INCIDENCE, MECHANISMS, AND CONSEQUENCES OF ADAPTIVE HABITAT SELECTION BY THE DICKCISSEL (*SPIZA AMERICANA*)

BY

SCOTT BRENT NELSON

DISSERTATION

Submitted in partial fulfillment of the requirements
for the degree of Doctor of Philosophy in Natural Resources and Environmental Sciences
in the Graduate College of the
University of Illinois at Urbana-Champaign, 2019

Urbana, Illinois

Doctoral Committee:

Associate Professor Robert L. Schooley, Chair
Professor James R. Miller, Director of Research
Associate Professor Jennifer M. Fraterrigo
Research Associate Professor Thomas J. Benson

ABSTRACT

Most animals display preferences when faced with the choice of habitats in which to settle. A key question that arises from these behaviors is whether preferences represent adaptive habitat selection—do animals occupying preferred habitats incur fitness benefits? A prediction based on natural selection suggests that preferences should increase fitness, but this prediction is not always supported. Several factors may cause preference-fitness mismatches, including temporal variability of variables driving reproductive success, tradeoffs across spatial scales or among fitness components, and anthropogenic changes disrupting historic relationships between habitat preferences and habitat quality.

This dissertation presents three studies I conducted on the habitat preferences and reproductive success of dickcissels (*Spiza americana*) in the Grand River Grasslands of southern Iowa. I first tested for signals of adaptive habitat selection, examining whether male and female birds' preferences among territories and larger habitat patches improve their ability to attract mates, avoid parasitism by brown-headed cowbirds (*Molothrus ater*), and produce robust offspring. Dickcissels engaged in adaptive habitat selection in some respects—such as preferring territories associated with high offspring condition and patches where parasitism was infrequent—but there was strong variation across sexes, spatial scales, years, and reproductive components.

Next, I examined whether dickcissels used vegetation cues to select high-quality habitats. I measured multiple vegetation features in territories and patches and compared these to dickcissel habitat preferences and fitness metrics. Although dickcissels preferred specific vegetation features (again, with variation across sexes and scales), and specific vegetation features were associated with fitness (again, with variation across reproductive metrics), I found limited evidence that vegetation mediated adaptive habitat selection.

Finally, I further studied the impacts of vegetation on dickcissel reproduction by focusing on the relative impacts of human-altered habitat components (invasive plants and broad-scale land cover) on nest survival and parasitism. I found that an invasive grass common throughout the Midwest region (tall fescue, *Schedonorus arundinaceus*) reduced nest survival and increased parasitism, whereas increasing woodland cover in the landscape reduced parasitism.

In these studies, I illuminated proximate and ultimate forces shaping the reproductive ecology of dickcissels. I demonstrated that habitat preferences—and thus the spatiotemporal dynamics of population distributions—benefit specific components of reproductive success at particular spatial scales, while benefits to other reproductive metrics are variable across time. These results show that because fitness results from a wide variety of ecological processes, accurate assessments of adaptive habitat selection require a complex perspective. In addition, I have contributed to our knowledge of how vegetation influences dickcissel settlement patterns, while showing that preferred vegetation components have little influence on fitness. Other mechanisms (e.g., site fidelity, conspecific attraction, food availability, predator abundance) may thus play a stronger role in facilitating adaptive habitat selection. At the same time, I found strong evidence that vegetation altered by human activity shapes dickcissel habitat quality, and my results suggest that controlling invasive tall fescue may improve dickcissel nest success.

This dissertation is dedicated to my mother, Therese Nelson, without whom I wouldn’t be here – either on Earth or in graduate school.

ACKNOWLEDGEMENTS

Graduate school blends isolation with collaboration and friendship. Isolation is needed to finish what needs to be done through long nights of reading, analysis, and writing. The company of others provides the fuel for those fires. Although my words here will fail to fully express how much I owe to people for getting to this point, I hope they will still know how grateful I am.

I begin by acknowledging Dr. Jim Miller, my adviser. Thank you for taking me into your lab in the first place and providing the space and resources to conduct my research. Thank you for helping me become a better writer and fostering an expectation of scientific rigor in our lab group. That atmosphere set a tone of professionalism and a clear directive for excellence that will continue to serve me in good stead.

I also thank the rest of my committee for their guidance. Bob, many of the insights you gave me in Wildlife Population Ecology and private conversations helped lead me to my research topic and make important decisions afterward. Jen, I appreciate the advice you gave me in meetings and on my manuscripts, as well as the thoughts you inspired through your Landscape Ecology course. Moreover, I could not have completed my research without the skills I learned in your GIS class. T.J., thank you for spending so many hours of your time looking over my statistical results and talking with me about birds. Without your advice—and your patience and generosity when you would meet with me for two or three hours at a time!—I would have been so much more lost regarding both data analysis and avian ecology.

I also appreciate my collaborators on the Grand River Grasslands project from outside the University of Illinois. Diane Debinski, Dave Engle, and Walt Schacht, the efforts you made to secure funding for our research and devise the broad framework of the project were critical for allowing me to conduct my personal research projects. Moreover, the advice you gave me on my

methods and manuscripts certainly improved the quality of my work. Thanks very much as well to Shannon and Josh Rusk for keeping the cattle stocked on our pastures, in the right places and the right times, and for showing me a thing or two about how to properly apply prescribed fire on a grassland (thanks also to Ryan Harr in that regard!).

I also want to give a huge acknowledgement to Karen Claus, who has always been there to answer my questions and get me through the administrative hoops of my Ph.D. program. Karen, I have always appreciated your willingness to immediately take time out of your extremely busy schedule whenever I come to your door for help.

My lab mates have also been fundamental to my growth and success. At the beginning, Jason Fischer was always there to listen to my ideas with a smiling face and a critical eye. Christine Parker and Sarah Schneider shared the first years of my program with me and set me on the path to learning how to mist-net, band, and process birds, while Henry Pollock, Sean MacDonald, and Todd Jones pushed my skills farther along. Tim Lyons helped steer me towards my project, his honesty not allowing him to hold back if an idea I had was thin. And without Courtney Duchardt it would have been difficult to get a firm grasp on how to conduct fieldwork and lead a field crew. Courtney, I owe you a lot for the time you invested in training me in my first field season (summer 2013) and for working on my 2014 crew.

As a related digression, thank you to the field technicians who helped gather data for this thesis. Annie Meyer, Matt Kneitel, Omar Garza, Kristen Malone, Tracy Park, Ben Vizzachero, Amy West, and Iris Bradley—you were indispensable. Special mentions are deserved: thanks to Annie for teaching me how to identify birds when I was a total novice; thanks to Kristen for teaching me how to find nests through behavioral observations; and thanks to Omar and Tracy for volunteering at the end of the field season beyond what we could pay you for. In parallel, I also thank the undergraduates who helped enter my data. First, thank you to Devin Jen, who did incredible work and invested huge amounts of time in my territory-mapping and nest data. Thanks also to Iris Bradley, Roshan Kumar, Magda Gustyn, April Wendling, Yanzhu Chen, Rachel Daughtridge, Jenna Mattes, and Jenna Johnson for helping to prepare my data.

Returning to my lab mates—now from the mid-late period of my program—I want to thank Lauren Lynch, Samniqueka Halsey, Adam Kranz, and Maddy Kangas for comments on my work in lab meetings and on manuscripts. Timothy Swartz, thank you for your companionship in the lab and the 2016 field season, for your philosophical conversations, and for your guidance in framing papers and analyses. Jane Capozzelli, I appreciate the time you’ve invested in reading my papers, the Vitamin D pills that kept my bones strong, and the focus and levity you helped me maintain while we basically lived in the annex over many otherwise stressful weeks.

And I would be far off base not to give the biggest shout-out of all time to my lab mate and super-collaborator, Jaime Coon. You have done so much for me. You collected—and coordinated the collection of—insane amounts of data (featured in this dissertation, our side projects, and our manuscripts yet to be written). You motivated me to apply for grants and helped me succeed in doing so. You helped keep me on pace to complete my dissertation. And, of course, you have just been fun and insightful as a friend. All this makes for a debt that won’t be easily repaid. We’ll just have to keep writing papers together to make it worth it!

I also appreciate those who mentored me in my early career. Aaron Turkewitz, you changed my life when you took me into your lab in college. You and Lydia Bright (thank you too!) set me on my path, providing a model of excellent science and pushing my professional skills. Moreover, your warm friendship has been an enduring joy in my life.

To Jennifer Thaler as well, I am extremely grateful. The responsibilities you gave me right out of college as your lab manager and technician provided crucial learning opportunities that made me a better scientist and worker. Thank you for taking a chance on me and for your patience when I made mistakes. I could not have made it here without you.

Many people from outside of academia have also brought me to this milestone. First is my mother, Therese Nelson. Mom, you have been the greatest influence on my life. You worked for decades to ensure I received my education, and your love of nature profoundly nurtured my own. You stressed the importance of work and provided life contexts where I developed the values and morals that make me who I am. In graduate school, there have been many times when I may not have persevered without your advice. Thank you forever for being you.

I may never be certain whether my next expression of appreciation will reach him, but I hold at once a solemn yet vibrant gratitude for my father, Daniel Nelson, who passed away when I was seven years old. Dad, even though you had to leave so much earlier than anyone would have wished, the gifts you gave me are indelible. Your passion for education inspired a lifelong love of learning, and I am certain that my sense of humor comes in a large part from you. I know you would have wished to be here to read this thesis.

To my sister and brother, Caroline and Allen Nelson, you have been with me since the beginning of my life, sculpting me in unfathomable and wonderful ways. I owe so much of who I am to having navigated the world with you. Our friendships are priceless, and I will always appreciate that I can lean on you in difficult times.

To my stepdad, Bob Vassar, I deeply respect your work ethic, and the way your equanimity and foresight have strengthened our family. I will always appreciate how you nurtured my love of biology in high school and have offered me career guidance as a friend and academic.

To my grandparents and close extended family, thank you for all of your company and support throughout my life. Grandma and Grandpa Nelson, thank you for helping me get my education. Your contributions made an incredible difference. Uncle Brent (Nelson), I got more than my middle name from you; your calm poise has always been a genuine inspiration to me.

I am eternally grateful as well for the close friends I have made and kept. Mackey Craven, Sai Li, Dawei Tang, Corbett Walsh, Jordan Pelander, Aaron Avellone, Bryan Munroe, Vanessa Gussick, Suzi Claflin, and more; I would not be who or where I am without the support, joy, and depth you have given me throughout my life. Mackey—I believe the strength of our particular bond emanates from not only our joy in what we share, but also in our differences. Thank you for always challenging me to think in new ways. In the last almost 20 years you have helped me grow into a more circumspect, confident, and (I mean this with humility) intelligent person.

To those who will not know I wrote this, but whose presence in my life played an inexpressible role in my success, I am grateful for Calvin, Hobbes, and Izzy—my feline roommates. Calvin, in particular, you’ve been around for the entirety of my program and are perhaps the only being to sit with me in the most difficult moments. Nothing compares to your unconditional love.

Last, but exactly the opposite of least, I give thanks to my amazing wife, Christine. This goes two ways. I appreciate graduate school itself for having met you in the first place; we would not likely have crossed paths had I not been here. Turning that around though, I am beyond grateful for the love, care, time, conversation, and patience you have given me throughout my program. Your ethical convictions and adventurous spirit have helped me find greater moral clarity and derive new meaning and joy from life. My life got a whole lot better when you showed up, and being with you gave me much of the motivation I needed to make it through the last half of my Ph.D. You are the ultimate fuel that got me to the finish line. You are my pillar, indeed.

TABLE OF CONTENTS

FOREWORD

I begin this dissertation committing an infraction against a scientific writer, Dr. Joshua Schimel, whose advice I hold in high regard. Whereas Dr. Schimel recommends that papers begin with the broadest reasonable framing and then narrow down to the specifics of the study (Schimel, 2012), I have chosen to start with what some might call a side story. No doubt, my dissertation will focus on much of the work I have conducted during my own doctoral studies, but I would be remiss to not acknowledge the logistical and academic context from which my work was born.

In 2006, my advisor, Dr. James Miller, then a professor at Iowa State University, decided to test the promising concept of 'Patch-burn Grazing,' developed by Dr. Dave Engle and Dr. Sam Fuhlendorf at Oklahoma State University. Patch-burn grazing is a method for managing grasslands, wherein a pasture is split into multiple "patches" and one patch is burned each year on a rotating basis, such that the entire pasture is burned over a multi-year cycle (Fuhlendorf & Engle, 2001, 2004). Each year, a herd of grazers (e.g., cattle, bison) have access to the entire pasture and the animals are expected to spend most of their time grazing the recently burned patch, which is replete with nutritious herbage and few dead plant stalks (Allred et al., 2011). This method is meant to increase vegetation heterogeneity through concentrated grazing in the burned areas and less restrained growth in the unburned areas. In turn, this increased heterogeneity is predicted to increase wildlife diversity (e.g., Fuhlendorf et al., 2010). While this method had been effective in the large rangelands of the Great Plains, Dr. Miller sought to test whether it would work in the highly fragmented grasslands in the central Midwest.

Working with Dr. Engle and Dr. Diane Debinksi at Iowa State University, with practitioners Josh Rusk, Shannon Rusk, and Ryan Harr, and years later with Dr. Walter Schacht at the University of Nebraska-Lincoln, Dr. Miller established a long-term research project in the Grand

River Grasslands of southern Iowa and northern Missouri. This is a working landscape, a 62,000-ha region where the predominant land use is for cattle grazing (Morton et al., 2010; Miller et al., 2012). But the Nature Conservancy has also identified this region as the best-known opportunity to restore a functional prairie system in the Tallgrass Prairie Ecoregion (TNC, 2008), due to its large area remaining in native and non-native grasses and its high percentage of protected area (managed by the Nature Conservancy, the Iowa Department of Natural Resources, and the Missouri Department of Conservation).

Before I joined the group in the fall of 2012 and set about asking my own questions in the Grand River Grasslands, this collaboration—the Conservation in Working Lands Research Group—had produced multiple manuscripts on the impacts of patch-burn grazing on multiple wildlife taxa (e.g., Debinski et al., 2011; Pillsbury et al., 2011; Hovick et al., 2012; Moranz et al., 2012); on the effects of a common invasive grass, tall fescue (*Schedonorus arundinaceus*), on plant diversity and fire in the region (e.g., McGranahan et al., 2012a; McGranahan et al., 2012b); and on the perspectives of private landowners on grassland management (Morton et al., 2010). As I have conducted my graduate studies, the knowledge produced on the ecology and social dynamics of the Grand River Grasslands has only expanded (e.g., Moranz et al., 2013; Harr et al., 2014; Lyons et al., 2015; Delaney et al., 2016; Duchardt et al., 2016; Jokela et al., 2016; Scasta et al., 2016; Coon et al., 2018a; Coon et al., 2018b; Swartz, 2018; Maresh Nelson et al., 2019).

