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Local and landscape effects on population dynamics of birds and butterflies in Iowa

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Local and landscape effects on population dynamics of birds and butterflies in Iowa

by

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A thesis submitted to the graduate faculty

in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

Major: Wildlife Ecology

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Iowa State University

Ames, Iowa

2016

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

Page

ACKNOWLEDGEMENTS

in the outdoors and wildlife might never have been awakened if Grandpa hadn't taken me to see those nighthawks zooming and diving over the school – or if Mom and Dad hadn't shown me the proper way to identify that Common Grackle out in the yard when I was just seven years old.

And now after looking back on times of happiness, I look ahead and dedicate this thesis to my two daughters – Natalie and Olivia – who will always inspire me to be my very best. We'll continue to make a lifetime of happy memories together.

CHAPTER 1. GENERAL INTRODUCTION

Background

Because of their ongoing popularity among nature enthusiasts (Sibley 2000, National

Geographic Society 2002, Brock and Kaufman 2006, Garrigues 2007), relative ease of

observation and utility as bio-indicators (Temple and Wiens 1989, Blair 1999, Thomas and

Clarke 2004, Thomas 2005, Van Swaay et al. 2006), both birds and butterflies continue to be

among the most heavily studied organisms on earth (Thomas 2005, Nowicki et al. 2008). With

both groups experiencing well-documented, widespread declines (Van Swaay et al. 2006, Van

Swaay et al. 2013, Sauer et al. 2014, North American Bird Conservation Initiative 2016), studies

of their status and conservation have proliferated in recent years. Furthermore, widespread,

comprehensive monitoring of birds and butterflies has been taking place in Iowa for more than a

decade via the Multiple Species Inventory and Monitoring (MSIM) program (Kinkead 2006).

There is now an opportunity to utilize advanced analytical tools (i.e., Program MARK) to

determine the manner in which landscape composition impacts the population dynamics of birds

and butterflies in Iowa's extensively fragmented habitats. For birds, this might be especially

useful with regard to the conservation of Neotropical migrants (Stotz et al. 1996), a nationally

declining group (Sauer et al. 2014) that is well-represented in many of Iowa's woods and second-

growth areas (Reeder and Clymer 2015, Teaming with Wildlife 2015). For butterflies, we can

gain deeper insights into the dual role of microhabitat and broad-scale habitat attributes, the latter

of which has only recently been studied in detail (Davis et al. 2007, Bried and Pellett 2011,

Fernández-Chacón et al. 2014, Puntenney and Schorr 2016).

Furthermore, two distinct opportunities exist to improve our understanding of a nearly

universal issue in bird and butterfly sampling methodology: the concept of detection probability,

defined as the probability that an organism is detected during a survey, given that it is present (Burnham and Anderson 1984). The majority of studies from the 20th Century ignored this concept (Mackenzie et al. 2005), especially in regard to butterflies (Kellner and Swihart 2014), which led to unreliable estimations of density and a barrier to understanding populations (Buckland et al. 2010). Among the survey methods available to account for imperfect detection are distance sampling and occupancy modeling. With distance sampling an observer assigns discrete detection distances to organisms during surveys (Buckland et al. 2004), thus enabling a detection probability and a corrected estimate of density to be estimated. With occupancy modeling, presence-absence data are used to estimate the probability of detection under an assumption of population closure (Mackenzie et al. 2002). The MSIM survey framework is designed to accommodate both analytical frameworks to be able to address a suite of questions about the status, conservation, and management of Iowa's wildlife.

<div align="center">Research Objectives</div>

Given this background information, the primary objectives of my study are to:

1. Compare the efficacy of unlimited-distance line-transect surveys that incorporate distance sampling to traditional Pollard-Yates transects to estimate butterfly density.

2. Evaluate habitat associations and landscape-level impacts on population dynamics of forest, savanna, and scrub-shrub birds in Iowa, while also incorporating estimates of detection probability.

3. Determine the effect of microhabitat and landscape-level variables on population dynamics of butterflies in Iowa, while also accounting for imperfect detection probability.

To complete the first objective, I designed and implemented a novel butterfly distance-sampling study that I personally conducted during my first field season of graduate school. I promptly analyzed data from these surveys in Program Distance during the subsequent semester and commenced writing a manuscript soon after. In that time interval, I also presented my findings at the 2014 meeting of the Iowa Chapter of The Wildlife Society (TWS). My research on this topic contributes to knowledge of distance sampling, detection probability, and density estimation of butterflies and should assist researchers in designing future studies of butterflies and other taxa.

For the second and third objectives, I performed extensive queries and extracted bird and butterfly data from the Multiple Species Inventory and Monitoring (MSIM) database, which functions as an ever-expanding archive and analytical tool for MSIM and related data collected across Iowa since 2006. I analyzed 2007-2014 bird point-count data and butterfly-transect data in RMARK (Laake 2013) to answer questions about habitat associations and the impacts of landscape composition on these taxa in Iowa. The comprehensive scope of the MSIM data and the robustness of the analyses also enabled me to summarize the results in such a way that they can be readily applied regionally and nationally. With that in mind, I gave a presentation at the 2015 Iowa TWS meeting on some encouraging preliminary results of these analyses, and I would welcome the opportunity to do so again – in Iowa or beyond.

Thesis Organization

This thesis is organized into chapters that have been formatted as journal papers. Chapter 1 provides a general introduction to the topics covered by these three chapters. Chapters 2, 3, and 4 address the research objectives outlined above. Chapter 5 provides a brief summary of findings and general conclusions.

Literature Cited

Blair, R. B. 1999. Birds and butterflies along an urban gradient: surrogate taxa for assessing biodiversity? Ecological Applications 9:164-170.

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.

Brock, J. P., and K. Kaufman. 2006. Butterflies of North America. Kaufman Field Guides.

Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas. 2004. Advanced distance sampling. Oxford University Press, Oxford, UK.

Buckland, S. T., J. L. Laake, and D. L. Borchers. 2010. Double-observer line transect methods: levels of independence. Biometrics 66:169-177.

Burnham, K. P., and D. R. Anderson. 1984. The need for distance data in transect counts. Journal of Wildlife Management 48:1248-1254.

Davis, J. D., D. M. Debinski, and B. J. Danielson. 2007. Local and landscape effects on the butterfly community in fragmented Midwest U.S.A. prairie habitats. Landscape Ecology 22:1341-1354.

Fernández-Chacón, A., C. Stefanescu, M. Genovart, J. D. Nichols, J. E. Hines, F. Paramo, M. Turco, and D. Oro. 2014. Determinants of extinction-colonization dynamics on Mediterranean butterflies: the role of landscape, climate, and local habitat features. Journal of Animal Ecology 83:276-285.

Garrigues, R. 2007. The Birds of Costa Rica. Comstock Publishing Associates.

Kellner, K. F. and R. K. Swihart. 2014. Accounting for imperfect detection in ecology: a quantitative review. PLOS ONE, 9(10), e111436.

Kinkead, K. E. 2006. Iowa multiple species inventory and monitoring program technical manual. Iowa Department of Natural Resources, Des Moines, Iowa, USA.

Laake, J. L. 2013. RMark: An R Interface for Analysis of Capture-Recapture Data with MARK. AFSC Processed Rep 2013-01, 25p. Alaska Fish. Sci. Cent., NOAA, Natl. Mar. Fish. Serv., 7600 Sand Point Way NE, Seattle WA 98115.

MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, J. A. Royle, C. A. Langtimm, 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology 83:2248-2255.

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

National Geographic Society. 2002. National Geographic field guide to the birds of North America, Fourth Edition. National Geographic Society, Washington, DC.

Reeder, K. F. and J. A. Clymer. 2015. Iowa's Wildlife Action Plan: Securing a future for fish and wildlife. Iowa Department of Natural Resources, Des Moines, Iowa, USA.

Puntenney, C. P. and R. A. Schorr. 2016. Patch occupancy and habitat of the hops azure (*Celastrina humulus*), a rare North American endemic butterfly: insights for monitoring and conservation. Journal of Insect Conservation 20:215-222.

Sauer, J. R., J. E. Hines, J. E. Fallon, K. L. Pardieck, D. J. Ziolkowski, Jr., and W. A. Link. 2014. The North American Breeding Bird Survey, Results and Analysis 1966-2013. Version 01.30.2015. USGS Patuxent Wildlife Research Center, Laurel, Maryland, USA.

Sibley, D. A. 2000. The Sibley guide to birds. Alfred A. Knopf, New York.

Stotz, D. F, J. W. Fitzpatrick, T.A. Parker III, and D. K. Moskovits. 1996. Neotropical birds: ecology and conservation. University of Chicago Press, Chicago, Illinois, USA.

Teaming with Wildlife. 2015. State Wildlife Action Plans: A strategic approach to conservation. <http: //www.teaming.com/state-wildlife-action-plans-swaps>. Accessed 10 July 2016.

Temple, S. A., and J. A. Wiens. 1989. Bird populations and environmental changes: can birds be bio-indicators? American Birds 43:260-270.

Thomas, J. A., and R. T. Clarke. 2004. Extinction rates and butterflies. Science 305:1563-1564.

Thomas, J. A. 2005. Monitoring change in the abundance and distribution of insects using butterflies and other indicator groups. Philosophical Transactions of the Royal Society of Biological Sciences 360:339-357.

Van Swaay, C. A. M., M. S. Warren, G. Lois. 2006. Biotope use and trends of European butterflies. Journal of Insect Conservation 10:189-209.

Van Swaay, C. A. M., A. Cuttelod, S. Collins, D. Maes, M. López Munguira, M. Šašic, J. Settele, R. Verovnik, T. Verstrael, M. Warren, M. Wiemers, and I. Wynhoff. 2010. European Red List of butterflies, IUCN Red List of Threatened Species - Regional Assessment - Office for Official Publications of the European Communities, Luxembourg. van Swaay, C. A. van Strien; A. Harpke; B. Fontaine; C. Stefanescu; D. Roy; E. Kühn; E. Õnuao; E. Regan and G. Švitra et al. 2013. *In* EEA Technical Reports 11/2013.

CHAPTER 2. A COMPARISON OF TWO METHODS TO ESTIMATE BUTTERFLY DENSITY

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Abstract

The Pollard-Yates transect is a widely used method for sampling butterflies. Data from these traditional transects are analyzed to produce density estimates, which are then used to make inferences about population status or trends. A key assumption of the Pollard-Yates transect is that detection probability is 1.0 out to a fixed distance (generally 2.5 m on either side of a transect line), although this assumption has not been well tested with field data. Our objectives were to (1) estimate detection probabilities for butterflies with differing natural histories, (2) compare butterfly density estimates from Pollard-Yates line transects to those that incorporate distance sampling, and (3) offer advice on future butterfly sampling techniques to estimate population density. We conducted Pollard-Yates transects and distance-sampling transects at four grassland sites in central Iowa in 2014. For comparison to densities derived from Pollard-Yates transects (number of detections/total area sampled), we used Program DISTANCE to model detection probability (p) and estimate density (D) for eight butterfly species representing a range of life-history attributes. Although we noted little variation in detectability within 2.5 m, we found that detection probability among species varied widely beyond 2.5 m, with

considerable variation apparent even within 5 m of the line. Such variation corresponded with

size and natural-history attributes of each butterfly species. Program DISTANCE provided more

robust density estimates at these greater distances, often considerably <1.0, particularly for

smaller, cryptic species. Estimated detection probabilities ranged from 0.53 to 0.79 across the

eight species. Thus, we recommend that researchers integrate distance sampling into butterfly

sampling and monitoring, particularly for studies utilizing survey transects >5 m wide. Narrower

transects are more likely to meet the assumption of perfect detection, but this assumption was

clearly violated for many species when transect widths exceeded 10 m.

Key Words: butterfly density, detectability, distance sampling, line transect, Pollard-Yates,

Program Distance

Introduction

Ecologists have often struggled with the need to estimate the probability that an organism

is detected during a survey, given that it is present. This concept is widely referred to as

detection probability (Burnham and Anderson 1984). Early studies tended to ignore this concept

and assumed that all organisms were detected during surveys (Mackenzie et al. 2005). Later

work shifted towards developing methods to directly estimate detection probability, which

include distance sampling (Eberhardt 1968, Gates 1968, Buckland et al. 2001, Buckland et al.

2004), multiple-covariate distance sampling (Marques et al. 2007), mark-recapture (e.g., Haddad

et al. 2008, Pellet et al. 2012), double observers (Nichols et al. 2000, Koneff et al. 2006), and a

synergy of distance-sampling and double-observer methods (Kissling and Garton 2006). If

detection probability is estimated to be less than 1.0, that information is used to correct estimates

of density and abundance to account for the fact that some fraction of the population is almost

always missed during surveys (Buckland et al. 2010). Still, despite heightened awareness of

imperfect detection and advances in statistical software, estimation of detection probability is widely lacking. For example, in a quantitative review of 537 papers from 1971-2011, Kellner and Swihart (2014) found that only 23% of ecological studies had accounted for imperfect detection.

Estimating population size is fundamental to understanding and conserving wildlife (Yoccoz et al. 2001, McGill 2006) and is thus closely linked to an understanding of detection probability. For decades, researchers have been using line transects to survey and derive population estimates, especially for birds (e.g., Childers and Dinsmore 2008, Newson et al. 2008) but also in diverse taxa such as desert tortoises (Swan et al. 2002), whales (Calambokidis and Barlow 2004), land plants (Buckland et al. 2007), and marsupials (Lollback et al. 2015). Traditional fixed-width transects include the assumption of perfect detection within a specified width. Distance sampling enables us to test this assumption by assigning a distance (or distance bin) to each individual detected. Program DISTANCE subsequently generates a detection probability and a "corrected" density estimate for each species (Buckland 2004, Thomas et al. 2010).

For butterfly surveys, the standard Pollard-Yates line transect has been the most extensively used means of surveying butterflies since the early 1990s (e.g., Brown and Boyce 2001, Collier et al. 2006, Nowicki et al. 2008). This method involves walking a slow pace (ca. 10 m/min) along a predetermined line and counting only butterflies seen within a prescribed width, often 5.0 m (i.e., 2.5 m to either side of the observer; Pollard and Yates 1993). A key assumption of these transects is that detection probability of butterflies is 1.0. Data from Pollard-Yates transects are often converted to density estimates and used to make inferences about populations. But a considerable body of research with varied taxa has illustrated that the assumption of

perfect detection, even within a small area, is often unmet (Mackenzie et al. 2005). Fortunately, there are additional survey methodologies that can be used to directly estimate detection probability and thus yield "corrected" density estimates. One such approach is distance sampling (Burnham and Anderson 1984). Prior to 2000, distance sampling was rarely used for butterflies (Brown and Boyce 1998), and imperfect detection as a concept was widely unaccounted for in the majority of invertebrate papers (Kellner and Swihart 2014). Since then, researchers have summarized the need to address sampling bias that stems from variation in butterfly detectability (Dennis et al. 2006, Kery and Plattner 2007, Haddad et al. 2008, Nowicki et al. 2008), and several recent studies have incorporated distance sampling into the traditional Pollard-Yates framework (Powell et al. 2007, Moranz 2010, Isaac et al. 2011). Detection is rarely perfect, even for conspicuous species, which hints at the need to adjust counts to reflect imperfect detection. Not accounting for imperfect detection can result in underestimates of true abundance (Burnham and Anderson 1984), which may have implications for conservation or management decisions.

In this study, our objectives were to (1) estimate detection probabilities for butterflies with differing natural histories, (2) compare butterfly density estimates from Pollard-Yates transects to those that incorporate distance sampling, and (3) offer advice on future butterfly sampling techniques to estimate population density.

Methods

Study Area and Site Selection

Our study was conducted at four public properties (Harrier Marsh Waterfowl Production Area, Marietta Sand Prairie State Preserve, McCoy Wildlife Management Area [WMA], and Rock Creek Marsh WMA) in central Iowa, each of which was included in the ongoing Iowa Multiple Species Inventory and Monitoring (MSIM) program (Kinkead 2006). Harrier Marsh

(170 ha) and McCoy WMA (177 ha) are located in the Des Moines Lobe of the Prairie Pothole

Region, while Marietta Sand Prairie (93 ha) and Rock Creek WMA (343 ha) lie nearby in the

Southern Iowa Drift Plain (Prior 1991). Although most of the former prairies, marshes, and

savannas in these landforms have been converted to row-crop agriculture (Reeder and Clymer

2015), our study sites collectively encompass a mixture of floodplain wetland, prairie-pothole

marsh, upland meadow, restored dry-mesic prairie, and shrubby thickets.

Lepidoptera surveys

To eliminate observer effects, a single observer conducted all surveys, which took place

between 24 July and 24 August 2014 to coincide with prolific flight periods for many species

common to this region (Schlicht et al. 2007). In accordance with MSIM protocol (Kinkead

2006), based on techniques developed by Shepherd and Debinski (2005), surveys were

conducted along a single 400-m long, 5-m wide line that had been placed on the centerline of an

established 10.4-ha sampling hexagon at each property. For the Pollard-Yates transect, the

observer walked at a steady pace (ca. 10 m/min) down the middle of the transect line and

recorded number and species for butterflies detected within the 5-m wide transect corridor.

Behavior (i.e., flying, nectaring, resting, basking, mineralizing, ovipositing, and courting) at

initial detection of each individual was also recorded. Butterfly nomenclature and taxonomic

sequence adhered to those of Opler et al. (2010).

On each site visit, I also conducted unlimited-distance line transects in the opposite

direction on the same transect line. All aspects of sampling techniques (e.g., pace during survey)

matched the methodology of the Pollard-Yates transects, with one key difference. For each

individual detected, the observer assigned it to one of nine distance bins based on its

perpendicular distance from the transect line (bin 1 = 0-1 m, bin 2 = 1-1.75 m, bin 3 = 1.75-2.5

m, bin 4 = 2.5-5.0 m, bin 5 = 5.0-10 m, bin 6 = 10-25 m, bin 7 = 25-50 m, and bin 8 = >50 m)

during the count. These detection-distance categories were arranged in such a way to allow for

comparison to the established 5-m sampling width of the Pollard-Yates line transects (S.

Shepherd, Iowa Department of Natural Resources, pers. comm.). To allow butterflies sufficient

time to settle following sampling disturbance, we waited 10 min before beginning the second

transect and we alternated the survey type (Pollard-Yates or distance sampling) that was

conducted first on a given visit. We completed all surveys between 9:00 a.m. and 6:00 p.m. and

during warm temperatures ($\geq 20°C$), low cloud cover (<70%), calm winds (<16 km/h), and no

precipitation. All weather variables were measured immediately before and after the completion

of each transect.

Data analyses

We selected a suite of eight butterfly species (least skipper [*Ancyloxypha numitor*],

cabbage white [*Pieris rapae*], clouded sulphur [*Colias philodice*], orange sulphur [*Colias

eurytheme*], little yellow [*Pyrisitia lisa*], eastern tailed-blue [*Cupido comyntas*], monarch

[*Danaus plexippus*], and viceroy [*Limenitis archippus*]) for analyses. Species were chosen to

meet the minimum sample size recommended by Thomas et al. (2010) for analysis in Program

Distance and to represent a range of life-history attributes (e.g., cryptic vs. brightly colored,

furtive vs. free-flying, small vs. large) that could contribute to detection probability.

Density was estimated differently for the two sampling approaches. For standard Pollard-

Yates transects, we calculated density (number/ha, or total number of detections divided by area

sampled) by site and across sites. We were unable to calculate a measure of precision for these

estimates because a) the number of surveys per site was low (7), and b) for some species there

was considerable variation in peak flights even within our short survey window. For unlimited-

distance transects, we used Program Distance (v6.2) to estimate detection probability (and associated sampling coefficient of variation [CV]) along with density for each species by site and across sites. We considered only the four models endorsed by Buckland et al. (2001) ([1] uniform key function with cosine adjustments, [2] half-normal key with cosine adjustments, [3] half-normal key function with Hermite polynomial adjustments, and [4] hazard rate key function with simple polynomial adjustments). These models demonstrate characteristics that meet the distance sampling assumption of monotonically decreasing probability of detection from the line. Model fit was evaluated using the chi-square goodness-of-fit test in Program Distance. We used AIC model selection (Burnham and Anderson 2002) to choose the best approximating model for each stratum, with truncations made at 50 m, 5 m, and 2.5 m. The latter two cut-points enabled further comparison to the densities produced via the 5-m wide Pollard-Yates transects.

