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ORIGINAL PAPER

Host plant patch size selection of an endangered butterfly, the mottled duskywing (*Erynnis martialis*), at a reintroduction site

Michelle Polley[1] · Jessica E. Linton[2] · Adrienne Brewster[3] · Alistair S. MacKenzie[4] · Nusha Keyghobadi[5] · Jessica Steiner[6,7] · Taylor Kerekes[6] · D. Ryan Norris[1]

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Abstract

Butterflies select host plants, which are an essential but often limiting resource, based on a variety of features, including characteristics of host plant distribution and patch size. Since selection is assumed to translate to fitness benefits, assessing characteristics butterflies use to select host plants at reintroduction sites could reveal catalysts for post-release success. To understand whether endangered Mottled Duskywing (*Erynnis martialis*) butterflies select their host plants based on patch size, we created a Resource Selection Function from 115 observations at a successful reintroduction site. We assessed selection of host plants distributed as individual plants (<1 m^2), small patches (<10 m^2), medium patches (<30 m^2), and large patches (>30 m^2) in females, males, and all observations combined (including unknown sex). All three classes of observations showed strong selection for large host plant patches, whereas medium host plant patches were moderately selected when all observations were considered, but not selected when males or females were considered separately. Individual plants and small patches were used in proportion to their availability. At two additional nearby sites where reintroduction of Mottled Duskywing was less successful, the density of large host plant patches was 25 and 44 times lower than the successful reintroduction site. Implications for insect conservation. Our results suggest that further reintroductions of Mottled Duskywing should consider availability and size of host plant patches at potential release sites. Our work highlights the value of post-release monitoring for assessing habitat preferences of reintroduced individuals and provides one example of how adaptive management could be used in reintroductions of endangered species.

Keywords Habitat use · *Hesperidae* · Resource selection function · Translocation · Species at risk

Introduction

For animal reintroductions to succeed, founders must be provided with resources that are sufficiently abundant and properly distributed to ensure that survival and reproductive rates result in positive population growth. However, defining the optimal abundance and distribution of resources at reintroduction sites can be challenging (IUCN/SSC 2013; Daniels et al. 2018; Berger-Tal et al. 2020). Knowledge about species' resource needs is usually derived from extant populations that may not face the same pressures that reintroduced populations would during colonization, such as extreme low density and abundance (IUCN/SSC 2013). More commonly, species' resource needs are not well known, even within extant populations, limiting the level of detail at which release-site resources can be assessed (IUCN/SSC 2013; Berger-Tal et al. 2020). One way to refine our understanding of optimal abundance and distribution of

✉ Michelle Polley
michelle.l.polley@gmail.com

1 Department of Integrative Biology, University of Guelph, Guelph, ON, Canada

2 Natural Resource Solutions Inc., Waterloo, ON, Canada

3 Cambridge Butterfly Conservatory, Cambridge, ON, Canada

4 Ontario Parks, Ministry of Environment, Conservation, and Parks, Pinery Provincial Park, Grand Bend, ON, Canada

5 Department of Biology, Western University, London, ON, Canada

6 Wildlife Preservation Canada, Guelph, ON, Canada

7 Present address: Wilder Institute, Calgary Zoo, Calgary, AB, Canada

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resources at reintroduction sites is to directly observe which resources founders choose, since selection of a resource, excluding ecological traps (Schlaepfer et al. 2002), is considered beneficial to an individual's performance (Boyce and McDonald 1999). Post-release selection could indicate which resources are advantageous for founder success, informing future reintroduction site selection or restoration efforts (Le Gouar et al. 2012; Osborne et al. 2022).