My dissertation research grew from the efforts of this group. Among the wildlife communities they have monitored over the last 13 years, grassland birds are a guild of critical conservation concern across the U.S. since many species have experienced sharp declines over the past 50 years (Vickery & Herkert, 1999; Brennan & Kuvlesky, 2005). Prior to my work, data on grassland birds from the project were primarily comprised of community surveys (Pillsbury et al., 2011; Duchardt et al., 2016) and focal studies on the nesting ecology of grasshopper sparrows (*Ammodramus savannarum*; Hovick et al., 2011; Hovick et al., 2012; Hovick & Miller, 2013; Lyons et al., 2015). However, when I began, few had explored the mechanisms by which birds in the Grand River Grasslands select breeding habitat, or whether their settlement decisions improve reproductive success (but see Duchardt, 2014). Also, although project data have shown that invasive grasses like tall fescue negatively impact nesting grasshopper sparrows (Hovick et al., 2012; Lyons et al., 2015), it was unclear whether these impacts are felt by more species.

It was with these primary knowledge gaps in mind that I began designing my research. Following my tendency toward detail, I chose to focus on a single species—a plucky bird known as the dickcissel (*Spiza americana*)—and set about attempting to quantify multiple aspects of their habitat preferences, reproductive outcomes, and the relationships between these two dimensions, while investigating how tall fescue influences this ecology. Along the way, I have collaborated with another Ph.D. student, Jaime Coon, which allowed us to expand the project even further. Most of the fruits of that work will be told in future papers. In this dissertation, I will focus on my original, animating questions, and the work and conclusions that sprang from them.

LITERATURE CITED

Allred, B. W., Fuhlendorf, S. D., Engle, D. M., & Elmore, R. D. (2011). Ungulate preference for burned patches reveals strength of fire-grazing interaction. *Ecology and Evolution*, **1**, 132-144. 10.1002/ece3.12

Brennan, L. A., & Kuvlesky, W. P. (2005). North American grassland birds: an unfolding conservation crisis? *Journal of Wildlife Management*, **69**, 1-13. 10.2193/0022-541x(2005)069<0001:nagbau>2.0.co;2

Coon, J. J., Morton, L. W., & Miller, J. R. 2018a. A survey of landowners in the Grand River Grasslands: Managing wildlife, cattle, and non-native plants. Report 2018-03, University of Illinois at Urbana-Champaign Department of Natural Resources and Environmental Sciences, Urbana, IL.

Coon, J. J., Nelson, S. B., West, A. C., Bradley, I. A., & Miller, J. R. (2018b). An observation of parental infanticide in dickcissels (*Spiza americana*): video evidence and potential mechanisms. *Wilson Journal of Ornithology*, **130**, 341-345. 10.1676/1559-4491-130.1.341

Debinski, D. M., Moranz, R. A., Delaney, J. T., Miller, J. R., Engle, D. M., Winkler, L. B., . . . Gillespie, M. K. (2011). A cross-taxonomic comparison of insect responses to grassland management and land-use legacies. *Ecosphere*, **2**, art131-art131.

Delaney, J. T., Moranz, R. A., Debinski, D. M., Engle, D. M., & Miller, J. R. (2016). Exotic-dominated grasslands show signs of recovery with cattle grazing and fire. *Plos One*, **11**, 10.1371/journal.pone.0165758

Duchardt, C. J. 2014. Habitat selection and breeding ecology of grassland birds in areas managed with fire and grazing. University of Illinois at Urbana-Champaign, University of Illinois at Urbana-Champaign.

Duchardt, C. J., Miller, J. R., Debinski, D. M., & Engle, D. M. (2016). Adapting the fire-grazing interaction to small pastures in a fragmented landscape for grassland bird conservation. *Rangeland Ecology & Management*, **69**, 300-309. 10.1016/j.rama.2016.03.005

Fuhlendorf, S. D., & Engle, D. M. (2001). Restoring heterogeneity on rangelands: ecosystem management based on evolutionary grazing patterns. *Bioscience*, **51**, 625-632. 10.1641/0006-3568(2001)051[0625:rhorem]2.0.co;2

Fuhlendorf, S. D., & Engle, D. M. (2004). Application of the fire-grazing interaction to restore a shifting mosaic on tallgrass prairie. *Journal of Applied Ecology*, **41**, 604-614. 10.1111/j.0021-8901.2004.00937.x

Fuhlendorf, S. D., Townsend, D. E., Elmore, R. D., & Engle, D. M. (2010). Pyric-herbivory to promote rangeland heterogeneity: evidence from small mammal communities. *Rangeland Ecology & Management*, **63**, 670-678. 10.2111/rem-d-10-00044.1

Harr, R. N., Morton, L. W., Rusk, S. R., Engle, D. M., Miller, J. R., & Debinski, D. (2014). Landowners' perceptions of risk in grassland management: woody plant encroachment and prescribed fire. *Ecology and Society*, **19**, 13. 10.5751/es-06404-190241

Hovick, T. J., & Miller, J. R. (2013). Broad-scale heterogeneity influences nest selection by brown-headed cowbirds. *Landscape Ecology*, **28**, 1493-1503. 10.1007/s10980-013-9896-7

Hovick, T. J., Miller, J. R., Dinsmore, S. J., Engle, D. M., Debinski, D. M., & Fuhlendorf, S. D. (2012). Effects of fire and grazing on grasshopper sparrow nest survival. *Journal of Wildlife Management*, **76**, 19-27. 10.1002/jwmg.243

Hovick, T. J., Miller, J. R., Koford, R. R., Engle, D. M., & Debinski, D. M. (2011). Postfledging survival of grasshopper sparrows in grasslands managed with fire and grazing. *Condor*, **113**, 429-437. 10.1525/cond.2011.100135

Jokela, K. J., Debinski, D. M., & Mcculley, R. L. (2016). Effects of tall fescue and its fungal endophyte on the development and survival of tawny-edged skippers (Lepidoptera: Hesperiidae). *Environmental Entomology*, **pii**, 1-10.

Lyons, T. P., Miller, J. R., Debinski, D. M., & Engle, D. M. (2015). Predator identity influences the effect of habitat management on nest predation. *Ecological Applications*, **25**, 1596-1605. 10.1890/14-1641.1

Maresh Nelson, S. B., Coon, J. J., Schacht, W. H., Miller, J. R. 2019. Cattle select against the invasive grass tall fescue in heterogeneous pastures managed with prescribed fire. *Grass and Forage Science*, **74**, in press. doi: 10.1111/gfs.12411.

McGranahan, D. A., Engle, D. M., Fuhlendorf, S. D., Miller, J. R., & Debinski, D. M. (2012a). An invasive cool-season grass complicates prescribed fire management in a native warm-season grassland. *Natural Areas Journal*, **32**, 208-214.

McGranahan, D. A., Engle, D. M., Wilsey, B. J., Fuhlendorf, S. D., Miller, J. R., & Debinski, D. M. (2012b). Grazing and an invasive grass confound spatial pattern of exotic and native grassland plant species richness. *Basic and Applied Ecology*, **13**, 654-662. 10.1016/j.baae.2012.09.011

Miller, J. R., Morton, L. W., Engle, D. M., Debinski, D. M., & Harr, R. N. (2012). Nature reserves as catalysts for landscape change. *Frontiers in Ecology and the Environment*, **10**, 144-152. 10.1890/100227

Moranz, R. A., Debinski, D. M., McGranahan, D. A., Engle, D. M., & Miller, J. R. (2012). Untangling the effects of fire, grazing, and land-use legacies on grassland butterfly communities. *Biodiversity and Conservation*, **21**, 2719-2746. 10.1007/s10531-012-0330-2

Moranz, R. A., Debinski, D. M., Winkler, L., Trager, J., McGranahan, D. A., Engle, D. M., & Miller, J. R. (2013). Effects of grassland management practices on ant functional groups in central North America. *Journal of Insect Conservation*, **17**, 699-713. 10.1007/s10841-013-9554-z

Morton, L. W., Regen, E., Engle, D. M., Miller, J. R., & Harr, R. N. (2010). Perceptions of landowners concerning conservation, grazing, fire, and eastern redcedar management in tallgrass prairie. *Rangeland Ecology & Management*, **63**, 645-654. 10.2111/rem-d-09-00041.1

Pillsbury, F. C., Miller, J. R., Debinski, D. M., & Engle, D. M. (2011). Another tool in the toolbox? Using fire and grazing to promote bird diversity in highly fragmented landscapes. *Ecosphere*, **2**, 10.1890/es10-00154.1

Scasta, J. D., Duchardt, C., Engle, D. M., Miller, J. R., Debinski, D. M., & Harr, R. N. (2016). Constraints to restoring fire and grazing ecological processes to optimize grassland vegetation structural diversity. *Ecological Engineering*, **95**, 865-875. 10.1016/j.ecoleng.2016.06.096

Schimel, J. 2012. Writing science: how to write papers that get cited and proposals that get funded. Oxford University Press, Oxford.

Swartz, T. M. 2018. Farm ponds of the eastern Great Plains: key challenges and opportunities for conserving amphibians in these novel ecosystems. University of Illinois at Urbana-Champaign, University of Illinois at Urbana-Champaign.

TNC (The Nature Conservancy). 2008. Grand River Grasslands conservation action plan. The Nature Conservancy, St. Louis, MO.

Vickery, P. D., & Herkert, J. R. (1999). Ecology and conservation of grassland birds of the Western Hemisphere. Proceedings of a conference, Tulsa, Oklahoma, October 1995. *Studies in Avian Biology*, **19**, i-viii, 1-299.

CHAPTER 1 – GENERAL INTRODUCTION

ADAPTIVE HABITAT SELECTION

Habitat selection has myriad ramifications for animal fitness. Alternative habitats vary markedly in resource availability (McLoughlin et al., 2007; Mosser et al., 2009; Nocera et al., 2009; Rauset et al., 2015), attractiveness to mates (Zimmerman, 1966; Hasselquist, 1998; Valcu & Kempenaers, 2008), and predation risk (Martin, 1995; Ishihara & Ohgushi, 2008; Klug et al., 2010; Rotem et al., 2013). Thus, an animal's choice of where to make its living can have profound effects on its ability to survive and reproduce. Given the fundamental importance of habitat selection, an intuitive prediction is that natural selection should engrain behaviors that maximize animals' abilities to recognize and settle in high-quality areas, leaving poor-quality habitats to only the least competitive or least fit (Jaenike & Holt, 1991; Clark & Shutler, 1999). Such behaviors have been referred to as adaptive habitat selection (Chalfoun & Schmidt, 2012).

Two classic theoretical models of habitat selection, the Ideal Free Distribution and Ideal Despotic Distribution (Fretwell & Lucas, 1969), are predicated upon an assumption of adaptive habitat selection. They predict that animals will preferentially colonize habitat patches in which they realize the greatest fitness, and only colonize lower-quality patches when density-dependent effects (under the Ideal Free Distribution) or competitive exclusion (under the Ideal Despotic Distribution) reduce the relative value of intrinsically high-quality sites.

These predictions and other tests of adaptive habitat selection have been supported in many empirical studies across multiple animal taxa (e.g., Weidinger, 2000; Chalfoun & Martin, 2007; Flaxman & deRoos, 2007; McLoughlin et al., 2007; Mosser et al., 2009; Perot & Villard, 2009; Quinlan & Green, 2012; Hache et al., 2013; Germain et al., 2015; Uboni et al., 2017). For example, holly leaf-miners (*Phytomyza ilicis*) demonstrate adaptive habitat selection, conforming to the Ideal Free Distribution as they oviposit eggs on holly bushes (Valladares & Lawton, 1991). Female leaf-miners oviposit on some individual holly bushes at far higher rates than on other bushes, but ultimately, all larvae achieve equal growth and survival rates due to density-dependent competition and parasitoid attack risk. In another example, male Bell's vireos (*Vireo bellii*) returning from migration to breed in Missouri express their territory-scale preferences by the order in which they occupy territories (earlier-settled territories being more highly preferred than later-settled territories; Joos et al., 2014). These birds exhibit adaptive habitat selection by conforming to the Ideal Despotic Distribution; males defending preferred territories produce more offspring than those in less preferred territories, indicating the preferred territories are also of higher quality. This effect is not just a product of high-quality birds occupying those territories or of favorable environmental conditions prevailing early in the breeding season (Joos et al., 2014). Similar examples have been demonstrated in other territorial birds (Aebischer et al., 1996; Hasselquist, 1998; Choi et al., 2010; Cooper et al., 2011; McKellar et al., 2013).

Evidence for adaptive habitat selection, however, is not universal. Multiple studies have failed to identify any relationships between habitat preferences and improved fitness (Davis, 2005; Jensen & Cully, 2005; Renfrew et al., 2005; Rahmig et al., 2009), and a large number have even identified apparent mismatches between habitat preferences and habitat quality (Remeš, 2003; Arlt & Pärt, 2007; Robertson & Hutto, 2007; Hawlena et al., 2010; Hollander et al., 2011; Rotem et al., 2013; Yoon & Read, 2016). For example, in southeast British Columbia, grizzly bears preferentially occupy urbanized valleys with high food availability, but bears in these valleys subsequently experience high mortality rates relative to surrounding areas (Lamb et al., 2017). The population has declined as a result. In another example, great tits (*Parus major*) in Estonia prefer to nest in patches of deciduous woodland versus coniferous woodland, but birds breeding in coniferous woods ultimately produce more young in better body condition while facing fewer energetic demands to provision their young (Mand et al., 2005; Magi et al., 2009).

The apparent lack of adaptive habitat selection in so many cases raises the question of why natural selection has not always produced this behavior (Chalfoun & Schmidt, 2012). One of the most commonly invoked explanations (for maladaptive preferences, in particular) is the phenomenon of the ecological trap. In these cases, habitat features historically associated with advantageous areas—and thus preferred by animals due to natural selection—become associated with poor-quality habitat due to anthropogenic changes (Kokko & Sutherland, 2001; Schlaepfer et al., 2002). The British Columbian grizzly bears mentioned earlier exemplify this phenomenon; their attraction to a high-quality resource (berries) in an urban habitat increases their mortality (Lamb et al., 2017). In other cases, ecological traps emerge when anthropogenic activity creates poor-quality habitats that mimic the structure of historically high-quality habitats (e.g., Robertson & Hutto, 2007; Hawlena et al., 2010; Hollander et al., 2011).

Unpredictable and temporally variable ecological conditions offer another potential explanation. For example, some authors studying songbird nest ecology have suggested that it might be difficult for birds to develop consistent habitat-selection strategies for enhancing nest survival because nest predators are ubiquitous or highly diverse (Filliater et al., 1994; Clark & Shutler, 1999; Renfrew et al., 2005). Different predator species forage in alternative microhabitats, limiting the availability of safe nesting sites (Phillips et al., 2004; Benson et al., 2010b; Cox et al., 2012; Ellison et al., 2013; Chiavacci et al., 2018).

Although each of these mechanisms may be responsible for limiting adaptive habitat selection in some cases, failure to detect this behavior may instead sometimes result from methodological shortcomings. For instance, while evaluations of lifetime fitness are often impossible in studies of highly mobile or long-lived animals (but see McLoughlin et al., 2007; Tarwater et al., 2018), many studies go to an opposite extreme and base their assessments of adaptive habitat selection on a single metric of fitness (e.g., Clark & Shutler, 1999; Misenhelter & Rotenberry, 2000; Remeš, 2003; Davis, 2005; Frei et al., 2013). This hinders investigators' abilities to draw firm conclusions because fitness is a product of a wide variety of processes. Consider an example of the common trade-off animals make between foraging effort and survival. Pied cormorants (*Phalacrocorax varius*) have low abundances in warm, shallow waters, even though fish abundances there are high (Heithaus, 2005). A study examining only food availability versus cormorant habitat selection would incorrectly conclude this pattern indicates maladaptive habitat selection. It is only upon determining that those shallow, food-rich habitats are often teeming with tiger sharks (*Galeocerdo cuvier*) that the adaptive behavior becomes clear. Examples of trade-offs among different fitness components exist across multiple animal taxa (Pitt, 1999; Pilastro et al., 2002; Cresswell, 2008; Inger et al., 2010; Utz et al., 2016).

