Evaluation of Karner Blue Butterfly Occupancy and Relationships to Management on State Lands in Michigan

Prepared By:

Michael J. Monfils and David L. Cuthrell
Michigan Natural Features Inventory
Michigan State University Extension
P.O. Box 13036
Lansing, MI 48901

Prepared For:

Michigan Department of Natural Resources
Wildlife Division

11/30/2018

MNFI Report No 2018-21

Michigan Natural Features Inventory
Discover. Define. Deliver.

MICHIGAN STATE UNIVERSITY | Extension

Suggested Citation:

Monfils, M. J., and D. L. Cuthrell. 2018. Evaluation of Karner blue butterfly occupancy and relationships to management on state lands in Michigan. Michigan Natural Features Inventory, Report Number 2018-16, Lansing, USA.

Cover: Karner blue butterfly taken by D. L. Cuthrell.

Table of Contents

List of Tables

List of Figures

Abstract

The Michigan Natural Features Inventory worked with the Michigan Department of Natural Resources (MDNR) to survey Karner blue butterfly (*Lycaeides melissa samuelis*; KBB) on State and private lands in southwestern Lower Michigan. Our objectives were to develop a monitoring program to track Karner blue occupancy over time, while also providing a long-term framework for evaluating the influence of prescribed fire and mowing on occupancy. We also wanted to analyze the four-year data set to estimate occupancy and other population parameters to assess the species' status, evaluate the influence of management variables on occupancy, and inform conservation planning. During 2016-2018, we surveyed sites occupied by KBB during pilot occupancy surveys conducted in 2015, unoccupied sites connected to or within 200 m of sites occupied in 2015, four previously occupied sites surveyed previously using distance sampling, and several occupied sites located on private lands. We conducted modified Pollard-Yates surveys in which surveyors followed a series of transects paralleling the outer boundary of the identified habitat patch. Locations of Karner blue observations were recorded using GPS and we characterized the habitat by ranking lupine cover, nectar source availability, and invasive plant species using the DAFOR system. We used occupancy models and Presence 2.12.17 software to estimate the probability of occupancy, detection, colonization, and extinction for Karner blue on State lands. The raw proportion of sites occupied by KBB appeared to be stable to increasing, with the pattern being similar whether all sites were considered (0.47 in 2015, 0.66 in 2018) or just those surveyed during all four years (0.55 in 2015, 0.66 in 2018). We observed a similar pattern in maximum second flight abundance, which increased each year when all sites were considered. Abundance for only those sites visited all four years varied by year but increased overall from 2015 (658 individuals) to 2018 (1,031 individuals). Our best-approximating model indicated an increasing trend in probability of occupancy, from 0.55 in 2015 to 0.69 In 2018, with the average rate of change in occupancy being greater than 1 for each transition from one year to the next. Detection probability was high, being estimated at 0.8 during the first visit and 0.7 for the second visit. Probability of colonization (0.27) was greater than extinction probability (0.09). Site area was positively associated with occupancy probability, but models containing other covariates received lower support. This project provides an example of how an occupancy-based program can be used to monitor KBB status. Our data suggest an increasing trend in occupancy on the State lands monitored over the four-year period, which may be indicative of a recovering Karner blue population since declines in 2012 associated with high spring temperatures and summer drought. We characterized habitat patches using variables that could be derived from management records (e.g., years since last burn) or easily measured in the field (e.g., lupine DAFOR ranking), but more detailed sampling of vegetation structure and composition and microclimate, as well as additional analyses, may better discern the factors associated with Karner occupancy. Assessing the influence of management on KBB populations is difficult, given that most of the occupied sites have had consistent management over many years.