Butterflies are the most commonly reintroduced insect group and would benefit from insights about post-release selection of their most critical resource: larval host plants (Schultz et al. 2008; Curtis et al. 2015; Daniels et al. 2018; Demarse et al. 2022). The presence of host plants is a prerequisite to release site selection but characteristics such as the size of host plant patches available could impact reintroduction outcomes if released butterflies prefer or avoid certain patches (Rabasa et al. 2005, 2008; Osborne et al. 2022; Crone and Schultz 2022). Outside of the context of reintroductions, host plant patch size has been shown to impact oviposition site selection (Čelik 2013; Pschera and Warren 2018; Dunskis et al. 2024) and the likelihood of patch occupancy (Brommer and Fred 1999; Puntenney and Schorr 2016; Macgregor et al. 2017), both of which would affect the outcomes of reintroduction efforts. Knowing the size of host plant patches that reintroduced butterflies select could facilitate adaptive management of butterfly reintroduction efforts, allowing refinement of site choice and site restoration, thereby increasing the effectiveness of subsequent reintroductions.

To understand selection of host plant patches at a butterfly reintroduction site, we used butterfly location data from extensive post-release monitoring of the first ever reintroduction of Mottled Duskywing (*Erynnis martialis*), which took place at Pinery Provincial Park ('Pinery') in southwestern Ontario (Polley et al. *In review*). Mottled Duskywing are a globally vulnerable species of skipper butterfly (family *Hesperidae*), considered at some level of risk throughout the entirety of their range (NatureServe 2025), including being listed as endangered in Canada and the province of Ontario (COSEWIC 2012; COSSARO 2014). Mottled Duskywing use a variety of habitat types such as dry prairies, oak savannas, pine barrens and alvars that have become globally rare due to a variety of anthropogenic causes (Linton 2015; Schweitzer et al. 2018). Host plants for Mottled Duskywing in Ontario are *Ceanothus herbaceous* and *Ceanothus americanus*, both of which are used for oviposition and larval feeding, larval and pupal shelter, and as nectar sources for adults (COSSARO 2014). It has been suggested that Mottled Duskywing use networks of patches of their host plants that are interspersed by scattered individual plants (Schweitzer et al. 2018; Demarse et al. 2023), though this preference has not been quantified.

We examined which host plants patches (individual plants [< 1 m^2] and small [< 10 m^2], medium [< 30 m^2], and large [> 30 m^2] patches) Mottled Duskywing butterflies selected during population establishment at one release site within Pinery. Using the results of this analysis, we then addressed whether the availability of host plant patches in preferred size classes may have affected post-release outcomes at two less successful Mottled Duskywing reintroduction sites in Pinery. Understanding reintroduced Mottled Duskywings' selection of host plant patches based on size could facilitate adaptive management of the reintroduction project in question, provide useful information when selecting and managing additional release sites for this species and offers an example of fine-scale habitat selection analysis and monitoring that can be achieved during butterfly reintroductions.

Methods

Mottled duskywing releases and release sites

We studied host plant patch size selection by reintroduced Mottled Duskywing (*Erynnis martialis*) in Pinery Provincial Park ("Pinery") in southwestern Ontario, Canada. Details of the releases can be found in Polley et al. (*In review*). Briefly here, the reintroduction included releases of captive-reared Mottled Duskywing (Brewster et al., *In review*) at three different life-stages (larvae, pupae and adults) in various combinations at three sites (sites A, B and C) where habitat was deemed appropriate for the species (Linton 2022). The precise locations of the study sites are withheld because of the endangered status of this species. *C. americanus* and *C. herbaceous* are referred to collectively as 'host plants', since the two species co-occur, often within the same patch, at release sites and were not differentiated during mapping.

Site A consisted of 7.48 ha of oak savanna that included wide swaths of open habitat and sparse canopy cover (Linton 2022). The site contained flowering plants, intermittent woody shrub growth (mainly *Rhus aromatica* and *Prunus virginia*), and both species of host plants. Mottled Duskywing were first reintroduced to site A in 2021 with the release of 310 individuals (138 pupae and 172 adults), which resulted in in-situ reproduction and persistence at the site. An additional 129 adults and 5 pupae were released at site A in 2023 (Polley et al. *In review*).