Another common methodological issue may arise when habitat preferences are only measured at a single spatial scale (e.g., Lloyd & Martin, 2005; Robertson & Hutto, 2007; Hollander et al., 2011; Uboni et al., 2017). Measuring preferences across multiple scales enables us to better understand the scales at which animals discriminate among their environments (Orians & Wittenberger, 1991) and the scales most clearly linked to different components of fitness. For example, Brewer's sparrows (*Spizella breweri*) in Montana produce offspring in superior body condition in preferred landscapes, but there is no relationship between offspring condition and preferences at the territory or nest-site scales (Chalfoun & Martin, 2007). Similarly, nest survival is greater in preferred nest sites and territories, but bears no relationship to broader-scale preferences (Chalfoun & Martin, 2007). Failure to have measured multiple fitness components and habitat preferences at multiple scales may have produced the incorrect conclusion that Brewer's sparrow habitat preferences do not improve their reproductive success.

Unfortunately, such detailed approaches are often avoided for simpler, yet potentially less revelatory, investigations. Without broad views of habitat preferences and fitness, it is difficult to make confident conclusions of the nature and extent of adaptive habitat selection.

MECHANISMS OF ADAPTIVE HABITAT SELECTION BY BIRDS

Investigating avian habitat selection and reproductive outcomes can improve our understanding of whether birds make advantageous settlement decisions, as well as of the cues they use to make these decisions. Several mechanisms have been demonstrated in different avian species.

Birds often use personal experience to select high-quality areas. In fact, the fact of having previously occupied a site often increases the site's quality to individual birds (Piper, 2011). For instance, prior residents may hold competitive advantages in territorial disputes with conspecifics (Krebs, 1982; Bruinzeel & van de Pol, 2004) or have detailed knowledge of local resources (e.g., high-quality nest sites and feeding areas) that improve their fitness (Pasinelli et al., 2007).

Site fidelity may particularly enable adaptive habitat selection if birds return more frequently to areas where they have been previously successful (Beletsky & Orians, 1987; Bollinger & Gavin, 1989; Serrano et al., 2001; Hoover, 2003)—a phenomenon known as the "win-stay, lose-switch" rule (Switzer, 1997; Chalfoun & Martin, 2010). Birds may also use "public information" on conspecific breeding success to identify high-quality sites (Danchin et al., 2004; Kelly & Ward, 2017). For example, male and female bobolinks (*Dolichonyx oryzivorus*) are less likely to disperse from a territory after nest failure if neighboring conspecifics were successful (Bollinger & Gavin, 1989). Similarly, a long-term study of collared flycatchers (*Ficedula al-*

bicollis) has shown that flycatcher immigration into patches increases and emigration decreases when total patch fledgling production is high (Doligez et al., 1999; Doligez et al., 2002). Furthermore, adult collared flycatchers seek public information during the breeding season, prospecting at active nests and settling in subsequent years near sites where parents displayed high feeding rates and vigilance (Doligez et al., 2004).

In addition to using personal and public information to judge habitat quality, birds may directly assess relevant habitat characteristics—such as vegetation (Hildén, 1965; Cody, 1981; Jones, 2001), food availability (Orians & Wittenberger, 1991; Germain et al., 2015; English et al., 2017), or predator and brood parasite abundance (Eggers et al., 2006; Forsman & Martin, 2009; Forsman et al., 2013). Habitat selection in response to vegetation characteristics has received a particularly large amount of research attention.

Birds frequently express habitat preferences based on vegetation structure and composition at multiple spatial scales (Orians & Wittenberger, 1991; Chalfoun & Martin, 2007). At the broadest scales, these influences are seen when migratory species choose to settle in specific ecosystem types (e.g. forests, shrublands, grasslands). Birds then discriminate among available habitats at finer scales within these ecosystems. For instance, species occurrence and abundance among habitat patches in landscapes often vary as a function of landscape context around patches (Drapeau et al., 2000; Davis et al., 2013; Shahan et al., 2017), patch size (Helzer & Jelinski, 1999; Johnson & Igl, 2001), and edge proximity (Jensen & Finck, 2004; Weldon & Haddad, 2005). At still finer scales, birds often discriminate among territories and nest sites of differing plant community composition and vegetation density or height (Zimmerman, 1971; Rotenberry & Wiens, 1980; Hoover & Brittingham, 1998; Misenhelter & Rotenberry, 2000; Harrison &

Green, 2010; Jacobs et al., 2012; Lemaitre et al., 2012; Quinlan & Green, 2012; Fogarty et al., 2017; Jedlikowski & Brambilla, 2017).

Because birds use vegetation features as habitat selection cues, a critical question is whether preferred features accurately depict habitat quality. This would suggest vegetation acts as a mechanism of adaptive habitat selection. Vegetation cues should approximate habitat quality when specific features are reliably correlated with reproductive success. For instance, as male yellow warblers (*Setophaga petechia*) arrive to breed in riparian habitats in British Columbia, they first establish territories in patches with high tree and shrub cover, high shrub diversity, and low total canopy cover before occupying other riparian patches (Quinlan & Green, 2012). Subsequently, male yellow warblers breeding in territories with those characteristics produce more fledglings than other males.

Birds can also increase reproductive success by selecting specific vegetation at nest sites. For instance, in the Mono Lake Basin, CA, female yellow warblers only select nest sites above 75 cm high that are 30-80% concealed (Latif et al., 2012). Within this range of microhabitats, nesting success does not vary, but experimental evidence shows that nests placed outside of these conditions are depredated more frequently. Thus, these yellow warblers consistently select nest microhabitats to minimize predation (Latif et al., 2012). In another example, tree foliage density in West Virginian forests is positively related to caterpillar abundance (Marshall & Cooper, 2004)—a variable commonly associated with high nestling provisioning rates and high nestling quality (Naef-Daenzer & Keller, 1999). In these forests, male red-eyed vireos (*Vireo olivaceus*) adjust the sizes of their territories in accordance with foliage density, presumably modulating their territory defense effort based on the availability of adequate resources with which to provision their nestlings (Marshall & Cooper, 2004). These examples show that vegetation may provide reliable signals of habitat quality and birds respond to these signals during habitat selection.

Even so, many studies have found that vegetation preferences do not improve reproductive success. Illustrating this fact, a review of songbird nest-site selection found that across 94 published instances of birds preferring particular nest-site vegetation features, 72% of the time, those features had no relation to nest success and in 7% of cases, they were in fact associated with reduced nest survival (Chalfoun & Schmidt, 2012).

Several causes may underlie such inconsistencies. In some cases, the plants that provide nest cover or food supplies for birds are still dormant when birds are selecting breeding sites, and so cannot provide information on site quality (Hahn & Silverman, 2006; Arlt & Pärt, 2007). Other explanations mirror those previously discussed. For example, preferred vegetation may have become deleterious due to recent anthropogenic changes (ecological traps; e.g., Lloyd & Martin, 2005; Robertson & Hutto, 2007; Hollander et al., 2011), or diverse nest predator communities could limit the ability of vegetation-based preferences to provide protection. Although predation rates by specific predators may be mediated by vegetation at nest-site, patch, or landscape scales, overall predation rates are often independent of vegetation (Renfrew et al., 2005; Benson et al., 2010b; Ellison et al., 2013; Lyons et al., 2015).

Despite these potential limits to vegetation-based adaptive habitat selection, it is still important to measure multiple components of fitness at multiple scales to make conclusions about the use of vegetation cues. The previous example of Brewer’s sparrows illustrates this need (Chalfoun & Martin, 2007). Brewer’s sparrows prefer landscapes with tall shrubs. This variable is correlated with nestling condition, but not with nest survival. Similarly, these sparrows prefer high shrub density in nest patches and territories. This feature improves nest survival but has no effect on nestling condition. It is only because habitat preferences and vegetation were measured at multiple scales—in conjunction with multiple fitness components—that this complex story came to light.

A similar approach is needed to rigorously discern whether other species engage in adaptive habitat selection through use of vegetation cues, or whether they rely more on other mechanisms (e.g., public information, personal experience, food abundance, predator abundance). This complex approach would also provide detailed evaluations of the impacts of habitat composition and structure on wildlife—a valuable applied contribution when working in ecosystems where generating knowledge for conservation is a key priority.

ANTHROPOGENIC EFFECTS ON GRASSLAND BIRDS

A clear example of such an ecosystem is the tallgrass prairie ecoregion of the central U.S. This system has undergone a near-total transformation in land use and land cover in the last century, with severe consequences for grassland wildlife. Primarily, tallgrass prairies have been plowed and converted to row-crop agriculture (corn and soybeans); less than 4% of tallgrass prairie has never been plowed (Samson & Knopf, 1994). Although some grassland has been restored for livestock farming and by the Conservation Reserve Program, conversion to agriculture is ongoing in some places, and subject to commodity prices (Wright & Wimberly, 2013).

On top of this extreme habitat loss, many remaining grasslands face more gradual degradation. For example, many grassland patches are experiencing woody encroachment due to overgrazing and infrequent use of prescribed fire (Briggs et al., 2005; Harr et al., 2014). Ultimately, this has the potential to replace grasslands and their native biota with shrublands (Coppedge et al., 2001; Engle et al., 2008). Also consequential, grassland restorations are often seeded with non-native, cool-season grasses rather than with native grasses and forbs (Flanders et al., 2006; Fisher & Davis, 2011). Introduced grasses may act as invasive species and encroach on native-dominated grasslands (McGranahan et al., 2012; Ellis-Felege et al., 2013).

These changes have strongly impacted grassland-dependent wildlife. In particular, more than half of all grassland bird species in North America have undergone range-wide population declines in the last 50 years (Peterjohn & Sauer, 1999; Sauer et al., 2017). These losses are due in large part to agricultural conversion (Warner, 1994; Murphy, 2003), but anthropogenic changes on and near remaining grasslands have also had negative effects. For example, many grassland bird species have minimum patch-size requirements, below which they may not occupy a grassland patch (Helzer & Jelinski, 1999; Johnson & Igl, 2001; Ribic et al., 2009). More generally, patterns of occupancy and abundance of grassland birds are frequently shaped by landscape context, including effects of nearby row-crop fields, woodlands, grasslands, and habitat edges (Cunningham & Johnson, 2006; Veech, 2006; Jacobs et al., 2012; Shahan et al., 2017). Within grassland patches, avian abundances are often lower in areas of increasing woody cover and invasive grass encroachment (Giuliano & Daves, 2002; Grant et al., 2004; Flanders et al., 2006; Hickman et al., 2006; Osborne et al., 2012; Osborne & Sparling, 2013), although these patterns are not universal (Nelson et al., 2017).

Another mechanism contributing to grassland bird declines is poor nest survival and fledgling production during the breeding season (Fletcher et al., 2006). Each of these parameters may be additionally reduced by brood parasitism by brown-headed cowbirds (*Molothrus ater*; Sealy, 1992; Hannon et al., 2009; Benson et al., 2010a; Hovick & Miller, 2013). While multiple studies have assessed how human-altered landscape context (Herkert et al. 2003; Ribic et al. 2012; Hovick and Miller 2013) and plant invasions (Lloyd & Martin 2005; Grant et al. 2006;

Nelson et al. 2017) have independently influenced nest survival and parasitism, little work has directly compared the relative effects of these factors. Moreover, our knowledge of the scales at which land-use change most impacts nest ecology is limited (Chiavacci et al. 2018). These uncertainties complicate grassland bird conservation since the extent to which managers should prioritize actions such as invasive grass removal, shrub removal, cowbird control, grassland expansion, and restoration of nearby row-crop fields is unclear. Research to clarify these priorities would aid managers seeking to improve conditions for grassland birds.

STRUCTURE OF THE DISSERTATION

I have introduced the prediction that animals should engage in adaptive habitat selection and highlighted hypotheses for why animals might not prefer high-quality habitats. I have also emphasized the value of measuring habitat preferences at multiple spatial scales and comparing these to multiple metrics of reproductive success. Chapter 2 of this dissertation describes my work to conduct this type of research in the Grand River Grasslands of Ringgold County, Iowa. Studying the dickcissel (*Spiza americana*; Fig 1.1), a species that breeds in central U.S. grasslands, I quantified the habitat preferences of male and female birds among territories and the larger patches in which they were embedded. I then assessed whether birds in preferred territories and patches enjoyed relatively high reproductive success based on four fitness metrics (mate attraction, avoidance of brood parasitism, fledgling production, and offspring body condition).

But understanding whether birds engage in adaptive habitat selection does not provide information on how this occurs. I have reviewed here multiple mechanisms by which birds might discern habitat quality, placing a particular emphasis on the potential use of vegetation cues. In Chapter 3 of this dissertation, I describe my work to evaluate whether male and female dickcissels use vegetation cues to engage in adaptive habitat selection. Using the same measurements as in Chapter 2, but also incorporating a slate of measurements of vegetation composition and structure (taken within territories and patches), I assessed which vegetation features were preferred at each scale and then tested whether preferred features mediated fitness metrics. This study also illuminated ways that dickcissels respond to and are affected by their grassland habitats.

I expanded on the latter element in my final study. In the third section of this chapter, I highlighted many ways in which anthropogenic changes (e.g., land-use change, invasive plants) have affected grassland birds, and suggested the importance of understanding the relative impacts of human-driven changes on the nest ecology of grassland birds. In Chapter 4, I describe my work to do this. I estimated nest survival and brood parasitism rates on dickcissel nests from 2013-2016, then used multi-model comparisons to determine the relative impacts on these outcomes of variables such as woody encroachment, row-crop cover, and the prevalence of the common invasive grass tall fescue (*Schedonorus arundinacea*).

THE DICKCISSEL

ECOLOGY

The dickcissel (Fig 1.1) is a Neotropical migratory passerine breeding primarily in grasslands of the central United States. Although their range is broad, its core is largely comprised of substantial portions of Kansas, Nebraska, Iowa, Missouri, and Oklahoma (Fig 1.2). This core includes the Grand River Grasslands, where I conducted my research. Dickcissels overwinter primarily in northern Venezuela, although some flocks stay in Central America and other parts of northern South America (Fig 1.2).

Dickcissels are considered obligate grassland birds (Vickery et al. 1999), but they occupy a broad range of grassland types. They frequently inhabit both grazed and ungrazed grasslands dominated by cool-season grasses, warm-season grasses, forbs, or legumes (Zimmerman 1971; Harmeson 1974; Finck 1984; Winter et al. 2000; Temple 2002; Dechant et al. 2003; Ramig et al. 2009). In some cases, they even occupy small-grain crop fields (Walk et al. 2010).

Territorial males defend exclusive breeding territories against conspecifics with frequent song displays (Schartz & Zimmerman 1971; Schook et al. 2008). Competition among males for mates is particularly fierce because dickcissels are facultatively polygynous, with multiple females often pairing with individual males while other males remain unmated (Zimmerman 1966; Fretwell & Lucas 1969; Harmeson 1974; Finck 1984).