Introduction

The Michigan Natural Features Inventory (MNFI) began working with the Michigan Department of Natural Resources (MDNR) in late 2014 to develop a new occupancy-based Karner blue (*Lycaeides melissa samuelis*; KBB) survey to address multiple monitoring goals. Long-term survey data are needed to 1) evaluate population status and progress toward recovery plan goals, 2) determine occupancy status of individual habitat patches to inform regulatory and management decisions, and 3) evaluate the response of KBB to management actions. An occupancy approach is well suited to smaller sites with low abundance, because it is easier and more efficient to implement compared to distance sampling. Furthermore, occupancy is often considered a better parameter for programs monitoring endangered or rare species occurring at population levels too low for reliable estimation of abundance (MacKenzie et al. 2005, 2006). Bried and Pellet (2012) suggested occupancy monitoring was a reasonable approach for tracking the status of a Karner blue population in New York.

After conducting pilot occupancy surveys in 2015, we refined the sample design in 2016 to focus the survey effort on recently occupied and nearby habitat patches and better connect monitoring to management efforts implemented as part of a three-year Competitive State Wildlife Grants project, which continued through 2018. Our monitoring objectives were to develop a survey that could track Karner blue occupancy over time, while also gathering information on abundance and providing a long-term framework for evaluating the influence of prescribed fire and mowing on occupancy. Prescribed fire and mowing are the primary techniques used to maintain and restore the open habitats required by Karner blue, so we designed the survey to monitor Karner blue occupancy and relative abundance concurrent with tracking management activities. We conducted occupancy modeling analysis on the four-year data set to estimate occupancy and other population parameters for Karner blue on lands managed by the MDNR to assess the species' status, evaluate the influence of management variables on occupancy, and inform conservation planning.

Study Area

We implemented this project in the southwestern portion of the Lower Peninsula of Michigan. Study sites consisted of areas occupied during 2015 pilot surveys and nearby (within 200 m) unoccupied areas with potential habitat. Most of the sites occurred in Allegan State Game Area (SGA; Allegan County), with a small number of areas surveyed further north in Flat River SGA (Montcalm and Ionia Counties) and on private lands (southern Newaygo County). The Allegan SGA sites were located within the Southern Lake Michigan Lake Plain (sub-subsection VI.3.2; Albert 1995) in areas regularly managed as oak savanna using prescribed fire and mowing. Sites in Flat River SGA fell within the Greenville sub-subsection (VI.4.2) and private land sites occurred in the Newaygo Outwash Plain (VII.3) and Manistee (VII.4) sub-subsections. Flat River SGA and private land sites also undergo periodic burning and/or mowing to maintain habitat for Karner blue.

Methods

Sample Design
The sample frame used for surveys during 2016-2018 consisted of sites occupied by KBB during pilot occupancy surveys conducted in 2015, unoccupied sites connected to or within 200 m of sites occupied in 2015, four previously occupied sites surveyed using distance sampling, and several occupied sites located on private lands for which the MDNR has provided management assistance. Monfils and Cuthrell (2015) described how the original pilot survey sites were developed. The final sample frame consisted of 64 sites totaling approximately 413 hectares (1,021 acres) of potential KBB habitat (Figure 1).

