Mark-Recapture Study and Habitat Assessment for the Northern Metalmark Butterfly, Calephelis borealis (Lepidoptera: Riodinidae)

Weston J. Henry  
*University of Connecticut - Storrs*, weston.henry@uconn.edu

Kristian S. Omland  
*Mergus Analytics*, komland@mergusanalytics.com

Henry Frye  
*University of Connecticut - Storrs*, henry.frye@uconn.edu

Wagner L. David  
*University of Connecticut - Storrs*, david.wagner@uconn.edu

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Corresponding Author: Weston Henry

weston.henry@uconn.edu

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Calephelis borealis (Lepidoptera: Riodinidae)

Weston J. Henry¹, Kristian S. Omland², Henry A. Frye¹, David L. Wagner¹

1. Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, Connecticut 06269–3043, USA

2. Mergus Analytics, LLC, Jericho, Vermont, USA

ORCID:
Weston Henry: 0000-0002-9312-8649
Kristian Omland: 0000-0002-6731-6080
Henry A. Frye: 0000-0002-2066-5742
David Wagner 0000-0002-7336-3334
ABSTRACT

Background: The northern metalmark (Calephelis borealis), is an exceedingly local, globally rare butterfly that is declining across the Midwestern and Northeastern USA. The principal stressors driving colony losses include afforestation and invasive plants that crowd out its larval hostplant (Packera ovata) and nectar resources.

Aims/Methods: To better understand its declines and guide restoration efforts, we 1) performed a mark-recapture study in Connecticut to document population trends where we were actively managing vegetation; 2) conducted a range-wide survey for evidence of phylogeographic structure, using cytochrome oxidase (CO1); 3) investigated abundance determinants of its larval foodplant, Packera ovata; and 4) visited northern metalmark populations across the Northeastern USA to identify common edaphic, structural, and community elements of its colonies.

Results: We document that the species is increasing at a managed colony in Connecticut, where we opened the canopy, removed invasive plants, and added nectar resources. Common habitat attributes in the Northeastern USA include limestone soil, eastern redcedar (Juniperus virginiana), and ecotonal woodland structure that allows its shade-loving, larval hostplant (Packera obovata) to be spatially proximate to sun-loving, nectar resources. Nectar limitation is hypothesized to be a driver of colony location and success.

Implications for insect conservation: Our results underscore how active plant management (canopy thinning, invasive plant removal, and the addition of nectar plants) was able to rescue an imperiled woodland butterfly, reinforce the increasingly recognized importance of nectar resources in butterfly conservation, and demonstrate how metapopulation structure can buffer against the vagaries of precipitation and other (increasingly variable) climatic factors.
Keywords: nectar limitation, ecotone, invasive plants, afforestation, mark-recapture, metapopulation structure, Packera obovata, Juniperus virginiana

DECLARATIONS

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Conflicts of interest/Competing interests: None.

Availability of data and material: Barcode sequences will be deposited in GenBank upon acceptance of this manuscript. Voucher specimens of the northern metalmark have been deposited at the University of Connecticut Insect Museum.

Code availability: Code for statistical analyses is available on GitHub (https://github.com/komland/NoMe). WJH, HAF, KSO, DLW contributed to writing; WJH designed plant sampling schema, collected field data, and carried out the mark-recapture study; KSO analyzed and visualized mark-recapture data; HAF analyzed vegetation data; DLW provided funding and oversight.

Ethical approvals: N/A
INTRODUCTION

Declines of insect populations are occurring globally, with steep downward rates documented from Europe and North America (Dirzo et al. 2014, Sanchez-Bayo and Wyckhuys 2019, Wagner 2020, Van Klink 2020, Wagner et al. 2021a). Of course, not all species and regions are in decline, and there is much taxonomic, spatial, and temporal heterogeneity in insect population trends (e.g., see Van Klink 2020, Crossley et al. 2021, and Wagner et al. 2021b). Butterflies are among the most-studied terrestrial invertebrates globally and include many detailed cases of downward population trends. In the USA, well-documented, multi-lineage butterfly declines have been reported from California (Forister et al. 2010), Ohio (Wepprich et al. 2019), and the Upper Midwest (Swengel et al. 2011, Van Klink et al. 2020). A recent meta-analysis across more than 70 locations in the American West, with census data spanning at least a decade for a set of >260 species, suggests that butterfly numbers have been declining by about 1.6% per year over the past four decades (Forister et al. 2021). Recently, Crossley et al. (2021) found considerable variability in butterfly abundances reported from Fourth of July Butterfly Counts across southern Canada and the USA: counts in western British Columbia and Washington had increasing numbers, while those from the Southwest were commonly in steep decline.