The dickcissel's facultative polygyny makes it an especially attractive species in which to study adaptive habitat selection. Females apparently have free choice among males, so the number of females paired with individual males presents a metric by which to estimate female preference among territories. Moreover, polygyny levels indicate male success in attracting mates, which corresponds to success in producing fledglings (Sousa & Westneat 2013). Thus, polygyny also offers a useful metric of male fitness.

CONSERVATION

Like many grassland bird species, dickcissel populations have sharply declined in the last half-century (Vickery & Herkert 1999; Brennan & Kuvlesky 2005; Sauer et al. 2017). Although the global population stabilized by the 1980s, data from the North American Breeding Bird Survey show that the dickcissel experienced an average annual population loss of 5.5% between 1966 and 1979 (Peterjohn & Sauer 1999). Even today, dickcissel population recoveries are heterogeneous across their breeding range, with increases in some areas offset by continued declines in other places (Fig 1.3).

Dickcissel declines have been attributed in part to mortality on the winter range (Basili & Temple 1999). Although territorial during summer, dickcissels often form winter flocks of over one million birds that forage and roost in rice fields, where they can cause substantial crop destruction. Many farmers in Latin America thus view dickcissels as agricultural pests, and some have implemented poisoning programs to reduce their numbers (Basili & Temple 1999).

These stresses are layered over the fact that dickcissels' primary grassland habitats have been converted to agriculture at extremely high rates (Vickery & Herkert 1999), while remaining grasslands are threatened by further conversion (Wright & Wimberly 2013), woody encroachment (Harr et al. 2014), and other invasive plants (Flanders et al. 2006; McGranahan et al. 2012; Ellis-Feledge et al. 2013). As a result, dickcissels and other grassland birds are considered species of conservation concern across many parts of their ranges (Rosenberg et al. 2016), including in Iowa, where I conducted my research (Zohrer et al. 2005).

LITERATURE CITED

Aebischer, A., Perrin, N., Krieg, M., Studer, J., & Meyer, D. R. (1996). The role of territory choice, mate choice and arrival date on breeding success in the Savi's warbler *Locustella luscinioides*. *Journal of Avian Biology*, **27**, 143-152. 10.2307/3677143

Arlt, D., & Pärt, T. (2007). Nonideal breeding habitat selection: a mismatch between preference and fitness. *Ecology*, **88**, 792-801. 10.1890/06-0574

Beletsky, L. D., & Orians, G. H. (1987). Territoriality among male red-winged blackbirds .1. Site fidelity and movement patterns. *Behavioral Ecology and Sociobiology*, **20**, 21-34. 10.1007/bf00292163

Benson, T. J., Anich, N. M., Brown, J. D., & Bednarz, J. C. (2010a). Habitat and landscape effects on brood parasitism, nest survival, and fledgling production in Swainson's warblers. *Journal of Wildlife Management*, **74**, 81-93. 10.2193/2008-442

Benson, T. J., Brown, J. D., & Bednarz, J. C. (2010b). Identifying predators clarifies predictors of nest success in a temperate passerine. *Journal of Animal Ecology*, **79**, 225-234. 10.1111/j.1365-2656.2009.01604.x

Bollinger, E. K., & Gavin, T. A. (1989). The effects of site quality on breeding-site fidelity in bobolinks. *Auk*, **106**, 584-594.

Briggs, J. M., Knapp, A. K., Blair, J. M., Heisler, J. L., Hoch, G. A., Lett, M. S., & McCarron, J. K. (2005). An ecosystem in transition - causes and consequences of the conversion of mesic grassland to shrubland. *Bioscience*, **55**, 243-254. 10.1641/0006-3568(2005)055[0243:aeitca]2.0.co;2

Bruinzeel, L. W., & van de Pol, M. (2004). Site attachment of floaters predicts success in territory acquisition. *Behavioral Ecology*, **15**, 290-296. 10.1093/beheco/arh019

Chalfoun, A. D., & Martin, T. E. (2007). Assessments of habitat preferences and quality depend on spatial scale and metrics of fitness. *Journal of Applied Ecology*, **44**, 983-992. 10.1111/j.1365-2664.2007.01352.x

Chalfoun, A. D., & Martin, T. E. (2010). Facultative nest patch shifts in response to nest predation risk in the Brewer's sparrow: a "win-stay, lose-switch" strategy? *Oecologia*, **163**, 885-892. 10.1007/s00442-010-1679-0

Chalfoun, A. D., & Schmidt, K. A. (2012). Adaptive breeding-habitat selection: is it for the birds? *Auk*, **129**, 589-599. 10.1525/auk.2012.129.4.589

Chiavacci, S. J., Benson, T. J., & Ward, M. P. (2018). Linking landscape composition to predator-specific nest predation requires examining multiple landscape scales. *Journal of Applied Ecology*, **55**, 2082-2092. 10.1111/1365-2664.13090

Choi, Y. S., Lee, Y. K., & Yoo, J. C. (2010). Relationships of settlement date and body size with reproductive success in male Oriental great reed warbler *Acrocephalus orientalis*. *Zoological Studies*, **49**, 398-404.

Clark, R. G., & Shutler, D. (1999). Avian habitat selection: pattern from process in nest-site use by ducks? *Ecology*, **80**, 272-287. 10.1890/0012-9658(1999)080[0272:ahspfp]2.0.co;2

Cody, M. L. (1981). Habitat selection in birds - the roles of vegetation structure, competitors, and productivity. *Bioscience*, **31**, 107-113. 10.2307/1308252

Cooper, N. W., Murphy, M. T., Redmond, L. J., & Dolan, A. C. (2011). Reproductive correlates of spring arrival date in the eastern kingbird *Tyrannus tyrannus*. *Journal of Ornithology*, **152**, 143-152. 10.1007/s10336-010-0559-z

Coppedge, B. R., Engle, D. M., Masters, R. E., & Gregory, M. S. (2001). Avian response to landscape change in fragmented southern Great Plains grasslands. *Ecological Applications*, **11**, 47-59. 10.2307/3061054

Cox, W. A., Thompson, F. R., & Faaborg, J. (2012). Landscape forest cover and edge effects on songbird nest predation vary by nest predator. *Landscape Ecology*, **27**, 659-669. 10.1007/s10980-012-9711-x

Cresswell, W. (2008). Non-lethal effects of predation in birds. *Ibis*, **150**, 3-17. 10.1111/j.1474-919X.2007.00793.x

Cunningham, M. A., & Johnson, D. H. (2006). Proximate and landscape factors influence grassland bird distributions. *Ecological Applications*, **16**, 1062-1075. 10.1890/1051-0761(2006)016[1062:palfig]2.0.co;2

Danchin, E., Giraldeau, L. A., Valone, T. J., & Wagner, R. H. (2004). Public information: from nosy neighbors to cultural evolution. *Science*, **305**, 487-491. 10.1126/science.1098254

Davis, S. K. (2005). Nest-site selection patterns and the influence of vegetation on nest survival of mixed-grass prairie passerines. *Condor*, **107**, 605-616. 10.1650/0010-5422(2005)107[0605:nspati]2.0.co;2

Davis, S. K., Fisher, R. J., Skinner, S. L., Shaffer, T. L., & Brigham, R. M. (2013). Songbird abundance in native and planted grassland varies with type and amount of grassland in the surrounding landscape. *Journal of Wildlife Management*, **77**, 908-919. 10.1002/jwmg.537

Doligez, B., Danchin, E., & Clobert, J. (2002). Public information and breeding habitat selection in a wild bird population. *Science*, **297**, 1168-1170. 10.1126/science.1072838

Doligez, B., Danchin, E., Clobert, J., & Gustafsson, L. (1999). The use of conspecific reproductive success for breeding habitat selection in a non-colonial, hole-nesting species, the collared flycatcher. *Journal of Animal Ecology*, **68**, 1193-1206. 10.1046/j.1365-2656.1999.00362.x

Doligez, B., Part, T., & Danchin, E. (2004). Prospecting in the collared flycatcher: gathering public information for future breeding habitat selection? *Animal Behaviour*, **67**, 457-466. 10.1016/j.anbehav.2003.03.010

Drapeau, P., Leduc, A., Giroux, J. F., Savard, J. P. L., Bergeron, Y., & Vickery, W. L. (2000). Landscape-scale disturbances and changes in bird communities of boreal mixed-wood forests. *Ecological Monographs*, **70**, 423-444. 10.1890/0012-9615(2000)070[0423:lsdaci]2.0.co;2

Eggers, S., Griesser, M., Nystrand, M., & Ekman, J. (2006). Predation risk induces changes in nest-site selection and clutch size in the Siberian jay. *Proceedings of the Royal Society B-Biological Sciences*, **273**, 701-706. 10.1098/rspb.2005.3373

Ellis-Felege, S. N., Dixon, C. S., & Wilson, S. D. (2013). Impacts and management of invasive cool-season grasses in the Northern Great Plains: challenges and opportunities for wildlife. *Wildlife Society Bulletin*, **37**, 510-516. 10.1002/wsb.321

Ellison, K. S., Ribic, C. A., Sample, D. W., Fawcett, M. J., & Dadisman, J. D. (2013). Impacts of tree rows on grassland birds and potential nest predators: a removal experiment. *Plos One*, **8**, e59151-e59151. 10.1371/journal.pone.0059151

Engle, D. M., Coppedge, B. R., & Fuhlendorf, S. D. 2008. From the Dust Bowl to the Green Glacier: human activity and environmental change in Great Plains grasslands. Pages 253-271 *in* O. W. Van Auken, editor. Western North American Juniperus Communities. Springer, New York, NY, USA.

English, P. A., Nocera, J. J., Pond, B. A., & Green, D. J. (2017). Habitat and food supply across multiple spatial scales influence the distribution and abundance of a nocturnal aerial insectivore. *Landscape Ecology*, **32**, 343-359. 10.1007/s10980-016-0454-y

Filliater, T. S., Breitwisch, R., & Nealen, P. M. (1994). Predation on northern cardinal nests: does choice of nest site matter? *Condor*, **96**, 761-768. 10.2307/1369479

Fisher, R. J., & Davis, S. K. (2011). Habitat use by Sprague's pipits (*Anthus spragueii*) in native pastures and planted, non-native hay fields. *Auk*, **128**, 273-282. 10.1525/auk.2011.10148

Flanders, A. A., Kuvlesky, W. P., Ruthven, D. C., Zaiglin, R. E., Bingham, R. L., Fulbright, T. E., . . . Brennan, L. A. (2006). Effects of invasive exotic grasses on South Texas rangeland breeding birds. *Auk*, **123**, 171-182. 10.1642/0004-8038(2006)123[0171:eoiego]2.0.co;2

Flaxman, S. M., & deRoos, C. A. (2007). Different modes of resource variation provide a critical test of ideal free distribution models. *Behavioral Ecology and Sociobiology*, **61**, 877-886. 10.1007/s00265-006-0316-8

Fletcher, R. J. Jr., Koford, R. R., & Seaman, D. A. (2006). Critical demographic parameters for declining songbirds breeding in restored grasslands. *Journal of Wildlife Management*, **70**, 145-157. 10.2193/0022-541x(2006)70[145:cdpfds]2.0.co;2

Fogarty, D. T., Elmore, R. D., Fuhlendorf, S. D., & Loss, S. R. (2017). Influence of olfactory and visual cover on nest site selection and nest success for grassland-nesting birds. *Ecology and Evolution*, **7**, 6247-6258. 10.1002/ece3.3195

Forsman, J. T., & Martin, T. E. (2009). Habitat selection for parasite-free space by hosts of parasitic cowbirds. *Oikos*, **118**, 464-470. 10.1111/j.1600-0706.2008.17000.x

Forsman, J. T., Monkkonen, M., Korpimaki, E., & Thomson, R. L. (2013). Mammalian nest predator feces as a cue in avian habitat selection decisions. *Behavioral Ecology*, **24**, 262-266. 10.1093/beheco/ars162

Frei, B., Fyles, J. W., & Nocera, J. J. (2013). Maladaptive habitat use of a North American woodpecker in population decline. *Ethology*, **119**, 377-388. 10.1111/eth.12074

Fretwell, S. D., & Lucas, H. L. J. (1969). On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheoretica*, **19**, 16-36.

Germain, R. R., Schuster, R., Delmore, K. E., & Arcese, P. (2015). Habitat preference facilitates successful early breeding in an open-cup nesting songbird. *Functional Ecology*, **29**, 1522-1532. 10.1111/1365-2435.12461

Giuliano, W. M., & Daves, S. E. (2002). Avian response to warm-season grass use in pasture and hayfield management. *Biological Conservation*, **106**, 1-9. 10.1016/s0006-3207(01)00126-4

Grant, T. A., Madden, E., & Berkey, G. B. (2004). Tree and shrub invasion in northern mixed-grass prairie: implications for breeding grassland birds. *Wildlife Society Bulletin*, **32**, 807-818. 10.2193/0091-7648(2004)032[0807:tasiin]2.0.co;2

Hache, S., Villard, M.-A., & Bayne, E. M. (2013). Experimental evidence for an ideal free distribution in a breeding population of a territorial songbird. *Ecology*, **94**, 861-869. 10.1890/12-1025.1

Hahn, B. A., & Silverman, E. D. (2006). Social cues facilitate habitat selection: American redstarts establish breeding territories in response to song. *Biology Letters*, **2**, 337-340. 10.1098/rsbl.2006.0472

Hannon, S. J., Wilson, S., & McCallum, C. A. (2009). Does cowbird parasitism increase predation risk to American redstart nests? *Oikos*, **118**, 1035-1043. 10.1111/j.1600-0706.2008.17383.x

Harr, R. N., Morton, L. W., Rusk, S. R., Engle, D. M., Miller, J. R., & Debinski, D. (2014). Landowners' perceptions of risk in grassland management: woody plant encroachment and prescribed fire. *Ecology and Society*, **19**, 13. 10.5751/es-06404-190241

Harrison, M. L., & Green, D. J. (2010). Vegetation influences patch occupancy but not settlement and dispersal decisions in a declining migratory songbird. *Canadian Journal of Zoology*, **88**, 148-160. 10.1139/z09-125

Hasselquist, D. (1998). Polygyny in great reed warblers: a long-term study of factors contributing to male fitness. *Ecology*, **79**, 2376-2390. 10.2307/176829

Hawlena, D., Saltz, D., Abramsky, Z., & Bouskila, A. (2010). Ecological trap for desert lizards caused by anthropogenic changes in habitat structure that favor predator activity. *Conservation Biology*, **24**, 803-809. 10.1111/j.1523-1739.2010.01477.x

Heithaus, M. R. (2005). Habitat use and group size of pied cormorants (*Phalacrocorax varius*) in a seagrass ecosystem: possible effects of food abundance and predation risk. *Marine Biology*, **147**, 27-35. 10.1007/s00227-004-1534-0

Helzer, C. J., & Jelinski, D. E. (1999). The relative importance of patch area and perimeter-area ratio to grassland breeding birds. *Ecological Applications*, **9**, 1448-1458.