Sites B and C were both smaller than site A, and habitat at each differed slightly from that at site A. Site B was 5.25 ha and was characterized by open, sandy soils and scattered stands of small White Pine (*Pinus strobus*) and Eastern Red Cedar (*Juniperus virginiana*; Linton 2022). Releases at site B consisted of 291 Mottled Duskywing larvae released in 2022 (Polley et al. *In review*). Site C was the smallest release site at 1.11 ha and contained hilly sections of unforested habitat bordered by tall, relatively dense oak-dominated forest (Linton 2022). Releases at site C included 392 larvae in 2021 and 92 adults in 2022 (Polley et al. *In review*). Mottled Duskywing occurred at very low densities at sites B and C following releases.

Mottled duskywing surveys

At site A, we used butterfly observations from distance sampling surveys (Isaac et al. 2011; Buckland et al. 2015) carried out from May – Aug. 2023 along 31 parallel linear transects 25–225 m in length which ran north-south and were spaced 20 m apart (Polley et al. *In review*). Transects were surveyed in dry weather conditions that met Pollard's (1997) criteria for butterfly counts: at 13–17 °C provided that there was no cloud cover, and at > 17 °C no matter the level of cloud cover. Total survey effort included 8–12 surveys of each transect over the course of the season. Transects were walked at a slow, consistent pace by a pair of surveyors, with the lead person responsible for sighting Mottled Duskywing butterflies and the second person responsible for navigating the transect and record keeping. When possible, Mottled Duskywing butterflies encountered during surveys were captured to determine sex. For each observation, we collected Universal Transverse Mercator (UTM) coordinates using a handheld GPS (Garmin Ltd., Olathe, Kansas). In total, we recorded 115 Mottled Duskywing butterfly observations made up of 46 females, 29 males, and 40 individuals of unknown sex. All butterflies were released at their location of capture. Given dimensions of the site are 1240 × 213 m and Mottled Duskywing butterflies have been recorded to move as far as 1985 m (Demarse 2022), we assumed that individual butterflies could access and select habitat over the entirety of the site.

Host plant patches and study area boundaries

Site boundaries were established prior to surveying for Mottled Duskywing and were drawn to include areas that met the definition of habitat for the species, with sparse canopy cover and relatively abundant food plants (COSEWIC 2012; Schweitzer et al. 2018; Linton 2022). Logical boundaries existed at the perimeter of each study site, where suitable habitat gave way to mixed forest with higher canopy cover, reducing the presence and size of host plants. Though *Ceanothus sp.* plants grow in the forest surrounding the sites, they are at low density and the relatively closed canopy does not suit the definition of habitat for Mottled Duskywing (Schweitzer et al. 2018).

To map Mottled Duskywing host plants at sites A and B in 2022 and site C in 2023, we used a high precision Trimble GPS (Model: SxBlue II GNSS) capable of recording locations within 1 m at 95% accuracy. Host plant patches > 1 m^2 were mapped as polygons. Any individual plants < 1 m^2 were mapped as points and later converted to uniform polygons (0.025 m^2, which was the mean area (m^2) of a random subset of individual plants at the site) to allow for their analysis alongside the polygons in other size classes (Fig. 1.1). Host plant data were processed in ArcGIS Pro (ESRI, version 2.8.8) and all host plant polygons were assigned to host plant patch size classes based on their area (m^2).

Resource selection function (RSF) for observations at site A

RSFs compare locations used by an animal ("used") to locations that were available to the animal (random locations deemed as "available"). This comparison provides the ability to assess positive (preference), negative (avoidance), or neutral (use = availability) selection for a given resource or habitat (Manly 2007, Boyce and McDonald 1999). We created a series of fourth-order RSF's to compare host plant resources at locations where Mottled Duskywing butterflies were observed ("used" locations, $n = 115$) to locations that were available to them ("available" locations, $n = 1150$; Manly et al. 2007). The number of "available" locations was consistent with the convention of employing a 10:1 ratio of "available" locations to "used" locations (Fig. 1.2; Nad'o and Kaňuch 2018). To assess selection of host plant patches, a 5 m circular buffer, sufficient to account for potential error in the UTM coordinates (0–3.79 m), was defined around each "used" and "available" location (Fig. 1.3). For each location, we used ArcGIS Pro to extract (1) the count of host plant patches in each size class that intersected, or were contained within, the buffer, and (2) the area (m^2) of host plant patches in each size class contained within the buffer.