Connecticut’s butterfly fauna was the subject of a five-year, statewide monitoring project from 1995 to 1999 (O’Donnell et al. 2007). At the time the work was completed, roughly one-fourth (26 of 99 species) of Connecticut’s resident butterfly fauna were regarded as either extirpated, rare, vulnerable, and/or declining (Wagner 2007). A similar portion of declining butterflies was recently reported for nearby Massachusetts (Michielini et al. 2020). Several of the Connecticut’s butterflies have been lost from the state over the two decades since the atlas was published (e.g., the Silvery Checkerspot [Chlosyne nycteis], Harris’ Checkerspot [C. harrisii],
Atlantis Fritillary \textit{(Speyeria atlantis)} [all Nymphalidae], and summer azure \textit{(Celastrina neglecta-major)} [Lycaenidae]), and many of the remaining (n=22) butterflies continue to decline. Thirteen of these species receive legal protection under the state’s Endangered Species Act (CT-DEEP 2015).

Principal stressors driving the declines of butterflies in Connecticut and elsewhere include habitat loss and destruction (which include urbanization and fragmentation), agricultural intensification, climate change, and invasive species; locally, pesticides and pollution also drive declines (Wagner 2007, Wepprich et al. 2019, Forister et al. 2021, Warren et al. 2021). In Connecticut and other forested regions, afforestation—i.e., the turnover of open, early successional habitats to closed-canopy forests—has played an additional role in butterfly declines (Wagner 2007, 2020, Schweitzer et al. 2011, Wagner et al. 2014). Fourteen of the 26 butterflies regarded to be Conservation Concern at the closure of the Connecticut Butterfly Atlas Project (O’Donnell et al. 2007) were identified as being associated with early successional habitats, i.e., dependent upon either manmade or natural disturbances for their habitats to persist.

Here we focus on one of Connecticut’s State Endangered butterflies, the northern metalmark \textit{(Calephelis borealis, Lepidoptera: Riodinidae)} (Fig. 1). The butterfly’s global status in NatureServe (2021) recently was upgraded from G3G4 (globally vulnerable to apparently secure) to G2G3 (globally imperiled to vulnerable). It is rare (ranked S1 [subnationally critically imperiled], S2 [subnationally imperiled], S2S3 [subnationally imperiled to vulnerable]) in 10 of the 14 states in which it is listed in NatureServe: Arkansas (no state rank), Connecticut (S1), Illinois (no state rank), Indiana (S1), Kentucky (S2), Maryland (S2), Missouri (S1), New Jersey (S3), New York (S1), Ohio (S1S3), Oklahoma (S2), Pennsylvania (S1S2), Virginia (S2S3), and West Virginia (S1). While currently regarded as an S3 species in New Jersey (NatureServe
2021), its rank is being revised to S1 (Robert Somes, NJ Department of Environmental Protection, pers. comm.). The Butterflies and Moths of North America website (BAMONA 2021) treats *C. borealis* as “G3 - Very rare or local throughout its range or found locally in a restricted range (21 to 100 occurrences) (Threatened throughout its range).” Many colonies that were known across Kentucky, New Jersey, Ohio, Pennsylvania, and Connecticut have been lost to forest succession; invasive plant encroachment has been a chronic threat to colonies in the Northeast (Schweitzer et al. 2011, Wagner and Henry 2020).

In the Northeast, the butterfly is a denizen of open woodlands, glades, forest edges, rides, powerline right-of-ways, or man-made openings in otherwise closed-canopy woodlands and forests (Fig. 2) (Iftner et al. 1992, O’Donnell et al. 2007, Schweitzer et al. 2011, Munroe and Wright 2017). Eastern populations of *Calephelis borealis* have one brood a year with a four-week flight season that peaks in the first week of July. Across its range, it uses a single larval hostplant: roundleaf ragwort (*Packera obovata*, Asteraceae; Scott 1986, Heitzman and Heitzman 1987, Iftner et al. 1992, O’Donnell et al. 2007, Schweitzer et al. 2011). Adults are avid flower visitors but also perch on flowers as a courtship post or resting site. Principal nectar sources in Connecticut include black-eyed Susan (*Rudbeckia hirta*), New Jersey tea (*Ceanothus americanus*), sunflowers (*Helianthus divaricatus*), and orange milkweed (*Asclepias tuberosa*) (O’Donnell et al. 2007). A summary of the insect’s biology, range, and conservation status is given in Schweitzer et al. (2011).

We have been involved in population monitoring, vegetation management, and restoration ecology on behalf of *C. borealis* in Connecticut since 2007. Both our censusing and vegetation management efforts were anchored to a colony in Litchfield County (Kent-1). Annual efforts at the site included (1) girdling or felling trees, with a goal of having 40% open canopy at
the core of the colony; (2) removing (thousands of) stems of invasive plants, the most
problematic of which have been autumn olive (*Elaeagnus umbellata*), oriental bittersweet
(*Celastrus orbiculatus*), winged euonymus (*Euonymus alatus*), and Merrow’s honeysuckle
(*Lonicera merrowi*); and (3) planting of nectar resources. We also began to enlarge the area of
habitat by felling trees about the periphery of the colony, which was less than an acre in extent in
2007.

For the first decade, daily counts at Kent-1 were worryingly modest; no more than a
dozen butterflies were seen in a single day over the first 11 years of study (Table S1,
Supplement-S3). Prior to 2016, our demographic data consisted of a daily walk-through along a
prescribed survey route, along which all individuals were counted. While such counts were
necessary to assess the colony status and population trends, and inform annual vegetation
management goals, these visual surveys left great uncertainty about the fraction of a population
that went unassessed. To more rigorously evaluate the species’ status in Connecticut and assess
how our daily sight counts compared to statistical population estimates, we carried out a three-
year, mark-recapture study of the colony.