Hickman, K. R., Farley, G. H., Channell, R., & Steier, J. E. (2006). Effects of old world bluestem (*Bothriochloa ischaemum*) on food availability and avian community composition within the mixed-grass prairie. *Southwestern Naturalist*, **51**, 524-530. 10.1894/0038-4909(2006)51[524:eoowbb]2.0.co;2

Hildén, O. (1965). Habitat selection in birds: a review. *Annales Zoologici Fennici*, **2**, 53-75.

Hollander, F. A., Van Dyck, H., Martin, G. S., & Titeux, N. (2011). Maladaptive habitat selection of a migratory passerine bird in a human-modified landscape. *Plos One*, **6**, 10.1371/journal.pone.0025703

Hoover, J. P. (2003). Decision rules for site fidelity in a migratory bird, the prothonotary warbler. *Ecology*, **84**, 416-430. 10.1890/0012-9658(2003)084[0416:drfsfi]2.0.co;2

Hoover, J. P., & Brittingham, M. C. (1998). Nest-site selection and nesting success of wood thrushes. *Wilson Bulletin*, **110**, 375-383.

Hovick, T. J., & Miller, J. R. (2013). Broad-scale heterogeneity influences nest selection by brown-headed cowbirds. *Landscape Ecology*, **28**, 1493-1503. 10.1007/s10980-013-9896-7

Inger, R., Harrison, X. A., Ruxton, G. D., Newton, J., Colhoun, K., Gudmundsson, G. A., . . . Bearhop, S. (2010). Carry-over effects reveal reproductive costs in a long-distance migrant. *Journal of Animal Ecology*, **79**, 974-982. 10.1111/j.1365-2656.2010.01712.x

Ishihara, M., & Ohgushi, T. (2008). Enemy-free space? Host preference and larval performance of a willow leaf beetle. *Population Ecology*, **50**, 35-43. 10.1007/s10144-007-0066-0

Jacobs, R. B., Thompson, F. R., Koford, R. R., La Sorte, F. A., Woodward, H. D., & Fitzgerald, J. A. (2012). Habitat and landscape effects on abundance of Missouri's grassland birds. *Journal of Wildlife Management*, **76**, 372-381. 10.1002/jwmg.264

Jaenike, J., & Holt, R. D. (1991). Genetic-variation for habitat preference - evidence and explanations. *American Naturalist*, **137**, S67-S90. 10.1086/285140

Jedlikowski, J., & Brambilla, M. (2017). The adaptive value of habitat preferences from a multi-scale spatial perspective: insights from marsh-nesting avian species. *Peerj*, **5**, 10.7717/peerj.3164

Jensen, W. E., & Cully, J. F. (2005). Density-dependent habitat selection by brown-headed cowbirds (*Molothrus ater*) in tallgrass prairie. *Oecologia*, **142**, 136-149. 10.1007/s00442-004-1709-x

Jensen, W. E., & Finck, E. J. (2004). Edge effects on nesting dickcissels (*Spiza americana*) in relation to edge type of remnant tallgrass prairie in Kansas. *American Midland Naturalist*, **151**, 192-199. 10.1674/0003-0031(2004)151[0192:eeonds]2.0.co;2

Johnson, D. H., & Igl, L. D. (2001). Area requirements of grassland birds: a regional perspective. *Auk*, **118**, 24-34. 10.1642/0004-8038(2001)118[0024:arogba]2.0.co;2

Jones, J. (2001). Habitat selection studies in avian ecology: a critical review. *Auk*, **118**, 557-562. 10.1642/0004-8038(2001)118[0557:hssiae]2.0.co;2

Joos, C. J., Thompson, F. R., III, & Faaborg, J. (2014). The role of territory settlement, individual quality, and nesting initiation on productivity of Bell's vireos *Vireo bellii bellii*. *Journal of Avian Biology*, **45**, 584-590. 10.1111/jav.00400

Kelly, J. K., & Ward, M. P. (2017). Do songbirds attend to song categories when selecting breeding habitat? A case study with a wood warbler. *Behaviour*, **154**, 1123-1144. 10.1163/1568539x-00003461

Klug, P. E., Jackrel, S. L., & With, K. A. (2010). Linking snake habitat use to nest predation risk in grassland birds: the dangers of shrub cover. *Oecologia*, **162**, 803-813. 10.1007/s00442-009-1549-9

Kokko, H., & Sutherland, W. J. (2001). Ecological traps in changing environments: ecological and evolutionary consequences of a behaviourally mediated Allee effect. *Evolutionary Ecology Research*, **3**, 537-551.

Krebs, J. R. (1982). Territorial defence in the great tit (*Parus major*): do residents always win? *Behavioral Ecology and Sociobiology*, **11**, 185-194. 10.1007/bf00300061

Lamb, C. T., Mowat, G., McLellan, B. N., Nielsen, S. E., & Boutin, S. (2017). Forbidden fruit: human settlement and abundant fruit create an ecological trap for an apex omnivore. *Journal of Animal Ecology*, **86**, 55-65. 10.1111/1365-2656.12589

Latif, Q. S., Heath, S. K., & Rotenberry, J. T. (2012). How avian nest site selection responds to predation risk: testing an adaptive peak hypothesis. *Journal of Animal Ecology*, **81**, 127-138. 10.1111/j.1365-2656.2011.01895.x

Lemaitre, J., Darveau, M., Zhao, Q., & Fortin, D. (2012). Multiscale assessment of the influence of habitat structure and composition on bird assemblages in boreal forest. *Biodiversity and Conservation*, **21**, 3355-3368. 10.1007/s10531-012-0366-3

Lloyd, J. D., & Martin, T. E. (2005). Reproductive success of chestnut-collared longspurs in native and exotic grassland. *Condor*, **107**, 363-374. 10.1650/7701

Lyons, T. P., Miller, J. R., Debinski, D. M., & Engle, D. M. (2015). Predator identity influences the effect of habitat management on nest predation. *Ecological Applications*, **25**, 1596-1605. 10.1890/14-1641.1

Magi, M., Mand, R., Tamm, H., Sisask, E., Kilgas, P., & Tilgar, V. (2009). Low reproductive success of great tits in the preferred habitat: a role of food availability. *Ecoscience*, **16**, 145-157. 10.2980/16-2-3215

Mand, R., Tilgar, V., Lohmus, A., & Leivits, A. (2005). Providing nest boxes for hole-nesting birds - does habitat matter? *Biodiversity and Conservation*, **14**, 1823-1840. 10.1007/s10531-004-1039-7

Marshall, M. R., & Cooper, R. J. (2004). Territory size of a migratory songbird in response to caterpillar density and foliage structure. *Ecology*, **85**, 432-445. 10.1890/02-0548

Martin, T. E. (1995). Avian life history evolution in relation to nest sites, nest predation, and food. *Ecological Monographs*, **65**, 101-127. 10.2307/2937160

McGranahan, D. A., Engle, D. M., Wilsey, B. J., Fuhlendorf, S. D., Miller, J. R., & Debinski, D. M. (2012). Grazing and an invasive grass confound spatial pattern of exotic and native grassland plant species richness. *Basic and Applied Ecology*, **13**, 654-662. 10.1016/j.baae.2012.09.011

McKellar, A. E., Marra, P. P., & Ratcliffe, L. M. (2013). Starting over: experimental effects of breeding delay on reproductive success in early-arriving male American redstarts. *Journal of Avian Biology*, **44**, 495-503. doi:10.1111/j.1600-048X.2013.00180.x

McLoughlin, P. D., Gaillard, J. M., Boyce, M. S., Bonenfant, C., Messier, F., Duncan, P., . . . Klein, F. (2007). Lifetime reproductive success and composition of the home range in a large herbivore. *Ecology*, **88**, 3192-3201. 10.1890/06-1974.1

Misenhelter, M. D., & Rotenberry, J. T. (2000). Choices and consequences of habitat occupancy and nest site selection in sage sparrows. *Ecology*, **81**, 2892-2901. 10.1890/0012-9658(2000)081[2892:cacoho]2.0.co;2

Mosser, A., Fryxell, J. M., Eberly, L., & Packer, C. (2009). Serengeti real estate: density vs. fitness-based indicators of lion habitat quality. *Ecology Letters*, **12**, 1050-1060. 10.1111/j.1461-0248.2009.01359.x

Murphy, M. T. (2003). Avian population trends within the evolving agricultural landscape of eastern and central United States. *Auk*, **120**, 20-34. 10.1642/0004-8038(2003)120[0020:aptwte]2.0.co;2

Naef-Daenzer, B., & Keller, L. F. (1999). The foraging performance of great and blue tits (*Parus major* and *P. caerulens*) in relation to caterpillar development, and its consequences for nestling growth and fledging weight. *Journal of Animal Ecology*, **68**, 708-718. 10.1046/j.1365-2656.1999.00318.x

Nelson, S. B., Coon, J. J., Duchardt, C. J., Fischer, J. D., Halsey, S. J., Kranz, A. J., . . . Miller, J. R. (2017). Patterns and mechanisms of invasive plant impacts on North American birds: a systematic review. *Biological Invasions*, 1-17. 10.1007/s10530-017-1377-5

Nocera, J. J., Forbes, G. J., & Giraldeau, L.-A. (2009). Aggregations from using inadvertent social information: a form of ideal habitat selection. *Ecography*, **32**, 143-152. 10.1111/j.1600-0587.2008.05614.x

Orians, G. H., & Wittenberger, J. F. (1991). Spatial and temporal scales in habitat selection. *American Naturalist*, **137**, 29-49.

Osborne, D. C., & Sparling, D. W. (2013). Multi-scale associations of grassland birds in response to cost-share management of conservation reserve program fields in Illinois. *Journal of Wildlife Management*, **77**, 920-930. 10.1002/jwmg.553

Osborne, D. C., Sparling, D. W., & Hopkins, R. L., II. (2012). Influence of conservation reserve program mid-contract management and landscape composition on northern bobwhite in tall fescue monocultures. *Journal of Wildlife Management*, **76**, 566-574. 10.1002/jwmg.258

Pasinelli, G., Mueller, M., Schaub, M., & Jenni, L. (2007). Possible causes and consequences of philopatry and breeding dispersal in red-backed shrikes *Lanius collurio*. *Behavioral Ecology and Sociobiology*, **61**, 1061-1074. 10.1007/s00265-006-0339-1

Perot, A., & Villard, M.-A. (2009). Putting density back into the habitat-quality equation: case study of an open-nesting forest bird. *Conservation Biology*, **23**, 1550-1557. 10.1111/j.1523-1739.2009.01272.x

Peterjohn, B. G., & Sauer, J. R. (1999). Population status of North American grassland birds from the North American Breeding Bird Survey, 1966-1996. *Studies in Avian Biology*, **19**, 27-44.

Phillips, M. L., Clark, W. R., Nusser, S. M., Sovada, M. A., & Greenwood, R. J. (2004). Analysis of predator movement in prairie landscapes with contrasting grassland composition. *Journal of Mammalogy*, **85**, 187-195. 10.1644/1545-1542(2004)085<0187:aopmip>2.0.co;2

Pilastro, A., Griggio, M., Biddau, L., & Mingozzi, T. (2002). Extrapair paternity as a cost of polygyny in the rock sparrow: behavioural and genetic evidence of the ‘trade-off’ hypothesis. *Animal Behaviour*, **63**, 967-974. http://dx.doi.org/10.1006/anbe.2002.1987

Piper, W. H. (2011). Making habitat selection more "familiar": a review. *Behavioral Ecology and Sociobiology*, **65**, 1329-1351. 10.1007/s00265-011-1195-1

Pitt, W. C. (1999). Effects of multiple vertebrate predators on grasshopper habitat selection: trade-offs due to predation risk, foraging, and thermoregulation. *Evolutionary Ecology*, **13**, 499-515. 10.1023/a:1006792726166

Quinlan, S. P., & Green, D. J. (2012). Riparian habitat disturbed by reservoir management does not function as an ecological trap for the yellow warbler (*Setophaga petechia*). *Canadian Journal of Zoology*, **90**, 320-328. 10.1139/z11-138

Rahmig, C. J., Jensen, W. E., & With, K. A. (2009). Grassland bird responses to land management in the largest remaining tallgrass prairie. *Conservation Biology*, **23**, 420-432. 10.1111/j.1523-1739.2008.01118.x

Rauset, G. R., Low, M., & Persson, J. (2015). Reproductive patterns result from age-related sensitivity to resources and reproductive costs in a mammalian carnivore. *Ecology,* **96**, 3153-3164. 10.1890/15-0262.1

Remeš, V. (2003). Effects of exotic habitat on nesting success, territory density, and settlement patterns in the blackcap (*Sylvia atricapilla*). *Conservation Biology*, **17**, 1127-1133. 10.1046/j.1523-1739.2003.01611.x

Renfrew, R. B., Ribic, C. A., & Nack, J. L. (2005). Edge avoidance by nesting grassland birds: a futile strategy in a fragmented landscape. *Auk,* **122**, 618-636. 10.1642/0004-8038(2005)122[0618:eabngb]2.0.co;2

Ribic, C. A., Koford, R. R., Herkert, J. R., Johnson, D. H., Niemuth, N. D., Naugle, D. E., . . . Renfrew, R. B. (2009). Area sensitivity in North American grassland birds: patterns and processes. *Auk,* **126**, 233-244. 10.1525/auk.2009.1409

Robertson, B. A., & Hutto, R. L. (2007). Is selectively harvested forest an ecological trap for olive-sided flycatchers? *Condor,* **109**, 109-121. 10.1650/0010-5422(2007)109[109:ishfae]2.0.co;2

Rotem, G., Ziv, Y., Giladi, I., & Bouskila, A. (2013). Wheat fields as an ecological trap for reptiles in a semiarid agroecosystem. *Biological Conservation*, **167**, 349-353. 10.1016/j.biocon.2013.08.028

Rotenberry, J. T., & Wiens, J. A. (1980). Habitat structure, patchiness, and avian communities in North American steppe vegetation - a multivariate analysis. *Ecology*, **61**, 1228-1250. 10.2307/1936840

Samson, F., & Knopf, F. (1994). Prairie conservation in North America. *Bioscience*, **44**, 418-421. 10.2307/1312365

Sauer, J. R., Niven, D. K., Hines, J. E., Ziolkowski, D. J. J., Pardieck, K. L., Fallon, J. E., & Link, W. A. 2017. The North American Breeding Bird Survey, results and analysis 1966 - 2015. Article 0004-8038, USGS Patuxent Wildlife Research Center, Laurel, MD.