To generate RSF estimates for each size class of host plant patches, we used binomial generalized linear models (GLMs) with a logit link function. All data processing and statistical analysis were performed with the R statistical computing software (version 4.2.0; R Core Team 2022). Our binary response variable represented whether a location was "used" (= 1) or "available" (= 0). Models were fit separately for all observations, observations of females, and observations of males, to identify any sex-dependent disparities in host plant resource selection. RSF's containing only female or only male 'used' points were created with random subsets of the total 1150 "available" locations to maintain a 10:1 ratio of "available" to "used" locations. For fixed effects, we considered two main variables which were modelled separately: (1) count (n) of host plant patches in each size class that intersected or were contained within the buffer(s), and (2) the measured area (m^2) of host plant patches in each

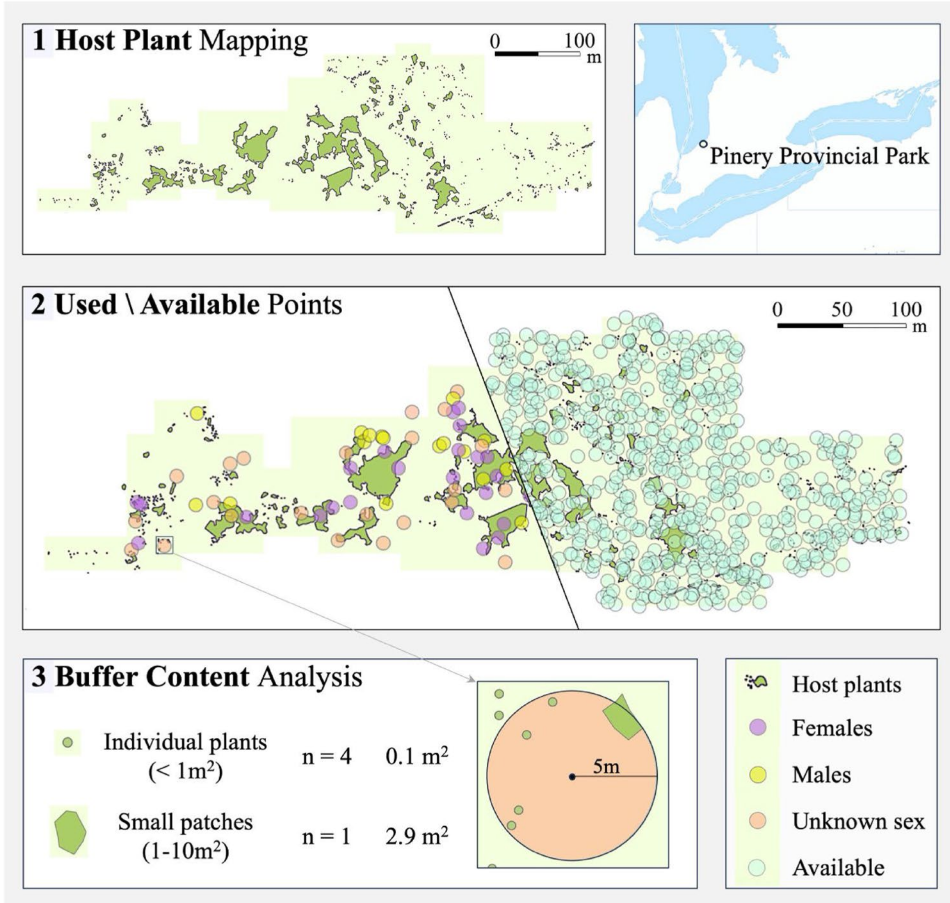

Fig. 1 The method used for estimating Mottled Duskywing host plant resource selection. (1) Host plants at a Mottled Duskywing reintroduction site (site A) in Pinery Provincial Park were mapped in detail. Host plant resources were then measured and divided into size classes: individual plants (<1 m^2), small patches (1–10 m^2), medium patches (10–30 m^2), and large patches (>30 m^2). (2) Map stylised to show 'used' (n=115 throughout the site; a subset of which are shown on left side of map) and 'available' (n=1150 throughout the site; a subset of which are shown on right side of map) locations. 'Used' locations were butterfly observations (females, males, and unknown sex) made during distance sampling surveys in 2023, and 'available' locations were randomly generated at a ratio of 10:1 ('used':'available'). A 5 m buffer radius was then created around all locations. (3) An example of how the count and area (m^2) of each size class of host plant patches was calculated within a buffer, which was used to create a Resource Selection Function. Map in the top right shows the location of Pinery Provincial Park in southwestern Ontario, Canada

size class that was contained within the buffer(s). However, within each model, the fixed effect was calculated for each of the four size classes of host plant patches, and all were included since correlations between the size classes were consistently low (<0.16). Therefore, six models were fit in total (2 for all observations, 2 for females-only, and 2 for males-only). The RSF output was a coefficient of selection (β) and was assessed at $\alpha=0.05$. A positive coefficient of selection ($\beta>0$) with a confidence interval not overlapping zero indicated selection for the relevant size class of host plant patches.