Given the northern metalmark's range across the Eastern USA, understanding the species’
phylogeographic structure could be important to conservation efforts, particularly if Northeastern
colonies were genetically isolated from the rest of its range. Indeed, Schweitzer et al. (2011)
recognized three population groups within the northern metalmark, with the Ozark population
cluster being the most isolated. Moreover, all eastern populations of the butterfly are univoltine
(Iftner et al. 1992), while those from the Ozark Region are double brooded (Clark and Clark
1951, Scott 1986, Heitzman and Heitzman 1987). Given that Ozark populations of several
lepidopteran lineages are unique [e.g., Baltimore (*Euphydryas phaeton ozarkae*) (Nymphalidae),
Heitzman’s lytrosis (*Lytrosis heitzmanorum*) (Geometridae), and Ozark swallowtail (*Papilio joanae*) (Papilionidae), and differ in brood number, we conducted a genetic survey of CO1 haplotypes across the species’ range to look for evidence of phylogeographic structure in the northern metalmark.

Lastly, to better circumscribe the northern metalmark’s critical habitat requirements, WJH conducted a demographic study of the metalmark’s larval foodplant, roundleaf ragwort (*Packera obovata*) with the goal of identifying common habitat elements—e.g., edaphic factors, vegetation structure, and associated plant species—that could guide management and restoration efforts in the Northeastern USA and elsewhere. A principal aim was to test the hypothesis that roundleaf ragwort was positively associated with the presence of redcedar, a nearly universal canopy species shared by metalmark colonies in the Northeast.

Below, we report results of our three-year mark-recapture study, initial genetic findings, and demographic data for the butterfly’s larval hostplant, roundleaf ragwort (*Packera obovata*). We close with a discussion of the butterfly’s management needs, including the importance of in-habitat nectar availability and relevance of metapopulation structure for *C. borealis*, particularly in the face of climate variability.

**METHODS**

**Study Site.** The study site is located near Kent, Litchfield County, Connecticut. Because *C. borealis* and several state-listed plants occur at the butterfly colony, its exact location is not reported here. The colony consists of three closely situated subpopulations of *C. borealis*, referred to here as Kent-1, Kent-2, and Kent-3 that run along a linear distance of ca. 800 m, with the subcolonies separated by 175 to 200 m of closed-canopy forest, where *C. borealis* is not
seen. Our daily survey route, initially established to conduct visual counts of all adults in years prior to our 2017-2019 mark-recapture study, traverses all locations where the metalmark is known to be active.

**Mark-Recapture.** Mark and recapture surveys were conducted in 2017, 2018, and 2019. Counts began the last week of June and continued into the third week of July, terminating when either (1) one or no adults were seen per day for three consecutive days, or (2) three or more continuous days of rain were forecast after the 18th of July. For each captured butterfly, the observer (1) recorded the site name, (2) applied a unique marking (ID number) to the wings or recorded the ID number of a previously marked individual, (3) recorded the sex of the individual, and (4) noted evidence of wing wear (fresh, worn, damaged, or very worn; and whether the wings were damaged in such a way as to have compromised the ID number markings). For newly captured individuals, each was marked with a unique ID number using a combination of fine, black dots applied with a Sharpie® to the undersides of forewings and hindwings (details are given in the Supplement-S1).

Models were fit in R version 3.6.3 (R Core Team 2020) using the RMark interface (Laake, 2013) to Program MARK (White and Burnham, 1999). Both Cormack-Jolly-Seber (CJS) and POPAN models were fit to the data to explore consistency of estimated apparent survival and resighting probability between models that estimated population size (POPAN) and ones that did not (CJS). In the POPAN models, probability of entry was held constant. Subcolony was not included in the modeling; movement among subpopulations was not sufficient to estimate transition probabilities and the number of marked individuals was not sufficient to model abundance, apparent survival, and resighting separately by subpopulation. Covariates considered that may have affected apparent survival and resighting were sex, observer, and date, although
staffing necessitated confounding of observer with phases of each season, therefore observer
may also be considered a surrogate variable for phase of the season. Model selection was based
on AIC. Real-value (back-transformed) estimates from supported models are reported with 95%
confidence limits.

**Genetic Data.** CO1 barcodes were obtained from 11 specimens of *Calephelis borealis* from 5
states (Connecticut, Missouri, New Jersey, New York, and Virginia). Additionally, 2 specimens
of *C. muticum* were sequenced from Missouri. These were compared with sequences for other
eastern North American *Calephelis* sequences in the Barcordes of Life Project (BOLD)
(www.boldsystems.org; Ratnasingham and Hebert, 2007) and GenBank for a total of 15 *C.
borealis*, 2 *C. muticum*, 8 *C. virginiensis*, and 1 *C. near virginiensis*. No additional states were
represented among the 4 barcodes for *Calephelis borealis* that were available through BOLD. A
neighbor-joining tree, using the default Kimura 2-P model, was generated by BOLD. DNA
extraction, PCR amplification, and CO1 barcode sequencing were performed at the Canadian
Centre for DNA Barcoding (Centre for Biodiversity Genomics – University of Guelph) using
their standard protocol (Wilson 2012).