Schlaepfer, M. A., Runge, M. C., & Sherman, P. W. (2002). Ecological and evolutionary traps. *Trends in Ecology & Evolution*, **17**, 474-480. 10.1016/s0169-5347(02)02580-6

Sealy, S. G. (1992). Removal of yellow warbler eggs in association with cowbird parasitism. *Condor*, **94**, 40-54. 10.2307/1368794

Serrano, D., Tella, J. L., Forero, M. G., & Donazar, J. A. (2001). Factors affecting breeding dispersal in the facultatively colonial lesser kestrel: individual experience vs. conspecific cues. *Journal of Animal Ecology*, **70**, 568-578. 10.1046/j.1365-2656.2001.00512.x

Shahan, J. L., Goodwin, B. J., & Rundquist, B. C. (2017). Grassland songbird occurrence on remnant prairie patches is primarily determined by landscape characteristics. *Landscape Ecology*, **32**, 971-988. 10.1007/s10980-017-0500-4

Sousa, B. F., & Westneat, D. F. (2013). Positive association between social and extra-pair mating in a polygynous songbird, the dickcissel (*Spiza americana*). *Behavioral Ecology and Sociobiology*, **67**, 243-255. 10.1007/s00265-012-1444-y

Switzer, P. V. (1997). Past reproductive success affects future habitat selection. *Behavioral Ecology and Sociobiology*, **40**, 307-312. 10.1007/s002650050346

Tarwater, C. E., Germain, R. R., & Arcese, P. (2018). Examination of context-dependent effects of natal traits on lifetime reproductive success using a long-term study of a temperate songbird. *Auk*, **135**, 609-621. 10.1642/auk-17-177.1

Uboni, A., Smith, D. W., Stahler, D. R., & Vucetich, J. A. (2017). Selecting habitat to what purpose? The advantage of exploring the habitat-fitness relationship. *Ecosphere*, **8**, 10.1002/ecs2.1705

Utz, J. L., Shipley, L. A., Rachlow, J. L., Johnstone-Yellin, T., Camp, M., & Forbey, J. S. (2016). Understanding tradeoffs between food and predation risks in a specialist mammalian herbivore. *Wildlife Biology*, **22**, 167-173. 10.2981/wlb.00121

Valcu, M., & Kempenaers, B. (2008). Causes and consequences of breeding dispersal and divorce in a blue tit, *Cyanistes caeruleus*, population. *Animal Behaviour,* **75**, 1949-1963. 10.1016/j.anbehav.2007.12.005

Valladares, G., & Lawton, J. H. (1991). Host-plant selection in the holly leaf-miner: does mother know best? *Journal of Animal Ecology*, **60**, 227-240. 10.2307/5456

Veech, J. A. (2006). A comparison of landscapes occupied by increasing and decreasing populations of grassland birds. *Conservation Biology*, **20**, 1422-1432. 10.1111/j.1523-1739.2006.00487.x

Warner, R. E. (1994). Agricultural land-use and grassland habitat in Illinois - future-shock for Midwestern birds. *Conservation Biology*, **8**, 147-156. 10.1046/j.1523-1739.1994.08010147.x

Weidinger, K. (2000). The breeding performance of blackcap *Sylvia atricapilla* in two types of forest habitat. *Ardea*, **88**, 225-233.

Weldon, A. J., & Haddad, N. M. (2005). The effects of patch shape on indigo buntings: evidence for an ecological trap. *Ecology*, **86**, 1422-1431. 10.1890/04-0913

Wright, C. K., & Wimberly, M. C. (2013). Recent land use change in the Western Corn Belt threatens grasslands and wetlands. *Proceedings of the National Academy of Sciences of the United States of America*, **110**, 4134-4139. 10.1073/pnas.1215404110

Yoon, S., & Read, Q. (2016). Consequences of exotic host use: impacts on Lepidoptera and a test of the ecological trap hypothesis. *Oecologia*, **181**, 985-996. 10.1007/s00442-016-3560-2

Zimmerman, J. L. (1966). Polygyny in the dickcissel. *Auk*, **83**, 534-546.

Zimmerman, J. L. (1971). The territory and its density dependent effect in *Spiza americana*. *Auk*, **88**, 591-612. 10.2307/4083752

FIGURES

Figure 1.1. Photos of study species.

(a) Dickcissel eggs and nestlings. Photo credit: Jaime J. Coon.

(b) Dickcissel (yellow bill) and brown-headed cowbird (white bill) nestlings. Photo credit: Jaime J. Coon.

Figure 1.1 continued…

(c) Dickcissel in the act of fledgling.

(d) Adult male dickcissel in mid-song (male has been fitted with USGS and color bands).

Figure 1.1 continued…

(e) Adult female dickcissel carrying a large praying mantis (en route to provision nestlings).

(f) Partially grazed mat of tall fescue. Photo credit: Jaime J. Coon.

Figure 1.2. Dickcissel breeding and winter ranges. Figure from Temple (2002).

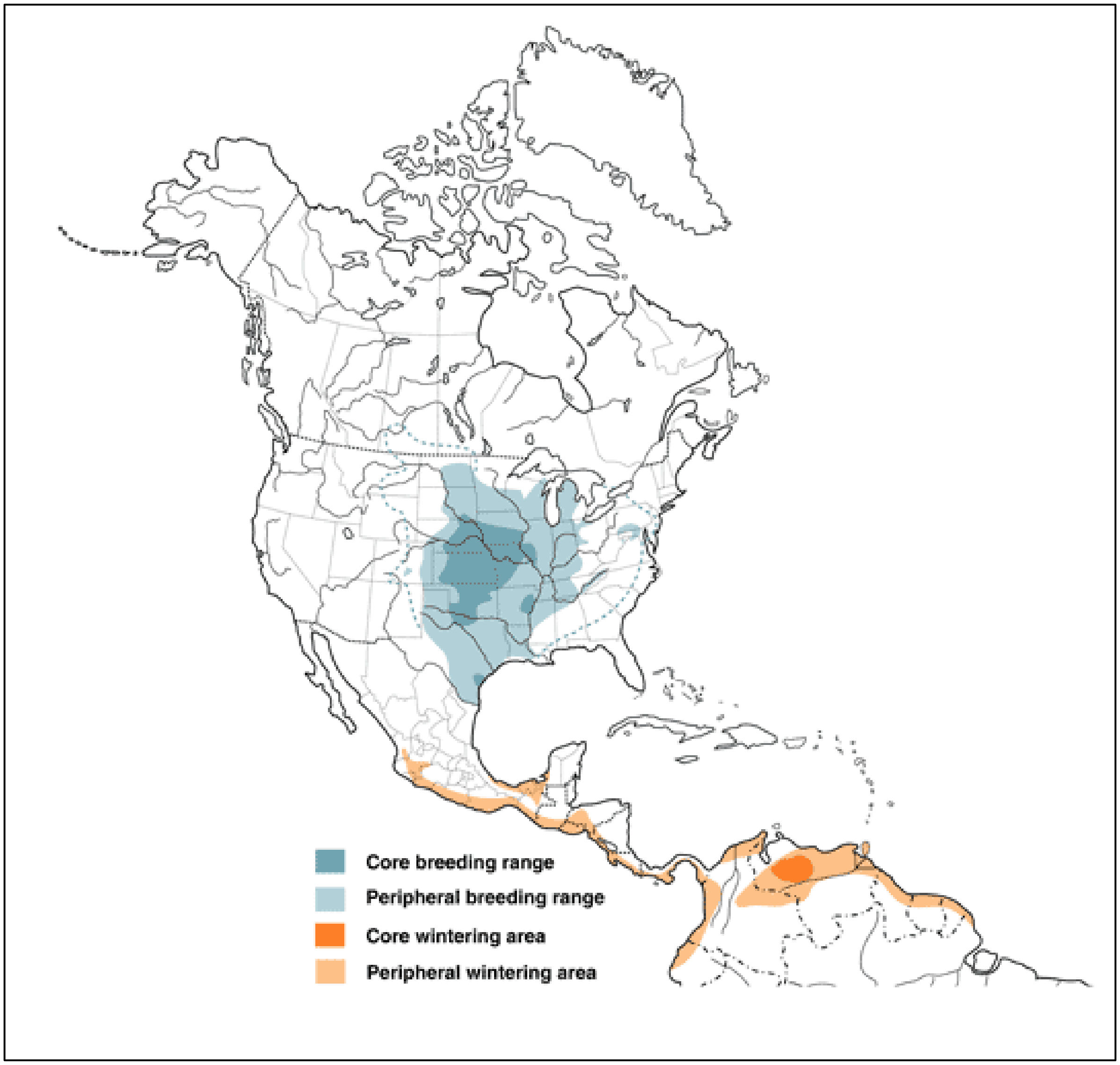
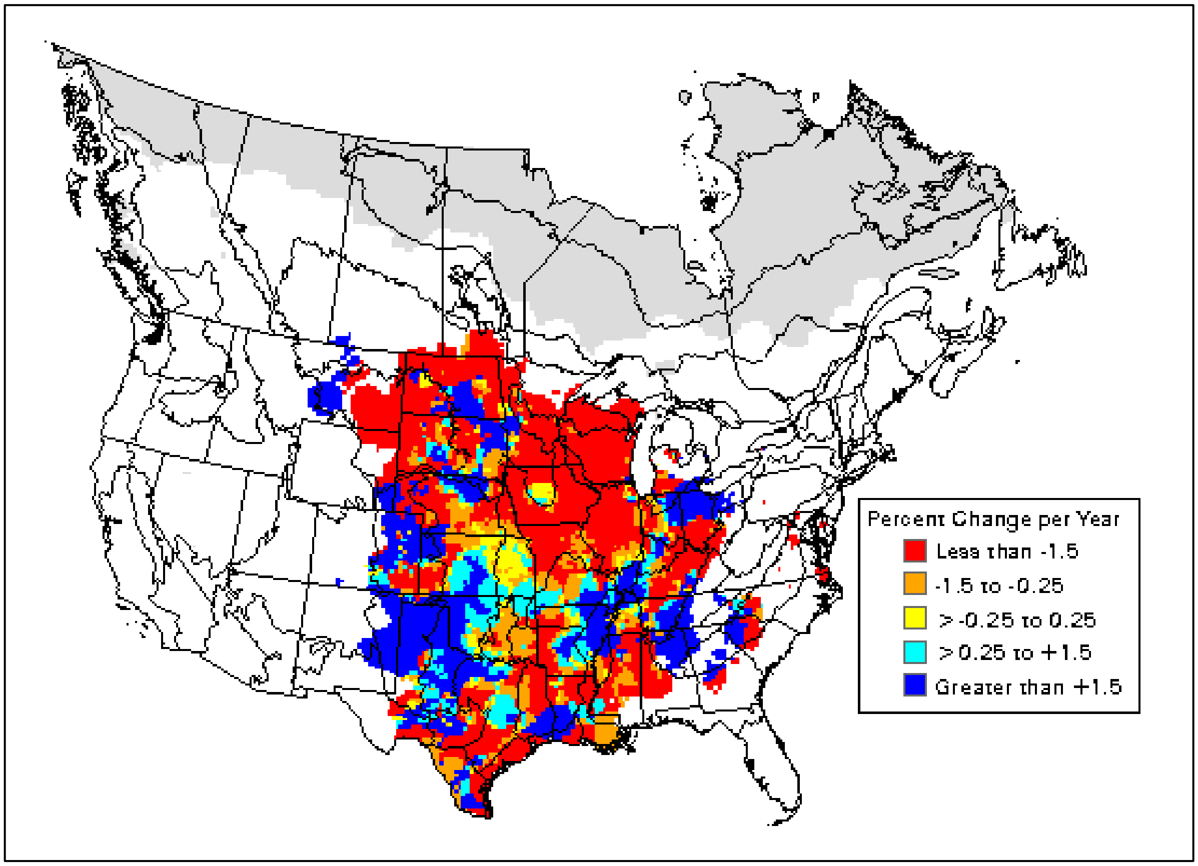


Figure 1.3. Rates of dickcissel breeding population change across the United States from 1966-2010. Data from the North American Breeding Bird Survey, provided by the USGS Patuxent Wildlife Research Center (Sauer et al. 2011).



CHAPTER 2 – ADAPTIVE HABITAT SELECTION VARIES ACROSS FITNESS METRICS, SPATIAL SCALES, SEXES, AND YEARS[1]

ABSTRACT

1. Animals are predicted to engage in adaptive habitat selection, preferring high-quality habitats over lower-quality areas. However, tests of this prediction often fail to address the broad diversity of factors mediating fitness and the multiple scales at which they operate.
2. We examined whether dickcissels (*Spiza americana*), a grassland songbird, exhibited adaptive habitat selection. We first measured male and female habitat preferences at two spatial scales (territories and patches), then tested whether preferences were associated with improvements in four reproductive metrics—mate attraction, avoidance of brood parasitism by brown-headed cowbirds (*Molothrus ater*), fledgling production, and offspring body condition. We examined whether preference-fitness relationships were consistent between years.
3. We mapped territories and searched for nests on 21 grassland patches in Ringgold County, IA, USA, from 2014-2015. We documented territory settlement order and patch territory densities to estimate male preferences, and measured female preferences based on territory polygyny levels and nest abundances in patches (adjusted for territory density). We then tested whether birds in preferred habitats experienced enhanced reproduction.
4. Males and females preferred territories where offspring attained superior body condition, and preferred patches where parasitism was infrequent. Female territory preferences were unrelated to fledgling production, but relationships of male territory preferences to mate attraction and fledgling production varied between years. In 2014, males in preferred territories attracted more mates and produced more fledglings. In 2015, males in *less*-preferred territories

---

[1] Authors: *S. B. Maresh Nelson, J. J. Coon, and J. R. Miller.*

were more successful. Improved success on preferred territories in 2014 corresponded with high female densities and nest survival early in the breeding season compared to 2015.

5. We should not conceive of adaptive habitat selection as a binary behavior. Fitness is a function of multiple processes, so habitat preferences may only improve specific aspects of fitness, and relationships may vary between sexes. Because many preference-fitness relationships only manifest at particular spatial scales, our ability to detect adaptive habitat selection depends on quantifying preferences at scales appropriate to measured metrics of fitness. Moreover, annual variation in conspecific population and predation dynamics may limit animal's abilities to consistently improve fitness through habitat selection.

INTRODUCTION

Animals are predicted to have evolved preferences for habitats that improve individual fitness—a behavior referred to as adaptive habitat selection (Clark & Shutler, 1999; Chalfoun & Schmidt, 2012). Adaptive habitat selection has been detected in some systems (e.g., McLoughlin et al., 2007; Germain et al., 2015), but not in others (e.g, Lloyd & Martin, 2005; Lamb et al., 2017). Some mismatches between habitat preferences and fitness may occur due to temporal variability in predator and competitor communities (Filliater et al., 1994; Martin & Martin, 2001; Chalfoun & Schmidt, 2012). Others result when cues historically associated with high-quality habitat are now associated with poor habitat due to anthropogenic change (Schlaepfer et al., 2002). Studies have identified such ecological traps (e.g., Lamb et al., 2017), but evidence is often based on a single fitness metric at one spatial scale (e.g., Remeš, 2003; Hawlena et al., 2010). Such limited measurements may not fully describe habitat preferences and fitness.

Lifetime fitness is difficult to quantify, particularly for long-lived or migratory animals (but see Tarwater et al., 2018). Even so, assessments of adaptive habitat selection over shorter periods can be improved by measuring multiple fitness components such as breeding effort, offspring production, offspring quality, and adult survival (Lloyd & Martin, 2005; Chalfoun & Martin, 2007; Uboni et al., 2017). This approach acknowledges that fitness is a product of many ecological processes and cannot be evaluated based on one metric. Moreover, it is critical to measure habitat preferences at multiple scales given uncertainty about the scales at which habitat affects fitness (Chalfoun & Martin, 2007; Bloom et al., 2013). For instance, food availability may be strongly influenced by home-range selection (Orians & Wittenberger, 1991; McLoughlin et al., 2007), whereas predation risk may be mediated by habitat composition at multiple scales corresponding to predator home-range sizes (Tewksbury et al., 2006; Chiavacci et al., 2018).