Results

Seven replicate surveys were conducted at each of the four sites (n = 28 surveys). Eight species had a sufficient number of detections for our analyses and included least skipper (n = 350), cabbage white (n = 117), clouded sulphur (n = 158), orange sulphur (n = 291), little yellow (n = 414), eastern tailed-blue (n = 247), viceroy (n = 88), and monarch (n = 301). The two smallest species, least Skipper and eastern tailed-blue, were detected in categories extending only out to the 5-10 m and 10-25 m bins respectively, whereas the other six species were recorded in all eight bins. However, in all instances, the two outermost bins accounted for a small proportion (<10%) of the detections, and the median detection distances occurred in the following bins for each species: least skipper (bin 2), cabbage white (bin 3), clouded sulphur (bin 4), orange sulphur (bin 4), little yellow (bin 4), eastern tailed-blue (bin 2), viceroy (bin 3), and Monarch (bin 4). For every species, >80% of individuals were identified as flying, basking or nectaring at time of

detection, with resting, mineralizing, courting/mating, and ovipositing butterflies composing the remainder.

Models to explain detection probability varied among the eight butterfly species in this study (Table 1). We found little variation in detectability among species within 2.5 m from the transect line. However, at the 2.5-5.0 m bin, which lies just outside the standard Pollard-Yates survey area, discrepancies in detectability were manifest and ranged from 0.53 for the Least Skipper to 0.79 for the much larger, more conspicuous monarch (Table 1). A post-hoc analysis also revealed a strong positive correlation ($r = 0.91$) between mean wing length and detection probability. At this distance, for all species, the minimum AIC value in Program DISTANCE was derived from a model with a hazard-rate key and simple polynomial adjustments. The corresponding species-specific densities varied, and for all species but little yellow and monarch, densities derived from Program Distance were greater than those estimated from the Pollard-Yates transects (Figure 1).

Discussion

Our study found that detection probabilities of eight common, widespread butterfly species in Iowa were at or near 1.0 in the standard Pollard-Yates transect, but dropped considerably when the sampling area extended >2.5 m from the line transect. Detection probability was positively correlated with mean wing size and was greatest for the largest, most conspicuous species. Below we discuss our findings in the larger context of methods to estimate butterfly densities, and then comment on how the inclusion of distance sampling can help with conservation and management decisions for this taxon.

Detectability and Natural History

As expected, detectability varied considerably among the eight butterfly species, with an upward trend that generally corresponded to median wing size. This matches the detailed findings of Moranz (2010) in comparable open landscapes of southwestern Missouri. The biggest exception in our study was that of little yellow, which produced the third-highest detection probability while having the third-smallest median wing length. Perhaps this detection probability stemmed from this species' tendency to flutter conspicuously just above the tops of *Chamaecrista fasciculate*, a widespread species that serves as the butterfly's favored hostplant in Iowa (Schlicht et al. 2007). The eastern tailed-blue and least skipper are equally short-winged. However, the eastern tailed-blue exhibits more conspicuous nectaring and breeding behavior, as males patrol tirelessly and females oviposit high on flower buds of favored host plants like the long-stemmed *Lespedeza capitata* (Opler et al. 2010), which was prevalent along our study transects (Iowa DNR MSIM program, unpublished data). On the other hand, the weak-flying least skipper often skulks low amongst grasses (Opler et al. 2010). Two very closely related species (orange sulphur and clouded sulphur) produced nearly identical detection probabilities, consistent with their strikingly similar size, life-history strategies, and interrelatedness (Wheat and Watt 2008, Opler et al. 2010, Dwyer et al. 2015). Likewise, the brightly colored, wide-ranging viceroy's detection rate was exceeded only by that of its larger, Mullerian co-mimic, the monarch (Ritland and Brower 1991, Ritland 1995).

Various studies have demonstrated that the Pollard-Yates line transect is susceptible to sampling bias resulting from differences in detectability (Dennis et al. 2006, Kery and Plattner 2007, Moranz 2010, Isaac et al. 2011). Although we did not find the expected variation in detectability close to the line (<2.5 m), we did find considerable differences in interspecific

detectability when considering detections at greater distances (>2.5 m) that exceeded the boundaries of the Pollard-Yates transect. Moranz (2010) and Isaac et al. (2011) provided the groundwork for utilizing distance data to transform Pollard-Yates data into population-density data. Kery and Platner (2007) and Isaac et al. (2011) noted differences in detectability among observers. The unique field methodology of our study (i.e., single observer, both survey types conducted on each visit) enabled direct assessment of specific-specific detectability, as well as a comparison of densities derived from distance sampling and standard Pollard-Yates transects, in the absence of observer bias. A useful follow-up to our study might involve assessment of site-specific (e.g., vegetation) effects, as Brown and Boyce (1998) and Haddad et al. (2008) also documented differences in detectability among sites.

Management Recommendations

Fixed-width transects assuming perfect detection may not provide the best estimate of density, thereby impacting our ability to make inferences about populations. But the degree to which distance sampling is needed depends upon transect width. In our study, variation in detectability was not manifest at the width employed by the traditional Pollard-Yates transect. As such, a narrow transect is more likely to meet that assumption of perfect detectability, but is this advantage traded against other considerations? Narrow transects might not adequately sample large habitat blocks, and avoidance behavior by larger, faster species (e.g., viceroy) might lead to poor counts. Nowicki et al. (2008) also detailed the inability of Pollard-Yates transects to account for detectability. Accordingly, considering the interspecific variation in detectability manifest in our study and other recent studies (Moranz 2010, Isaac et al. 2011), and the observer variation summarized by Kery and Plattner (2007) and Isaac et al. (2011), we recommend incorporating distance sampling whenever possible, even when narrow transects are used.

Line transects are straightforward in their implementation and can be used to repeatedly sample butterflies at multiple sites across a broad region in a short window of time. Distance sampling can be easily incorporated into the line-transect framework and analyzed using Program Distance (Buckland 2006), which provides density estimates and associated measures of precision. As such, distance sampling, especially when used in conjunction with other methods like mark-recapture, represents an effective tool to survey butterflies and guide the management and conservation of butterfly populations.

Acknowledgements

Literature Cited

Barlow, J., T. Gerrodette, and J. Forcada. 2001. Factors affecting perpendicular sighting distances on shipboard line-transect surveys for cetaceans. Journal of Cetacean Research and Management 3:201-212.

Brown, J. A., and M. S. Boyce. 1998. Line transect sampling of Karner blue butterflies (Lycaeides Melissa samuelis). Environmental and Ecological Statistics 5:81-91.

Brown, J. A., and M. S. Boyce. 2001. A survey design for monitoring butterflies. Statistica 61:291-299.

Buckland, S. T. 2006. Point-transect surveys for songbirds: Robust methodologies. Auk 123:345-357.

Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas. 2001. Introduction to Distance Sampling: estimating abundance of biological populations. Oxford University Press, Oxford, UK.

Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas. 2004. Advanced distance sampling. Oxford University Press, Oxford, UK.

Buckland, S. T., D. L. Borchers, A. Johnston, P. A. Henrys, and T. A. Marques. 2007. Line transect methods for plant surveys. Biometrics 63:989-998.

Buckland, S. T., J. L. Laake, and D. L. Borchers. 2010. Double-observer line transect methods: levels of independence. Biometrics 66:169-177.

Burnham, K. P., and D. R. Anderson. 1984. The need for distance data in transect counts. Journal of Wildlife Management 48:1248-1254.

Burnham, K. P. and D. R. Anderson. 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretical Approach. 2nd Ed. Springer-Verlag, New York City, USA.

Calambokidis, J., and J. Barlow. 2004. Abundance of blue and humpback whales in the eastern North Pacific estimated by capture-recapture and line-transect methods. Marine Mammal Science 20:63-85.

Childers, T. M., and S. J. Dinsmore. 2008. Density and abundance of Mountain Plovers in northeastern Montana. The Wilson Journal of Ornithology 120:700-707.

Collier, N., D. A. Mackay, K. Benkendorff, A. D. Austin, and S. M. Carthew. 2006. Butterfly communities in South Australian urban reserves: Estimating abundance and diversity using the Pollard walk. Austral Ecology 31:282-290.

Dennis, R. L. H., T. G. Shreeve, N. B. Isaac, D. B. Roy, P. B. Hardy, R. Fox, and J. Asher. 2006. The effects of visual apparency on bias in butterfly recording and monitoring. Biological Conservation 128:486.

Dwyer, H. E., M. Jasieniuk, M. Okada, and A. M. Shapiro. 2015. Molecular evidence for hybridization in Colias (Lepidoptera: Pieridae): are Colias hybrids really hybrids? Ecology and Evolution. 5:2865-2877.

Eberhardt, L. L. 1968. A preliminary appraisal of line transects. Journal of Wildlife Management 32:82-88.

Gates, C.E. 1968. Line transect method of estimating grouse population densities. Biometrics 24:135-145.

Haddad, N. M., B. Hudgens, C. Damiani, K. Gross, D. Kuefler, and K. Pollock. 2008. Determining optimal population monitoring for rare butterflies. Conservation Biology 22:929-940.

Isaac, N. J. B., K. L. Cruickshanks, A.M. Weddle, J.M. Rowcliffe, T.M. Brereton, R.L.H. Dennis, D.M. Shuker, C.D. Thomas. 2011. Distance sampling and the challenge of monitoring butterfly populations. Methods in Ecology and Evolution 2:585-559.

Kellner, K. F. and R. K. Swihart. 2014. Accounting for imperfect detection in ecology: a quantitative review. PLOS ONE, 9(10), e111436.

Kery, M., and M. Plattner. 2007. Species richness estimation and determinants of species detectability in butterfly monitoring programmes. Ecological Entomology 32:53-61.

Kinkead, K. E. 2006. Iowa multiple species inventory and monitoring program technical manual. Iowa Department of Natural Resources, Des Moines, Iowa, USA.

Kissling, M. L. and E. O. Garton. 2006. Estimating detection probability and density from point-count surveys: a combination of distance and double-observer sampling. The Auk 123:735-752.

Koneff, M. D., J. A. Royle, M. C. Otto, J. S. Wortham, and J. K. Bidwell. 2006. A double-observer method to estimate detection rate during aerial waterfowl surveys. The Journal of Wildlife Management 72:1641-1649.

Lollback, G. W., R. Mebberson, N. Evans, J. D. Shuker, and J-M Hero. 2015. Estimating the abundance of the bilby (*Macrotis lagotis*): a vulnerable, uncommon, nocturnal marsupial. Australian Mammalogy 37:75-85.

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

Marques, T. A., L. Thomas, S. G. Fancy, and S. T. Buckland. 2007. Improving estimates of bird density using multiple-covariate distance sampling. The Auk 124:1229-1243.

McGill, B. J. 2006. A renaissance in the study of abundance. Science 314:770-772.

Moranz, R. A. 2010. The effects of ecological management on tallgrass prairie butterflies and their nectar sources. Dissertation, Oklahoma State University, USA.

Newson, S. E., Evans, K. L., Noble, D. G., Greenwood, J. J. D., and Gaston, K. J. 2008. Use of distance sampling to improve estimates of national population sizes for common and widespread breeding birds in the UK. Journal of Applied Ecology 45:1330-1338.

Nichols, J. D., J. E. Hines, J. R. Sauer, F. W. Fallon, J. E. Fallon, and P. J. Heglund. 2000. A double-observer approach for estimating detection probability and abundance from point counts. The Auk 117:393-408.

Nowicki, P., J. Settele, P. Y. Henry, and M. Woyciechowski. 2008. Butterfly monitoring methods: The ideal and the real world. Israel Journal of Ecology & Evolution 54:69-88.

Opler, P. A. 1998. A field guide to eastern butterflies. Houghton Mifflin, Boston, Massachusetts, USA.

Opler, P. A., K. Lotts, and T. Naberhaus, coordinators. 2010. Butterflies and moths of North America. Bozeman, MT: Big Sky Institute. http://www.butterfliesandmoths.org/ (Version 6-12-2015).

Pellet, J., J. T. Bried, D. Parietti, A. Gander, P. O. Heer, and Cherix D., et al. 2012. Monitoring butterfly abundance: beyond Pollard walks. PLOS ONE, 7(7), e111436.

Pollard, E., Yates, T.J., 1993. Monitoring Butterflies for Ecology and Conservation: The British Butterfly Monitoring Scheme. Chapman & Hall, London, UK.

Powell, A. W. H. Busby, and K. Kindscher. 2007. Status of the regal fritillary (*Speyeria idalia*) and effects of fire management on its abundance in northeastern Kansas, USA. Journal of Insect Conservation 11:299-308.

Prior, J. C. 1991. Landforms of Iowa. University of Iowa Press, Iowa City, Iowa, USA.

Reeder, K. F. and J. A. Clymer. 2015. Iowa's Wildlife Action Plan: Securing a future for fish and wildlife. Iowa Department of Natural Resources, Des Moines, Iowa, USA.

Ritland, D. B. 1995. Comparative unpalatability of mimetic viceroy butterflies (*Limenitis archippus*) from four south-eastern United States populations". Oecologia 103:327-336.

Ritland, D. B., and L. P. Brower. 1991. The viceroy butterfly is not a batesian mimic. Nature 350:497-498.

Schlicht, D. W., J. C. Downey, and J. C. Nekola. 2007. The Butterflies of Iowa. University of Iowa Press, Iowa City, Iowa, USA.

Shepherd, S. and D. M. Debinski. 2005. Evaluation of isolated and integrated prairie reconstructions as habitat for prairie butterflies. Biological Conservation 126:51-61.

Swann, D. E., R. C. Averill-Murray, and C. R. Schwalbe. 2002. Distance sampling for Sonoran Desert tortoises. Journal of Wildlife Management 66:969-975.

Thomas, L., S. T. Buckland, E. A. Rexstad, J. L. Laake, S. Strindberg, S. Hedley, J. R. B. Bishop, T. A. Marques, and K. P. Burnham. 2010. Distance software: Design and analysis of distance sampling surveys for estimating population size. Journal of Applied Ecology 47:5-14.

Wheat, C. W., and W. B. Watt. A mitochondrial-DNA-based phylogeny for some evolutionary-genetic model species of Colias butterflies (Lepidotera, Pieridae). 2008. Molecular Phylogenetics Evolution 47:893-902.

Yoccoz, N. G., J. D. Nichols, and T. Boulinier. 2001. Monitoring of biological diversity in space and time. Trends in Ecology & Evolution 16:446-453.

Table 1. Model selection results, species-specific detection probability (p), and associated coefficient of variation (CV) for eight butterfly species in Iowa, 2014. Estimates are from distance sampling analyses where data were truncated at a distance of 5.0 m. Only the best model is shown for each species and was used for all inferences (see text for details). Included here are model name and expansion term with the number of expansion adjustments in parentheses. Species are ordered by increasing median wing length (mm) (Opler et al. 2010).

Species (median wing length)	Model, expansion (no. adjustments of orders)	AICc	p	CV (%)
Least skipper (2.55 mm)	Hazard rate key, cosine (1)	583.26	0.53	16.75
Eastern tailed-blue (2.55 mm)	Uniform key, simple polynomial (2)	393.76	0.57	11.91
Little yellow (3.80 mm)	Hazard rate key, cosine (1)	408.28	0.67	16.19
Cabbage white (5.15 mm)	Hazard rate key, cosine (4)	182.47	0.61	16.18
Orange sulphur (5.25 mm)	Hazard rate key, cosine (1)	334.96	0.66	13.45
Clouded sulphur (5.40 mm)	Hazard rate key, Hermite polynomial (4)	335.13	0.66	15.69
Viceroy (7.45 mm)	Uniform key, simple polynomial (2)	127.34	0.76	16.71
Monarch (10.5 mm)	Hazard rate key, cosine (1)	544.98	0.79	16.19
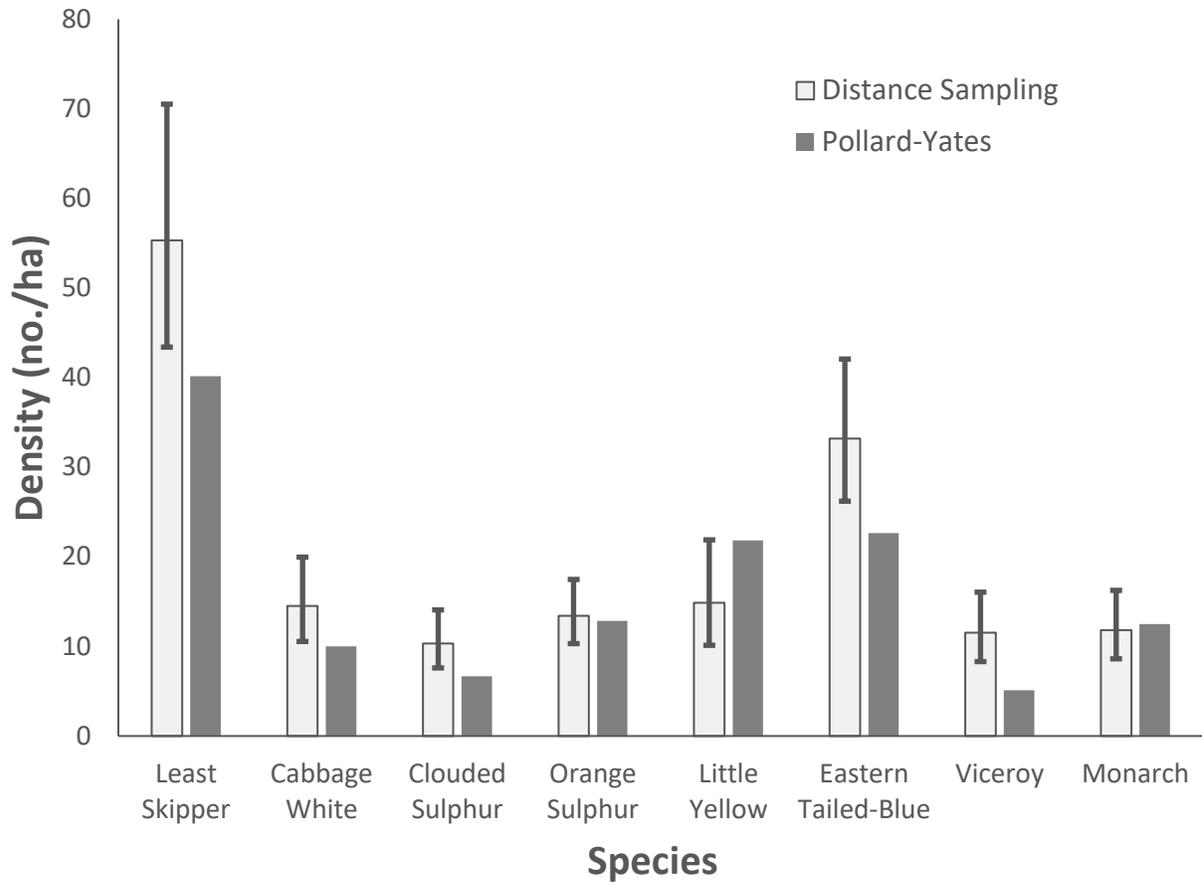
Figure 1. Comparison of species-specific densities (number/ha) of eight Iowa butterflies derived from Pollard-Yates line transects and transects incorporating distance sampling (with truncation at 5 m), Iowa, 2014. Vertical bars depict 95% confidence intervals.

CHAPTER 3: LANDSCAPE EFFECTS ON WOODLAND, SAVANNA, AND SCRUB-SHRUB BIRDS AT MULTIPLE SCALES IN IOWA

A paper to be submitted to *Condor*

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Abstract

North American birds across multiple guilds continue to experience widespread declines. As a result, there has been increasing interest in defining habitat associations and the impact of landscape configuration on avian population dynamics, especially in increasingly fragmented landscapes. Using bird-survey data collected at 476 sites across Iowa during the Multiple Species Inventory and Monitoring (MSIM) program from 2007-2014, we estimated rates of occupancy, colonization, and extinction for 10 bird species of forest, savanna, and scrub-shrub habitats. We used presence-absence data in robust design occupancy models to estimate the effects of landscape-habitat metrics (edge density and percentage of landscape in grassland, agriculture, and woodland) at multiple scales (200 m, 500 m, 1000 m, and 5000 m). We also modeled the impact of weather covariates (temperature, cloud cover, and wind speed) on detection probability. Occupancy probability ranged from 0.021 for Pileated Woodpecker to 0.610 for Eastern Wood-Pewee. Colonization probability (mean = 0.159) was estimated for all ten species and ranged from 0.021 for Kentucky Warbler to 0.508 for Eastern Wood-Pewee while extinction

probability (mean = 0.239) ranged from 0.069 for Eastern Wood-Pewee to 0.398 for Wood Thrush. Our results suggested that habitat associations and dynamics of site colonization and extinction varied by species and spatial scale. The contrasting positive impacts of woodland and negative effect of row-crop agriculture in the landscape were evident for multiple forest birds, particularly area-sensitive species, whereas savanna and scrub-shrub birds showed more species-specific results. Wind speed had a negative impact on detectability across guilds. Our results provide further insight into the habitat associations of birds spanning multiple habitats and serve as a means to enhance management and conservation of birds in highly fragmented landscapes.