Comparison of host plant patch size density to sites B and C

To compare the relative host plant patch availability at two other reintroduction sites at Pinery (sites B and C), we compiled the count and density (m^2/ha) of host plant patches in all size classes at all three sites (Table 1). Host plants at sites B and C were mapped and classified in the same manner as at site A, allowing for comparison of host plant patch availability between the three sites. RSF's were not able to be created for sites B and C due to very few ($n<10$) observations of Mottled Duskywing butterflies at those sites.

Results

Resource selection function for observations at site A

Individual host plants and small host plant patches (1–10 m^2) were used by all groups (females, males and all observations pooled) in proportion to their availability (Table 1; Fig. 2). There was moderate evidence for selection for medium patches (10–30 m^2) when all observations were pooled and only weak evidence ($0.10>p>0.05$) for selection of medium patches when females and males were analyzed separately (Table 1; Fig. 2). All groups showed strong selection for large patches of host plants (>30 m^2; Table 1; Fig. 2).

Comparison of host plant patch size density to sites B and C

At site B, individual plant, small patch, and medium patch size classes were slightly less dense (1.3, 1.5 and 1.9 times, respectively) than at site A (Table 2). Similarly, at site C, individual plants were 1.6 times less dense than at site A.

Table 1 Results of a resource selection function estimating mottled Duskywing (*Erynnis martialis*) butterflies' selection of host plant (*Ceanothus herbaceous* and *Ceanothus americanus*) resources in different size classes at a reintroduction site (site A) in pinery provincial Park, Ontario, Canada

Group	Host plant size class	Selection coefficient (β)	2.5% CI	97.5% CI	p
Count within buffers					
All observations	Individual plant	0.025	− 0.103	0.129	0.67
	Small	0.058	− 1.123	0.930	0.91
	Medium	0.969	0.397	1.487	**<0.001***
	Large	1.376	1.039	1.720	**<0.001***
Females	Individual plant	0.106	− 0.053	0.241	0.14
	Small	− 0.167	− 3.034	1.345	0.87
	Medium	0.934	− 0.205	1.887	0.07
	Large	1.832	1.269	2.436	**<0.001***
Males	Individual plant	0.018	− 0.309	0.267	0.9
	Small	0.037	− 2.846	1.634	0.97
	Medium	1.005	− 0.179	2.027	0.06
	Large	1.130	0.448	1.809	**<0.001***
Area within buffers					
All observations	Individual plant	0.167	− 0.54	0.736	0.6
	Small	0.032	− 0.258	0.231	0.79
	Medium	0.092	0.02	0.155	**0.006***
	Large	0.033	0.024	0.041	**<0.001***
Females	Individual plant	0.642	− 0.245	1.341	0.1
	Small	0.072	− 0.397	0.344	0.67
	Medium	0.117	− 0.031	0.231	0.06
	Large	0.045	0.031	0.058	**<0.001***
Males	Individual plant	0.040	− 1.829	1.481	0.96
	Small	− 0.101	− 1.543	0.328	0.77
	Medium	0.104	− 0.036	0.224	0.09
	Large	0.035	0.017	0.053	**<0.001***

