and the Ministry of Transportation of Ontario (MTO) for allowing us to do research on their land along Highway 40. We also thank the David Suzuki Foundation for outreach and advice on this research project, as well as three anonymous reviewers for helpful comments that improved this manuscript.

References

Alcock, J., Brower, L.P., Williams Jr., E.H., 2016. Monarch butterflies use regenerating milkweeds for reproduction in mowed hayfields in northern Virginia. J. Lepidopterists' Soc. 70, 177–181.

Ausden, M., 2007. Habitat Management for Conservation: a Handbook of Techniques. Oxford University Press on Demand.

Batalden, R.V., Oberhauser, K., Peterson, A.T., 2007. Ecological niches in sequential generations of eastern North American monarch butterflies (Lepidoptera: danaidae): the ecology of migration and likely climate change implications. Environ. Entomol. 36, 1365–1373.

Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67, 1–48.

Berg, Å., Ahrné, K., Öckinger, E., Svensson, R., Wissman, J., 2013. Butterflies in semi-natural pastures and power-line corridors—effects of flower richness, management, and structural vegetation characteristics. Insect conservation and diversity 6, 639–657.
Borders, B., Lee-Mäder, E., 2014. Milkweeds: a conservation practitioner's guide. Portland, OR: xerces society for invertebrate conservation. Proc. R. Soc. B 282, 9.
Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Maechler, M., Bolker, B.M., 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. The R Journal 9, 378–400.
Brower, L.P., 1995. Understanding and misunderstanding the migration of the monarch butterfly (Nymphalidae) in North America: 1857-1995. J. Lepidopterists' Soc. 49, 304–385.
Brower, L.P., Castilleja, G., Peralta, A., Lopez-Garcia, J., Bojorquez-Tapia, L., Díaz, S., Melgarejo, D., Missrie, M., 2002. Quantitative changes in forest quality in a principal overwintering area of the monarch butterfly in Mexico, 1971–1999. Conserv. Biol. 16, 346–359.
Brower, L.P., Taylor, O.R., Williams, E.H., Slayback, D.A., Zubieta, R.R., Ramirez, M.I., 2012. Decline of monarch butterflies overwintering in Mexico: is the migratory phenomenon at risk? Insect Conservation and Diversity 5, 95–100.
COSEWIC, 2016. COSEWIC Assessment and Status Report on the Monarch *Danaus plexippus* in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa. Xiii-59. http://www.registrelep-sararegistry.gc.ca/default.asp?lang=en&n=24F7211B-1.
Dale, B.C., Martin, P.A., Taylor, P.S., 1997. Effects of hay management on grassland songbirds in Saskatchewan. Wildl. Soc. Bull. 25, 616–626.
Davis, A.K., Schroeder, H., Yeager, I., Pearce, J., 2018. Effects of simulated highway noise on heart rates of larval monarch butterflies, *Danaus plexippus*: implications for roadside habitat suitability. Biol. Lett. 14, 20180018.
Durant, D., Tichit, M., Kerneis, E., Fritz, H., 2008. Management of agricultural wet grasslands for breeding waders: integrating ecological and livestock system perspectives—a review. Biodivers. Conserv. 17, 2275–2295.
Entsminger, E.D., Jones, J.C., Guyton, J.W., Strickland, B.K., Leopold, B.D., 2017. Evaluation of mowing frequency on right-of-way plant communities in Mississippi. Journal of Fish and Wildlife Management 8, 125–139.
Fischer, S.J., Williams, E.H., Brower, L.P., Palmiotto, P.A., 2015. Enhancing monarch butterfly reproduction by mowing fields of common milkweed. Am. Midl. Nat. 173, 229–240.