Key Words: bird, detection probability, habitat association, Iowa, landscape effect, Neotropical migrant, occupancy model, robust design

Introduction

Precipitous declines in North American bird populations across multiple habitat guilds have been widely documented (Sauer et al. 2014, North American Bird Conservation Initiative 2016). Of special interest are those species defined as area-sensitive, wherein occurrence and density of a given species diminishes accordingly with decreasing patch size (Robbins 1989) and birds whose population dynamics are impacted by proximity to habitat edges (Whitcomb et al. 1981, Freemark and Collins 1992, Ehrlich 1996). So it is not surprising that many studies have addressed these issues, especially for grassland birds (e.g., Herkert 1994, Johnson and Igl 2001, Brennan and Kuvlesky 2005, Jacobs et al. 2005, Hamer et al. 2006, Winter et al. 2006, Askins et al. 2007, Renfrew and Ribic 2008), which continue to undergo some of the steepest declines of any avian suite in North America (Sauer et al. 2014). Johnson (2001) and later Ribic et al. (2009) summarized the area-sensitivity of these grassland-obligate birds and illustrated that occurrence

and density increased with habitat patch size in a majority of species. Emblematic cases on each end of the size spectrum include Henslow's Sparrow (*Ammodramus henslowii*), whose density and occurrence respond positively to large grassland patches in the landscape (Herkert 1994, Bollinger 1995, Heckert et al. 2002), much like nesting densities of the Northern Harrier (*Circus cyaneus)* (Johnson and Igl 2001, Skinner 2004). However, consistent patterns do not hold for all species in this well-studied suite. Winter et al. (2006) found that the effect of patch size on Bobolink (*Dolichonyx oryzivorus*) density varied among regions and years - and landscape effects were not associated with patch size, whereas others (e.g. Skinner 2004, Renfrew and Ribic 2008) found a recurrently positive relationship between patch size and Bobolink density.

In forested landscapes, in which area-sensitive birds have also received considerable attention for decades (Whitcomb et al. 1981, Robbins 1988, Robinson 1992, Martin and Finch 1995, Rosenberg et al. 2003, Radford et al. 2005), the varied impacts of landscape composition are also manifest, particularly among Neotropical migrants (Stotz et al. 1996). For example, Acadian Flycatcher (*Empidonax virescens*) and Wood Thrush (*Hylocichla mustelina*), which are both classified as area sensitive (Kroodsma 1984, Robbins et al. 1989, Groom and Grubb 2002, Whitehead and Taylor 2002, Evans et al. 2011), respond more strongly at broad spatial scales than woodland generalists like Eastern Wood-Pewee (*Contopus virens*) and Indigo Bunting (*Passerina cyanea*) (Fauth et al. (2000), Howell et al. (2000), Dunford and Freemark 2005, Reidy et al. 2014). Embodying seemingly disparate life-history traits in this regard is the Yellow-throated Vireo (*Vireo flavifrons*), which exhibits aspects of area-sensitivity (responding favorably to larger forest tracts in the landscape), while also readily occupying both the interior and edges of the sizable forests it selects (Rodewald and James 2011). Elsewhere, interest in landscape-habitat relationships has extended to birds of shrubby or semi-open habitats. Knick

and Rotenberry (2002) demonstrated that shrub-steppe birds of intermountain regions are highly sensitive to habitat fragmentation at scales much larger their respective home territory. In the more patchy landscapes of the Midwest, Reidy et al. (2014) found a wide range of local and landscape effects on scrub-shrub and savanna birds. Many species from these suites are of added interest due to their reliance on both grassland and forest components in the landscape (Carey et al. 2008, Scharf et. 2010, Frei 2015.).

There exists further opportunity to determine the manner in which forest and scrub-shrub birds are impacted by landscape composition, even in an extensively fragmented landscape like Iowa's. Although 57% of the original woodland habitat has been lost and now comprises less than 10% of the overall landscape in the state (Reeder and Clymer 2015), many forest birds were found to be of widespread occurrence on the Iowa Breeding Bird Atlas II, 2008-2012. Savanna habitats, which are of considerable conservation concern in the Midwest (Nelson 2005, Mabry et al. 2010), are also home to several declining species (Sauer et al. 2014, Teaming with Wildlife 2015). Accordingly, Midwestern savanna contains both a grassland and woodland component (McPherson 1997, Anderson et al. 1999), and it provides breeding habitat for scrub-shrub birds in addition to many open-woodland species (Davis et al. 2000, Brawn 2006, Barrioz et al. 2013). Information on woodland, savanna, and scrub-shrub birds should prove especially useful in the conservation of Neotropical migrant songbirds (Stotz et al. 1996), a nationally declining group that is also well-represented in many of Iowa's woodlands and second-growth habitats (Teaming with Wildlife 2015, U.S. Fish and Wildlife Service 2015).

Historically, researchers used various indices to survey birds. However, population indices have received considerable criticism, largely because they assume a detection probability (p) of 1.0, when in reality detection varies widely and is often imperfect (Anderson 2001,

Anderson 2003, Mackenzie et al. 2006). Conversely, occupancy models enable us to incorporate

detection probability, thereby providing better estimates of population dynamics (Mackenzie et

al. 2003). Fauth et al. (2000), Howell et al. (2000), and Lee et al. (2002) described how

woodland birds, especially Neotropical migrants, respond favorably to higher forest coverage in

the landscape at multiple scales. Additionally, Dunford and Freemark (2005) also showed that

the varying impact of agriculture on forest birds occurs at multiple spatial scales. Neotropical

migrant songbirds, which have received much attention nationally due to widespread, long-term

declines (Stotz et al. 1996, Sauer 2014), stood out as the most negatively impacted group in the

aforementioned studies. Furthermore, Mabry et al. (2010) and Reidy (2014) highlighted the

importance of forest and grassland coverage on the diversity and occupancy of savanna and

early-successional (i.e., scrub-shrub) birds in the Midwestern U.S. Many of these savanna and

scrub-shrub birds prefer a patchy juxtaposition of forested and open habitats (Carey et al. 2008,

Kus et al. 2010, Scharf et al. 2010, Reidy et al. 2014). Additionally, studies from North America

and Europe have shown that species from forest and shrub-steppe communities respond variably

to forest coverage at varying scales (e.g., McClure et al. 2011, Huhta and Jokimäki 2015),

highlighting the need to assess habitat associations of forest and scrub-shrub species at multiple

spatial scales in Iowa.

In this study, we used multi-season, robust design occupancy models (MacKenzie et al.

2003) to evaluate landscape-level habitat associations of 10 bird species representing forest,

savanna, and scrub-shrub habitats. Data were collected from across Iowa through inventory and

monitoring efforts developed under the Iowa Wildlife Action Plan (hereafter IWAP; Reeder and

Clymer 2015). Our purpose here is to incorporate presence-absence data into the robust design

occupancy framework to model the impact of broad-scale impacts of habitat on birds of forest,

savanna, and scrub-shrub habitats in Iowa. Specifically, we want to understand how coarse landscape composition, at differing spatial scales, affects the site occupancy and dynamics (extinction and colonization probabilities) of these birds in Iowa. We hope that this information will be useful for land managers in the conservation of bird populations in these habitat types, especially in increasingly fragmented environments of the Midwest.

Methods

Survey site selection

Our site selection and bird sampling techniques followed the methodology of the Iowa Multiple Species Inventory and Monitoring (MSIM) Program (Kinkead 2006). We selected sites for bird surveys using a stratified random sampling design from three Iowa property classifications: public lands (federal, state, and county owned), Wetland Reserve Program (WRP) easements, and Landowner Incentive Program (LIP) easements. We chose these classifications because they are managed specifically for wildlife habitat. All public properties in Iowa >97 ha were classified according to 19 habitat types outlined in the IWAP (Reeder and Clymer 2015). We then stratified properties into four management districts that consisted of the northeastern, southeastern, northwestern, and southwestern quarters of Iowa to allow for equal selection of different habitat types across the state. In addition, we considered only public properties >97 ha to constrain our sampling frame due to financial and logistical constraints. We selected new properties without replacement each year from 2007-2014 such that properties of a certain habitat type were chosen from each management district. We also retained up to five properties from the sample of properties each year to constitute a sample of properties surveyed multiple years for comparison purposes. These permanent properties were selected using the

same stratified random procedure outlined above. We used a similar method to allocate WRP and LIP sites, including a subset of each that were surveyed across multiple years, except that these properties had to meet a minimum threshold of 16.2 ha or 40 acres.

We established a core area on each MSIM and LIP property that consisted of the assigned habitat type of that property. Within the core area, we placed six points approximately 200 m apart and in a hexagonal shape (plus one point in the geometric center) to allow for adequate coverage of the core area while minimizing double-counting of birds (Blondel et al. 1981). We used an analogous approach to establish survey points on the WRP sites, but with up to three additional points placed symmetrically at 200-m intervals around the main hexagon.

Bird surveys

We conducted bird surveys at selected properties April-October each year from 2007 to 2014. We partitioned the survey year into three seasons to focus on both breeding and migratory birds: spring (April – May) and fall (September – October) focused on migratory birds and summer (June – July) focused on breeding birds. We conducted three visits to each property at least 4 days apart in each of the three seasons for a total of 9 visits to each property in a survey year. On each visit, we employed standardized, unlimited radial-distance point-count methodology (Buckland et al. 2001, 2004) consisting of 10-min point counts with distance sampling at all survey points from 30 min before sunrise to 4.5 hr after sunrise. We recorded all birds seen or heard to species, number, and sex/age (when identifiable). Many species, especially those nesting in densely forested habitats, are detected far more frequently by sound than sight (Brewster and Simons 2009). Therefore, to account for difficulties in estimating distances, we assigned all detections to one of five distance bins: 1 to 25 m, 26 to 50 m, 51 to 75 m, 76 to 100 m, and >100 m. In accordance with the primary assumption of distance sampling (Buckland et al.

2001), we recorded the distance to each individual bird when it was first observed and did not

record any subsequent observations. Prior to bird surveys, we measured wind speed (km/h),

cloud cover (%), and temperature (°C) and did not conduct bird surveys during periods of fog,

prolonged precipitation, or high winds (>20 km/h).

Landscape habitat covariates

Using ArcGIS (ver. 10.1; ESRI, 2012), we measured various landscape-level habitat

variables within a 200-m, 500-m, 1000-m, and 5000-m radius of each sampled site. We placed a

buffer around each of our sampled sites using the buffer tool in ArcGIS toolbox (Analysis Tools,

Proximity, Buffer; ESRI, 2012). We then clipped the 2009 Iowa Landcover file to our site

buffers using the "clipraster" command in the tools extension package Geospatial Modeling

Environment (GME; Beyer 2012). The 2009 Iowa Landcover file provides information on the

land use classification of the Iowa landscape in 2009 using satellite imagery. This is currently the

most recent land use classification for Iowa. We repeated the above two steps for all radii to

obtain the land use description within each radius of the center point of our surveyed properties.

We estimated our landscape-level habitat characteristics for each radius using

FRAGSTATS (ver. 4.2; McGarigal et al. 2012). FRAGSTATS is a computer program that

analyzes spatial patterns based on categorical maps and allows the user to pick from a variety of

metrics to assess landscape configuration (McGarigal et al. 2012). For our analyses, we selected

the percentage of landscape (PLAND) and edge density (ED). Percentage of landscape measures

the area of the focal land-use classification standardized by the total area of the landscape,

whereas ED measures the amount of edge on the landscape corresponding to a single land-use

classification standardized by landscape area. We performed these two calculations on the two

land-use classifications for each radius, in addition to distance to the nearest roadway and

distance to the nearest river, resulting in 15 landscape-level variables to be included as covariates

in our models.

Among the wide variety of land-use classifications in our landcover file, we selected the

"woodland", "grassland", and "agriculture" classifications for our analysis because these were

the classifications we believed would most influence our 10 focal species. "Agriculture" in this

Iowa context refers to industrial row-cropping (e.g., corn-soybean rotational systems). We chose

to make calculations about habitat availability and configuration at four widely different spatial

scales (200, 500, 1000, and 5000 m) surrounding the centroid of each property. The 200-m scale

effectively characterized the actual survey hexagon, while the greater radii captured conditions at

differing distance around the property.

Occupancy models

We utilized the robust design occupancy model framework (MacKenzie et al. 2003) via

the RMARK (Laake 2013) interface in Program Mark (White and Burnham, 1999) to evaluate

the effects of the above-mentioned landscape-level habitat characteristics on terrestrial birds in

Iowa. The robust design occupancy model estimates four parameters: 1) probability of

occupancy (ψ) (i.e., the probability that the species of interest occupied a sampled site), 2)

probability of colonization (γ), or the probability that a site will be colonized at time $t+1$ given

the site was not occupied at time t, 3) probability of extinction (ε), or the probability that a site

went extinct at time $t+1$ given the site was occupied at time t, and 4) detection probability, or the

probability of detecting the species of interest given it was present at the sampled site (p;

MacKenzie et al. 2003). Unlike the single-season occupancy model where sites are closed to

changes in occupancy state during the primary sampling season (MacKenzie et al. 2002), the

robust design occupancy model assumes sites are closed to changes in occupancy state between

secondary sampling intervals (e.g., sampling occasions within a year) but are open to changes in

occupancy state between primary sampling intervals (e.g., years; MacKenzie et al. 2003). This

allows for the evaluation of metapopulation dynamics through the process of determining the

probability a site will remain occupied, go locally extinct, or become locally colonized. In

addition, the robust design occupancy model allows covariates to be modeled on the parameters

to improve parameter estimates and provide information on characteristics that might influence

the various parameters. Based on recommendations by Doherty et al. (2010), we ran all possible

models (62,500 models total) for each species. For model evaluation, we used Akaike's

Information Criterion, corrected for small sample size (AICc), to order models, and we used the

top model for each species to represent the best estimate of covariate effects on four parameters

of interest (occupancy, colonization, extinction, and detection probability). We evaluated the

strength of model effects (betas) by examining the 95% confidence interval and whether it

included zero; effects for which the confidence interval did not include zero were considered

strong while those with minimal overlap were considered weak effects. We considered a

covariate to have no effect when the 95% confidence interval included zero.

We modeled the aforementioned landscape-level habitat variables on the probability of

occupancy, colonization, and extinction on a group of ten species comprised of eight songbirds

and two woodpeckers, spanning scrub-shrub, savanna, and forest habitats. Seven of these birds

(Red-headed Woodpecker, Eastern Wood-Pewee, Acadian Flycatcher, Bell's Vireo, Wood

Thrush, Kentucky Warbler, and Field Sparrow) are listed as Species of Greatest Conservation

Need (SGCN) by the IWAP (Reeder and Clymer 2015). All eight of the songbirds are classified

as Neotropical migrants (Stotz et al. 1996), whereas Red-headed Woodpecker and Pileated

Woodpecker are respectively a short-distance migrant and a resident species in Iowa (Kent and

Dinsmore 1996). The primary sampling intervals were the years during which bird surveys were conducted (2007-2014), and the secondary sampling intervals were the survey occasions (days) within each sampling year (April-October). We estimated all parameters on an annual basis. We truncated data sets to include only surveys conducted during June-July (i.e., within the peak breeding season), thereby ensuring closure among the secondary sampling occasions. Because we had landcover data from only one year (2009), we assumed the landscape and the corresponding effects on occupancy, colonization, and extinction did not change among our survey years and pooled all survey years for analysis. For detection probability we considered three weather covariates (percent cloud cover, wind speed, and temperature at beginning of survey) that are known to be important correlates with this parameter (O'Connor and Hicks 1980, Lindenmayer et al. 2009, McClure et al. 2011).

We made the following general hypotheses regarding the four parameters of interest (site occupancy, colonization, extinction, and detection probability) for our 10 study species:

1) Percentage of woodland in the landscape and edge density of woodland will yield a strong positive influence on the population dynamics of forest birds at multiple scales, with area-sensitive species like Acadian Flycatcher and Wood Thrush experiencing a greater impact at broader spatial scales than a woodland generalist like Eastern Wood-Pewee (Fauth et al. (2000), Howell et al. (2000), Dunford and Freemark 2005, Reidy et al. 2014).

2) Savanna species, such as Red-headed Woodpecker and Orchard Oriole, will experience positive effects of both forest and grassland metrics at multiple scales, owing to their preference for a mixture of each habitat type (Scharf et al. 2010, Reidy et al. 2014, Frei et al. 2015).

3) Scrub-shrub inhabitants like Bell's Vireo and Field Sparrow will also respond

positively to both grassland and forest at multiple scales because their nesting

requirements (shrubs and low trees) will be more readily available in both of these

habitats (Carey et al. 2008, Kus et al. 2010, Reidy et al. 2014).

4) Detection probabilities of all species will be negatively affected by wind speed and to

a lesser extent by cloud cover and temperature, based on findings in other forested

and semi-forested habitats (e.g., O'Connor and Hicks 1980, Lindenmayer et al. 2009,

McClure et al. 2011).

Results

We conducted breeding season surveys for ten species of birds at 476 sites throughout

Iowa from 2007 to 2014. The number of sites across all years at which a species was detected

during these surveys ranged from 28 (Kentucky Warbler) to 346 (Eastern Wood-Pewee). Among

focal species, the mean number of sites at which a species was detected was 156 (SD = 42).

Habitat effects

Our models describing the habitat associations of forest, savanna, and scrub-shrub birds

in Iowa showed varying patterns across the ten species with respect to habitat covariates and

differing spatial scales (Table 1). Among the seven species for which there were strong covariate

effects on site occupancy, woodland emerged as a positive correlate for three forest birds

(Pileated Woodpecker, Eastern Wood-Pewee, and Yellow-throated Vireo) while agriculture

negatively impacted site occupancy of Red-headed Woodpecker and Wood Thrush. Edge density

of agriculture at the 5000-m scale was positively associated with site occupancy of two scrub-

shrub songbirds: Field Sparrow and Orchard Oriole.

At multiple spatial scales, the percentage of the landscape in woodland was the most prevalent covariate affecting colonization rates of forest birds. Acadian Flycatcher (200 m), Eastern Wood-Pewee (500 m), Wood Thrush (500 m), and Pileated Woodpecker (1000 m) all had colonization rates that were positively influenced by woodland coverage. Likewise, Kentucky Warbler's colonization rate was best explained by increasing woodland edge density at the 5000-m scale. Colonization for another forest bird, Yellow-throated Vireo, was negatively associated with the percentage of land in agriculture at 5000 m. Covariate effects on colonization of scrub-shrub birds revealed the positive impact of grassland (Red-headed Woodpecker with percentage of grassland at 5 km and Orchard Oriole with grassland edge density at 200 m). There was also an apparent mixed influence of agricultural edge density where Bell's Vireo was influenced positively at the 5 km scale and Field Sparrow negatively at the 1 km scale.

Covariate effects on site extinction rates were strong in only six species and showed varying results. Percentage of grassland in the landscape at 500 m was positively correlated with the extinction of two forest birds (Eastern Wood-Pewee and Yellow-throated Vireo). In the scrub-shrub group, agricultural edge density at 5000 m was negatively associated with extinction of Field Sparrow and Orchard Oriole. Red-headed Woodpecker's extinction rate was negatively linked with woodland edge density at 1 km, whereas agricultural edge density at this same scale positively influenced Pileated Woodpecker's extinction rate in wooded habitats. Furthermore, percentage of the landscape in woodland at 500 m and 1000 m respectively for Acadian Flycatcher and Wood Thrush exhibited a moderate negative correlation with extinction rates of these two interior-forest species. Extinction probability could not be estimated for Kentucky Warbler, possibly because of small sample or high degree of variance in the data.

Detection probabilities

Wind speed had a strong negative impact on the detection probabilities of Red-headed Woodpecker, Eastern Wood-Pewee, and Field Sparrow, and it was also present in the top model for Acadian Flycatcher. The only other covariate with a strong negative effect on detection probability was cloud cover (Yellow-throated Vireo), which was also present as a weak effect in Bell's Vireo. Three species (Wood Thrush, Kentucky Warbler, and Orchard Oriole) had no covariate effect on detection probability in the top model, and temperature showed a weak negative influence on the detection probability of Pileated Woodpecker.