**Statistical modeling of larval host, Packera obovata.** We collected a variety of habitat data to
assess the effects of small-scale environmental factors on local distribution of *Packera obovata.*
Along the adult mark-recapture survey route, twelve linear transects were created. Within each
transect, four 1-m² quadrats were established that represented different densities of *Packera*, for
a total of 48 quadrats. One quadrat represented the greatest *Packera* cover in the general transect
area, one represented the lowest *Packera* cover within the area, one represented *Packera* cover
between the two, and one quadrat contained no *Packera.* Along a given transect, quadrats were
established approximately equidistantly from one another.
We modified a quadrat-based method from Mueller-Dombios and Ellenberg (2002) to estimate percent cover of *Packera*, competitor plant species, invasive species, nectar plants, open soil, exposed rocks, and bryophytes for each quadrat. We only included vegetation growing within 1-m of the soil surface. We also took five measurements of slope, aspect, and soil depth per quadrat. Canopy cover measurements were taken using a fisheye lens camera, and Gap Light Analyzer was used to quantify canopy cover and total transmitted light (Frazer et al. 1999). All canopy trees growing over each quadrat were identified to species, resulting in presence-absence data for each.

We modeled *Packera* presence/absence and abundance using a Bayesian beta hurdle regression (Ospina & Ferrari, 2010). Presence/absence was modeled with a Bernoulli distribution and the abundance portion with a Beta distribution. Covariates of the presence/absence portion of the model included factors we thought could regulate *Packera* establishment and persistence: competitor cover, canopy openness, eastern hemlock (*Tsuga canadensis*) presence/absence, eastern redcedar (*Juniperus virginiana*) presence/absence, and bare ground coverage. The abundance portion of the model included factors that we thought could be important to *Packera* persistence once established: canopy openness, competitor coverage, and aspect. We provide an ordination of woody species and environmental factors that helped guide our modeling approach in the Supplement-S4.

Analysis was done in R version 4.0.3 (R Core Team 2020) using the R2jags package (Su and Yajima 2020). The posterior distribution for coefficients was estimated using three, parallel, MCMC chains at 10,000 iterations, with a burn-in of 1,000. Convergence of chains was assessed visually and by Gelman-Rubin diagnostics. We used normally distributed non-informed priors (mean = 0, variance = 1,000) for the coefficients.
Critical Habitat Characterization. To better understand common habitat elements of *C. borealis* colonies and inform future management and restoration efforts in Connecticut and elsewhere in the Northeast, WJH and DLW visited many of the known metalmark populations across the Northeastern United States: three in CT, four in New Jersey (NJ-1, NJ-2, NJ-3, and NJ-4), two in New York (NY-1 and NY-2), and two colonies in southeastern Ohio. A photograph and brief site description for six of these colonies are provided in Supplement-S5; again, exact locations are not reported. To get a sense of the current conservation status of the butterfly across its (global) range, we spoke with biologists familiar with the *C. borealis* populations in eleven states: John Shuey (Illinois), Jim Vargo (Indiana), Loran Gibson (Kentucky), Jennifer Selfridge (Maryland), Phillip Koenig (Missouri), Anthony McBride and Robert Somes (New Jersey), John Howard and Jim McCormack (Ohio), Richard Boscoe and David Wright (Pennsylvania), Steve Roble (Virginia), James Utter (New York), and Linda Williams (Missouri).

RESULTS

Mark-Recapture. A database of 924 butterfly sightings was assembled (2017: 349; 2018: 246; 2019: 329). These records included initial capture-and-mark encounters, recaptures of previously marked butterflies, resightings where re-netting was not needed, and sightings of butterflies that evaded us (these included unmarked butterflies as well as resightings of marked butterflies whose identity was not discernable before they flew off). The proportion of sightings that were unmarked butterflies was 19% in 2017, 33% in 2018, and 32% in 2019. Butterflies were active from the last days of June through about July 20. Peak activity was 6-13 July in 2017, 1-8 July in 2018, and 1-6 July in 2019 (Fig. 3).
In total, 81 butterflies (35 F, 45 M, 1 undetermined) were marked in 2017; 87 (46 F, 38 M, 3 undetermined) in 2018; and 117 (48 F, 69 M) in 2019. Numbers marked within subcolonies changed substantially over the three years. At Kent-1, we marked 14, 33, and 80 individuals respectively; at Kent-2, corresponding numbers were 33, 30, and 12; at Kent-3, they were 34, 24, and 25, underscoring the dynamic nature of the year-to-year counts across the three subpopulations.

Marked individuals were resighted as many as 11 times, with males often showing high site fidelity. Males were more likely than females to be resighted (Table 1, Fig. 5). Only 51% of marked females were seen one or more times after their initial marking (66 of 129), while 68% of marked males were re-sighted (103 of 152). The longest interval between the date when a butterfly was marked and the date it was last seen (i.e., maximum adult longevity) was 17 days: which was observed for one male in year 1 and one female in year 2.