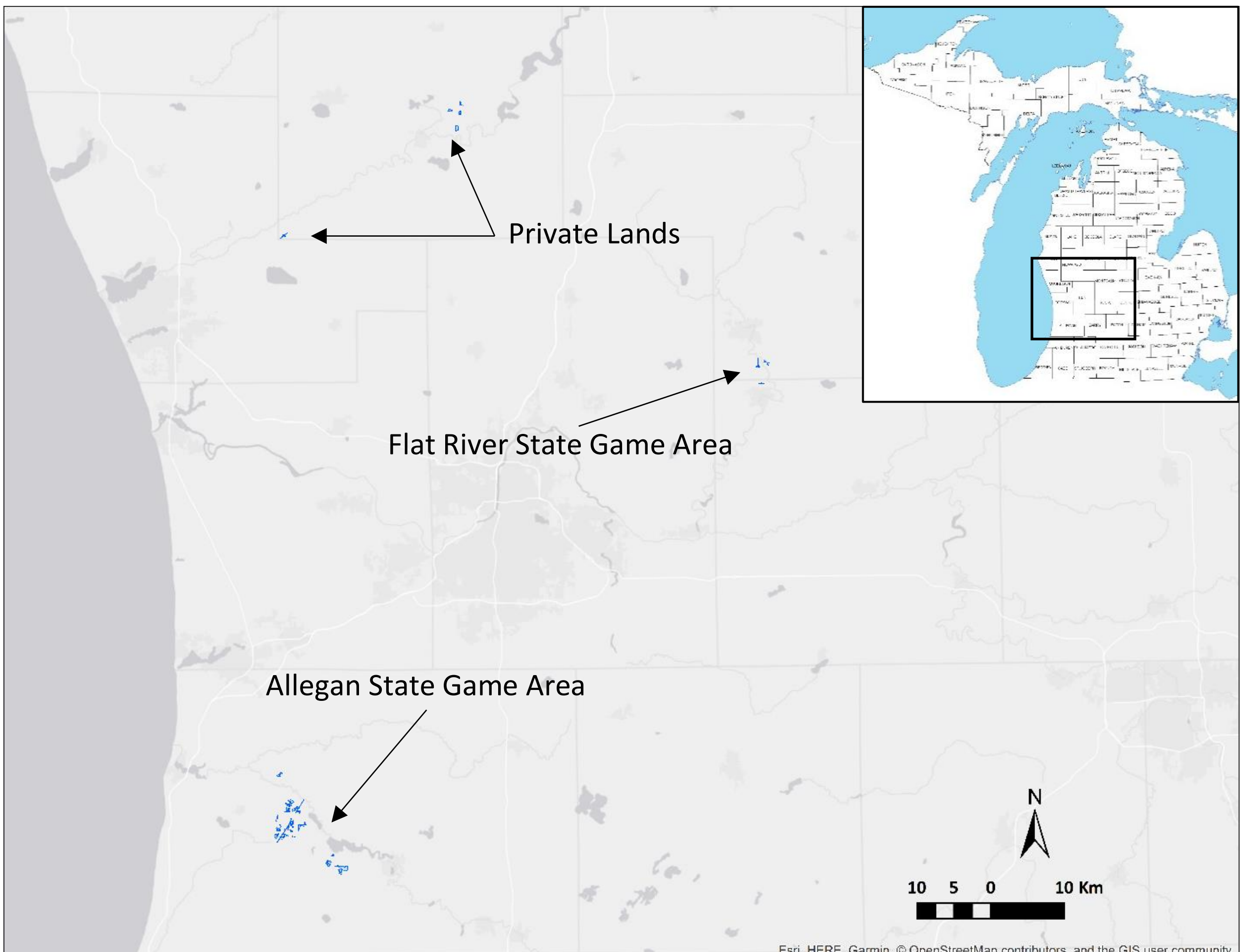

Figure 1. Karner blue butterfly survey locations (blue shading) in southwestern Lower Michigan visited during 2015-2018.

Butterfly Surveys
We designed the survey to be flexible, allowing survey routes to be modified over time in the field as vegetation conditions changed. Polygons defining the survey sites were uploaded to

tablet computers to assist surveyors as they navigated among and within sites using a GPS application. We focused surveys on areas having ≤ 60% tree canopy cover (Grundel et al. 1998). Areas within the polygons having one or more of the following conditions were excluded from the survey: 1) > 60% tree canopy cover; 2) > 75% bare soil and no lupine; and 3) planted crops or ground cover (e.g., grassland, lawn) lacking lupine and nectar sources. Areas of potential habitat (i.e., ≤ 60% canopy cover with lupine/nectar sources) located immediately outside of the identified polygons were added to the survey.