Parameter estimates

Our occupancy models produced meaningful estimates of most parameters for most species, except for problems with site occupancy and extinction probability for three species (Table 2). Occupancy probability (mean = 0.248) ranged from 0.038 for Bell's Vireo to 0.610 for Eastern Wood-Pewee. Occupancy probability was not estimated for Kentucky Warbler. Colonization probability (mean = 0.159) was estimated for all ten species and ranged from 0.021 for Kentucky Warbler to 0.508 for Eastern Wood-Pewee. The lowest site extinction probability (0.069) was estimated for Eastern Wood-Pewee, and the highest (0.398) for Wood Thrush. Extinction probability (mean = 0.239) was not estimated for Acadian Flycatcher, Bell's Vireo, and Kentucky Warbler. Detection probability (mean = 0.598) was estimated for all species, spanning a woodland representative (Kentucky Warbler [0.332]) and a scrub-shrub denizen (Orchard Oriole [0.395]) at the low end of the spectrum to Eastern Wood-Pewee (0.858) and Field Sparrow (0.804) representing each guild at the top.

The annual estimate of site occupancy showed differing patterns by species (Table A1). For six species (Red-headed and Pileated woodpeckers, Eastern Wood-Pewee, Yellow-throated Vireo, Field Sparrow, and Orchard Oriole) the pattern was one of a steady increase across the study period. For the other four species (Acadian Flycatcher, Bell's Vireo, Wood Thrush, and Kentucky Warbler) the occupancy probabilities were essentially unchanged across years. (Table A1).

Discussion

This study represents the first use of multi-season, robust design occupancy models to examine the influence of habitat associations at differing spatial scales for forest, savanna, and scrub-shrub breeding birds in Iowa. As predicted, the negative impact of agriculture and the positive impact of grassland and woodland at multiple scales best defined site occupancy among our study species. Our models revealed that the extent of woodland was the best predictor of forest-bird colonization at differing spatial scales, as expected. Colonization for savanna species (i.e., Red-headed Woodpecker and Orchard Oriole) was best defined by grassland components in the landscape. However, contrary to our predictions, scrub-shrub birds (Bell's Vireo and Field Sparrow) showed colonization positively impacted by agricultural components. Extinction probabilities were more difficult to estimate for some species, but grassland and agricultural influences had the most substantial impact. Detection probability was most strongly influenced by wind speed for a majority of species. Below, we discuss the landscape-habitat effects in greater detail and suggest how this information might be used to benefit the management and conservation of Iowa's avian community.

Habitat effects and parameter estimates

Our conclusion that habitat associations, and the dynamics of site colonization and extinction, vary by species and spatial scale has important implications for understanding concepts like area-sensitivity and edge effects on Neotropical migrants. Our results for Acadian Flycatcher and Wood Thrush further support the notion that area-sensitive forest species respond favorably to percentage of woodland at multiple scales and negatively to row-crop agriculture. Wood Thrush is of particular interest in this regard. In addition to its classification as a Neotropical migrant (del Hoyo et al. 2005), it is considered area sensitive (Groom and Grubb 2002, Evans et al. 2011) and has been experiencing steady, moderate population declines across much of its nesting range (Sauer et al. 2014) to such a point that that it was recently assigned Near Threatened status by the International Union for Conservation of Nature and Natural Resources (IUCN) (BirdLife International 2014). Likewise, Acadian Flycatcher has received considerable conservation attention as an interior-forest denizen that relies on large tracts of forest on both its nesting and wintering grounds (Kroodsma 1984, Robbins et al. 1989, Probst and Thompson 1996, Whitehead and Taylor 2002), while also showing high suitability as an indicator species in old-growth deciduous forests of eastern North America (Urban et al. 2012). We found that woodland coverage in the landscape positively impacts site colonization, while showing the negative association of agriculture with occupancy for both species (and strongly so for Wood Thrush) in Iowa's intensively row-cropped landscape. Similarly, our results revealed the dual impact of forest (positive for site occupancy) and agriculture (negative for colonization) on Yellow-throated Vireo, an area sensitive species that that readily occupies the edges of expansive forests, in addition to the interior (Rodewald and James 2011). This suggests that

although Yellow-throated Vireo inhabits the periphery of forests, it is less likely to colonize such habitats when surrounded by agriculture at a broad scale.

Eastern Wood-Pewee, which is numerous across much of Iowa (Kent and Dinsmore 1996) and eastern North America (Sauer et al. 2014), showed strong covariate effects of woodland on both occupancy and colonization. This species also registered considerably higher parameter estimates for occupancy and colonization compared to extinction rate, which was more closely associated with grassland. Collectively, this shows that Eastern Wood-Pewee is a widespread bird in Iowa's forests, which it readily colonizes by keying into woodland extent at moderate spatial scales; once a site is occupied, this species rarely vacates it except in areas with a strong grassland presence surrounding the forest.

Pileated Woodpecker, the lone resident species in our study suite, is not generally listed as a species of targeted conservation concern in Iowa or elsewhere. However, this cavity excavator's vital role as a keystone species in mature, old-growth forest communities is well documented (Martin and Eadie 1999; Bonar 2000, Aubry and Raley 2002, Bull and Jackson 2011), and its presence, along with other woodpeckers, likely influences overall bird diversity on a landscape scale (Mikusiński et al. 2001, Roberge and Angelstam 2006). As such, our findings, which showed the positive impact of woodland in the landscape on both occupancy and colonization for Pileated Woodpecker, hint at the importance of these metrics for many other forest species. Baumgardt et al. (2014), however, did not find a strong association between Pileated Woodpecker occupancy and canopy-cover percentage on the landscape. Their results came from data collected in a landscape (north-central Idaho) that is much more heavily forested than most of Iowa. Furthermore, Pileated Woodpecker's extinction rate in our study was positively correlated with agricultural edge density at a broad scale, and the parameter estimate

was much greater (albeit with a higher SE) than that of the colonization rate. This once again highlights an Iowa forest bird that apparently does not persist well when sites are extensively bordered by agriculture, even when such sites meet the species' forest-coverage requirements for colonization.

Red-headed Woodpecker, an iconic savanna species that is declining both regionally and nationally (Melcher 1998, Mueller 2002, Sauer et al. 2014, Birdlife International 2016), exhibited colonization substantially tied to a grassland aspect on a broad scale. This association may stem from (1) the species' attraction to semi-open habitats with at least a few scattered large trees/snags to provide nesting cavities (Bent 1939, Kahl et al. 1985, Blake and Carr 1987, Kent and Dinsmore 1996, Brawn 2006), and (2) the need for an open-ground (i.e., grassland) component from which to forage for mast (i.e., acorns) and hunt for insects adjacent to woodland edges with requisite nesting snags (Frei 2015). This conspicuous species also exhibited the buoying effect of woodland edge density on extinction rate, perhaps again owing to its preference for grassland-woodland juxtaposition. Orchard Oriole, another species of savanna or park-like environs (Scharf et al. 2010), also had colonization strongly impacted by grassland (edge density at 200 m), along with occupancy and extinction tied most closely to agricultural edge density at a larger scale (1000 m and 5000 m respectively). Perhaps this species' attraction to patchy habitats, such as wooded rural homesteads or traditional farmland with scattered trees and groves (Robbins 1991, Kent and Dinsmore 1996), might explain the positive influence of these two open landcover classifications.

Bell's Vireo, a denizen of sunny, shrubby habitats in Iowa (Kent and Dinsmore 1996) and across much of its range (Kus et al. 2010), was impacted by grassland edge density on occupancy (weak effect) and agriculture on colonization (stronger effect). Perhaps in each case,

the shrubby, open-canopy nesting preferences of this species are better met by some sort of non-forested habitat, such as shrubby hedgerows in rural landscapes. Furthermore, Field Sparrow, another species of early-stage shrublands (Peterjohn and Rice 1991, Carey et al. 2008), showed mixed effects of agricultural edge density at a broad scale for occupancy, colonization, and extinction, which again may indicate that the preferred nest sites (shrubs and low trees) are in some way more closely associated with open, disturbed landscapes than with forests or pure prairie in Iowa.

Although substantial, discernible effects were evident in some species, extinction patterns were not as clear overall as those for occupancy and colonization. For example, no parameter estimate was produced on extinction for Acadian Flycatcher, Bell's Vireo, and Kentucky Warbler. Additionally, Bell's Vireo's extinction rate was only very weakly associated with a covariate (agricultural edge density at 200 m). However, each of these species comprised (or had) comparatively few detections in our study, with Kentucky Warbler having the fewest.

Detection probability

Specific detection probabilities from occupancy modeling for our study species are scarce in the literature, but some comparisons from recent studies are available. From point-count data on forest birds on the Virginia Peninsula, Watson (2013) found a considerably lower range of detection probabilities for five woodpecker species (<0.500), including a particularly small value for Pileated Woodpecker (~0.200), compared to our results (0.725) for that species. Conversely, our detection probabilities for Acadian Flycatcher (0.693) and Wood Thrush (0.488) were within the range of probabilities reported by Watson (2013), who described methodological contrasts that likely accounted for this differentiation. Watson (2013) used a smaller point-count area (<75 m) for analyses and a shorter count duration on survey visits to each site. This may have allowed

a similar detection rate for songbirds, which sing frequently (i.e., early enough in the count interval), but resulted in a lower detection probability for woodpeckers, which may vocalize less often (and thus are not as frequently detected during the count interval). Likewise, Baumgardt et al. (2014), who used surveys with much shorter count duration, found Pileated Woodpecker detection probabilities to be approximately half that estimated in our study. Our songbird detection probabilities are also consistent with the wide range established by De Wan et al. (2009) for various forest songbirds in the Hudson Valley Ecoregion. Further support for these findings is presented in a seminal bird-monitoring work by Ralph et al. (1995), who illustrated that many songbirds, including four of our specific study species (Eastern Wood-Pewee, Acadian Flycatcher, Wood Thrush, and Kentucky Warbler) are detected nearly as frequently in short counts (e.g., 3 min) as they are in longer counts (e.g., 10 min), whereas woodpeckers exhibit a marked increase in detection frequency during a longer survey period.

Influences of weather-related variables on detection probabilities were largely consistent with our expectations and with findings from previous studies (e.g., O'Connor and Hicks 1980, Lindenmayer et al. 2009, McClure et al. 2011). Increasing wind speed, cloud cover, and temperature all negatively impacted detection, in descending order of magnitude. Our results also support the protocol utilized by other large-scale bird monitoring projects (Ralph et al. 1995). For example, North American Breeding Bird Survey protocol continues to instruct observers to conduct counts on mornings where wind speed is <8 mph, except in open-prairie regions, where up to 12 mph is acceptable (Robbins et al. 1986, Sauer et al. 1997, Sauer et al. 2014).

Conservation Implications

Our study fills important knowledge gaps regarding multi-scale habitat associations of forest, savanna, and scrub-shrub birds in a highly fragmented Midwestern landscape. Additionally, our suite of study species includes various declining, area-sensitive birds that are of conservation concern not only in Iowa (Teaming with Wildlife 2015), but also regionally and nationally (Sauer et al. 2014, U.S. Fish and Wildlife Service 2015.). By offering insights into how landscape-level habitat factors impact site colonization and extinction rates of these species, and at what spatial scales, we provide a potential framework for enhanced management of these and similar birds across much of their nesting range. For instance, our findings further validate the Iowa DNR's efforts to conserve large-scale landscapes via the Bird Conservation Area (BCA) model. Likewise, our findings could help to enhance decisions regarding SGCN status for declining or range-restricted birds by showing which species are most susceptible to landscape changes and fragmentation. We also underscored the importance of incorporating detection probabilities into analyses of bird-survey data to provide more robust estimates and enable well-justified solutions to managing bird populations.

Bishop, Kelly Smith, Doug Harr, Bruce Ehresman, and Paul Frese), the U.S. Fish and Wildlife Service, USDA Natural Resource Conservation Service (particularly Monica Monk), and various County Conservation Boards provided logistical support and access to properties. Private landowners enrolled in the Landowner Incentive Program and Wetland Reserve Program also provided access to their properties for data collection.

Literature Cited

Anderson, D. R. 2001. The need to get the basics right in wildlife field studies. Wildlife Society Bulletin 29:1294-1297.

Anderson, D. R. 2003. Response to Engeman: index values rarely constitute reliable information. Wildlife Society Bulletin 31:288-291.

Askins, R. A., F. Chávez-Ramírez, B. C. Dale, C. A. Haas, J. R. Herkert, F. L. Knopf, and P. D. Vickery. 2007. Conservation of grassland birds in North America: Understanding ecological processes in different regions. Ornithological Monographs 64:1-46.

Aubry, K. B., and C. M. Raley. 2002. The Pileated Woodpecker as a keystone habitat modifier in the Pacific Northwest. Pages 257-274 *in* Proc. Symposium on the ecology and management of dead wood in western forests. (Laudenslayer, Jr., J. P., P. J. Shea, B. E. Valentine, C. P. Weatherspoon, and T. E. Lisle, Eds.) U. S. Dep. Agric., For. Serv., Gen. Tech. Rep. PSW-GTR-181, Berkeley, California, USA.

Bakker, K. K., D. E. Naugle, and K. F. Higgins. 2002. Incorporating landscape attributes into models for migratory grassland bird conservation. Conservation Biology 16:1638-1646.

Barrioz, S., P. Keyser, D. Buckley, D. Buehler, and C. Harper. 2013. Vegetation and avian response to oak savanna restoration in the mid-south USA. American Midland Naturalist 169:194-213.

Baumgardt, J. A., J. D. Sauder, and K. L. Nicholson. 2014. Occupancy modeling of woodpeckers: maximizing detections for multiple species with multiple spatial scales. Journal of Fish and Wildlife Management 5:198-207.

Bent, A. C. 1939. Life histories of North American woodpeckers. U. S. National Museum Bulletin 174.

Beyer, H. L., 2012. Geospatial Modelling Environment ver. 0.7.2.1. <http://www.spatialecology.com/gme.>. Accessed 12 June 2016.

BirdLife International. 2000. Threatened birds of the world. Lynx Edicions and BirdLife International, Barcelona, Spain and Cambridge, UK.

BirdLife International. 2014. *Hylocichla mustelina*. The IUCN Red List of Threatened Species 2014. Downloaded on 10 July 2016.

Birdlife International. 2016. Species factsheet: *Melanerpes erythrocephalus*. Downloaded on 10 July 2016.

Blake, J. G., and J. R. Karr. 1987. Breeding birds in isolated woodlots: area and habitat relationships. Ecology 68:1724-1734.

Blondel, J., C. Ferry, and B. Frochot. 1981. Points counts with unlimited distance. Studies in Avian Biology 6:414-420.

Bollinger, E. K. 1995. The effects of habitat selection and vegetation selection on the breeding dispersion of birds nesting in eastern hayfields Auk 112:720-730.

Bonar, R. L. 2000. Availability of Pileated Woodpecker cavities and use by other species. Journal of Wildlife Management 64:52-59.

Brawn, J. D. 2006. Effects of Restoring Oak Savannas on Bird Communities and Populations. Conservation Biology 20:460-469.

Brennan, L. A., and W. P. Kuvlesky, Jr. 2005. North American grassland birds: an unfolding crisis? Journal of Wildlife Management 69:1-13.

Brewster, J. P., and T. R. Simons. 2009. Testing the importance of auditory detections in avian point counts. Journal of Field Ornithology 80:178-182.

Brotons, L., W. Thuiller, M. B. Araújo, and A. H. Hirzel. 2004. Presence-absence versus presence-only modelling methods for predicting bird habitat suitability. Ecography 27:437-448.

Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas. 2001. Introduction to Distance Sampling: Estimating Abundance of Biological Populations. Oxford University Press, Oxford, UK.

Bull, E. L., and J. A. Jackson. 2011. Pileated Woodpecker (*Dryocopus pileatus*). No. 148. *In* (A. Poole, Ed.). The Birds of North America Online. Cornell Lab of Ornithology, Ithaca, New York, USA.

Burnham, K. P., and D. R. Anderson. 2002. Model Selection and Multimodal Inference: A Practical Information-theoretic Approach. Springer-Verlag, New York, New York, USA.

Carey, M., M. Carey, D. E. Burhans, and D. A. Nelson. 2008. Field Sparrow (*Spizella pusilla*). No. 103. *In* (A. Poole, Ed.). The Birds of North America Online. Cornell Lab of Ornithology, Ithaca, New York, USA.

Chesser, R. T., K. J. Burns, C. Cicero, J. L. Dunn, A. W. Kratter, I. J. Lovette, P. C. Rasmussen, J. V. Remsen Jr., J. D. Rising, D. F. Stotz, and K. Winter. 2016. Fifty-seventh supplement to the American Ornithologists' Union Checklist of Northern American Birds. The Auk 133:544-560.

Comte, L., and G. Grenouillet. 2013. Species distribution modelling and imperfect detection: comparing occupancy versus consensus methods. Diversity and Distributions 19:996-1007.

Cunningham, M., and D. H. Johnson. 2006. Proximate and landscape factors influence grassland bird distributions. Ecological Applications 16:1062-1075.

Davis, M. A., D. W. Peterson, P. B. Reich, M. Crozier, T. Query, E. Mitchell, J. Huntington, and P. Bazakas. 2000. Restoring savanna using fire: Impact on the breeding bird community. Restoration Ecology 8:30-40.

del Hoyo, J., A. Elliott, and D. Christie. 2005. Handbook of the Birds of the World, vol. 10: Cuckoo-shrikes to Thrushes. Lynx Editions, Barcelona, Spain.

De Wan, A. A., P. J. Sullivan, A. J. Lembo, C. R. Smith, J. C. Maerz, J. P. Lassoie, and M. E. Richmond. 2009. Using occupancy models of forest breeding birds to prioritize conservation planning. Biological Conservation 142:982-991.

Doherty, P. F., G. C. White, and K. P. Burnham. 2010. Comparison of model building and selection strategies. Journal of Ornithology.

Dunford, W., and K. Freemark. 2005. Matrix matters: effects of surrounding land uses on forest birds near Ottawa, Canada. Landscape Ecology 20:497.

Ehrlich, P. R. 1996. Conservation in temperate forests: what do we need to know and do? Forest Ecology and Management 85:9-19.

Environmental Services Research Institute (ESRI). 2012. ArcGIS ver. 10.1. http://www.esri.com. Accessed 12 June 2016.

Evans, M., E. Gow, R. R. Roth, M. S. Johnson, and T. J. Underwood. 2011. Wood Thrush (*Hylocichla mustelina*). No. 246. *In* (A. Poole, Ed.). The Birds of North America Online. Cornell Lab of Ornithology, Ithaca, New York, USA.

Fauth, P. T., E. J. Gustafson, and K. N. Rabenold. 2000. Using landscape metrics to model source habitat for Neotropical migrants in the Midwestern U.S. Landscape Ecology 15:621-631.

Frei, B., K. G. Smith, J. H. Withgott, and P. G. Rodewald. 2015. Red-headed Woodpecker (*Melanerpes erythrocephalus*). No. 518. *In* (A. Poole, Ed.). The Birds of North America Online. Cornell Lab of Ornithology, Ithaca, New York, USA.

Groom, J. D., and Grubb Jr., T.C., 2002. Bird species associated with riparian woodland in fragmented, temperate-deciduous forest. Conservation Biology 16:832-836.

Hamer, T. L., C. H. Flather, and B. R. Noon. 2006. Factors associated with grassland bird species richness: the relative roles of grassland area, landscape structure, and prey. Landscape Ecology 21:569-583.

Herkert, J. R. 1994. The effects of habitat fragmentation on Midwestern grassland bird communities. Ecological Applications 4:461-71.

Herkert, J. R., P. D. Vickery, and D. E. Kroodsma. 2002. Henslow's Sparrow (*Ammodramus henslowii*). No. 672. *In* (A. Poole, Ed.). The Birds of North America Online. Cornell Lab of Ornithology, Ithaca, New York, USA.

Herkert, J. R., D. L. Reinking, D. A. Wiedenfeld, M. Winter, J. L. Zimmerman, W. E. Jensen, E. J. Finck, R. R. Koford, D. H. Wolfe, S. K. Sherrod, M. A. Jenkins, J. Faaborg, and S. K. Robinson. 2003. Effects of prairie fragmentation on the nest success of breeding birds in the midcontinental United States. Conservation Biology 17:587-594.

Howell, C. A., S. C. Latta, T. M. Donovan, P. A. Porneluzi, G. R. Parks, and J. Faaborg. 2000. Landscape effects mediate breeding bird abundance in Midwestern forests. Landscape Ecology 15:547-562.

Huhta, E., and J. Jokimäki. 2015. Landscape matrix fragmentation effect on virgin forest and managed forest birds: a multi-scale study. Pages 95-111 *in* J.A. Daniels (Ed.). Advances of Environmental Sciences. Nova Science Publishers, Hauppauge, New York, USA.

Jacobs, R. B., R. R. Koford, F. R. Thompson III, H. Woodward, M. Hubbard, J. A. Fitzgerald, and J. R. Herkert. 2005. Grassland Bird Conservation Efforts in Missouri and Iowa: How Will We Measure Success? In USDA Forest Service Gen. Tech. Rep. PSW-GTR-191. Pp. 78-82.