A large majority of resightings (269 of 285 or 94% of marked individuals) were within the same subcolony. Sixteen butterflies were re-sighted in a patch other than where they had been initially marked; one individual also returned to its initial patch and one traveled three times between two patches. Eleven of the 16 butterflies that traveled between subpopulations were male and five were female.

In each of the first two seasons, model selection supported estimating a common apparent survival parameter between the two sexes but different re-sighting probability (Table 1). Data from 2019 also indicated no support for different apparent survival rates; however, they also indicated an effect of observer on resighting probability. Model fitting was unstable using three levels of observer, therefore the second and third sets of observers were consolidated to represent the later phase of the season when resighting probability was low. The best-supported model had
resighting dependent on both phase of the season (early/observer A, late/observers B-C) and butterfly sex (Table S3, Supplement-S2). Modeling two versus three levels of observer (phase of season) entailed only a minor loss of goodness of fit (deviance). 

Apparent daily survival was about 0.9 each year [2017: 0.91 (0.88, 0.93), 2018: 0.86 (0.82, 0.90), 2019: 0.84 (0.78, 0.89); Table 1]. Male resighting probability was 0.24 to 0.34 per day except for the later observers in 2019, when it was 0.01 [2017: 0.33 (0.28, 0.39), 2018: 0.24 (0.17, 0.32), 2019 early: 0.35 (0.26, 0.44), 2019 late: 0.01 (0.00, 0.06)]; female resighting probability was 0.11 to 0.25 per day except for by the later observers 2019, when it was 0.06 [2017: 0.21 (0.16, 0.27), 2018: 0.11 (0.07, 0.17), 2019 early: 0.25 (0.17, 0.36), 2019 late: 0.06 (0.03, 0.13)].

Including the population size parameter, the POPAN model also supported similar structure (common apparent survival, resighting dependent on sex the first two years, and dependent on both sex and observer/phase-of-season in 2019) with similar estimates for Φ and p. Population estimates were 110 (95% CI 97, 125), 152 (124, 187), and 345 (262, 455) for the three seasons, respectively (Fig. 4). However, in 2019, inclusion of the observations when resighting probability was substantially lower greatly inflated the estimate (implying greater than doubling from 2018) as well as its uncertainty, therefore we also report the estimate based only of the work of the first observer as a minimum estimate (172, 95% CI 146, 202), which still reflects population increase over all three years.

**Genetic Data.** To assess whether eastern populations of the metalmark might be genetically distinct from those of the Ozarks, we barcoded 11 *Calephelis borealis* individuals from five colonies in Connecticut, Missouri, New Jersey, New York, and Virginia. Barcodes were available for an additional 4 *Calephelis borealis*, 2 *C. muticum*, and 9 *C. virginiensis* through the
Barcodes of Life Projects (BOLD) (www.boldsystems.org) (Ratnasingham and Hebert, 2007).

Unexpectedly, all fifteen CO1 sequences, from across the range of C. borealis, were identical. A neighbor-joining tree for Calephelis is shown in Fig. 6. Each of the three species comes out as monophyletic (recognizing that C. virginiensis includes a segregate in South Carolina that differs from Florida populations by 2%). Except for the two haplotypes for C. virginiensis, haplotype diversity across the genus Calephelis is notably lacking.

**Determinants of Packera populations.** Almost all 95% credible intervals of model coefficients overlapped zero suggesting that either the covariates were unimportant or our sample sizes were too small to distinguish sizeable effects (Fig. 7). The only exception was that of competitor coverage predicting Packera presence/absence. Based on the mean value of the posterior distribution ($\mu = -0.941$, $\sigma^2 = 0.456$), an approximate 10% increase in competitor coverage in a plot would lead to ~20% decrease in the probability of Packera presence. Presence/absence factors recorded for Packera quadrats (e.g., Tsuga canadensis and Juniperus virginiana) were not strong and had wide credible intervals. Packera density may be weakly and negatively affected by canopy openness, competitor cover, and aspect. However, none of these had strong impacts individually on the abundance for the 36 Packera plots.

**DISCUSSION**

**Mark-Recapture.**

Beginning in 2017, we began marking butterflies to estimate populations more rigorously for each of the three subcolonies. Daily counts remained low at least at Kent-1, the focal site of management efforts for thirteen years, until 2018, when we saw the population numbers double and then double again in 2019 (see below), therein reinforcing a common outcome of insect
conservation efforts, i.e., that favorable habitat management can quickly reverse insect declines (e.g., Schultz and Crone 2015, Gifford et al. 2020, Warren et al. 2021).

The estimate for 2019 has greater uncertainty, possibly related to a change in observers; unsanctioned vegetation management practices at Kent-3 on 8 July, which included the felling of trees and trampling; or still other reasons. Regardless of the explanation, we observed an abrupt diminishment of adult sightings after the first week of July. Our estimate of 345 butterflies for the Kent metapopulation in 2019 seems excessive since only 117 butterflies were marked in total: 105 in the first 10 days by observer A and only 12 additional butterflies in the remaining 13 days. The population estimate from the first 10 days was 172, then doubled to 345 based on the addition of just a dozen butterflies—an estimate, for whatever reason, that we believe to be unreliable. Regardless of our uncertainty, much of the population increase in 2019 traces to high numbers at Kent-1, the site of thirteen years of yearly C. borealis habitat management.