Estimates of the selection coefficient (β) from a binomial GLM with the logit link function and associated 2.5% and 97.5% confidence intervals (CI) are shown. Fixed variables for models were '*count within buffers*' (the number of each size class of host plant patch within buffers) and *'area within buffers'* (the total area [m^2] of each size class of host plant patch within buffers). Positive estimates of β with upper and lower confidence intervals that do not overlap with zero indicate selection for a particular size class (* indicates significance at α = 0.05)

However, small and medium patches at site C were 7.3 and 2.2 times denser than site A (Table 2). In contrast to smaller host plant patches, the disparity in the availability of large host plant patches between the three sites was considerable: large patches at sites B and C were 44 and 25 times less dense than at site A (Table 2).

Discussion

We provide evidence of strong selection for large patches (> 30 m^2) of host plants (*Ceanothus herbaceous* and *Ceanothus americanus*) by Mottled Duskywing butterflies during successful colonization of a reintroduction site (site A). Selection for large host plant patches was exhibited by each sex and when all observations were pooled (including individuals of unknown sex). We suggest that the availability of large host plant patches was beneficial for species establishment at site A. As of 2025, site A hosts a dense population of Mottled Duskywing that has shown signs of persistence in the four years since releases began (Polley et al. *In review*; M.P., J.E.L., D.R.N. *pers. obs.*). Given Mottled Duskywing are endangered in Canada and are declining or extirpated in much of their U.S. range (COSEWIC 2012), it is crucial to maximize the probability that founders will reproduce and make a genetic contribution to the next generation. The apparently successful reintroduction of Mottled Duskywing at site A was achieved by releasing a total 444 animals (Polley et al. *In review*) and, after three years of reintroductions, genetic diversity at this site is considered comparable to the source population (A. Aboulnaga, S. Kroze, N.K., D.R.N., J.E.L. M.P., A.B., *unpubl. data*.).

The availability of large host plant patches could impact reintroduction outcomes by influencing the retention of Mottled Duskywing adults at release sites. Some butterfly species have been shown to disperse in search of host plant patches that meet size or spatial configuration preferences (Brommer and Fred 1999) or to access habitat of higher quality (Matter and Roland 2002), so the presence of preferred patch sizes at release sites may prevent or reduce Mottled Duskywing dispersal post-release. As a result, released Mottled Duskywing may be present at higher density at sites where large host plant patches are available, resulting in greater probability of encountering mates. The availability of large host plant patches may also increase the fecundity of released Mottled Duskywing if non-dispersers conserve time and energy that would otherwise be spent on dispersal movement during a brief reproductive window (Henry and Schultz 2013; Crone and Schultz 2022).

It is also possible that medium or small host plant patches and individual plants are less effective resources to support Mottled Duskywing colonization. In contrast to strong selection for large host plant patches, we found only moderate evidence for selection of medium patches (10–30 m^2), and no significant evidence of selection for small host plant patches (1–10 m^2) or individual plants (< 1 m^2). Additional evidence to support this hypothesis comes from comparing the availability of host plant resources in all patch size classes at site A to two additional reintroduction sites (sites B and C), where there were low post-release abundances