We conducted surveys when the temperature was above 15° C (60° F), there was no rain, and when winds were ≤ 25 km/h (15 mph). If temperatures were 15 - 21° C (60 - 70° F), surveys were only conducted when cloud cover was ≤ 50% of the sky. There was no cloud cover restriction if the temperature was above 21° C (70° F). If weather conditions deteriorated during a visit, observers terminated the survey and resurveyed the entire site on a suitable day. Surveys were conducted between 9 AM and 6 PM (EDT). Two surveys of each site were completed during the second Karner blue flight (approximately early July through early August).

We conducted modified Pollard-Yates (Pollard and Yates 1993) surveys in which surveyors followed a series of transects paralleling the outer boundary of the identified patch of potential habitat (e.g., savanna, grassland). The first transect began 5 m inward from the outer edge of the patch, with one surveyor slowly walking along the first transect until the entire periphery of the site was surveyed. A second transect was located 10 m inward from the first transect and was surveyed in the same manner. Additional transects were added until the entire patch was surveyed. For long narrow sites (e.g., utility corridors), surveyors used short transects traversing the width of the corridor (i.e., perpendicular to longest axis) and surveyed the transects back and forth, moving from one end of the corridor to the other, to avoid repeat counts of butterflies. At some large sites, two to five people conducted the survey together, with transects spaced 10 m apart. Observers looked for and counted butterflies within an area 5 m to either side of the transect, 5 m forward along the transect, and 5 m above the transect (10 m x 5 m x 5 m, rectangular survey area). Surveyors walked at a steady, slow speed of approximately 35 m/min. If Karner blues flew ahead of an observer, they were ignored if the surveyor was certain the individual was already counted. When an observer was uncertain as to whether an individual was tallied, it was counted and considered a new individual.

To facilitate an accurate count of Karner blues and understand their distribution within and among sites, we collected geospatial information using GPS units or tablet computers. In most cases, a waypoint was collected for each individual Karner observed. For example, if five butterflies were seen on one nectar source, five waypoints were collected at the same location. However, at a few of the most densely populated sites, surveyors recorded locations at the periphery of observations and documented the number of individuals detected. Observers tried to avoid flushing butterflies when collecting waypoints as much as possible. We also recorded survey transects by gathering track locations at 30-sec intervals during the first visit to sites. During the second survey and visits during subsequent years, observers followed the same tracks to ensure consistency among surveys.

We characterized KBB activity and condition by assigning the total number of individuals detected within several categories. We recorded the number of Karner blues observed within the following behavioral classes: nectaring, flying, perched, copulating, and ovipositing. The condition of Karner blues was ranked according to the following 1 – 5 numeric scale presented by Watt et al. (1977): 1) freshly emerged, wings still damp; 2) wings and other cuticle dry and hard, no visible damage; 3) noticeable wear of scales from wings or body; 4) wings showing fraying or tearing in their cuticle; and 5) wings with extensive scale wear and cuticle damage.

Other butterfly species detected during Karner blue surveys were recorded on a checklist for each site. Because estimating relative abundance would be difficult for multiple species and would distract observers from surveying for Karners, observers did not attempt to count species other than Karner blue.

Site Characterization

Observers characterized environmental and habitat characteristics at each site during each visit. We collected information on variables that may influence Karner blue detection and occupancy and could be included in models used to estimate population parameters. At the start and end of a survey, surveyors recorded the temperature (°C), percent relative humidity, cloud cover (expressed as the % of sky occluded), and maximum wind speed (km/h). Surveyors collected general information about potential threats to KBB and its habitats and ranked the relative abundance of lupine, nectar sources, and invasive plant species. We used the DAFOR scale to rank the relative abundance of lupine, potential nectar sources, and invasive species as dominant (D), abundant (A), frequent (F), occasional (O), or rare (R). Because lupine is both the larval host plant and a potential nectar source for Karner blue, we ranked relative abundance of flowering lupine and all lupine (both flowering and non-flowering plants) separately.