Our estimated apparent survival for C. borealis was consistent over all three seasons and between CJS and POPAN models, indicating that our estimate is robust. Estimated apparent daily survival was relatively high at approximately 0.9, i.e., about 10% of the population disappeared each day, whether by perishing or emigrating. Results from previous studies lend support for our own findings. For instance, apparent daily survival estimated by Arnold (1983) for Lange’s metalmark (Apodemia mormoa langei) was 0.7-0.925 over a three-year study. Schultz and Dlugosch (1999) also reported a daily survivorship estimate of 0.9 for the Fender’s blue butterfly (Icaricia icarioides fenderi) (Lycaenidae).

Our mark-recapture data reflect a surprising degree of subcolony fidelity for both male and female northern metalmarks: only 16 of 285 marked individuals were observed to have moved between the subpopulations, which were separated from each other by less than 800m.
Males were commonly observed on consecutive days in the same location along the survey route. One male was observed in the same isolated light gap over a period of 10 days in 2019. The generally non-overlapping confidence intervals for resighting probabilities of females and males indicate that females were significantly more sedentary or cryptic in habit than males (Fig. 5). This is consistent with the findings of Arnold (1983) that more males than females of the Lange’s metalmark were marked.

**Genetic Data.** Were the northern metalmark found to consist of two or more population segments, the conversation status of each would be significantly elevated, possibly leading to the recognition of Ozark colonies as worthy of federal protection under the (Amended) Endangered Species Act (1982). While we initially believed that we would find genetic evidence that Ozark populations of the northern metalmark would be genetically distinct or at least represent distinct population segments, CO1 data revealed the opposite: we found no genetic variation in CO1 barcodes from across the states that span the global range of the butterfly. We are surprised by this finding, given the metalmark’s small body size, its weak flight, localized and often isolated populations, small population sizes, and high site fidelity (Schweitzer et al. 2011, Munroe and Wright 2017; and this study). The absence of haplotype diversity suggests that *C. borealis* dispersed across its range relatively recently, perhaps spreading from its site of origin during the 18th, 19th, and first half of the 20th century, when much of the eastern United States was cleared for agriculture. Wooded tracts with eastern redcedar (*Juniperus virginiana*), a widespread successional species in pastures of eastern North America, would have provided habitat for the butterfly and its hostplant in a march across the eastern USA. Nick Grishin’s lab (in litt.) at UT Southwestern Medical Center has generated genomic data for multiple northern...
metalmark accessions. Consistent with our findings, they have found surprisingly modest genetic variation across their nuclear markers for *C. borealis*.

**Metapopulation Dynamics at Kent.** Over the last four flight seasons, we observed considerable fluctuation in adult numbers across the three Kent subpopulations. In 2016 and 2017, Kent-3 yielded the largest daily counts among the subpopulations, but numbers decreased in 2018, and further still in 2019 (due in part to unsanctioned and unsupervised tree removal activities in both years). Kent-2 numbers also declined in 2018 and then again in 2019; here, nectar availability may have been limiting due to canopy closure (see below). By contrast, the Kent-1 population doubled in size in 2018, and then doubled again in 2019 (Supplement-S2, S3), presumably due to ongoing, annual management efforts on behalf of the northern metalmark that include canopy-thinning, invasive plant removal, and supplemental nectar planting.

It is our hypothesis that both vegetation management efforts and weather played roles in these inter-colony (and opposite) population estimates. At Kent-1, the site where the most extensive, scheduled canopy thinning occurred, *Packera* and other plants on the southwest-facing slope wilt during hot, droughty years (as happened over the summer of 2016). Adult metalmark sightings at Kent-1 dropped off markedly in 2017, the year following the drought. (2017 metalmark adults result from larvae that eclosed and started feeding in July of 2016). In years with normal or above-average rainfall, the same slope yields abundant nectar resources—*Rudbeckia*, *Ceanothus*, *Helianthus*, and *Asclepias*. Regardless of the drivers, our results highlight the vagaries of insect population dynamics, the potential importance of metapopulation structure, and the role that weather can play across years even when subpopulations are closely situated [also noted by Williams (2011) and Oliver et al. (2015)]. These fluxes underscore how important it can be to preserve and manage multiple habitat patch for butterflies and other insects,
especially as climate instability increases. Several recent studies have linked below-average rainfall and elevated annual temperatures to butterfly declines across the American West (Forister et al. 2018, 2021, Crossley et al. 2021, Halsch et al. 2021). There is much reason to believe that episodes of elevated temperatures and diminished precipitation likewise affect local areas and populations of butterflies elsewhere, and argue for the necessity of striving to acquire and manage a set of proximate tracts that differ somewhat in their physical attributes and thus mitigate responses to year-to-year climatic vagaries. Because the metalmark exhibits high site fidelity (evidenced by its modest tendency to disperse), fostering connectivity among subpopulations and suitable habitat patches should be a management goal. Such will serve to increase rates of recolonization following local extirpations, and could prevent some local extirpations through the rescue effect (Kalarus and Nowicki 2015).