These complexities are illustrated by the breeding ecology of territorial songbirds. Offspring production is a product of many processes, including mate attraction (Sousa & Westneat, 2013a), nest and fledgling survival (Ricklefs, 1969; Jones et al., 2017), and avoidance of brood parasites, such as brown-headed cowbirds (*Molothrus ater*), which often compete with or kill host young (Dearborn et al., 1998). These processes are each mediated by multiple factors. Mate attraction is mediated by territory and individual quality (Zimmerman, 1966; Hasselquist, 1998), predation and parasitism by predator and parasite habitat selection and perception (Hahn et al., 1999; Tewksbury et al., 2006), and fledgling mortality by predation and fledgling condition—itself a function of parasitism and food availability (Dearborn et al., 1998; Jones et al., 2017). Because reproduction depends on multiple processes operating at a range of scales, birds must consider many variables to assess habitat quality. Accordingly, evaluations of adaptive habitat selection must account for many fitness metrics at multiple scales.

Proper evaluations also require appropriate metrics of habitat preference. In some cases, avian densities indicate relative preferences among habitat patches, but this assumption must be validated since high densities can indicate low-quality habitats in strongly territorial species (Fretwell & Lucas, 1969; Van Horne, 1983). For migratory species that select new habitats every year, preferences may also be approximated by the order of settlement among habitat options (e.g., territories or patches; Sergio & Newton, 2003; Robertson & Hutto, 2006; Joos et al., 2014).

In this study, we tested the hypothesis that animals exhibit adaptive habitat selection by examining the breeding ecology of dickcissels (*Spiza americana*)—a migratory songbird of U.S. grasslands. Given the complex links between habitat selection and fitness, we used a multi-pronged approach. We examined whether male and female birds in preferred habitats attracted more mates, experienced lower rates of cowbird parasitism, produced more fledglings, or produced offspring in superior body condition relative to birds in less-preferred habitats. We compared these fitness metrics to habitat preferences among both territories and broader patches, and evaluated the consistency of preference-fitness relationships across breeding seasons to understand whether they depend on temporally variable conditions.

METHODS

FOCAL SPECIES

Dickcissels are an ideal species for evaluating adaptive habitat selection. They inhabit many types of grasslands (e.g., prairies, old-fields, hayfields), but densities and reproduction vary among patches, suggesting that habitat preferences may relate to fitness (Zimmerman, 1971). The fact that dickcissels engage in facultative polygyny (i.e., some males pair with multiple females, others with one, and others attract no mates at all) is also advantageous. Polygyny accentuates differences in individual male fitness and provides a metric of female preferences among territories (Zimmerman, 1966; Sousa & Westneat, 2013a). Finally, because dickcissels have low rates of site fidelity (10-49%; Fletcher et al., 2006; Zimmerman & Finck, 1989), their annual habitat choices may be based not only on settlement decisions made in prior years, but also on conditions in the current year.

STUDY AREA

We investigated dickcissel habitat preferences and reproductive success in 2014-2015 on seven pastures (17.6-41.1 ha in area) in the Grand River Grasslands of Ringgold County, Iowa (Fig 2.1). This 62,000-ha region is characterized by high levels (~70%) of herbaceous land cover, interspersed with row-crop agriculture and woodlands (Duchardt et al., 2016). The average daily temperature from May-August was 21.0°C in 2014 and 21.6°C in 2015. Total May-August rainfall was 28.8 inches in 2014 and 27.4 inches in 2015 (National Climatic Data Center). There were more pronounced differences in monthly climate data (Appendix A).

Our study pastures were spaced at an average pairwise distance of 5.96 km (range: 0.7-13.3). Each pasture was divided into three patches (21 patches total, 3.5-15.6 ha) that demarcated management units (Appendix B). Differential management among patches (e.g., prescribed burns, cattle grazing, herbicide application) has generated divergent plant and bird communities (Duchardt et al., 2016). We thus considered patches as distinct replicates.

MEASURING HABITAT PREFERENCES

To document settlement patterns, we mapped dickcissel territories from 7 May-13 August in 2014 and 8 May-22 August in 2015. To aid mapping, we captured as many singing males as possible via targeted mist-netting with recorded playbacks, banding each with a USGS band and a unique combination of color bands. We mapped territories on each pasture every 3-7 d ($\bar{x}$±SD =

4.9±1.4 d) for a total of 18-23 (median=20) surveys per pasture per year (Sousa & Westneat, 2013a; Joos et al., 2014). Survey routes and pasture survey order varied among mapping rounds to reduce sampling bias (Bibby et al., 2000). Surveys were conducted between 0500-1300 h, and not during precipitation or high wind. Surveyors recorded band combinations and throat markings of each male to aid identification, and conducted focal observations (9.4±6.1 min) of each male in each survey, using a GPS to mark all perches (3.4±1.8 perches per focal observation).

We only considered males territorial if observed in ≥2 surveys. Perches recorded in different surveys were only considered part of the same territory if at least one was within 30 m of a perch used by the same male in another survey. Territory tenure was the number of days between the male's first detection and the day after last detection. We drew territory boundaries in ArcMap10.5 (ESRI, Redlands, CA, USA), grouping points based on bands, throat markings, perch proximity, and simultaneous sightings of males (Bibby et al., 2000). Boundaries were minimum convex polygons around all perches where the male sang or was seen with a female (28.7±17.6 perches recorded per territory).

We quantified male territory preferences based on the relative order in which territories were first established (Sergio & Newton, 2003; Joos et al., 2014). Territories seen in the first survey round were assigned Settlement Rank=1 (most preferred), in the second round, Settlement Rank=2, and so forth. Multiple males sometimes established territories in the same location in a given year (overlap >50%), with later males either displacing existing territory holders or resettling abandoned areas. We assigned later-settled territories the same rank as the earliest-settled territory in the same location (Joos et al., 2014) because the habitat within the later-settled territories was more preferred than an unmodified rank would indicate. Although we cannot distinguish whether preferences were a function of site fidelity or habitat characteristics, settlement rank indicates which territories males prioritized.

We quantified relative preferences of males among patches based on the maximum territory density recorded on each patch each year (Chalfoun & Martin, 2007). Territories overlapping two patches were considered half territories in each patch. Maximum densities were greater on patches with an early date of first settlement, so we considered density a reliable indicator of preference (GLM: $F_{1,\,31} = 12.53$, $p = 0.001$, $R^2 = 0.288$, $\beta_{\text{First Territory Date}} = -0.008 \pm 0.002$ SE).

We measured female territory preferences based on territory polygyny levels; territories selected by more females were considered more highly preferred (Orians & Wittenberger, 1991). Polygyny level was the maximum number of simultaneously active nests on the territory (Sousa & Westneat, 2013a). We located nests by observing adults (Martin & Geupel, 1993), dragging a rope through vegetation (Higgins et al., 1969), and watching for incidental flushes. We visited nests every 1-3 days after discovery to record the number of dickcissel and cowbird eggs and nestlings (Ralph et al., 1996). Nests empty before chicks were ≥7 days old—the age at which they are able to fledge—were considered depredated. Nests were considered successful when ≥1 nestling fledged. We confirmed fledging based on parental behavior.

To determine territory polygyny levels, we calculated nest initiation dates (date first egg laid in each nest, following Maresh Nelson et al. 2018; Chapter 4) and noted nest end dates from monitoring data. Matching nests with territories based on nest locations and interactions of females with nearby males, we determined how many nests were simultaneously active on each territory. However, we deemed it likely that we failed to find nests in some territories (22 of 193); specifically, in territories with no known nests where we observed a female in ≥2 surveys or saw parents feeding fledglings. We increased the polygyny level for these territories by one.

We estimated female patch preferences by dividing the total number of nests built on each patch each year by the total number of territories on the patch (nest-to-territory ratios; Zimmerman, 1971). We adjusted nest abundances by territory abundances because patch selection by females is more constrained by mate availability than patch size. Nest-to-territory ratios were greater in patches where the first nest was initiated earlier, suggesting that these ratios reveal similar preference patterns compared to settlement timing (GLM: $F_{1, 27} = 7.03$, $p = 0.013$, $R^2 = 0.207$, $\beta_{\text{First Nest Date}} = -0.012 \pm 0.004$ SE).

MEASURING REPRODUCTIVE SUCCESS

We measured multiple fitness metrics: mate attraction, cowbird parasitism rates, fledgling production, and nestling body condition. We evaluated male mate attraction based on territory polygyny levels (see above) and quantified parasitism by the presence or absence of cowbird eggs or nestlings in nests (Benson et al., 2010).

We quantified fledgling production by males as the total number of dickcissels fledged per territory (territory productivity; Sousa & Westneat, 2013a). In seven cases, we observed parents feeding fledglings from an unfound nest. We assumed these nests each produced two dickcissel chicks—the median number fledged from successful nests—and added these to the productivity of the respective territories.

Evaluating fledgling production by females required a different approach, since fledglings from polygynous territories are often the offspring of multiple females. We thus counted how many dickcissels fledged from individual nests that produced at least one fledgling (nest productivity). We included nests from which only cowbirds fledged in this analysis, counting them as having produced zero dickcissel fledglings (Benson et al., 2010). Because dickcissels rarely build additional nests after producing a successful brood, nest productivity is likely a good estimate of annual fledgling production by individual females (Walk et al., 2004).

To quantify nestling body condition, we weighed chicks and measured their tarsus lengths 4-6 days after hatching. We then regressed mass vs. tarsus length (GLM: $F_{1,\,214} = 629.37$, $p<0.001$, $R^2 = 0.746$; $\beta_{\mathrm{Tarsus}} = 1.11 \pm 0.04$ SE) and calculated an index of body condition for each chick as its residual from this linear relationship (Vitz & Rodewald, 2011). This metric has been shown to influence post-fledging survival of dickcissels (Jones et al., 2017), and using it allowed us to control for variation in mass due to nestling age and frame size.

DATA ANALYSIS

We conducted seven analyses to assess whether dickcissels engage in adaptive habitat selection (Table 2.1). Analyses related reproductive metrics (response variables) to male and female habitat preferences at the territory and patch scales (explanatory variables). All analyses were performed in SAS 9.4 using PROC GLIMMIX (SAS Institute, Cary, NC, USA). Analyses of cowbird parasitism risk used a binomial distribution. We chose a distribution for the other reproductive metrics by testing whether a Gaussian, negative binomial, or Poisson distribution yielded the lowest $\mathrm{AIC_c}$ score. We only accepted distributions yielding Pearson chi-squared/df ratios <1.2 to avoid overdispersion (Littell et al., 2006). We used likelihood-ratio tests to decide whether to include ‘Pasture’, ‘Year’, or ‘Pasture × Year’ as random effects in each analysis. We tested for non-independence between territories defended by the same male—within or between years—by conducting a likelihood-ratio test on models including ‘MaleID’ as a random effect. This did not improve model fit, so we did not retain this random effect. However, we did include ‘NestID’ as a random effect in analyses of nestling condition to account for among-sibling similarities.

In all analyses, we conducted a two-stage model-selection process to relate fitness to habitat preferences. In Stage 1, we selected covariate fixed effects by comparing AIC_c scores of models including covariates to a random-effects-only model. Covariates represented variables not strictly related to habitat preferences that may have influenced fitness (e.g., temporal variables, nest contents, etc.). We considered a covariate supported if its respective model contributed to the cumulative top 90% of model weights, as long as it also had model weight greater than the random-effects-only model (Burnham & Anderson, 1998: p. 127). Random variables and selected covariates were included in all Stage-2 models.

In Stage 2, we related reproduction to habitat preferences. Candidate model sets for analyses of male preferences included 'Settlement Rank' and 'Maximum Territory Density', our metrics of male territory- and patch-scale preferences. Analyses of female preferences included models for 'Territory Polygyny level' and 'Nest-to-Territory Ratio', our parallel metrics of female preferences. To evaluate the consistency of preference-fitness relationships from 2014-2015, Stage-2 model sets also included interactions between each preference metric and 'Year'.

For each Stage-2 analysis, we compared AIC_c scores of candidate models to a base model with only random effects and covariates. We considered models supported if they contributed to the cumulative top 90% of weights in their respective model set and were ranked above the base. We computed predicted values of fitness metrics across observed ranges of preference metrics, holding covariates at average values (Shaffer & Thompson, 2007). We generated 85% confidence intervals around predicted values since AIC selects variables at this level (Arnold, 2010).

In two analyses—the comparison of male preferences to territory polygyny levels and territory productivity—each territory represented one unit of replication. However, there were many locations where multiple males occupied the same location (at different times) within a breeding season. Thus, to avoid pseudoreplication, we only included the territory with the longest tenure occupying a given location, and thereby excluded 37 territories from those analyses.

RESULTS

DATA STRUCTURE AND ANNUAL VARIABILITY

In 2014, we used data from only six pastures (18 patches) because dickcissels vacated the seventh after an intense June storm. We used 3235 of 3737 recorded perches to map 107 territories (2014 territory size: $\bar{x}$±SD = 0.75±0.91 ha; median = 0.51 ha). We banded 42 males, 40 of which maintained territories on our pastures in 2014. At least 8 of the 107 territories were secondary, established by banded males that moved within the season, and one was a tertiary territory. There were 24 instances where a male either displaced or encroached upon another territory. We found 149 nests in 2014, from which we measured 140 nestlings. Forty-six nests were successful, producing 113 dickcissel fledglings. We estimated that there were another seven unfound nests, three of which produced fledglings. Of the 129 nests surviving to incubation, 65 (50.4%) were parasitized, producing 34 cowbird fledglings.

Thirteen of the males banded in 2014 returned to our pastures in 2015, yielding a site-fidelity rate of 30.1% for banded males (13/42). The site-faithful birds had all been banded on the same pasture in 2014. Of the returning males, three exhibited no spatial overlap in 2015 with their 2014 territory, four exhibited 1-50% overlap, four exhibited >50% overlap, and two had not held known territories in 2014. We banded an additional 11 males in 2015.

In 2015, we mapped 86 territories across all 7 pastures (21 patches), using 2303 of 2486 recorded perches (2015 territory size: $\bar{x}$±SD = 1.01±0.84 ha; median = 0.87 ha). No banded males moved to secondary territories. There were 13 instances where a male either displaced or encroached upon another territory. We found 59 nests, from which we measured 42 nestlings. Thirteen nests were successful, producing 31 dickcissel fledglings. We estimated there were 15 unfound nests, four of which produced fledglings. Of the 52 nests surviving to incubation, 19 (36.5%) were parasitized, producing only 3 cowbird fledglings.

Males and females colonized the study region more quickly and at higher densities in 2014 than 2015 (Fig 2.2). The average territory-establishment date was 18 days earlier in 2014 (27 May vs. 14 June), the first nest was built 4 days earlier in 2014 (11 May vs. 15 May), and peak nest density was 15 days earlier in 2014 (20 June vs. 5 July). Before July, the ratio of males (i.e., territories) to females (i.e., nests) across all pastures was lower in 2014 than 2015, but this pattern reversed in July, after which the male-to-female ratio was lower in 2015 (Appendix C). Dickcissels continued breeding later in 2015. The last remaining male departed its territory eight days earlier in 2014 than in 2015 (12 August vs. 20 August), and the last surviving nest finished eight days earlier in 2014 than in 2015 (24 August vs. 1 September). Reproductive success in 2015 was relatively poor. Average territory productivity was nearly 2.5 times higher in 2014 (1.09 vs. 0.44 fledglings per territory), and only 11.5% of territories were polygynous in 2015 compared to 29.4% in 2014 (Fig 2.3).