Johnson, D. H., and L. D. Igl. 2001. Area requirements of grassland birds: A regional perspective. Auk 118:24-34.

Kahl, R. B., T. S. Baskett, J. A. Ellis, and J. N. Burroughs. 1985. Characteristics of summer habitats of selected nongame birds in Missouri. University of Missouri-Columbia, College of Agriculture, Agricultural Experiment Station Resource Bulletin 1056.

Kent, T. H., and J. J. Dinsmore. 1996. Birds in Iowa. Iowa City, Iowa, USA.

Kinkead, K. E. 2006. Iowa multiple species inventory and monitoring program technical manual. Iowa Department of Natural Resources, Des Moines, Iowa, USA.

Kroodsma, R. L. 1984. Effect of edge on breeding forest bird species. Wilson Bulletin 96:426-436.

Kus, B., S. L. Hopp, R. R. Johnson, and B. T. Brown. 2010. Bell's Vireo (*Vireo bellii*). No. 035. *In* (A. Poole, Ed.). The Birds of North America Online. Cornell Lab of Ornithology, Ithaca, New York, USA.

Laake, J. L. 2013. RMark: An R Interface for Analysis of Capture-Recapture Data with MARK. AFSC Processed Rep 2013-01, 25p. Alaska Fish. Sci. Cent., NOAA, Natl. Mar. Fish. Serv., 7600 Sand Point Way NE, Seattle WA 98115.

Lee, M., L. Fahrig, K. Freemark, and D. J. Currie. 2002. Importance of patch scale vs landscape scale on selected forest birds. Oikos 96:110-118.

Lindenmayer, D. B, J.T. Wood, and C. MacGregor. 2009. Do observer differences in bird detection affect inferences from large-scale ecological studies? Emu 109:100-106.

Mabry, C. M., L. A. Brudvig, and R. C. Atwell. 2010. The confluence of landscape context and site-level management in determining Midwestern savanna and woodland breeding bird communities. Forest Ecology and Management 260:42-51.

MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, J. A. Royle, and C. A. Langtimm. 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology 83:2248-2255.

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.

Martin, K., and J. Eadie. 1999. Nest webs: a community-wide approach to the management and conservation of cavity-nesting birds. Forest Ecology and Management. 115:243-257.

Martin, T. E., and D. M. Finch, Eds. 1995. Ecology and management of Neotropical migratory birds: a synthesis and review of critical issues. Oxford University Press, New York.

Melcher, B. 1998. Red-headed Woodpecker. Pages 250-251 *in* Colorado breeding bird atlas. (Kingery, H. E., Ed.) Colorado Bird Atlas Partnership and Colorado Division of Wildlife, Denver, Colorado, USA.

McClure, C. J. W., L. K. Estep, and G. E. Hill. 2011. Using public land cover data to determine habitat associations of breeding birds in Tuskegee National Forest, Alabama. Southern Journal of Applied Forestry 29:199-209.

McGarigal, K., S. A. Cushman, and E. Ene. 2012. FRAGSTATS v4: Spatial Pattern Analysis Program for Categorical and Continuous Maps. Computer software program produced by the authors at the University of Massachusetts, Amherst. Available at the following web site: <http://www.umass.edu/landeco/research/fragstats/fragstats.html>.

Mikusiński, G., M. Gromadzki, and P. Chylarecki. 2001. Woodpeckers as indicators of forest bird diversity. Conservation Biology 15:208-217.

Mueller, W. P. 2002. The population decline of the Red-headed Woodpecker in Wisconsin and Illinois. Meadowlark 11:130-132.

Nelson, P. W. 2005. The Terrestrial Natural Communities of Missouri. Missouri Natural Areas Committee, Jefferson City, Missouri, USA.

O'Connor, R. J., and R. K. Hicks. 1980. The influence of weather conditions on the detection of birds during common bird census fieldwork. Bird Study 27:137-151.

Peterjohn, B. G., and D. L. Rice. 1991. The Ohio breeding bird atlas. Ohio Department of Natural Resources, Columbus, Ohio, USA.

Probst, J. R., and F. R. Thompson III. 1996. A multi-scale assessment of the geographic and ecological distribution of Midwestern Neotropical migratory birds. Pages 22-40 *in* Management of Midwestern landscapes for the conservation of Neotropical migratory birds. (Thompson III, F. R., Ed.). U.S. Department of Agriculture General Technical Report NC187.

Radford, J. Q., A. F. Bennett, and G. J. Cheers. 2005. Landscape-level thresholds of habitat cover for woodland-dependent birds. Biological Conservation 124:317-337.

Ralph, C. J., J. R. Sauer, and S. Droege. 1995. Monitoring bird populations by point counts. USDA Forest Service General Technical Report PSW-GTR-149.

Reeder, K. F. and J. A. Clymer. 2015. Iowa's Wildlife Action Plan: Securing a future for fish and wildlife. Iowa Department of Natural Resources, Des Moines, Iowa, USA.

Reidy, J. L., F. R. Thompson, and S. W. Kendrick. 2014. Breeding bird response to habitat and landscape factors across a gradient of savanna, woodland, and forest in the Missouri Ozarks. Forest Ecology and Management 313:34-46.

Renfrew, R. B., and C. A. Ribic. 2008. Multi-scale models of grassland passerine abundance in a fragmented system in Wisconsin. Landscape Ecology 23:181-193.

Ribic, C. A., and D. W. Sample. 2001. Associations of grassland birds with landscape factors in southern Wisconsin. American Midland Naturalist 146:105-121.

Robbins, C. S., D. Bystrak, and P. H. Geissler. 1986. The Breeding Bird Survey: its first fifteen years, 1965-1979. U.S. Fish and Wildlife Service, Resource Publication 157.

Robbins, C. S. 1988. Forest fragmentation and its effects on birds. Pages 61-65 *in* Managing North Central forests for non-timber values. (J.E. Johnson Ed.). SAF publication 88-04. Society of American Foresters.

Robbins, C. S., J. R. Sauer, R. S. Greenberg, and S. Droege. 1989. Population declines in North American birds that migrate to the Neotropics. Proceedings of the National Academy of Science 86:6758-7662.

Robbins, S. D., Jr. 1991. Wisconsin birdlife: Population and distribution past and present. University of Wisconsin Press, Madison, Wisconsin, USA.

Robinson, S. K. 1992. Population dynamics of breeding Neotropical migrants in a fragmented Illinois landscape. *In* Ecology and conservation of Neotropical migrant landbirds. (J.M. Hagan and D.W. Johnston, Eds.). Washington, DC: Smithsonian Institution Press 408-418.

Roberge, J. M., and P. Angelstam. 2006. Indicator species among resident forest birds–a cross-regional evaluation in northern Europe. Biological Conservation 130:134-147.

Rodewald, P. G. and R. D. James. 2011. Yellow-throated Vireo (*Vireo flavifrons*). No. 247. *In* (A. Poole, Ed.). The Birds of North America Online. Cornell Lab of Ornithology, Ithaca, New York, USA.

Rosenberg, K. V., R. S. Hames, R. W. Rohrbaugh, Jr., S. Barker Swarthout, J. D. Lowe, and A. A. Dhondt. 2003. A land manager's guide to improving habitat for forest thrushes. The Cornell Lab of Ornithology, Ithaca, New York, USA.

Sauer, J. R., J. E. Hines, G. Gough, I. Thomas, and B. G. Peterjohn. 1997. The North American Breeding Bird Survey Results and Analysis. Version 96.4. Patuxent Wildlife Research Center, Laurel, Maryland, USA.

Sauer, J. R., J. E. Hines, J. E. Fallon, K. L. Pardieck, D. J. Ziolkowski, Jr., and W. A. Link. 2014. The North American Breeding Bird Survey, Results and Analysis 1966-2013. Version 01.30.2015. USGS Patuxent Wildlife Research Center, Laurel, Maryland, USA.

Scharf, W. C., and J. Kren. 2010. Orchard Oriole (*Icterus spurius*). No. 255. *In* (A. Poole, Ed.). The Birds of North America Online. Cornell Lab of Ornithology, Ithaca, New York, USA.

Skinner, S. P. 2004. Linking decision support systems for ducks with relative abundance of other grassland bird species. Thesis. University of Saskatchewan, Saskatoon, Canada.

Stotz, D. F, J. W. Fitzpatrick, T.A. Parker III, and D. K. Moskovits. 1996. Neotropical birds: ecology and conservation. University of Chicago Press, Chicago, Illinois, USA.

Teaming with Wildlife. 2015. State Wildlife Action Plans: A strategic approach to conservation. <http://www.teaming.com/state-wildlife-action-plans-swaps>. Accessed 10 July 2016.

Urban, N. A., R. K. Swihart, M. C. Malloy, and J. B. Dunning, Jr. 2012. Improving selection of indicator species when detection is imperfect. Ecological Indicators 15:188-197.

U.S. Fish and Wildlife Service. 2015. Midwest birds of concern. <http://www.fws.gov/midwest/midwestbird/concern.html>. Accessed 10 July 2016.

Watson, K. 2013. A comparison of single-day vs multiple-day samplings designs using occupancy modeling. College of William & Mary Undergraduate Honors Theses. Paper 645.

Whitcomb, R. F., C.S. Robbins, J. F. Lynch, B. L. Whitcomb, M. K. Kliemkiewicz, and D. Bystrak. 1981. Effects of forest fragmentation on avifauna of the eastern deciduous forest. Pp. 125-205 in Forest island dynamics in man-dominated landscapes. R. L. Burgess and D. M. Sharpe (eds). Springer-Verlag, New York, New York, USA.

White, G. C., and Burnham, K. P. 1999. Program MARK: Survival estimation from populations of marked animals. Bird Study 46:120-139.

Whitehead, D. R., and T. Taylor. 2002. Acadian Flycatcher (*Empidonax virescens*). No. 614. *In* (A. Poole, Ed.). The Birds of North America Online. Cornell Lab of Ornithology, Ithaca, New York, USA.

Winter, M., D. H. Johnson, J. A. Shaffer, T. M. Donovan, and W. D. Svedarsky. 2006. Patch size and landscape effects on density and nesting success of grassland birds. Journal of Wildlife Management 70:158-17.

Table 1. Model effects (95% confidence limits) from the best model to explain habitat associations of forest and scrub-shrub birds in Iowa, 2007-2014. Covariates modeled on site occupancy (Psi), colonization (Gamma), and extinction (Epsilon) are as follows: "Ag" represents agriculture, "Grass" represents grassland, "Wood" represents woodland, "200" represents the 200-m spatial scale, "500" represents the 500-m spatial scale, "1K" represents the 1000-m spatial scale, "5K" represents the 5000-m spatial scale, "PLAND" represents percentage of the landscape, and "ED" represents edge density. Covariates modeled on detection probability (p) are the following: "Wind" represents wind speed (km/h), "Cloud" represents cloud cover (%), "Temp" represents temperature (converted from °F to °C), and "." represents a constant effect. Bold text indicates a significant effect (i.e., confidence interval did not include zero). Some parameters could not be estimated ("Not estimated"), while for other parameters there was no covariate effect and it was the intercept model ("No effect"). Species nomenclature follows the four-letter alpha codes delineated by Chesser et al. (2016).

Species	Psi	Gamma	Epsilon	p
RHWO	Ag200ED	Grass5KPLAND	Wood1KED	Wind
	-0.001 (-0.002, -0.000)	**0.017 (0.002, 0.033)**	**-0.012 (-0.019, -0.005)**	**-0.072 (-0.133, -0.011)**
PIWO	Wood5KPLAND	Wood1KPLAND	Ag1KED	Temp
	0.149 (0.069, 0.229)	**0.031 (0.015, 0.048)**	**0.015 (0.001, 0.029)**	-0.022 (-0.055, 0.010)
EAWP	Wood200ED	Wood500PLAND	Grass500PLAND	Wind
	0.005 (0.002, 0.007)	**0.068 (0.038, 0.097)**	**0.039 (0.017, 0.061)**	**-0.150 (-0.200, -0.010)**
ACFL	Ag500ED	Wood200PLAND	Wood500PLAND	Wind
	-0.008 (-0.013, 0.002)	**0.023 (0.013, 0.034)**	-0.186 (-0.392, 0.020)	-0.140 (-0.282, 0.001)
BEVI	Grass5KED	Ag5KED	Ag200ED	Cloud
	0.081 (-0.034, 0.196)	**0.007 (0.004, 0.011)**	-1.725 (-4.359, 0.909)	-0.007 (-0.016, 0.002)
YTVI	Wood200PLAND	Ag5KPLAND	Grass500PLAND	Cloud
	0.040 (0.021, 0.059)	**-0.036 (-0.051, -0.020)**	**0.067 (0.035, 0.099)**	**-0.003 (-0.007, -0.000)**
WOTH	Ag500PLAND	Wood500PLAND	Wood1KPLAND	.
	-0.033 (-0.064,-0.003)	**0.034 (0.017, 0.051)**	-0.030 (-0.060, 0.001)	No effect
KEWA	Wood200PLAND	Wood5KED	Ag1KED	.
	0.049 (-0.010, 0.108)	**0.010 (0.003, 0.016)**	Not estimated	No effect
FISP	Ag5KED	Ag1KED	Ag5KED	Wind
	0.011 (0.006, 0.016)	**-0.002 (-0.004, -0.000)**	**-0.007 (-0.011, -0.004)**	**-0.098 (-0.161, -0.035)**
OROR	Ag1KED	Grass200ED	Ag5KED	.
	0.006 (0.000, 0.0105)	**0.001 (0.000, 0.002)**	**-0.008 (-0.016, -0.001)**	No effect

Table 2. Parameter estimates (SE) from the best model to explain habitat associations of forest and scrub-shrub birds in Iowa, 2007-2014. Parameter estimates are for site occupancy (Psi) colonization (Gamma), extinction (Epsilon), and detection probability (p). "N/E" denotes parameter was not estimated.

Species	Psi (SE)	Gamma (SE)	Epsilon (SE)	p (SE)
Red-headed Woodpecker	0.451 (0.051)	0.156 (0.032)	0.120 (0.043)	0.624 (0.024)
Pileated Woodpecker	0.021 (0.016)	0.052 (0.011)	0.222 (0.106)	0.725 (0.219)
Eastern Wood-Pewee	0.610 (0.069)	0.508 (0.113)	0.069 (0.018)	0.858 (0.012)
Acadian Flycatcher	0.056 (0.035)	0.064 (0.014)	N/E	0.693 (0.040)
Bell's Vireo	0.038 (0.011)	0.069 (0.015)	N/E	0.515 (0.075)
Yellow-throated Vireo	0.357 (0.071)	0.203 (0.035)	0.319 (0.072)	0.544 (0.032)
Wood Thrush	0.214 (0.053)	0.109 (0.032)	0.398 (0.132)	0.488 (0.031)
Kentucky Warbler	N/E	0.021 (0.009)	N/E	0.332 (0.097)
Field Sparrow	0.403 (0.063)	0.245 (0.036)	0.186 (0.034)	0.804 (0.017)
Orchard Oriole	0.050 (0.035)	0.160 (0.030)	0.358 (0.107)	0.395 (0.034)

Appendix

Table A1. Annual derived estimates of Psi (95% confidence limits) from the best model for 10 bird species of forest, savanna, and scrub-shrub habitats in Iowa, 2007-2014. "N/E" denotes that parameter was not estimated.

Species	Year	Psi-hat	SE	Lower	Upper
Red-headed Woodpecker	2007	0.4514	0.0506	0.3522	0.5507
	2008	0.4832	0.0331	0.4182	0.5481
	2009	0.5061	0.0298	0.4477	0.5645
	2010	0.5227	0.0349	0.4543	0.5911
	2011	0.5347	0.0417	0.4530	0.6164
	2012	0.5434	0.0478	0.4497	0.6370
	2013	0.5496	0.0528	0.4462	0.6531
	2014	0.5542	0.0567	0.4430	0.6654
Pileated Woodpecker	2007	0.0207	0.0164	0.0115	0.0529
	2008	0.0671	0.0149	0.0379	0.0963
	2009	0.1008	0.0181	0.0654	0.1362
	2010	0.1253	0.0229	0.0804	0.1701
	2011	0.1430	0.0285	0.0871	0.1989
	2012	0.1559	0.0344	0.0885	0.2232
	2013	0.1652	0.0399	0.0870	0.2435
	2014	0.1720	0.0449	0.0839	0.2600
Eastern Wood-Pewee	2007	0.6101	0.0695	0.4739	0.7463
	2008	0.7658	0.0428	0.6819	0.8496
	2009	0.8315	0.0370	0.7589	0.9040
	2010	0.8592	0.0309	0.7986	0.9197
	2011	0.8709	0.0273	0.8174	0.9243
	2012	0.8758	0.0256	0.8256	0.9260
	2013	0.8779	0.0249	0.8290	0.9267
	2014	0.8788	0.0246	0.8304	0.9271
Acadian Flycatcher	2007	0.0565	0.0348	0.0116	0.1246
	2008	0.0611	0.0131	0.0354	0.0868
	2009	0.0608	0.0120	0.0372	0.0843
	2010	0.0608	0.0121	0.0371	0.0845
	2011	0.0608	0.0121	0.0371	0.0845
	2012	0.0608	0.0121	0.0371	0.0845
	2013	0.0608	0.0121	0.0371	0.0845
	2014	0.0608	0.0121	0.0371	0.0845

Table A1 (continued).

Species	Year	Psi-hat	SE	Lower	Upper
Bell's Vireo	2007	N/E			
	2008	0.0695	0.0146	0.0409	0.0982
	2009	0.0647	0.0126	0.0400	0.0894
	2010	0.0650	0.0128	0.0399	0.0901
	2011	0.0650	0.0128	0.0400	0.0900
	2012	0.0650	0.0128	0.0400	0.0901
	2013	0.0650	0.0128	0.0400	0.0901
	2014	0.0650	0.0128	0.0400	0.0901
Yellow-throated Vireo	2007	0.3579	0.0713	0.2181	0.4977
	2008	0.3741	0.0368	0.3020	0.4462
	2009	0.3819	0.0327	0.3178	0.4460
	2010	0.3856	0.0360	0.3151	0.4561
	2011	0.3873	0.0386	0.3117	0.4630
	2012	0.3882	0.0401	0.3096	0.4668
	2013	0.3886	0.0409	0.3084	0.4687
	2014	0.3888	0.0413	0.3078	0.4697
Wood Thrush	2007	0.2150	0.0528	0.1116	0.3184
	2008	0.2154	0.0265	0.1634	0.2674
	2009	0.2156	0.0242	0.1682	0.2630
	2010	0.2157	0.0273	0.1622	0.2692
	2011	0.2157	0.0296	0.1577	0.2738
	2012	0.2157	0.0309	0.1552	0.2763
	2013	0.2158	0.0316	0.1539	0.2776
	2014	0.2158	0.0319	0.1532	0.2783
Kentucky Warbler	2007	N/E			
	2008	0.0216	0.0091	0.0037	0.0395
	2009	0.0213	0.0088	0.0040	0.0386
	2010	0.0213	0.0088	0.0040	0.0387
	2011	0.0213	0.0088	0.0040	0.0386
	2012	0.0213	0.0088	0.0040	0.0386
	2013	0.0213	0.0088	0.0040	0.0386
	2014	0.0213	0.0088	0.0040	0.0386

Table A1 (continued).