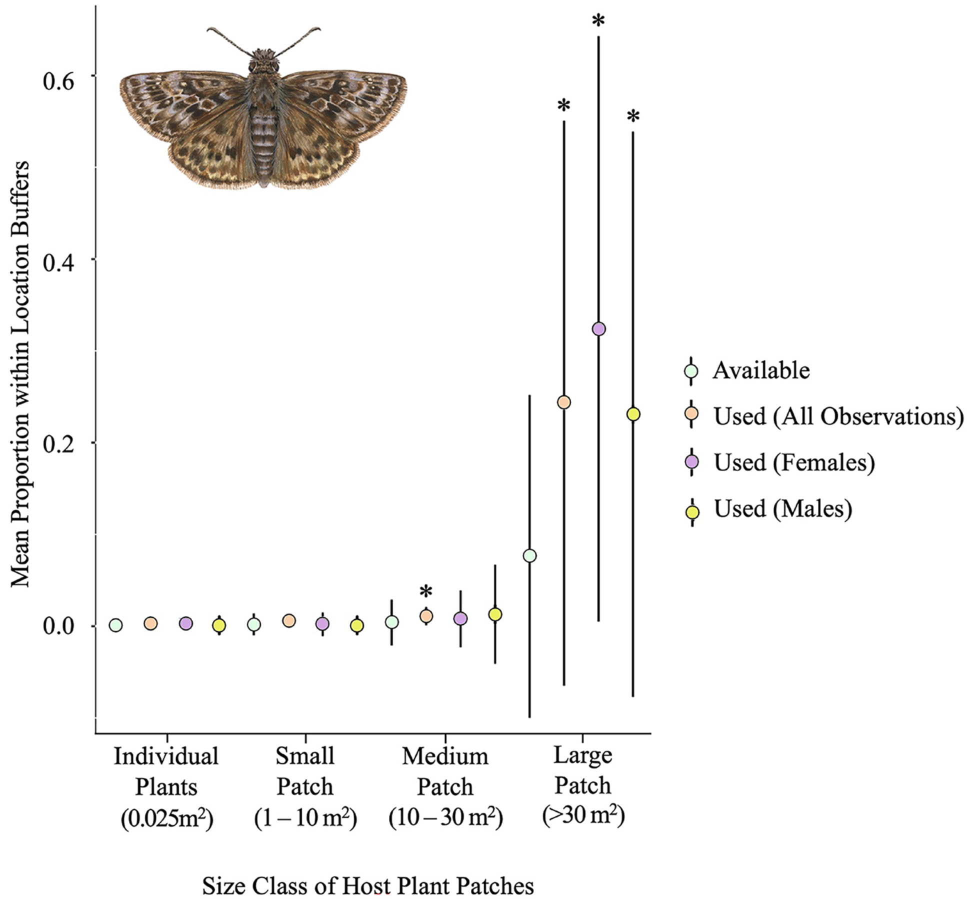

Fig. 2 Mean (±SD) proportion of host plant (*Ceanothus herbaceous* and *Ceanothus americanus*) patches in four size classes within 5 m buffers of Mottled Duskywing (*Erynnis martialis*) 'used' locations (all observations [females, males and unknown sex]: $n=115$; females: $n=46$; males: $n=29$) and within buffers of 'available' locations (randomly generated, used at a ratio of 10 available locations for each used location in a given subset of observations) at a reintroduction site (Site A), Pinery Provincial Park, Ontario, Canada. An * above SD error bar indicates statistically significant (α=0.05) selection relative to available points according to resource selection function model. Inset: Mottled Duskywing butterfly, copyright Suzane M Matheson 2020

Table 2 Summary of host plant (*Ceanothus herbaceous* and *Ceanothus americanus*) patches (count and density) at three mottled Duskywing (*Erynnis martialis*) reintroduction sites in pinery provincial Park, Ontario, Canada

Site →	A		B		C	
Area (ha) →	7.48		5.25		1.11	
Size class (m²)	Count (n)	Density (m²/ha)	Count (n)	Density (m²/ha)	Count (n)	Density (m²/ha)
Individual plant (<1)	1619	5	729	4	116	3
Small patch (1–10)	28	21	26	14	52	154
Medium patch (10–30)	28	67	10	35	11	149
Large patch (>30)	29	798	3	18	1	31

Host plant resources were divided into four size classes (individual plants, small, medium and large patches) to describe the site-wise availability of host plants and host plant patches

(<10 observations annually following releases) of Mottled Duskywing butterflies (Polley et al. *In review*). Site B had lower density of host plant resources across all size classes compared to site A, including 40 times lower density of large patches (Table 2). Mottled Duskywing have shown poor recruitment at site B, with very few ($n=11$) observations over three years post-release (Polley at al. *In review*). Site C contained small and medium host plant patches at a higher density than site A but had a 25 times lower density of large patches (Table 2). Site C has shown evidence of some Mottled Duskywing recruitment since reintroduction began in 2021, but abundances have been low and whether a sustainable population will be established there remains uncertain (Polley at al. *In review*).