Flockhart, D.T.T., Wassenaar, L.I., Martin, T.G., Hobson, K.A., Wunder, M.B., Norris, D.R., 2013. Tracking multi-generational colonization of the breeding grounds by monarch butterflies in eastern North America. Proceedings of the Royal Society B 280, 20131087.
Flockhart, D.T.T., Pichancourt, J.-B., Norris, D.R., Martin, T.G., 2015. Unravelling the annual cycle in a migratory animal: breeding-season habitat loss drives population declines of monarch butterflies. J. Anim. Ecol. 84, 155–165.
Flockhart, D.T.T., Larrivee, M., Prudic, K.L., Norris, D.R., 2019. Estimating the annual distribution of monarch butterflies in Canada over 16 years using citizen science data. Facets. https://doi.org/10.1139/facets-2018-0011 (in press).
Forman, R.T.T., Sperling, D., Bissonette, J.A., Clevenger, A.P., Cutshall, C.D., Dale, V.H., Fahrig, L., France, R.L., Heanue, K., Goldman, C.R., Jones, J., 2003. Road Ecology: Science and Solutions. Island Press.
Haan, N.L., Landis, D.A., 2019. Grassland disturbance increases monarch butterfly oviposition and decreases arthropod predator abundance. Biol. Conserv. 233, 185–192.
Hartzler, R.G., 2010. Reduction in common milkweed (*Asclepias syriaca*) occurrence in Iowa cropland from 1999 to 2009. Crop Protect. 29, 1542–1544.
Kantola, T., Tracy, J.L., Baum, K.A., Quinn, M.A., Coulson, R.N., 2019. Spatial risk assessment of eastern monarch butterfly road mortality during autumn migration within the southern corridor. Biol. Conserv. 231, 150–160.
Keilsohn, W., Narango, D.L., Tallamy, D.W., 2018. Roadside habitat impacts insect traffic mortality. J. Insect Conserv. 22, 183–188.
Kasten, K., Stenoien, C., Caldwell, W., Oberhauser, K.S., 2016. Can roadside habitat lead monarchs on a route to recovery? J. Insect Conserv. 20, 1047–1057.
Lark, T.J., Salmon, J.M., Gibbs, H.K., 2015. Cropland expansion outpaces agricultural and biofuel policies in the United States. Environ. Res. Lett. 10, 044003.
Lensu, T., Komonen, A., Hiltula, O., Päivinen, J., Saari, V., Kotiaho, J.S., 2011. The role of power line rights-of-way as an alternative habitat for declined mire butterflies. J. Environ. Manag. 92, 2539–2546.
Malcolm, S.B., Brower, L.P., 1986. Selective oviposition by monarch butterflies (*Danaus plexippus L.*) in a mixed stand of *Asclepias curassavica L.* and *A. incarnata L.* in south Florida. J. Lepidopterists' Soc. 40, 255–263.
McKenna, D.D., McKenna, K.M., Malcom, S.B., Bebenbaum, M.R., 2001. Mortality of Lepidoptera along roadways in central Illinois. Journal-lepidopterists society 55, 63–68.
Munguira, M.L., Thomas, J.A., 1992. Use of road verges by butterfly and burnet populations, and the effect of roads on adult dispersal and mortality. J. Appl. Ecol. 29, 316–329.
Noordijk, J., Delille, K., Schaffers, A.P., Sýkora, K.V., 2009. Optimizing grassland management for flower-visiting insects in roadside verges. Biol. Conserv. 142, 2097–2103.
Oberhauser, K., Peterson, A.T., 2003. Modeling current and future potential wintering distributions of eastern North American monarch butterflies. Proc. Natl. Acad. Sci. Unit. States Am. 100, 14063–14068.
Patterson, M.P., Best, L.B., 1996. Bird abundance and nesting success in Iowa CRP fields: the importance of vegetation structure and composition. Am. Midl. Nat. 135, 153–167.
Pecenka, J.R., Lundgren, J.G., 2015. Non-target effects of clothianidin on monarch butterflies. Sci. Nat. 102, 19.