Species	Year	Psi-hat	SE	Lower	Upper
Field Sparrow	2007	0.4030	0.0634	0.2788	0.5273
	2008	0.4745	0.0345	0.4069	0.5421
	2009	0.5152	0.0262	0.4639	0.5665
	2010	0.5383	0.0268	0.4858	0.5908
	2011	0.5514	0.0290	0.4945	0.6083
	2012	0.5589	0.0309	0.4983	0.6195
	2013	0.5631	0.0322	0.5000	0.6263
	2014	0.5655	0.0331	0.5007	0.6304
Orchard Oriole	2007	0.0502	0.0350	-0.0184	0.1188
	2008	0.1843	0.0260	0.1334	0.2352
	2009	0.2488	0.0270	0.1959	0.3017
	2010	0.2798	0.0304	0.2201	0.3394
	2011	0.2947	0.0353	0.2254	0.3639
	2012	0.3018	0.0394	0.2246	0.3791
	2013	0.3053	0.0422	0.2226	0.3880
	2014	0.3069	0.0439	0.2210	0.3929

CHAPTER 4: LOCAL AND LANDSCAPE EFFECTS ON BUTTERFLIES AT MULTIPLE SCALES IN IOWA

A paper to be submitted to *Insect Conservation and Diversity*

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Abstract

Butterflies are declining around the globe, and they are particularly at risk in increasingly fragmented landscapes, such as those found in the Midwestern USA. Growing concern over these taxa, which are often regarded as proxies for other insects and the environment as a whole, has intensified interest in understanding the impacts of local and broad-scale features on butterfly population dynamics. Using butterfly-survey data collected at 314 sites across Iowa during the Multiple Species Inventory and Monitoring (MSIM) program 2007-2014, we estimated occupancy, colonization, and extinction probabilities for four butterfly species: giant swallowtail (*Papilio cresphontes*), summer azure (*Celastrina neglecta*), viceroy (*Limenitis archippus*), and pearl crescent (*Phyciodes tharos*). We used presence-absence data in robust design occupancy models to estimate the effects of microhabitat characteristics (litter depth, canopy cover, visual obstruction, and presence/absence of larval food plant), as well as landscape-habitat metrics (edge density and percentage of landscape in grassland, agriculture, and woodland) at multiple scales (100 m, 200 m, 500 m, 1000 m, and 5000 m). We also modeled the impact of weather covariates (temperature, cloud cover, and wind speed) on detection probability. Occupancy

probability ranged from 0.16 for *P. cresphontes* to 0.73 for *P. tharos*. Likewise, colonization

probability spanned from 0.083 for *P. cresphontes* to 0.409 for *P. tharos* and extinction

probability ranged from 0.141 for *L. archippus* to 0.437 for *C. neglecta*. Landscape covariates

surfaced in the top model on occupancy for all four species and on colonization rates for three

species. Microhabitat variables impacted colonization for one species and extinction for two

species; the direction of these effects were positive in each case. Woodland and grassland at

differing spatial scales were each more prevalent than agriculture in the best models. Wind

showed a strong negative impact on detection for two species, while percent cloud cover

(negative effect) and temperature (positive effect) moderately impacted one species each. In

what may be the first robust design occupancy study of butterflies in North America, we hope

our findings will provide new insights into the life histories and conservation of butterflies in

Iowa and beyond.

Key Words: butterfly, detectability, habitat association, larval host plant, Iowa, landscape effects,

occupancy model, robust design, Pollard-Yates

Introduction

Butterflies as a whole are declining globally (Van Swaay et al. 2010). A particularly

striking illustration involves the steep, short-term decline summarized by the European

Grassland Butterfly Indicator for Grassland Species (Van Swaay et al. 2015), which found that

butterfly numbers in European grasslands have dropped by approximately 50% since 1990.

Landscape alteration and land-use changes, along with pesticide increased pesticide use and

climate change, are suspected causes (Cane and Tepedino 2001, Kerr 2001). Habitat

fragmentation is but one of the land-use changes that has negatively impacted many butterfly

species; suitable patches of habitat are isolated to the extent that they cannot sustain a population,

nor be colonized by nearby source population (Fahrig 2003). Considering the highly fragmented nature of Midwestern landscapes, wherein the original prairie has been reduced by more than 99% (Samson and Knopf 1994) and forest habitats by 57% (Zohrer 2006), Iowa's butterfly representatives are presumably headed in the same direction. Currently, 51 out of 124 (over one-third) of Iowa's butterfly species are listed as Species of Greatest Conservation Need (SGCN) (Reeder and Clymer 2015), highlighting the need to understand how these species respond to landscape-level habitat configurations.

Understanding habitat associations and the impact of increasingly altered landscapes should prove critical in the conservation of these invertebrates, which often serve as indicators of insect and other wildlife health (Kremen et al. 1993, Blair 1999, Thomas and Clarke 2004, Thomas 2005, van Swaay et al. 2006). As a result, butterflies have been the focus of a growing number of ecological studies worldwide (Thomas 2005, Nowicki et al. 2008). Although many butterfly studies have taken place in regions that differ from the intensively agricultural landscapes of the central U.S., researchers in Iowa have nonetheless addressed butterflies in a diverse array of contexts. This includes movement patterns at habitat edges (Ries and Debinski 2001), the value of prairie restoration in species richness and abundance (Shepherd and Debinski 2005), and the response of butterflies to various microhabitat and landscape factors (Davis et al. 2007). However, none of these studies has addressed how large-scale landscape configurations affect long-term occupancy dynamics of multiple butterfly species.

Since the 1990s, Pollard-Yates transects (Pollard and Yates 1993) have served as the predominant method for sampling butterflies (Nowicki et al. 2008). Data from Pollard-Yates transects produce density estimates and have been used to make inferences about populations. A key assumption of these transects is that detection probability of butterflies is 1.0, but a

considerable body of research with varied taxa has illustrated that the assumption of perfect

detection, even within a small area, is often violated (Anderson 2001, Anderson 2003,

Mackenzie et al. 2005). As a result, many researchers (e.g., Dennis et al. 2006, Kery and Plattner

2007, Haddad et al. 2008, Nowicki et al. 2008) have highlighted the need to account for

imperfect detection probability in butterfly surveys. One response has been to conduct transects

that incorporate distance sampling (Powell et al. 2007, Moranz 2010, Isaac et al. 2011), which

enables estimation of detection probabilities and, therefore, corrected values for density

(Burnham and Anderson 1984).

Another approach is to use occupancy modeling, which accounts for imperfect

detectability (i.e., <1.0) and estimates the probability that a species will occupy a site (Mackenzie

et al. 2002), thus enabling better insights into population dynamics than methodologies which

ignore detection probability (Mackenzie et al. 2005). Recent butterfly studies (Bried and Pellett

2011, Puntenney and Schorr 2016) have incorporated presence-absence data into single-season

occupancy modeling of uncommon species. Moreover, in a long-term study of butterflies in

northeastern Spain, Fernández-Chacón et al. (2014) utilized multi-season occupancy models in

program Presence (Hines 2006) to assess the influence of numerous site covariates (e.g., habitat

area, topography, and climate) on colonization and extinction patterns.

Here, we took butterfly-transect data from surveys conducted in 2007-2014 at sites across

Iowa and converted them to presence-absence values to assess the impact of microhabitat

variables (larval food plant, litter depth, visual obstruction, and canopy cover) and landscape

composition (edge density and percentage of landscape in agriculture, grassland, and forest at

scales of 100 m, 200 m, 500 m, 1000 m, and 5000 m) on the population dynamics of four

butterfly species: giant swallowtail (*Papilio cresphontes*), summer azure (*Celastrina neglecta*),

viceroy (*Limenitis archippus*), and pearl crescent (*Phyciodes tharos*). These species are each numerous and widespread and collectively represent assorted open, semi-open, and forested habitats in Iowa and elsewhere (Schlicht et al. 2007, Opler et al. 2010, Reese 2016), have well-defined larval food plants in Iowa (Schlicht 2007, Opler et al. 2010), and are all likely susceptible to the apparent deleterious effects of agriculture on butterflies (Cane and Tepedino 2001, Kerr 2001). Furthermore, across the spectrum of size and life-history strategies, butterflies undergo dispersal and daily movements spanning from <200 m for many smaller genera through 5km or more for some larger species (Brown 1973, Emmel 1986, Harrison 1989, Wahlberg et al. 2002, Schneider et al. 2003, Auckland et al. 2004, Stasek et al. 2008, Xerces Society 2008). Thus, we consider the above spatial scales relevant to habitat associations and landscape-level effects on Iowa butterflies, including our four study species.

Methods

Study site

Our site selection, butterfly sampling, and vegetation sampling techniques followed the methodology of the Iowa Multiple Species Inventory and Monitoring (MSIM) Program (Kinkead 2006). We selected sites for butterfly surveys using a stratified random sampling design from Iowa public lands (federal, state, and county owned). We chose these classifications for ease of access and because they are managed specifically for wildlife habitat. All public properties in Iowa >97 ha were classified according to 19 habitat types outlined in the IWAP (Zohrer 2006). We then stratified properties into four districts that consisted of the northeastern, southeastern, northwestern, and southwestern quarters of Iowa to allow for equal selection of different habitat types across the state. In addition, we considered only public properties >97 ha to constrain our

sampling frame due to financial and logistical constraints. We selected new properties without replacement each year from 2007-2014 such that properties of a certain habitat type were chosen from each management district. We also retained up to five properties from the sample of properties each year to constitute a sample of properties surveyed multiple years for comparison purposes. We established a core area on each public property that consisted of the assigned habitat type of that property. Within the core area, we established one transect for butterfly surveys.

Butterfly surveys

We conducted four butterfly visits, at least 14 d apart, at selected properties from 15 May to 15 September annually from 2007 to 2014. On each visit, we employed Pollard-Yates transect survey methodology (Pollard and Yates 1993), as modified by Shepherd and Debinski (2005), in which a single observer walked along a 400-m long, 5-m wide line that had been placed through the center of the sampling plot at each property. The observer walked at a steady pace (ca. 10 m/min) down the middle of the transect line and recorded number and species for butterflies detected within the 5-m wide transect corridor. Behavior (i.e., flying, nectaring, resting, basking, ovipositing, and courting/mating) at initial detection of each individual was also recorded. We completed all surveys between 0900 and 1800 hours as well as during warm temperatures ($\geq$ 20°C), low cloud cover (<70%), calm winds (<16 km/h), and no precipitation. All weather variables were measured immediately before and after the completion of each transect. Butterfly nomenclature and taxonomic sequence adhered to those of Opler et al. (2010).

Vegetation sampling

Terrestrial vegetation sampling followed the protocol set forth in the MSIM technical

manual (Kinkead 2006). We established ten 0.3 ha sampling plots within a 200 m radius of the

center of the transect described above; seven plots were arranged in a hexagon shape (including

the center point), and one to three (but typically one) additional plots were placed 36.4 m from

the center of center point at angles of 120^0, 240^0, and 360^0. Within each plot, the following

measurements relevant to these analyses were made: Litter depth (mm) was measured at three

distances (2.5 m, 5 m, 7.5 m) along sub-transects within each plot, and four Robel pole readings

(visual obstruction) were taken within each large plot. Using a densitometer, four binary

estimates of tree-canopy cover were made around the perimeter of a 0.017-ha subplot in the four

cardinal directions within each vegetation sampling plot. A vegetative species list for larval host

plants was compiled through two methods: estimates of cover class within 2 1-m^2 plots and a

timed (5 minute) canvas of the 0.017-ha subplot. This list was then used to compile

presence/absence values for larval food plant genera of butterfly species. At each property, all

occurrences of any given plant species in a survey season were collapsed into a single

presence/absence value for that property.

Landscape and microhabitat covariates

Using ArcGIS (ver. 10.1; ESRI, 2012), we measured various landscape-level habitat

variables within a 100 m, 200 m, 500 m, 1000 m, and 5000 m radius of each sampled site. We

placed a buffer around each of our sampled sites using the buffer tool in ArcGIS toolbox

(Analysis Tools, Proximity, Buffer; ESRI, 2012). We then clipped the 2009 Iowa Landcover file

to our site buffers using the "clipraster" command in the tools extension package Geospatial

Modeling Environment (GME; Beyer 2012). The 2009 Iowa Landcover file provides information

on the land use classification of the Iowa landscape in 2009 using satellite imagery. This is currently the most recent land use classification for Iowa. We repeated the above two steps for all radii to obtain the land use description within each radius our surveyed sites. Among the wide variety of land-use classifications in the Landcover file, we selected the "woodland", "grassland", and "agriculture" classifications for our analysis because these were the classifications we believed would most influence our focal species based on their aforementioned life-history traits.

We estimated our landscape-level habitat characteristics for each radius using FRAGSTATS (ver. 4.2; McGarigal et al. 2012). FRAGSTATS is a computer program that analyzes spatial patterns based on categorical maps and allows the user to pick from a variety of metrics to assess landscape configuration (McGarigal et al. 2012). As edge effects (Ries and Debinski 2001) and percentage of habitat in the landscape (Davis et al. 2007) have both been shown to impact butterfly dynamics in Iowa, we selected the percentage of landscape (PLAND) and edge density (ED) from FRAGSTATS. Percentage of landscape measures the area of the focal land-use classification standardized by the total area of the landscape, whereas ED measures the amount of edge on the landscape corresponding to a single land-use classification standardized by landscape area.

We also selected four vegetation measurements from all sites to serve as microhabitat covariates in our analyses. These included litter depth, which relates to overwintering habitat for larvae of *P. tharos* (Kopper et al. 2000) and was modeled on this species by Davis et al. (2007); visual obstruction and canopy cover, both of which could affect the growth of the shade-intolerant plants (Burns and Honkala 1990) that serve as larval food sources of all four species (Schlicht et al. 2007, Opler et al. 2010) and also affect butterfly behavior (Pivnik and McNeil

1987, Krauss et al. 2004, Wikström et al. 2009, Bried and Pellett 2012, Cormont et al. 2011, Fernández-Chacón 2014 et al., Puntenney and Schorr 2016*)*; and finally presence-absence of larval food-plant genera for each species, which are universally known to be essential to a butterfly's life cycle. Larval food plants were based on summaries by Schlicht et al. (2007) and Opler et al. (2010) and observations made by the authors during MSIM surveys. They consisted of the following plant genera by butterfly species: wafer-ash (*Ptelea*) and prickly-ash (*Zanthoxylum*) for *P. cresphontes*; New Jersey tea (*Ceanothus*), dogwood (*Cornus*), elderberry (*Sambucus*), wingstem (*Verbesina*), and viburnum (*Viburnum*) for *C. neglecta*; aspen and cottonwood (*Populus*) and willow (*Salix*) for *L. archippus*; and aster (*Aster*) for *P. tharos*.

Occupancy models

We converted butterfly detections from Pollard-Yates transects into presence-absence values for each species on each survey visit. We utilized the robust design occupancy model framework (MacKenzie et al. 2003) via the RMARK interface (Laake 2013) with Program Mark (White and Burnham 1999) to evaluate the effects of the above-mentioned microhabitat and landscape-level habitat characteristics on our four study species. Robust design occupancy model estimates four parameters: 1) probability of occupancy (ψ), (i.e., the probability that the species of interest occupied a sampled site), 2) probability of colonization (γ), or the probability that a site was colonized at time $t+1$ given the site was not occupied at time t, 3) probability of extinction (ε), or the probability that a site went extinct at time $t+1$ given the site was occupied at time t, and 4) detection probability, or the probability of detecting the species of interest given it was present at the sampled site (p; MacKenzie et al. 2003). Unlike the single-season occupancy model where sites are closed to changes in occupancy state during the primary sampling season (MacKenzie et al. 2002), the robust design occupancy model assumes sites are closed to changes

in occupancy state between secondary sampling intervals (e.g., sampling occasions within a year) but are open to changes in occupancy state between primary sampling intervals (e.g., years; MacKenzie et al. 2003). This allows for the evaluation of metapopulation dynamics through the process of determining the probability a site will remain occupied, go locally extinct, or become locally colonized. In addition, the robust design occupancy model allows covariates to be modeled on the parameters to improve parameter estimates and provide information on characteristics that might influence the various parameters.

Based on recommendations by Doherty et al. (2010), we ran all possible models (270,000 total) for each species. For model evaluation, we used Akaike's Information Criterion, corrected for small sample size (AICc), to order models, and we used the top model for each species to represent the best estimate of covariate effects on four parameters of interest (occupancy, colonization, extinction, and detection probability). We evaluated the strength of model effects (betas) by examining the 95% confidence interval and whether it included zero; effects for which the confidence interval did not include zero were considered strong while those with minimal overlap were considered weak effects.

We modeled the aforementioned landscape-level and microhabitat variables on the probability of occupancy, colonization, and extinction of our four study species. The primary sampling intervals were the years during which butterfly surveys were conducted (2007-2014), and the secondary sampling intervals were the survey occasions (days) within each sampling year (May-September). We estimated all parameters on an annual basis. We truncated data sets to include only surveys conducted during June-August to ensure closure among the secondary sampling occasions. We had landcover data from only one year (2009), and so we assumed the landscape and the corresponding effects on occupancy, colonization, and extinction did not

change among our survey years and pooled all survey years for analysis. For detection

probability, we considered three weather covariates (percent cloud cover, wind speed, and

temperature all from the start of the survey) that are known to be important correlates with this

parameter for butterflies (Krauss et al. 2004, Wikström et al. 2009, Bried and Pellett 2012,

Cormont et al. 2011, Fernández-Chacón et al. 2014, Puntenney and Schorr 2016).

We hypothesized the following regarding the site occupancy, colonization and extinction

probability, detection probability, and host-plant interactions of four Iowa butterflies:

1. Vegetation structure and landscape metrics at multiple scales will define the

   population (i.e., site occupancy) dynamics of our study species, which each utilize

   host plants that are common and associated with a wide variety of habitats across

   Iowa.

2. Woodland at multiple scales will positively influence dynamics of *P. cresphontes* and

   C. neglecta, whereas grassland will have the most explanatory power for *L. archippus*

   and *P. tharos*. Any impacts of agriculture within landscape configuration will be

   negative.

3. Larger butterflies (*P. cresphontes* and *L. archippus*), which tend to have greater long-

   distance capabilities, will be more influenced by broad-scale metrics (500 m, 1000 m,

   5000 m) than smaller species (*C. neglecta* and *P. tharos*), which will be impacted at

   smaller scales (100 m and 200 m).

4. Detection probabilities for all species will be strongly influenced by weather

   covariates, particularly cloud cover and wind.

Results

We conducted butterfly surveys on a total of 314 properties from 2007 to 2014. During those surveys, we detected *P. cresphontes* at 35 properties, *C. neglecta* at 51 properties, *L. archippus* at 73 properties, and *P. tharos* at 130 properties.

Habitat effects

Our models describing the habitat associations of four butterfly species in Iowa showed varying patterns with respect to microhabitat and landscape-level covariates at differing spatial scales (Table 1). Regarding occupancy, colonization, and extinction, microhabitat covariates emerged as the explanatory variable in the best model for three species. The presence of the larval food plant, prickly-ash (*Zanthoxylum*), strongly affected colonization rate of *P. cresphontes*, visual obstruction showed a weak positive effect on extinction rate of *C. neglecta,* and canopy cover increased the extinction rate of *P. tharos*. All other parameters were best explained by landscape-level covariates. Among those, percentage of the landscape in woodland at 500 m exhibited a substantial positive impact on site occupancy of *P. cresphontes*, while woodland edge density at 200 m and percentage of grassland in the landscape at 200 m each produced strong positive effects on the corresponding colonization rates of *C. neglecta* and *P. tharos*. Weather covariates exhibited a negative impact on detection probabilities of all four species. Wind showed strong negative effects on detection probabilities of both the very large *P. cresphontes* and the much smaller *P. tharos* while cloud and temperature each demonstrated weak effects on *C. neglecta* and *L. archippus*, respectively.

Host plant interactions

Our models describing the impact of species-specific larval food plant(s) on the population dynamics generally showed mild to moderate effects for the three parameters of interest, and in most cases the effect did not appear in a competing model (Table 2). More than half of the betas associated with the host plant covariates were not estimated at all, and many of the remaining effects were estimated poorly.

Parameter estimates

Our models produced meaningful estimates on occupancy, colonization, extinction, and detection probability for all four study species (Table 3, Figure 1). Occupancy probability (mean = 0.433) ranged from 0.16 for *P. cresphontes* to 0.73 for *P. tharos*, colonization probability (mean = 0.285) ranged from 0.083 for *P. cresphontes* to 0.409 for *P. tharos*, and extinction probability (mean = 0.294) ranged from 0.141 for *L. archippus* to 0.329 for *P. cresphontes*. Detection probability (mean = 0.329) was generally low for all species and ranged from to 0.250 for *P. cresphontes* to 0.461 for *P. tharos*.

Discussion

This study represents the first use of multi-season, robust design occupancy models to examine the influence of local and landscape effects at differing spatial scales for butterflies in North America. Landscape covariates surfaced in the top model on occupancy for all four species and on colonization for three species. Microhabitat variables impacted colonization for one species and extinction for two species. Woodland and grassland at differing spatial scales were each more prevalent than agriculture in the best models. Regarding detection probability, wind showed a strong negative impact for two species, while percent cloud cover (negative

effect) and temperature (positive effect) moderately impacted one species each. Below, we discuss microhabitat and landscape-level effects in greater detail and show how this information could be helpful in the conservation of butterflies in Iowa's fragmented landscape.

Habitat effects

Although a unified pattern did not emerge across our study, connections to the life-history requirements of each species are evident. For example, percentage of woodland in the landscape at the 500-m scale strongly influenced site occupancy of *P. cresphontes*, which is widespread in shrubby woodland margins across much of Iowa (Schlicht et al. 2007). This species' larval food plant, *Zanthoxylum americanum* (Schlicht et al. 2007, Opler et al. 2010), is also prevalent in similar wooded contexts, where it thrives in a variety of soils and moisture conditions along sunny edges and forest clearings (Van Der Linden and Farrar 2011, Iowa State University Forestry Extension 2016). This sort of widespread habitat association may explain why the butterfly's site occupancy was most readily defined by the degree of woodland present. We likewise found a moderate additive effect of woodland at a broad scale (1000 m) on the extinction of *P. cresphontes*. Furthermore, site colonization itself was best described by presence of *Zanthoxylum americanum*, indicating that this large butterfly may focus on sites with its host plant during dispersal, and stay there as long as a certain threshold of forest remains to support both the butterfly and its common larval food source. Collectively, this information reveals that this species occupies Iowa landscapes with a greater amount of woodland at intermediate spatial scales, colonizes sites that contain its preferred host plant, and will disappear from occupied sites with too little woodland at moderate spatial scales.