Analysis

We estimated Karner blue occupancy probabilities, or the estimated proportion of sites occupied given imperfect detection, using the single species, multi-season occupancy model presented by MacKenzie et al. (2003, 2006). The primary goal of surveys was to track Karner blue occupancy of MDNR-managed sites over time, but we were also interested in the potential influence of management and other habitat factors on Karner blue occurrence. By using multi-season occupancy models, we also estimated probabilities of colonization (probability an unoccupied site becomes occupied) and extinction (probability an occupied site becomes unoccupied). Occupancy models were produced using Presence (version 2.12.17, Hines [2006]). We began by first comparing the four model parameterizations available for the multi-season model using Akaike's Information Criterion (AIC). The parameterization that estimates initial (year 1) occupancy, colonization, extinction, and detection probabilities directly, and subsequent years of occupancy through recursive equations, performed the best based on AIC values, so that parameterization was used in all subsequent models.

We used a tiered approach to developing candidate models. Detection probability was modeled first by comparing four models: one assuming constant probability of detection across survey periods and seasons, a second incorporating variable detection probabilities by survey period within seasons, a third with detectability varying by year, and a fourth with detectability varying by year and season. The best-supported configuration of the four models, as indicated by AIC values, was used in subsequent models. We then compared three models each containing one of three covariates that could influence KBB detection (temperature, cloud cover, and wind speed). The best-approximating detection model was included in all subsequent occupancy models. We modeled the occupancy parameter next by comparing a model with no occupancy covariates with models containing one of the following variables: site area (hectares), years since last burn, years since last mowing, years since last disturbance (burning or mowing), and total lupine availability (DAFOR ranking). Variables describing the time since last management action were transformed to 0 – 1 scale. When years since last management were 1 – 9, we divided by 10 (i.e., 0.1 – 0.9); we assigned a value of 1 when the number of years was ≥ 10. Sites having no record or evidence of previous management were also assigned a value of 1. The best occupancy configuration was included in all remaining models. We next modeled the colonization parameter by first comparing two models, one with constant probability across all years and the second with probability varying by year. We used the best configuration in subsequent models containing one of the same variables used for the occupancy parameter (i.e., area, years since burn, years since mowing, years since disturbance, and lupine). Finally, we modeled the extinction parameter using the same procedure used for colonization probability. Because records of past management were not available for the private land sites, we conducted our analysis using data from 57 patches of potential KBB habitat on State lands.

Results

Karner Blue Surveys

Changes in the sample frame made between the 2015 and 2016 field seasons were reflected in the survey results. The broad-scale pilot survey conducted in 2015 visited 134 potential habitat patches that included areas with no previous or recent record of Karner blue, with 51 of the sites covered in 2015 also being surveyed during at least one of the following three years. There were 44 sites consistently surveyed during all four years. Naïve occupancy, or the raw proportion of sites occupied, appeared to be stable to possibly increasing (Table 1). Maximum second flight abundance increased each year when all sites were considered, but abundance for only those sites visited in all four years was more variable across the period (Table 1).

Table 1. Summary of results from surveys conducted for Karner blue on State and private lands in Michigan during 2015-2018.

Measure	2015	2016	2017	2018
Number of sites surveyed	51	62	63	58
Proportion of sites occupied				
All sites surveyed	0.471	0.672	0.672	0.655
Sites visited every year (*n* = 44)	0.546	0.682	0.727	0.659
Maximum second flight abundance (sum of largest number detected between two surveys of each site)				
All sites surveyed	658	4,986	4,867	5,384
Sites visited every year (*n* = 44)	658	1,704	1,596	1,031

Occupancy Modeling

We ran 27 models in our candidate set, of which 21 successfully converged (Table 2). The best-approximating model contained area as an occupancy covariate, had detectability varying by survey period within season, and had no colonization or extinction covariates. However, three similar models also received relatively strong support; two of these models contained extinction covariates (area, lupine) and one had area as a colonization covariate (Table 2). Although these three models appeared to be well supported by the data, the colonization and extinction covariates distinguishing these models from the best-approximating model did not appear to be significant (i.e., 95% confidence intervals of parameter estimates included 0).