**Common Habitat Elements and Habitat Management.** We did not find strong evidence for any particular site characteristic that led to greater *Packera* abundance or establishment across all sites (Kent-1-3). The only factor that we measured that had any significant effect on *Packera* establishment was competitor cover, which seemed to decrease the probability of *Packera* being present. Variables that were indicative of overall site characteristics (with *Tsuga canadensis* presence suggesting wetter and cooler sites, and *Juniperus virginiana* suggesting drier and more exposed sites) did not yield strong signals either (Fig. 7). Given our small plot sizes and sample numbers, these results highlight the need for a larger-scale study that extends beyond the Kent population.

Our visits to eleven populations in Connecticut, New Jersey, New York, and Ohio revealed several common habitat requirements of *C. borealis*. Most colonies in the Northeast are on limestone-based soils. Preferred habitat appears to be a mosaic of eastern redcedar (*Juniperus*
virginiana) woodland and openings (glades), with both hostplant (*Packera obovata*) and nectar resources interspersed or in close proximity. *Packera* is often a dominant constituent of the ground herbaceous layer in areas where the butterfly is locally common; black-eyed susan (*Rudbeckia hirta*) is present (and in bloom) at nearly all sites, and a preferred nectar source and perching site (see Supplement-S5).

The butterfly is absent from closed-canopy forests and woodlands as well as from expansive open fens, fields, fields, and prairies, although adults routinely frequent the ecotone between woodlands and open habitats to take advantage of nectar sources. Accordingly, powerline corridors running through redcedar woodlands often support northern metalmark populations. Other Northeastern *C. borealis* habitats include successional redcedar woodlands associated with human activity (Kent-2, NJ-1, NY-1, NY-2, NJ-4); wetland and pond edges (Kent-1, NJ-3, NY-2); edges of dry limestone ridges (NY-2) and quarries; and natural dry, semi-open redcedar glades (NJ-1) (see Supplement-S5).

Eastern redcedar provides no obvious resource to the butterfly, and thus why it is so commonly a dominant element in northern metalmark colonies remains a conundrum. Most simply, it may just indicate a stage of succession, where the plant community is midway between open pasture or grassland and a closed canopy forest, with both open sunny areas (for nectar) and shady habitats (for the larval foodplant) existing side-by-side. Our initial hypothesis was that because redcedar is allopathic and excludes many plants (Teixeira de Silva 2015), *Packera obovata* might be favored by the lack of competitors; however, our data failed to identify a strong association between the two plants (Fig. 7). While our results around the importance of redcedar are inconclusive, it seems advisable that redcedar should not be removed from *C.*
borealis habitat, except for where it is so common that canopy closure threatens the survival of nectar resources (see below).

Succession and canopy closure are considered a primary threat for the species in the Midwest and Northeast (Schweitzer et al. 2011). Given that most colonies across the northern metalmark’s range are small—as are all three of Connecticut’s surviving colonies—it is our guess that many of the species’ remaining colonies will not persist without active management. Only the Appalachian populations associated with shale barren habitats of West Virginia, Maryland, and Virginia are regarded to be secure by Schweitzer et al. (2011). In these, soils are so nutrient-poor and thin that trees are disfavored, and the threat of canopy closure is diminished.

Invasive plants (especially those species listed in Introduction) are a chronic threat to the butterfly at all the Kent subpopulations, elsewhere in Connecticut, and at NJ-1. These plants are best removed on an annual basis, as lapses of just a few years threaten both the butterfly’s nectar and larval hostplant resources. Our management efforts at all three Kent sites over the past thirteen years have involved the manual removal of invasive plants supplemented with herbicidal applications at Kent-1, which is presently Connecticut’s most viable colony. At NY-2, cut-and-paint herbicidal applications of autumn olive have created one of the largest expanses of northern metalmark habitat in the region (James Utter pers. comm.).

Nectar Limitation. We have not collected data that would allow us to know if nectar availability is a limiting factor for C. borealis, but that working hypothesis has driven our on-site vegetation management efforts. At Kent-1, where funding has been available for on-site restoration efforts, we have actively managed for midsummer nectar resources by (1) canopy thinning, (2) planting dozens of nectar plants (Ceanothus americanus, Asclepias tuberosa, and Rudbeckia hirta), and (3) erecting a deer fence to protect key nectar plants from deer browsing. Counts at Kent-1 have
been increasing, while those at the other two (unmanaged) Kent subpopulations decreased over the 2018 and 2019 field seasons (Fig. S3).