Our findings also revealed the strong positive impact of woodland (edge density at 200 m) on the colonization of *C. neglecta*. This corresponds nicely to the species' preference for patchy woodland edges and shrubby meadows where its various larval food genera (*Cornus*, *Sambucus*, *Verbesina*, and *Ceanothus*) prevail (Schlicht et al. 2007, Opler et al. 2010). Site extinction for *C. neglecta* was best defined by degree of visual obstruction. Perhaps this butterfly chooses certain types of woodland environs and remains there until such habitats become too overgrown for the sun-loving larval food plants. A weak negative impact of agriculture also surfaced for occupancy, hinting at how heavily row-cropped landscapes may not fully suit *C. neglecta's* life-history requirements.

P. tharos, which is the most abundant of the many Nymphalid species in Iowa (Schlicht et al. 2007), exhibited colonization-extinction dynamics closely tied to known habitat requirements. A strong positive impact of grassland on a small scale (200 m) emerged for colonization, while extinction rate was substantially hastened by canopy cover (i.e., trees). Each result fits the species' affinity to various open and semi-open habitats (Davis et al. 2007, Schlicht et al. 2007, Opler et al. 2010, Reese 2016), which regularly contain one or more of the many plant species (e.g., 13 documented during our vegetation surveys) that comprise this butterfly's favored host genera. In other words, *P. tharos* keys in on grassland habitats on a small scale and occupies those areas until they become too heavily shaded.

The contrasting influence of grassland and forested landscapes also surfaced for *L. archippus,* as edge density of grassland at 200 m showed a strong positive effect on colonization, while percentage of the landscape in woodland at broader scales (1000 m and 5000 m respectively) negatively impacted occupancy and reinforced extinction rate. This suggests that its population dynamics may be linked to habitat association with larval food sources: *Salix* and

Populus (Opler and Krizek 1984, Schlicht et al. 2007, Opler et al. 2010). All representatives of these tree and shrub genera are considered to be shade intolerant and thrive in meadows or margins of water bodies (Burns and Honkala 1990). Overall, *L. archippus*, much like the preceding species, readily colonizes grasslands at a small scale and abandons sites in which much of the surrounding landscape has transitioned to woodland.

Although larval food plant did not frequently appear as an explanatory variable in the best models across our study species, there is still an indication that the population dynamics of these butterflies are in some way related to host plant, albeit via habitat association. Another noticeable pattern in our study is that the two larger species (*P. cresphontes* and *L. archippus*) were both more strongly impacted at broader landscape scales than the two smaller species (*C. neglecta* and *P. tharos*), perhaps indicating that size may play a role in how a butterfly disperses and responds to landscape factors. Accordingly, in a comparison of two species in south-central Ohio, Stasek et al. (2008) found that *P. tharos* moved far less frequently among habitat patches than the much larger great spangled fritillary (*Speyeria cybele*), which exhibited a demonstrably higher degree of inter-patch movement.

Long-distance flights are also well known among swallowtails. For instance, individuals of the Schaus' swallowtail (*Papilio aristodemus*), have been tagged and observed dispersing distances of up to 5.8 km among habitat patches in southern Florida (Brown 1973, Emmel 1986, Xerces Society 2008). *P. cresphontes* might be capable of similar long-distance movements, as evidenced by the broad landscape influence on its occupancy and extinction probabilities in our study. Conversely, members of *C. neglecta's* family (Lycaenidae) are known to have peak dispersal distances around 100 m (Knutson et al. 1999, Maes et al. 2004), matching the small scale at which this species is apparently operating in Iowa.

Detection probability

Incorporating detection probabilities into butterfly analyses is a relatively new practice, but recent occupancy studies and butterfly behavioral research provide context for our findings. For example, although cloud cover surfaced only once (a mild effect on *C. neglecta*) as the explanatory variable for detection probability among our four species, this agrees with recent findings for the closely related hops azure (*Celastrina humulus*) by Puntenney and Schorr (2016) in a single-season occupancy study in Colorado. Exposure to sunlight is a driving force behind butterfly activity (Pivnick and McNeil 1987, Wikström et al. 2009), and thus increased cloud cover would diminish a butterfly's propensity to fly, nectar, and bask. These behaviors collectively constitute a majority of the detections (>80%) in our dataset. Therefore, we are somewhat surprised that only once did cloud cover best explain detection probability for our study species.

Our results showing the substantial negative effect of wind on detection probability of species near both ends of the size spectrum (*P. cresphontes* and *P. tharos*) are supported by Cormont et al. (2011), who described the significant influence of fluctuating wind speed on butterfly flight dynamics. Detectability might also be affected in this way. Likewise, Krauss et al. (2004) demonstrated that detection probability of the small blue (*Cupido minimus*) is strongly impacted by wind speed. On the other hand, Wikström et al. (2009) found no effect of wind on butterfly species richness or abundance, and Bried and Pellet (2011) did not find detection probability to be strongly influenced by wind during their single-season occupancy study of Karner blue (*Lycaeides melissa samuelis*). Rather, they revealed the positive impact of temperature, which corresponds to the moderate effect of increasing temperature on detection probability of *L. archippus* in our study. This again likely relates to the importance of sunlight to

butterfly activity (and thus detectability), as rising temperature typically correlates with peak solar exposure during the day.

Future considerations

As one of very few studies (e.g., Fernández-Chacón et al. 2014) to model butterfly population dynamics across multiple seasons (and apparently the only one to do so via robust design occupancy in the Program MARK framework) we are confident that our results will shed new insights into local and landscape effects on butterflies in Iowa. Our study might also provide a template for future work seeking to link butterfly occupancy patterns to the dynamics of colonization and extinction of those sites. Below, we discuss some important caveats to this work.

All four of our study species are multivoltine, with overlapping broods emerging across late spring, summer, and early fall in Iowa (Schlicht et al. 2007) and most of their respective ranges (Iftner et al. 1992, Opler et al. 2010, Beth 2012, Reese 2016). As such, a potential problem with our analysis is that the data season possibly encompassed multiple flight periods (i.e., broods) during each primary sampling occasion, meaning that we may have violated the closure assumption of occupancy studies (Mackenzie et al. 2002, Mackenzie and Royle 2005). However, the frequency and degree to which these butterflies disperse in Iowa is not well known (Schlicht et al. 2007) and may not be great enough to enable colonization among our study sites within a single season. Additionally, for robust design occupancy, the timing of specific brood-sampling periods might prove to be difficult on a yearly basis, and we noted that the emergence dates and flight windows of these and other common butterflies were unpredictable and varied widely among study years (S. Patterson, pers. obs.).

Another potential issue relates to our vegetation sampling technique. We used only presence-absence of the larval food plant at each site as a binary covariate on occupancy, colonization, and extinction. Other recent studies have indicated that butterfly occupancy is more closely related to host-plant area than presence-absence of host plant alone (Krauss et al. 2004, Pocewicz et al. 2009, Sanford et al. 2011, Puntenney and Schorr 2016), suggesting that a continuous variable based on specific measurements (e.g., percent ground coverage of larval food-plant genera) would be preferable. However, for our purposes, and because of differences among butterfly flight times and peak growth periods of larval food plants, such data would require a more comprehensive vegetation-sampling scheme than what is currently used by the MSIM program. The emphasis of MSIM is on a single microhabitat survey in August that is designed to capture a wide range of plant measures (species composition, structure, etc.) and correlate them to the presence-absence of multiple vertebrate and invertebrate taxa (Kinkead 2006). Any such expansion of survey protocol would likely pose logistical and financial problems for a program that is already intensively sampling a wide array of taxa across a broad region.

Conservation implications

Butterflies in other parts of the world have proven to be in wide decline (Van Swaay et al. 2015). Although North America does not have sufficient trend data on terrestrial invertebrates, it is reasonable to suspect that butterflies on this continent are experiencing a similar fate, especially in heavily degraded landscapes of the central USA. Through our findings in what may be the first robust design occupancy study of butterflies on this continent, we think that our conclusions concerning the effect of landscape composition and microhabitat conditions on butterfly population dynamics will provide new insight into the conservation of butterflies.

Acknowledgements

Literature Cited

Anderson, D. R. 2001. The need to get the basics right in wildlife field studies. Wildlife Society Bulletin 29:1294-1297.

Anderson, D. R. 2003. Response to Engeman: index values rarely constitute reliable information. Wildlife Society Bulletin 31:288-291.

Auckland, J. N., D. M. Debinski, and W. R. Clark. 2004. Survival, movement, and resource use of the butterfly *Parnassius clodius*. Ecological Entomology 29:139-149.

Beth, J. E. 2012. Butterflies of Indiana: A Field Guide. Indiana University Press, Bloomington, Indiana, USA.

Beyer, H. L., 2012. Geospatial Modelling Environment ver. 0.7.2.1. <http://www.spatialecology.com/gme.>. Accessed 10 July 2016.

Blair, R. B. 1999. Birds and butterflies along an urban gradient: surrogate taxa for assessing biodiversity? Ecological Applications 9:164-170.

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.

Brown, L.N. 1973. Populations of *Papilio andraemon bonhotei* Sharpe and *Papilio aristodemus ponceanus* Schaus in Biscayne National Monument, Florida. Journal of Lepidopterists' Society 27:136-140.

Burnham, K. P., and D. R. Anderson. 1984. The need for distance data in transect counts. Journal of Wildlife Management 48:1248-1254.

Burns, R. M. and B. H. Honkala. 1990. Silvics of North America: Vol. 1. Agriculture handbook No. 654. U.S. Department of Agriculture, Forest Service, Washington D.C., USA.

Cane, J. H., and V. J. Tepedino. 2001. Causes and extent of declines among native North American invertebrate pollinators: detection, evidence, and consequences. Conservation Ecology 5:1.

Cormont, A., A. H. Malinowska, O. Kostenko, V. Radchuk, L. Hemerik, M. F. Wallis-DeVries, and J. Verboom. 2011. Effect of local weather on butterfly flight behavior, movement, and colonization: significance for dispersal under climate change. Biodiversity Conservation 20:483-503.

Davis, J. D., D. M. Debinski, and B. J. Danielson. 2007. Local and landscape effects on the butterfly community in fragmented Midwest U.S.A. prairie habitats. Landscape Ecology 22:1341-1354.

Dennis, R. L. H., T. G. Shreeve, N. B. Isaac, D. B. Roy, P. B. Hardy, R. Fox, and J. Asher. 2006. The effects of visual apparency on bias in butterfly recording and monitoring. Biological Conservation 128:486.

Emmel, T. C. 1986. Status survey and habitat requirements of Florida's endemic Schaus swallowtail butterfly. Florida Game and Fresh Water Fish Commission, Final Report GFC-84-028. Tallahassee, Florida, USA.

Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. Annual Review of Ecology, Evolution, and Systematics 34:487–515.

Fernández-Chacón, A., C. Stefanescu, M. Genovart, J. D. Nichols, J. E. Hines, F. Paramo, M. Turco, and D. Oro. 2014. Determinants of extinction-colonization dynamics on Mediterranean butterflies: the role of landscape, climate, and local habitat features. Journal of Animal Ecology 83:276-285.

Haddad, N. M., B. Hudgens, C. Damiani, K. Gross, D. Kuefler, and K. Pollock. 2008. Determining optimal population monitoring for rare butterflies. Conservation Biology 22:929-940.

Harrison, S. 1989. Long-distance dispersal and colonization in the bay checkerspot butterfly, *Euphydryas editha bayensis*. Ecology 70:1236-1243.

Hines, J. E. 2006. PRESENCE2 – Software to estimate patch occupancy and related parameters. PSGS-PWRC. http://www.mbr-pwrc.gov/software/presence.html.

Isaac, N. J. B., K. L. Cruickshanks, A. M. Weddle, J. M. Rowcliffe, T. M. Brereton, R. L. H. Dennis, D. M. Shuker, and C. D. Thomas. 2011. Distance sampling and the challenge of monitoring butterfly populations. Methods in Ecology and Evolution 2:585-559.

Iftner, D. C., J. A. Shuey, and J. V. Calhoun. 1992. Butterflies and Skippers of Ohio. Ohio Biological Survey Bulletin. New Series Bol. 9 No. 1. College of Biological Sciences. The Ohio State University, Columbus, Ohio, USA.

Iowa State University Forestry Extension. 2016. Trees of Iowa: An Interactive Key. <http://www.extension.iastate.edu/forestry/iowa_trees/trees/prickly_ash.html>. Accessed 15 July 2016.

Kerr, J. T. 2001. Butterfly species richness patterns in Canada: energy, heterogeneity, and the potential consequences of climate change. Conservation Ecology 5:10.

Kery, M., and M. Plattner. 2007. Species richness estimation and determinants of species detectability in butterfly monitoring programmes. Ecological Entomology 32:53-61.

Kinkead, K. E. 2006. Iowa multiple species inventory and monitoring program technical manual. Iowa Department of Natural Resources, Des Moines, Iowa, USA.

Knutson, R. L., J. R. Kwilosz, and R. Grundel. 1999. Movement patterns and population characteristics of the Karner blue butterfly (*Lycaeides melissa samuelis*) at Indiana Dunes National Lakeshore. Natural Areas Journal 19:109-120.

Kopper, B.J., R. E. Charlton, D. C. Margolies. 2000. Oviposition site selection by the regal fritillary, *Speyeria idalia*, as affected by proximity of violet host plants. Journal of Insect Behavior 13:651–665.

Krauss, J., I. Steffan-Dewenter, and T. Tscharntke. 2004. Landscape occupancy and local population size depends on host plant distribution in the butterfly *Cupido minimus*. Biological Conservation 120:355-361.

Kremen, C., R. K. Colwell, T. L. Erwin, D. D. Murphy, R. F. Noss, and M. A. Sanjayan. 1993. Terrestrial arthropod assemblages: their use in conservation planning. Conservation Biology 7:796-808.

Laake, J. L. 2013. RMark: An R Interface for Analysis of Capture-Recapture Data with MARK. AFSC Processed Rep 2013-01, 25p. Alaska Fish. Sci. Cent., NOAA, Natl. Mar. Fish. Serv., 7600 Sand Point Way NE, Seattle WA 98115.

Maes, D., W. Vanreuse, W. Talloen, and H. Van Dyck. 2001. Functional conservation units for the endangered Alcon Blue butterfly *Maculinea alcon* in Belgium (Lepidoptera: Lycaenidae). Biological Conservation 120:229-241.

McGarigal, K., S. A. Cushman, and E. Ene. 2012. FRAGSTATS v4: Spatial Pattern Analysis Program for Categorical and Continuous Maps. Computer software program produced by the authors at the University of Massachusetts, Amherst. Available at the following web site: <http://www.umass.edu/landeco/research/fragstats/fragstats.html>.

MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, J. A. Royle, C. A. Langtimm, 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology 83:2248-2255.

MacKenzie, D. I., J. D. Nichols, J. E. Hines, M. G. Knutson, 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, and N. Sutton. 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 efficient occupancy studies: general advice and tips on allocation of survey effort. Journal of Applied Ecology 42:1105-1114.

Manley, P. N., and K. K. McIntyre. 2004. Multiple species inventory and monitoring protocol Region 3 study plan: implementation of the point count survey method. U.S. Department of Agriculture Forest Service Pacific Southwest Research Station, Albany, California, USA.

Moranz, R. A. 2010. The effects of ecological management on tallgrass prairie butterflies and their nectar sources. Dissertation, Oklahoma State University, Stillwater, Oklahoma, USA.

Nowicki, P., J. Settele, P. Y. Henry, and M. Woyciechowski. 2008. Butterfly monitoring methods: The ideal and the real world. Israel Journal of Ecology & Evolution 54:69-88.

Opler, P. A., and G. N. Krizek. 1984. Butterflies east of the Great Plains. Johns Hopkins University Press, Baltimore, Maryland, USA.

Opler, P. A., K. Lotts, and T. Naberhaus, coordinators. 2010. Butterflies and moths of North America. Bozeman, MT: Big Sky Institute. http://www.butterfliesandmoths.org/ (Version 6-12-2015).

Pivnick, K. A., and J. M. McNeil. 1987. Diel patterns of activity of *Thymelicus lineola* adults (Lepidoptera: Hesperiidae) in relation to weather. Ecological Entomology 12:197-207.

Pocewicz, A., P. Morgan, and S. D. Eigenbrode. 2009. Local and landscape effects on butterfly density in northern Idaho grasslands and forests. Journal of Insect Conservation 13:593-601.

Pollard, E., and Yates, T. J., 1993. Monitoring Butterflies for Ecology and Conservation: The British Butterfly Monitoring Scheme. Chapman & Hall, London, United Kingdom.

Powell, A., W. H. Busby, and K. Kindscher. 2007. Status of the regal fritillary (*Speyeria idalia*) and effects of fire management on its abundance in northeastern Kansas, USA. Journal of Insect Conservation 11:299-308.

Puntenney, C. P. and R. A. Schorr. 2016. Patch occupancy and habitat of the hops azure (*Celastrina humulus*), a rare North American endemic butterfly: insights for monitoring and conservation. Journal of Insect Conservation 20:215-222.

Reeder, K. F. and J. A. Clymer. 2015. Iowa's Wildlife Action Plan: Securing a future for fish and wildlife. Iowa Department of Natural Resources, Des Moines, Iowa, USA.

Reese, M. 2016. Wisconsin Butterflies. <http://www.wisconsinbutterflies.org>. Accessed 21 July 2016.

Ries, L., and D. M. Debinski. 2001. Butterfly responses to habitat edges in the highly fragmented prairies of Central Iowa. Journal of Animal Ecology 70:840-852.

Samson, F., and F. Knopf. 1994. Prairie conservation in North America. BioScience 44:418-421.

Sanford, M. P., Murphy, D. D., and P. F. Brussard. 2011. Distinguishing habitat types and the relative influences of environmental factors on patch occupancy for a butterfly metapopulation. Journal of Insect Conservation 15:775-785.

Schlicht, D. W., J. C. Downey, and J. C. Nekola. 2007. The Butterflies of Iowa. University of Iowa Press, Iowa City, Iowa, USA.

Schneider, C., J. Dover, and G. L. A. Fry. 2003. Movement of two grassland butterflies in the same habitat network: The role of adult resources and size of the study area. Ecological Entomology 28:219-227.

Shepherd, S. and D. M. Debinski. 2005. Evaluation of isolated and integrated prairie reconstructions as habitat for prairie butterflies. Biological Conservation 126:51-61.

Stasek, D. J., C. Bean, and T. O. Crist. 2008. Butterfly abundance and movements among prairie patches: the roles of habitat quality, edge, and forest matrix permeability. Environmental Entomology 37:897-906.

Stevens, V. M., C. Turlure, and M. Baguette. 2010. A meta-analysis of dispersal in butterflies. Biological Reviews 85:625-642.

Teaming with Wildlife. 2015. State Wildlife Action Plans: A strategic approach to conservation. <http://www.teaming.com/state-wildlife-action-plans-swaps>. Accessed 15 July 2016.

Thomas, J. A. 2005. Monitoring change in the abundance and distribution of insects using butterflies and other indicator groups. Philosophical Transactions of the Royal Society of Biological Sciences 360:339-357.

Thomas, J. A. and R. T. Clarke. 2004. Extinction rates and butterflies: response. Nature 305:1563-1564.

Van Der Linden, P. J. and D. R. Farrar. 2011. Forest and Shade Trees of Iowa. University of Iowa Press, Iowa City, Iowa, USA.

Van Swaay, C. A. M., A. Cuttelod, S. Collins, D. Maes, M. López Munguira, M. Šašic, J. Settele, R. Verovnik, T. Verstrael, M. Warren, M. Wiemers, and I. Wynhoff. 2010. European Red List of butterflies, IUCN Red List of Threatened Species - Regional Assessment - Office for Official Publications of the European Communities, Luxembourg. Van Swaay, C. A. Van Strien; A. Harpke; B. Fontaine; C. Stefanescu; D. Roy; E. Kühn; E. Õnuao; E. Regan and G. Švitra et al. 2013. *In* EEA Technical Reports 11/2013.