Table 2. Results of occupancy model analysis for Karner blue on State lands in Michigan during 2015-2018.				
Model[1]	**AIC**	**∆ AIC**	**AIC Weight**	**No. Parameters**
psi(A),gamma(.),eps(.),p(S)	460.76	0.00	0.2209	6
psi(A),gamma(.),eps(L),p(S)	461.90	1.14	0.1249	9
psi(A),gamma(.),eps(A),p(S)	462.65	1.89	0.0859	7
psi(A),gamma(A),eps(),p(S)	462.67	1.91	0.0850	7
psi(A),gamma(.),eps(M),p(S)	463.08	2.32	0.0693	9
psi(.),gamma(.),eps(.),p(S)	463.57	2.81	0.0542	5
psi(A),gamma(.),eps(B),p(S)	464.01	3.25	0.0435	9
psi(A),gamma(.),eps(Y),p(S)	464.20	3.44	0.0396	8
psi(.),gamma(.),eps(.),p(S,C)	464.26	3.50	0.0384	6
psi(.),gamma(.),eps(.),p(S,W)	464.45	3.69	0.0349	6
psi(A),gamma(.),eps(D),p(S)	464.77	4.01	0.0297	9
psi(.),gamma(.),eps(),p(S,T)	465.04	4.28	0.0260	6
psi(B),gamma(.),eps(),p(S)	465.21	4.45	0.0239	6
psi(.),gamma(.),eps(.),p(Y)	465.34	4.58	0.0224	7
psi(L),gamma(.),eps(.),p(S)	465.52	4.76	0.0204	6
psi(D),gamma(.),eps(.),p(S)	465.54	4.78	0.0202	6
psi(M),gamma(.),eps(.),p(S)	465.56	4.80	0.0200	6
psi(.),gamma(.),eps(.),p(.)	466.24	5.48	0.0143	4
psi(.),gamma(.),p(.)	466.39	5.63	0.0132	3
psi(.),eps(.),p(.)	466.39	5.63	0.0132	3
psi(.),gamma(.),eps=1-gamma,p(.)	510.07	49.31	0.0000	3

[1]Model notation as follows: psi = occupancy probability; gamma = colonization probability; eps = extinction probability; p = detection probability; A = area (ha); B = years since last burn; D = years since last disturbance; L = lupine cover ranking; M = years since last mowing; S = survey period; Y = year; C = cloud cover proportion; T = temperature (°C); and W = wind speed (km/s).

Estimates from the model best supported by the data indicate detectability differed by survey period but was consistent across seasons (Table 3). Probability of detection was about 0.8 during the first visit and 0.7 during the second visit. The addition of detection covariates did not improve the performance of the models. Yearly occupancy estimates increased each year, with the average rate of change in occupancy (psi_t+1/psi_t) being greater than 1 for each transition from one year to the next (Table 3). Site area was positively associated with occupancy probability. Probability of extinction (i.e., probability an occupied site in year *t* becomes unoccupied in year *t*+1) was 0.09, whereas colonization probability (i.e., probability an unoccupied site in year *t* becomes occupied in year *t*+1) was 0.27. Including covariates for the extinction and colonization parameters did not improve model fit.

Table 3. Parameter estimates from best-approximating multi-season occupancy model for Karner blue on State lands in Michigan during 2015-2018.				
Parameter	**Estimate**	**Standard Error**	**Lower Confidence Limit**	**Upper Confidence Limit**
Naïve occupancy (modeled sites)				
2015	0.471	---	---	---
2016	0.636	---	---	---
2017	0.655	---	---	---
2018	0.635	---	---	---
Occupancy probability				
2015	0.546	0.091	0.368	0.712
2016	0.618	0.066	0.488	0.747
2017	0.664	0.065	0.537	0.791
2018	0.694	0.069	0.559	0.829
Detection probability				
2015-2018, period 1	0.816	0.040	0.737	0.895
2015-2018, period 2	0.697	0.043	0.612	0.782
Occupancy rate of change				
2015-2016	1.187	0.145	0.903	1.471
2016-2017	1.091	0.056	0.982	1.201
2017-2018	1.050	0.029	0.994	1.107
Extinction probability	0.091	0.037	0.018	0.163
Colonization probability	0.268	0.068	0.134	0.401