Pelton, E., McKnight, S., Fallon, C., Code, A., Hopwood, J., Hoyle, S., Jepsen, S., Black, S.H., 2018. Managing for monarchs in the west: best management practices for conserving the monarch butterfly and its habitat. In: The Xerces Society for Invertebrate Conservation. Portland, Oregon, USA, p. 106. Available online at: www.xerces.org.
Pitman, G.M., Flockhart, D.T.T., Norris, D.R., 2018. Patterns and causes of oviposition in monarch butterflies: implications for milkweed restoration. Biol. Conserv. 217, 54–65.
Pleasants, J., 2017. Milkweed restoration in the Midwest for monarch butterfly recovery: estimates of milkweeds lost, milkweeds remaining and milkweeds that must be added to increase the monarch population. Insect Conservation and Diversity 10, 42–53.
Pleasants, J.M., Oberhauser, K.S., 2013. Milkweed loss in agricultural fields because of herbicide use: effect on the monarch butterfly population. Insect Conservation and Diversity 6, 135–144.
Pleasants, J.M., Zalucki, M.P., Oberhauser, K.S., Brower, L.P., Taylor, O.R., Thogmartin, W.E., 2017. Interpreting surveys to estimate the size of the monarch butterfly population: pitfalls and prospects. PLoS One 12, e0181245.
R Core Team, 2018. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.
Ries, L., Debinski, D.M., Wieland, M.L., 2001. Conservation value of roadside prairie restoration to butterfly communities. Conserv. Biol. 15, 401–411.
Scott, J.M., Goble, D.D., Haines, A.M., Wiens, J.A., Neel, M.C., 2010. Conservation-reliant species and the future of conservation. Conservation Letters 3, 91–97.
Semmens, B.X., Semmens, D.J., Thogmartin, W.E., Wiederholt, R., López-Hoffman, L., Diffendorfer, J.E., Pleasants, J.M., Oberhauser, K.S., Taylor, O.R., 2016. Quasi-extinction risk and population targets for the Eastern, migratory population of monarch butterflies (Danaus plexippus). Sci. Rep. 6, 23265.
Skórka, P., Lenda, M., Moroń, D., Kalarus, K., Tryjanowski, P., 2013. Factors affecting road mortality and the suitability of road verges for butterflies. Biol. Conserv. 159, 148–157.
Snell-Rood, E.C., Espeset, A., Boser, C.J., White, W.A., Smykalski, R., 2014. Anthropogenic changes in sodium affect neural and muscle development in butterflies. Proc. Natl. Acad. Sci. Unit. States Am. 201323607.
Urquhart, F.A., 1960. The Monarch Butterfly. University of Toronto Press.
Vidal, O., Rendón-Salinas, E., 2014. Dynamics and trends of overwintering colonies of the monarch butterfly in Mexico. Biol. Conserv. 180, 165–175.
Zalucki, M.P., 1982. Temperature and rate of development in *Danaus plexippus L.* and *D. chrysippus L.* (Lepidoptera: nymphalidae). Aust. J. Entomol. 21, 241–246.

Zalucki, M.P., Kitching, R.L., 1982. Dynamics of oviposition in *Danaus plexippus* (Insecta: Lepidoptera) on milkweed, Asclepias spp. J. Zool. 198, 103–116.
Zalucki, M.P., Suzuki, Y., 1987. Milkweed patch quality, adult population structure, and egg laying in the monarch butterfly. J. Lepidopterists' Soc. 41, 13–22.
Zalucki, M.P., Parry, H.R., Zalucki, J.M., 2016. Movement and egg laying in monarchs: to move or not to move, that is the equation. Austral Ecol. 41, 154–167.
Zartman, R.E., McKenney, C.B., Wester, D.B., Sosebee, R.E., Borrelli, J.B., 2013. Precipitation and mowing effects on highway rights-of-way vegetation height and safety. Landsc. Ecol. Eng. 9, 121–129.