Van Swaay, C. A. M., A. Van Strien, K. Aghababyan, S. Astrom, M. Botham, T. Brereton, P. Chambers, S. Collins, M. Domenech Ferre, R. Escobes, R. Feldman, J. M. Fernandez-Garcia, B. Fontaine, S. Goloshchapova, A. Gracianteparaluceta, A. Harpke, J. Heliola, G. Khanamirian, R. Julliard, E. Kuhn, A. Lang, P. Leopold, J. Loos, D. Maes, X. Mestdagh, Y. Monasterio, M. L. Munguira, T. Murray, M. Musche, E. Ounap, L. Pettersson, S. Popoff, I. Prokofev, T. Roth, D. Roy, J. Settele, C. Stefanescu, G. Svitra, S. N. Teixeira, A. Tiitsaar, R. Verovnik, M. Warren. 2015. The European Butterfly Indicator for grassland species: 1990-2013. Wageningen, The Netherlands.

Wahlberg, N., T. Klemetti, and I. Hanski. 2002. Dynamic populations in a dynamic landscape: the metapopulation structure of the marsh fritillary butterfly. Ecography 25:224-232.

White, G. C. and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46 Supplement: 120-138.

Wikstrom, L., P. Milberg, and K. O. Bergman. 2009. Monitoring butterflies in semi-natural grasslands: diurnal variation and weather effects. Journal of Insect Conservation 13:203-211.

Xerces Society. 2008. Multi-species recovery plan for south Florida: Schaus swallowtail butterfly (*Herclides aristodemus ponceanus*). <http://www.xerces.org/wp-content/uploads/2008/09/schaus_swallowtail_recovery_plan_1999_revised.pdf>. Accessed 21 July 2016.

Zohrer, J. J. 2006. The Iowa Comprehensive Wildlife Action Plan. Iowa Department of Natural Resources, Des Moines, Iowa, USA.

Table 1. Model effects (95% confidence limits) from the best model to explain habitat associations of four butterfly species in Iowa, 2007-2015. For each species and parameter combination, the top cell lists the covariate effect and the bottom cell gives the beta estimate (95% confidence limits). Covariates modeled on site occupancy (Psi), colonization (Gamma), and extinction (Epsilon) are as follows: "Ag" represents agriculture, "Grass" represents grassland, "Wood" represents woodland, "100" represents the 100-m scale, "200" represents the 200-m spatial scale, "500" represents the 500-m spatial scale, "1K" represents the 1000-m spatial scale, "5K" represents the 5000-m spatial scale, "PLAND" represents percentage of the landscape, "ED" represents edge density, "Canopy" represents canopy cover, "Visual Obstruction" represents mean Robel reading, and "*Zanthoxylum*" represents *Zanthoxylum americanum*, a larval food plant of *Papilio cresphontes* in Iowa. Covariates modeled on detection probability (p) are the following: "Wind" represents wind speed (km/h), "Cloud" represents cloud cover (%), "Temp" represents temperature (°C), and "." represents a constant effect. Bold text indicates a significant effect (i.e., confidence interval did not include zero). Some parameters could not be estimated ("Not estimated").

| Species	Psi	Gamma	Epsilon	p
P. cresphontes	**Wood500PLAND**	*Zanthoxylum*	Wood1KPLAND	**Wind**
	0.076 (0.008, 0.143)	**Not estimated**	-0.142 (-0.303, 0.019)	**-0.143 (-0.266, -0.021)**
C. neglecta	Ag500PLAND	**Wood200ED**	Visual Obstruction	Cloud
	-0.291 (-0.769, 0.188)	**0.004 (0.002, 0.007)**	0.036 (-0.013, 0.084)	-0.004 (-0.010, 0.001)
L. archippus	Wood1KED	**Grass200ED**	Wood500PLAND	Temp
	0.023 (-0.022, 0.067)	**0.002 (0.000, 0.002)**	0.069 (-0.007, 0.145)	0.020 (-0.001, 0.042)
P. tharos	Wood200PLAND	**Grass200PLAND**	**Canopy**	**Wind**
	Not estimated	**0.032 (0.011, 0.053)**	**2.642 (0.969, 4.316)**	**-0.005 (-0.009, -0.001)**

Table 2. Model effects (95% confidence limits) taken from the best model (represented by ΔAICc) for each species-specific larval food-plant genera to explain its effect on population dynamics of four butterfly species in Iowa, 2007-2014. For each species and parameter combination, the top cell lists the ΔAICc value of the best model containing that host plant and the bottom cell gives the beta estimate (95% confidence limits). Species-specific larval food-plant genera (based on information from Schlicht 2007, Opler 2010, and observations made by the authors during surveys) are modeled as covariates on site occupancy (Psi), colonization (Gamma), and extinction (Epsilon). Some parameters could not be estimated ("Not estimated"). Excluded from this table is the genus *Ptelea*, which is a known food source for *P. cresphontes* larva in Iowa but was not found during our vegetation sampling.

Butterfly Species	Larval Food Plant(s)	Psi	Gamma	Epsilon
Papilio cresphontes	*Zanthoxylum*	1.524	0	8.132
		Not estimated	Not estimated	-4.646 (-17.50, 8.203)
Celastrina neglecta	*Ceanothus*	1.5261	23.2797	1.7119
		Not estimated	Not estimated	Not estimated
	Cornus	3.5517	26.346	2.6735
		-0.006 (-0.077, 0.064)	-0.671 (-1.215, -0.126)	-0.019 (-0.052, 0.014)
	Sambucus	2.5560	1337.2987	3.2326
		0.010 (-0.112, 0.132)	-0.624 (-1.142, -0.106)	0.077 (-0.335, 0.181)
	Verbesina	0.8744	26.2149	3.0333
		Not estimated	0.066 (-0.139, 0.270)	-0.122 (-0.506, 0.263)
	Viburnum	1.3869	23.096	2.0697
		Not estimated	Not estimated	Not estimated
Limenitis archippus	*Populus*	8.659	25.0555	25.0774
		Not estimated	Not estimated	Not estimated
	Salix	0.0776	7.5881	7.4699
		Not estimated	0.187 (0.046, 0.328)	Not estimated
Phyciodes tharos	*Aster*	7.934	18.7865	10.7371
		Not Estimated	1.230 (-2.179, 4.641)	0.546 (-1.383, 2.475)

Table 3. Parameter estimates (SE) from the best model to explain habitat associations of four butterfly species in Iowa, 2007-2015. Parameter estimates are for site occupancy (Psi) colonization (Gamma), extinction (Epsilon), and detection probability (p). "N/E" denotes parameter was not estimated.

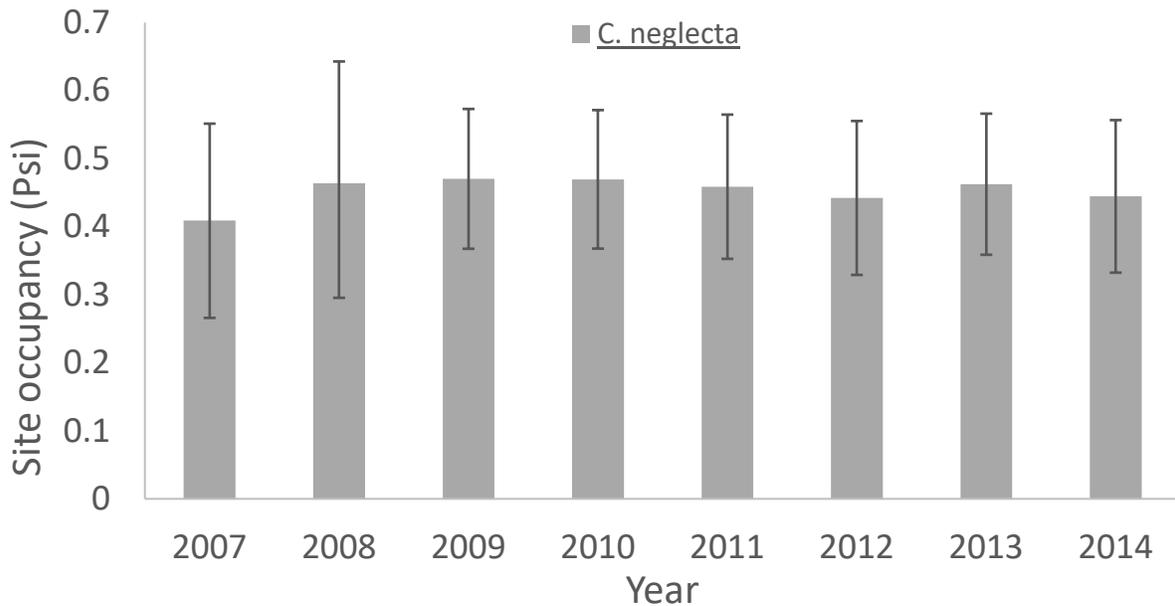| Species	Psi (SE)	Gamma (SE)	Epsilon (SE)	p (SE)
Papilio cresphontes	0.646 (0.149)	0.083 (0.042)	0.329 (0.125)	0.250 (0.038)
Celastrina neglecta	0.409 (0.072)	0.408 (0.073)	0.437 (0.082)	0.300 (0.030)
Limenitis archippus	0.286 (0.067)	0.240 (0.069)	0.141 (0.108)	0.303 (0.032)
Phyciodes tharos	0.730 (0.050)	0.409 (0.089)	0.270 (0.050)	0.461 (0.023)

(a)
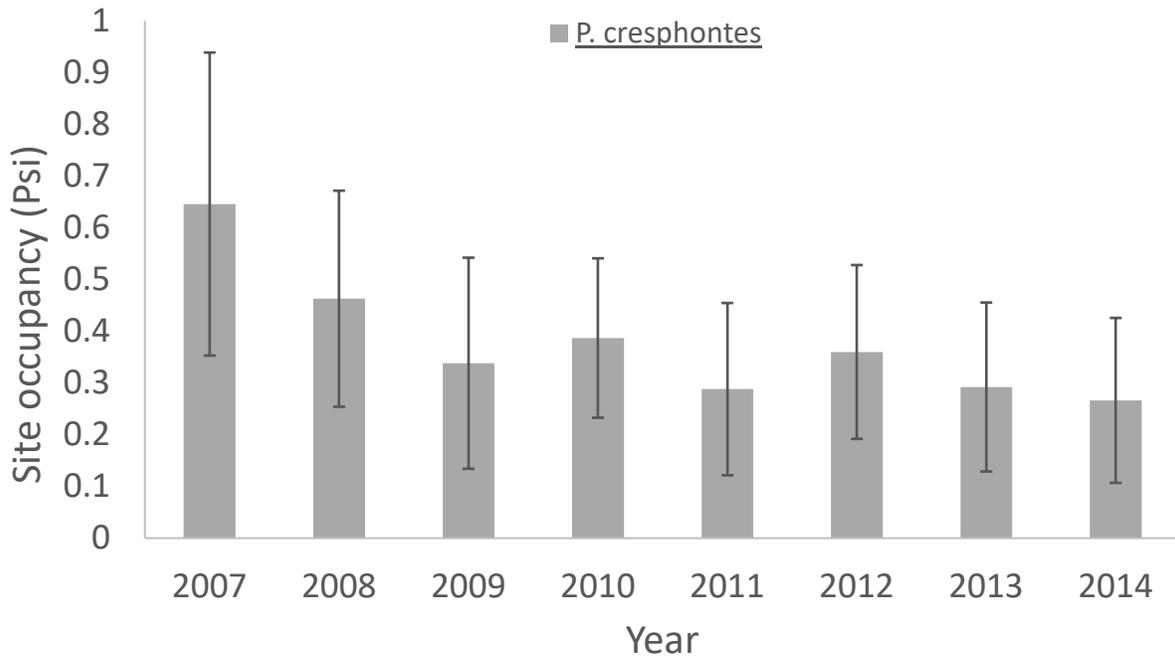
(b)

Figure 1. Parameter estimates (bars indicate 95% confidence limits) from the best model to explain habitat associations of four butterfly species in Iowa, 2007-2014. Parameter estimates are for derived site occupancy (Psi) for (a) *P. cresphontes*, (b) *C. neglecta*, (c) *L. archippus*, and (d) *P. tharos*.
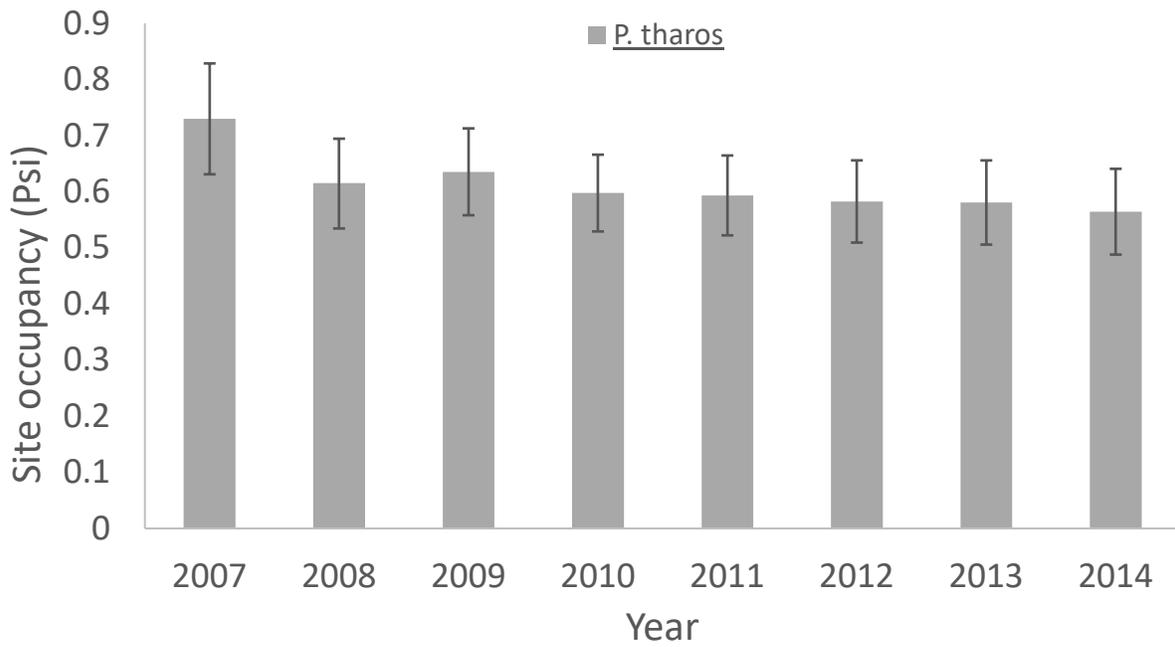
(c)
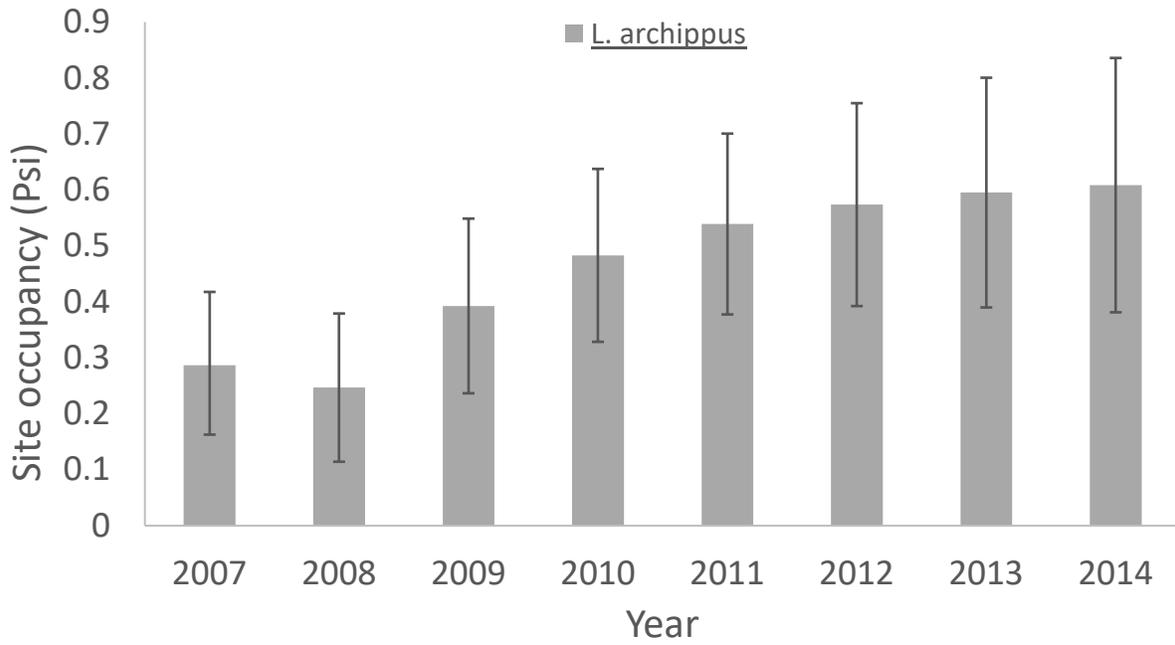
(d)

Figure 1 (continued).

CHAPTER 5. GENERAL CONCLUSIONS

This project's stated goals were to: 1) compare the efficacy of unlimited-distance line-transect surveys that incorporate distance sampling to traditional Pollard-Yates transects to estimate butterfly density; 2) evaluate habitat associations and landscape-level impacts on population dynamics of forest, savanna, and scrub-shrub birds in Iowa, while also incorporating estimates of detection probability; and 3) determine the effect of microhabitat and landscape-level variables on population dynamics of butterflies in Iowa, while also accounting for imperfect detection probability.

To meet the first goal, I implemented a direct comparison of Pollard-Yates transects and distance-sampling transects by conducting each survey type back-to-back on repeated visits at four grassland sites in central Iowa in 2014. I used Program DISTANCE to model detection probability (p) and estimate density (D) for eight butterfly species representing a range of life-history attributes. I found that detection probabilities were at or near 1.0 in the standard Pollard-Yates transect, but dropped considerably when the sampling area extended >2.5 m from the line transect. I also noted that detection probability was tied to morphology (i.e., wing size). Because of interspecific variation in detectability, I recommended incorporating distance sampling whenever possible, even when narrow transects are used. Line transects are straightforward in their implementation and can be used to repeatedly sample butterflies at multiple sites across a broad region in a short window of time. Distance sampling can be easily incorporated into the line-transect framework and analyzed using Program Distance, which provides density estimates and associated measures of precision. As such, distance sampling, especially when used in conjunction with other methods like mark-recapture, represents an effective tool to survey butterflies and guide the management and conservation of butterfly populations.

For the second goal, I used robust design occupancy models to examine the influence of habitat associations at differing spatial scales for forest, savanna, and scrub-shrub breeding birds in Iowa. As predicted, I demonstrated that the impact of agriculture (negative), as well as grassland and woodland (both largely positive), best defined site occupancy among our study species. I showed that the extent of woodland was the best predictor of forest-bird colonization at differing spatial scales - whereas colonization for savanna species was characterized by grassland components in the landscape. I also discovered, contrary to my predictions, that scrub-shrub birds had colonization positively impacted by agricultural landscape components. Conversely, I demonstrated that open habitats (grassland and agricultural) had the greatest effect on extinction probabilities of forest birds. Lastly, I confirmed that detection probability was most strongly influenced by wind speed for most study species. By offering insights into how landscape-level habitat factors and spatial scale impact colonization-extinction rates of declining species, especially Neotropical migrant songbirds, these results further emphasize the importance of conserving habitat on a large scale for these and similar birds in Iowa and many other regions.

For the study's third stated goal, I utilized robust design occupancy models to examine the influence of local and landscape effects at differing spatial scales for butterflies. Landscape covariates surfaced in the top model on occupancy for all four species and on colonization for three species. Microhabitat variables impacted colonization for one species (giant swallowtail) and extinction for two species (summer azure and pearl crescent). Woodland and grassland at differing spatial scales were each more prevalent than agriculture in the best models. Regarding detection probability, wind showed a strong negative impact for two species, while percent cloud cover (negative effect) and temperature (positive effect) moderately impacted one species each. I also noted that many patterns showed plausible connections to the known life-history

requirements of each species. As one of very few studies to model butterfly population dynamics across multiple seasons, I am confident that these results will provide new insights into local and landscape effects on butterflies. Our study might also provide a template for future work seeking to link butterfly occupancy patterns to the dynamics of colonization and extinction. Finally, I also explored two potential modifications regarding butterfly-research methodology: 1) timing butterfly surveys to more closely match presumed peak flight periods and 2) designing vegetation sampling in such a way to fully represent the area covered by species-specific larval host plants during established flight periods.

In aggregate, these findings contributed further insights into the variable impact of habitat characteristics and landscape-level metrics on birds and butterflies in Iowa, while also demonstrating how judicious use of study design and analytical tools can lead to a better representation of these impacts.