Discussion

Our surveys and analysis provide an example of how an occupancy-based program can be used to monitor the status of Karner blue. Occupancy analysis produces parameters, such as occupancy, extinction, and colonization probabilities, that can be used to track population status over time when estimating abundance is more problematic (e.g., because of small sites, low abundance, variation associated with timing/peaks of abundance). For example, probability of detecting Karner blue was high (0.7-0.8) under our project, so the species was likely to be detected when present at a site, yet accurately estimating abundance may be difficult when resources are not available to conduct the repeated surveys needed to ensure the peak of abundance during the second flight is detected. Given our estimates of detectability and occupancy, two surveys during the second flight is probably optimal for a program, such as ours, in which all sites are surveyed the same number of times within a season (MacKenzie and Royle 2005). Bried and Pellet (2012) suggested the minimal survey effort for Karner blue occupancy surveys in New York was 360 (40 sites x 9 visits) in the first flight and 200 (20 sites x 10 visits) in the second flight. However, the authors had lower probabilities of occupancy and detection compared to our study and their sample design focused on sites with sparse populations. Huron-Manistee National Forest personnel conduct surveys of some smaller habitat patches on U.S. Forest Service (USFS) lands using a protocol similar to our occupancy-based approach. There is potential to use the USFS data to conduct a larger-scale occupancy analysis, which could provide a better assessment of the overall Michigan Karner blue population.

Our analysis suggests an increasing trend in occupancy on the State lands monitored over the four-year period, with the probability of colonization being greater than the probability of extinction. This pattern may be indicative of a Karner blue population in recovery since declines in 2012 associated with record high spring temperatures and summer drought. Although Grundel and Pavlovic (2007) observed that spatial pattern, resource availability, matrix quality, and microclimate accounted for similar levels of variation in patch occupancy by Karner blue in Wisconsin and Indiana sites, Walsh (2017) found that heat load explained most of the variation (64-67%) in logistic regression models of occupied and restored sites in Michigan and Ohio. Additional occupancy modeling of our data set with climate and weather variables would be valuable.

We were interested in evaluating if occupancy, extinction, and colonization probabilities were associated with management, site area, and lupine availability. Years since last burn, mowing, or disturbance (burning/mowing) were used as indicators of management. Our best-approximating model included area as an occupancy covariate, but models containing management variables received less support. Grundel and Pavlovic (2007) found that habitat patch size explained 30% of the variation in Karner blue occupancy of sites within the Indiana Dunes Lakeshore. Consistent with our project, King (2003) found no significant difference in Karner density among burned, mowed, and control sites in Wisconsin, yet differences in herbaceous layer components were detected. We attempted to describe the habitat patches using variables that could be quickly and easily measured in the field, but more detailed sampling of vegetation structure and composition and microclimate variables could be needed to discern the factors associated with Karner occupancy.

Evaluating the influence of management on Karner blue populations is a difficult endeavor because nearly all the occupied sites are regularly managed by prescribed fire and mowing in an alternating sequence. Previously occupied sites that have not undergone regular management have likely converted to forest no longer suitable for Karner blue. Given that most of the sites now occupied by KBB have had consistent management over long periods, it is not surprising that management variables did not appear associated with occupancy, because unmanaged sites were not sampled. Often only a portion of an individual habitat patch underwent management and the areas covered and techniques used within the patch changed over time, further complicating our ability to discern the effects of management. Although the direct effects of management on Karner blue remains unknown, the species is unlikely to survive without the continued periodic disturbance to occupied patches. Strict experimental management with occupied control sites and a long-term approach would likely be needed to understand how Karner blue responds to management, which could result in declines or temporary extirpation of the species in control sites.