Furthermore, it is possible that host plants are in better condition when they are located with larger patches compared to individual plants or those within small and medium sized patches. In 2021, for example, the relatively small and isolated host plants at site B were in poor condition, which we attributed to the combined effects of late frost and extensive Spongy Moth (*Lymantria dispar*) larval herbivory (J.E.L., A.M. *pers. observ.*). Also in 2023, host plants at site C were reduced in area and quantity, possibly due to Spongy Moth herbivory and overgrowth of competing plants such as Common Dewberry (*Rubus flagellaris*) (M.P., J.E.L. *pers.*

observ.). At both sites B and C, the relative lack of large, dense patches of host plants may have left Mottled Duskywing larvae without refugia and Mottled Duskywing adults with fewer nectar sources when host plant conditions deteriorated. In contrast, the large host plant patches at site A remained relatively intact throughout reintroduction, possibly buffered from damage by their larger-than-average size and more well-established growth, thus providing superior quality resources for Mottled Duskywing establishment.

While our findings align with the suggestion that Mottled Duskywing are commonly associated with networks of patches of their host plants (Schweitzer et al. 2018) and are consistent with evidence that other butterflies select host plants based on patch size (Dickins et al. 2013; Čelik 2013; Dunskis et al. 2024), we also acknowledge that the factors affecting reintroduction outcomes are likely more complex. First and foremost, the three reintroduction sites differed substantially in total area, ranging from 1.11 to 7.48 ha, and their size co-varied with the number of large patches at the sites, from 1 to 29 (Table 2). Second, founders at release sites may also have faced challenges caused by the life-stage at which they were released (Cabrera 2020; Polley et al., *In review*), or by the quantity of animals released, both of which varied by site. Site A received the highest quantity (444 founders) of what are apparently the most effective founder life-stages (pupae and adults; Polley et al., *In review*), which may have provided additional advantages at that site beyond those afforded by host plant resources. It is also possible that it is not pertinent to apply a hard rule for host plant patch resource requirements across different sites since patch density and patch size may be interactive factors. For example, very densely arranged individual plants, small and/or medium patches might provide equivalent host plant resources at sites where large patches are not present (Grundel and Pavlovic 2007).

In summary, we demonstrate that Mottled Duskywing butterflies selected large patches (>30 m^2) of their host plants in the early years of recolonization at a successful reintroduction site. Ensuring the presence of comparable host plant resources at future reintroduction sites should be a consideration moving forward. Existing reintroduction sites should also be managed to maintain or create larger patches of host plants whenever possible. Next steps include examining whether high densities of individual plants or small and medium host plant patches can provide equivalent resources in places where large host plant patches are absent or cannot be created. Mottled Duskywing are an endangered species in Ontario and Canada and their reintroduction to additional sites is ongoing. Information presented here will inform reintroduction site selection, restoration, and management for this species. In terms of the larger field of butterfly reintroduction, we present one avenue through which reintroduction outcomes can be monitored and connected to possible contributing factors, facilitating the advancement of techniques in the field in the context of adaptive management.

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Author contributions Author contributions. MP, JL, DRN contributed to the study conception and design. Funding acquisition by DRN, JL, AB, NK, AM. Field work and data collection and preparation performed by MP and JL. Data analysis, figure preparation and manuscript writing done by MP and DRN. All authors reviewed and approved the manuscript.

Data availability Data used within the manuscript is available online at https://doi.org/10.6084/m9.figshare.28612382.v1.

Declarations

Competing interests The authors declare no competing interests.

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