It is significant that *C. borealis* feeds on nectar at all, as most woodland-dwelling, midsummer-flying butterflies in the Northeastern USA are not reliant upon flowers or shun them. Satyrines (*Enodia, Megisto*), anglewings (*Polygonia*), and tortoiseshells (*Nymphalis*) (all Nymphalidae) feed at tree wounds, sap fluxes, rotting fruits and berries, or animal dung (O’Donnell et al. 2007, Wagner and Gagliardi 2015). There are five forest-dwelling hairstreak butterflies in the genus *Satyrium* (Lycaenidae) across New England. While all will feed at flowers, there is increasing evidence that these forest-dwelling hairstreaks more commonly feed at honeydew, gall secretions, and extrafloral nectaries (Wagner and Gagliardi 2015, Gagliardi and Wagner 2016). Given the general scarcity of nectar resources in woodlands and forests of the Northeast, during midsummer when metalmark adults are active, it is easy to imagine that nectar scarcity could be a limiting factor in the butterfly’s biology.

*Packera obovata*, the sole larval foodplant, is much more widespread than the northern metalmark. It is common at many locales across western Connecticut, but many of these areas are closed-canopy woodlands without nectar resources. Likewise, there are several limestone areas in northwestern New Jersey that support extensive *Packera* growth, but those with closed canopies do not support metalmark colonies. The fact that we are unable to identify an association between *Packera* density and metalmark numbers (Fig. S3, Supplement-S4) indirectly suggests that nectar sources or some other factor is playing a key role in the butterfly’s ecology.

The importance of nectar resources to adult butterflies is increasingly recognized as critical. Diminished late-summer nectar resources are correlated with higher mortality rates for
migrating monarchs (Brower et al. 2006, Inamine et al. 2016, Saunders et al. 2019). Schultz and Dlugosch (1999) found that nectar availability was strongly correlated with adult population numbers of Fender’s blue (*Icaricia icarioides fenderi*), and that adults leave their natal sites if nectar is unavailable. Other studies have linked nectar access to both longevity and egg production in butterflies (e.g., Hill and Pierce 1989, Hill 1992, Boggs and Ross 1993). All but one of the studies cited above, documenting nectar limitation, involve lycaenid butterflies (the sister family to metalmarks).

### CONCLUDING REMARKS

Mark-recapture data confirm that New England’s largest northern metalmark population remains perilously small and that adults exhibit high site fidelity to their natal habitat patch. Most colonies of this species in the Northeastern USA are in (redcedar) woodlands with interspersed glades suitable for midsummer floral resources, or the ecotone between closed redcedar woodlands and open fields. Our observations suggest that nectar availability could play a key role in the metalmark’s ability to colonize and persist in woodlands even where the larval hostplant (*Packera obovata*) grows in abundance. To effectively manage and restore critical habitat, larger (replicated) ecological studies are needed to better understand the microhabitat requirements of *Packera* as well as the midsummer nectar resources required by the adults. Barcode (CO1) sequences from across the butterfly’s global range yielded only a single haplotype; a perplexing finding suggesting that the butterfly’s current range was only recently colonized. Year-to-year vagaries in weather appear to drive fluctuating subcolony numbers at Kent, and underscore the importance of metapopulation structure for this and other butterflies. Given the site fidelity suggested by our data, metalmark subcolonies would need to be proximate
to one another or connected by habitat-appropriate corridors. Like many early successional taxa, continued habitat management will be needed to maintain populations of the metalmark, with succession (afforestation) and exotic plant species representing chronic threats to its colonies across much of eastern North America.

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Table 1. CJS model estimates for best-supported models. Φ apparent daily survival and p resighting probability. Two sets of estimates are displayed for 2019, one for Φ(~1)p(~obs2:sex) fit to all of the data and a second set for Φ(~1)p(~sex) fit to the data collected only by observer A (the first 10 days of the season).

<table>
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Figures 1, 2. Northern metalmark. (1) Adult female. (2) Habitat at Kent-1 with two recently girdled trees to right.

Figure 3. Seasonal pattern of butterfly activity over three seasons. Butterflies that evaded capture or whose identity could not be discerned (e.g., because their wings had worn, and identity was ambiguous despite remaining evidence of marking) were all grouped as “Unmarked.” No visits were on 2018-06-28, 2018-07-22 and 23; 2019-07-21 through 23.
**Figure 4.** Population estimates with 95% confidence intervals over three years: both sexes (gray), females (magenta), and males (blue). Two sets of estimates are shown for 2019: filled bars indicate estimates from the first 10 days of the season; hashed bars indicate estimates over whole season with greater uncertainty.
Figure 5. Recaptures by sex over three years. Female northern metalmarks are more sedentary and/or secretive in habit and generally have a lower probability of being sighted. The mean number of sightings (marked or resighted) was 1.7 for females (CL 1.4-2.1), while this number was 2.1 for males (CL 1.8-2.4).
Figure 6. Kimura-2P neighbor-joining tree for CO1 for 15 *Calephelis borealis* and 11 other *Calephelis* collections for USA, based on all Barcodes of Life Database (BOLD) (Ratnasingham and Hebert 2007) (sequences accessed March 2021).
Figure 7: Parameter coefficients and 95% credible intervals from a Bayesian beta hurdle regression predicting *Packera* presence/absence and abundance. Parameters in black have 95% credible intervals that do not overlap zero while open dots indicated that parameters with 50% credible intervals overlapping zeros. Parameters modeling the presence/absence portion of the model are labeled as pertaining to establishment.