Acknowledgements

Funding for this project was provided through the Cooperative State Wildlife Grants program grant number F15AP00895 in cooperation with the U.S. Fish and Wildlife Service, Wildlife and Sport Fish Restoration Program. We thank the following DNR staff for their advice and assistance: Maria Albright, Amy Derosier, Donna Jones, Dan Kennedy, Mark Mills, Mike Parker, John Niewoonder, and Mark Sargent. Thanks to Helen Enander (MNFI) for help with delineating openings based on aerial photo interpretation. Several MNFI field technicians conducted surveys: Kailyn Atkinson, Michael Belitz, Selena Creed, Aaron Cuthrell, Daniel Earl, Kristen Finch, Lillian Hendrick, Michelle Nichols, Mary Parr, Rachel Patterson, Clint Pogue, Henry Pointon, and Melanie Schott. John Bagley and several volunteers from the Michigan Nature Association also assisted with surveys. Administrative support was provided by Brian Klatt, Ashley Atkinson, Sue Ridge, and Nancy Toben (MNFI).

Literature Cited

Albert, D. A. 1995. Regional landscape ecosystems of Michigan, Minnesota and Wisconsin: a working map and classification. General Technical Report NC-178, U.S. Dept. of Agriculture, Forest Service, North Central Forest Experiment Station, St. Paul, Minnesota, USA.

Bried, J. T., and J. Pellet. 2012. Optimal design of butterfly occupancy surveys and testing if occupancy converts to abundance for sparse populations. Journal of Insect Conservation 16:489–499.

Hines, J. E. 2006. PRESENCE- Software to estimate patch occupancy and related parameters. USGS-PWRC. <http://www.mbr-pwrc.usgs.gov/software/presence.html>.

King, R. S. 2003. Habitat management for the Karner blue butterfly (*Lycaeides melissa samuelis*): evaluating the short-term consequences. Ecological Restoration 21:101-106.

Grundel, R., N. B. Pavlovic, and C. L. Sulzman. 1998. Habitat use by the endangered Karner blue butterfly in oak woodlands: the influence of canopy cover. Biological Conservation 85:47-53.

Grundel, R., and N. B. Pavlovic. 2007. Resource availability, matrix quality, microclimate, and spatial pattern as predictors of patch use by the Karner blue butterfly. Biological Conservation 135:135-144.

Mackenzie, D. I., J. D. Nichols, J. E. Hines, M. G. Knutson, and A. B. Franklin. 2003. Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. Ecology 84:2200–2207.

Mackenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. L. Bailey, and J. E. Hines. 2006. Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. Elsevier Publishing, Inc., Amsterdam, The Netherlands.

Mackenzie, D. I., J. D. Nichols, N. Sutton, K. Kawanishi, and L. L. Bailey. 2005. Improving inferences in population studies of rare species that are detected imperfectly. Ecology 86:1101-1113.

Mackenzie, D. I., and J. A. Royle. 2005. Designing occupancy studies: general advice and allocating survey effort. Journal of Applied Ecology 42:1105–1114.

Monfils, M. J., and D. L. Cuthrell. 2015. Development and implementation of an occupancy survey for Karner blue butterflies. Michigan Natural Features Inventory, Report Number 2015-15, Lansing, USA.

Pollard E., and T. J. Yates. 1993. Monitoring butterflies for ecology and conservation. Chapman & Hall, London, Great Britain.

Walsh, R. P. 2017. Microclimate and biotic interactions affect Karner blue butterfly occupancy and persistence in managed oak savanna habitats. Journal of Insect Conservation 21:219–230.

Watt, W. B., F. S. Chew, L. R. G. Snyder, A. G. Watt, and D. E. Rothschild. 1977. Population structure of Pierid butterflies: I. Numbers and movements of some montane *Colias* species. Oecologia 27:1-22.