MALE HABITAT PREFERENCES AND MATE ATTRACTION

Examining covariates in Stage 1, territory polygyny level increased with tenure ($\beta_{Tenure} = 0.022 \pm 0.005$ SE), indicating males attracted more mates by holding territories for longer. We found no evidence that territory size influenced polygyny. Including tenure as a covariate in Stage 2, the interaction between territory settlement rank and year was the best-supported habitat preference model (Table 2.2A). Males in territories settled earlier achieved marginally greater polygyny in

2014, while males in *later* territories attracted more mates in 2015 (Fig 2.4A). Territories in high-density patches achieved greater polygyny levels ($\beta_{\text{Max Density}}$ = 0.416 ± 0.201 SE; Fig 2.4B).

HABITAT PREFERENCES AND COWBIRD PARASITISM

Nests initiated later in the season were less likely to be parasitized (Stage 1; $\beta_{\text{Initiation Date}}$ = -0.036 ± 0.010 SE). In Stage 2, neither male nor female territory preferences influenced parasitism risk. However, patch preferences of both sexes ranked above their respective base models (Table 2.2B, 2.2C). Nests in patches with high territory density (Fig 2.5A) and with high nest-to-territory ratios (Fig 2.5B) were less likely to be parasitized ($\beta_{\text{Max Density}}$ = -0.800 ± 0.542 SE; $\beta_{\text{Nest-to-Territory Ratio}}$ = -0.888 ± 0.449 SE).

HABITAT PREFERENCES AND FLEDGLING PRODUCTION

Territory productivity—our metric of fledgling production by males—was greater in territories where more nests were built (Stage 1; $\beta_{\text{Total Nests}}$ = 0.429 ± 0.147 SE). This covariate had much more support than either tenure or territory size. In Stage 2, the best-supported model was the interaction between territory settlement rank and year (Table 2.2D). More dickcissels fledged from territories with low ranks (i.e., preferred by males) in 2014. In 2015, however, territories with high ranks produced more fledglings (Fig 2.6A). In addition, territories in patches with high territory density produced more fledglings ($\beta_{\text{Max Density}}$ = 0.657 ± 0.365 SE; Fig 2.6B).

In contrast to territory productivity, nest productivity—our metric of fledgling production by females—was unrelated to territory-scale preferences (Table 2.2E). However, there was a mild tendency for nest productivity to be greater in patches preferred by females ($\beta_{\text{Nest-to-Territory Ratio}}$ = 0.184 ± 0.119 SE; Fig 2.7). No covariates were supported in Stage 1 of this analysis.

HABITAT PREFERENCES AND NESTLING BODY CONDITION

Nestlings measured later in the day were in superior body condition (Stage 1: $\beta_{\text{Time of Day}} = 0.156 \pm 0.032$ SE). Controlling for this in Stage 2 of the analysis of male habitat preferences, territory settlement rank was the best-supported model (Table 2.2F). Nestlings attained superior condition when reared in territories established earlier in the season ($\beta_{\text{Settlement Rank}} = -0.067 \pm 0.023$ SE; Fig 2.8A). Interannual differences in nestling condition predicted by the settlement-rank-year interaction were small, so we did not consider the interaction model competitive.

Again controlling for time of day, territory polygyny levels and patch nest-to-territory ratios were both supported in Stage 2 of the analysis of female habitat preferences (Table 2.2G). Nestlings reared in territories with high polygyny levels ($\beta_{\text{Polygyny Level}} = 0.266 \pm 0.122$ SE; Fig 2.8B) and in patches with high nest-to-territory ratios ($\beta_{\text{Nest-to-Territory Ratio}} = 0.250 \pm 0.139$ SE; Fig 2.8C) attained superior condition.

DISCUSSION

Our study provides a complex portrait of adaptive habitat selection. Dickcissel habitat preferences improved every metric of reproduction we measured—polygyny, cowbird parasitism, nestling body condition, and fledgling production—but every relationship was context dependent. Habitat preferences only improved reproduction at particular spatial scales, and relevant scales of preference differed among fitness metrics (Chalfoun & Martin, 2007; Bloom et al., 2013). Moreover, male and female birds faced differing limitations. Whereas male habitat preferences at both the territory and patch scales enhanced their fledgling production, fledgling production by females was only improved by patch-scale preferences. Adding to this complexity, male territory preferences only improved mate attraction and fledgling production in one year of the study—evidence of temporal variation in adaptive habitat selection (Mosser et al., 2009).

We acknowledge that we could not examine whether individual quality of males and females influenced fitness, and thus whether preference-fitness relationships were in part a product of high-quality birds occupying preferred habitats (Hasselquist, 1998). However, other work has found few impacts of male traits (at least) on annual reproduction, suggesting this may not be an issue (Sousa & Westneat, 2013b). We also note that we were unable to follow individual birds across their entire lifespans (e.g., Tarwater et al., 2018) and thus test whether habitat preferences improved lifetime fitness (McLoughlin et al., 2007). Despite this limitation, multiple signals of adaptive habitat selection manifested in the two years of our study.

One of the strongest patterns was that both males and females preferred territories that produced offspring in superior body condition. Males selected these territories early in the breeding season and females nested on them in high numbers. Similarly, offspring in patches preferred by females attained superior condition. Because increasing body condition improves post-fledging survival in dickcissels (Suedkamp Wells et al., 2007; Jones et al., 2017), these results indicate that habitat preferences improved parental fitness through offspring recruitment.

Why did preferred habitats produce robust offspring? Dickcissels may prefer habitats containing high-quality resources for offspring growth (e.g. abundant arthropods; Orians & Wittenberger, 1991; Germain et al., 2015). However, if resource availability was responsible for increased polygyny levels, this would contradict the Polygyny Threshold Hypothesis (Orians, 1969). Although this hypothesis predicts that polygyny increases with territory quality, it also predicts that intra-female competition should then equalize realized fitness among territories.

Another potential line of evidence for adaptive habitat selection was that territory densities and nest-to-territory ratios—our respective metrics of male and female patch preferences—were higher on patches where cowbird parasitism was infrequent. Parasitism increases parental energy costs and reduces offspring condition and productivity (Hoover & Reetz, 2006), so escaping it enhances fitness. Our results would indicate adaptive patch selection if dickcissels actively detect and avoid cowbirds during settlement, as observed in other systems (Forsman & Martin, 2009). It is possible instead though that nests in high-density patches were parasitized less often because cowbirds there could not lay enough eggs to parasitize all nests. In this scenario, it would be unclear whether dickcissels settled near each other *in order* to reduce parasitism—a form of adaptive habitat selection—or whether infrequent parasitism was a by-product of clustering for another purpose. A third alternative may be that patches with less parasitism have accumulated large dickcissel populations over time because adults are more site-faithful or recruitment is higher (Hoover & Reetz, 2006). We do not believe recruitment drove our results, however, because we observed no natal philopatry from 2014-2016 (SBMN, unpublished data).

Additional research is needed to determine whether dickcissels actively avoid cowbirds at the patch scale, but our results provide no evidence that territory preferences reduced parasitism. Avoidance of parasitism through territory selection may be difficult either because cowbirds maintain large laying ranges (2.6-32.2 ha; Hahn et al., 1999) relative to dickcissel territory size, or because parasitism in our study region is mediated by habitat features at broad spatial scales (i.e., woodland cover in the landscape; Hovick & Miller, 2013; Maresh Nelson et al., 2018).

We also observed scale-dependency with respect to nest productivity—the number of dickcissel chicks that fledged from successful nests. While likely an important metric of female reproductive success (Walk et al., 2004), nest productivity was unrelated to female territory preferences. In preferred patches, however, successful nests tended to produce more dickcissel fledglings. These patterns may be related to brood parasitism. Cowbirds remove host eggs when they parasitize nests (Hoover & Reetz, 2006), and successful dickcissel nests in our study region produce fewer conspecific fledglings if they are parasitized (Maresh Nelson et al., 2018). Thus, the fact that females did not prefer territories where parasitism risk was low may have prevented them from preferring territories where nest productivity was high. In contrast, nests in preferred patches were infrequently parasitized, and thus may have produced more dickcissel chicks.

In contrast to females, males engaged in adaptive territory selection with respect to fledgling production and mate attraction—albeit inconsistently. In 2014, males conformed to the model of adaptive settlement formulated in the Ideal Despotic Distribution (Fretwell & Lucas, 1969). Early-arriving males selected high-quality territories where they attracted multiple females and produced many fledglings, while later-arriving males were relegated to lower-quality territories unless they displaced an early bird (Aebischer et al., 1996; Joos et al., 2014). Males in 2014 may have accurately evaluated territory quality during settlement based on vegetation cues or food availability (Chalfoun & Martin, 2007; Germain et al., 2015), or prior experience may have allowed site-faithful birds to return to high-quality territories (Forstmeier, 2002).

But despite the evidence for adaptive territory selection in 2014, males in preferred territories performed poorly in 2015. We offer two hypotheses to explain this reversal. First, nest survival rates were high early in the 2014 season and decreased over time, but were low early in 2015 and *increased* over time (Maresh Nelson et al., 2018). These patterns could have allowed males on early territories to produce more fledglings in 2014, but fewer in 2015. The source of these differing predation dynamics is uncertain, but might be explained by temporal variation in predator foraging behavior or community composition between years (Borgmann et al., 2013).

Differences in climate between our study years could have influenced predation dynamics, as grassland bird nest success is often poor early in the breeding season when early-season precipitation levels are high (Zuckerberg et al., 2018) and May precipitation was greater in 2015 than 2014 (3.73 inches in 2014 vs. 6.79 inches in 2015; National Climatic Data Center).

A second explanation for annual inconsistency in adaptive habitat selection may stem from variability in dickcissel population dynamics. In 2014, both sexes began arriving in early May and increased rapidly in abundance. In 2015, however, the earliest males still arrived in early May, but females began nesting and peaked in abundance later in the summer. The male-to-female ratio was relatively low early in 2014, reducing mate competition for early arriving males and thus increasing fledgling production. But in 2015, early arriving males faced more intense mate competition, and late males may have performed especially well since many early males abandoned their territories after attracting no mates.

It is unclear why population dynamics differed between years. Dickcissels are known for their erratic distributions (Temple 2002), but the causes of these changes are not fully understood. A possible explanation for the patterns we observed may be that a strong El Niño event occurred in 2015. Some Neotropical migrants delay spring migration during El Niño events, and may even experience poor adult survival (Mazerolle et al., 2005; González-Prieto & Hobson, 2013). It is unknown whether dickcissels are affected this way.

In either case, temporal variability in preference-fitness relationships underscores a key limitation to adaptive habitat selection: reproduction is mediated in part by factors animals cannot evaluate while selecting habitat. Other authors have noted that microhabitat preferences with respect to nest-site selection may be of little adaptive value due to unpredictable predation risk (e.g., Filliater et al., 1994), and our data suggest that inter-annual variability in predation may also limit adaptive territory selection. Moreover, although inter-specific competition has been known to prevent adaptive habitat selection (Martin & Martin, 2001), to our knowledge, our study is the first to suggest that intra-specific competition might do the same.

The complexity of adaptive habitat selection presents logistical challenges for ecologists. Our study illustrates that specific fitness metrics are often only enhanced by habitat preferences at specific spatial scales. If investigators quantify preferences at scales irrelevant to measured metrics, habitat preferences may appear unrelated to animal fitness. Because relevant scales are often unknown *a priori*, we recommend measuring preferences at multiple scales. Similarly, we suggest measuring multiple fitness components, as some may be more strongly influenced by habitat selection, and we urge authors to evaluate how preference-fitness relationships vary over time to better understand the mechanisms underlying adaptive habitat selection. Finally, we recommend examining relationships among animal sexes independently. Males and females are often subject to different life-history constraints, and may thus vary in habitat-selection strategies.

LITERATURE CITED

Aebischer, A., Perrin, N., Krieg, M., Studer, J., & Meyer, D. R. (1996). The role of territory choice, mate choice and arrival date on breeding success in the Savi's warbler *Locustella luscinioides*. *Journal of Avian Biology*, **27**, 143-152. 10.2307/3677143

Arnold, T. W. (2010). Uninformative parameters and model selection using Akaike's Information Criterion. *Journal of Wildlife Management*, **74**, 1175-1178. 10.2193/2009-367

Benson, T. J., Anich, N. M., Brown, J. D., & Bednarz, J. C. (2010). Habitat and landscape effects on brood parasitism, nest survival, and fledgling production in Swainson's warblers. *Journal of Wildlife Management*, **74**, 81-93. 10.2193/2008-442

Bibby, C. J., Burgess, N. D., & Hill, D. A. 2000. Bird census techniques. 2nd edition. Academic Press, Inc., London.

Bloom, P. M., Clark, R. G., Howerter, D. W., & Armstrong, L. M. (2013). Multi-scale habitat selection affects offspring survival in a precocial species. *Oecologia*, **173**, 1249-1259. 10.1007/s00442-013-2698-4

Borgmann, K. L., Conway, C. J., & Morrison, M. L. (2013). Breeding phenology of birds: mechanisms underlying seasonal declines in the risk of nest predation. *Plos One,* **8**, 10. 10.1371/journal.pone.0065909

Burnham, K. P., & Anderson, D. R. (1998). Model selection and inference: a practical information-theoretic approach. Springer, New York, NY.

Chalfoun, A. D., & Martin, T. E. (2007). Assessments of habitat preferences and quality depend on spatial scale and metrics of fitness. *Journal of Applied Ecology*, **44**, 983-992. 10.1111/j.1365-2664.2007.01352.x

Chalfoun, A. D., & Schmidt, K. A. (2012). Adaptive breeding-habitat selection: is it for the birds? *Auk,* **129**, 589-599. 10.1525/auk.2012.129.4.589

Chiavacci, S. J., Benson, T. J., & Ward, M. P. (2018). Linking landscape composition to predator-specific nest predation requires examining multiple landscape scales. *Journal of Applied Ecology*, **55**, 2082-2092. 10.1111/1365-2664.13090

Clark, R. G., & Shutler, D. (1999). Avian habitat selection: pattern from process in nest-site use by ducks? *Ecology*, **80**, 272-287. 10.1890/0012-9658(1999)080[0272:ahspfp]2.0.co;2

Dearborn, D. C., Anders, A. D., Thompson, F. R., & Faaborg, J. (1998). Effects of cowbird parasitism on parental provisioning and nestling food acquisition and growth. *Condor*, **100**, 326-334. 10.2307/1370273

Duchardt, C. J., Miller, J. R., Debinski, D. M., & Engle, D. M. (2016). Adapting the fire-grazing interaction to small pastures in a fragmented landscape for grassland bird conservation. *Rangeland Ecology & Management*, **69**, 300-309. 10.1016/j.rama.2016.03.005

Filliater, T. S., Breitwisch, R., & Nealen, P. M. (1994). Predation on northern cardinal nests: does choice of nest site matter? *Condor*, **96**, 761-768. 10.2307/1369479

Fletcher, R. J., Koford, R. R., & Seaman, D. A. (2006). Critical demographic parameters for declining songbirds breeding in restored grasslands. *Journal of Wildlife Management*, **70**, 145-157.

Forsman, J. T., & Martin, T. E. (2009). Habitat selection for parasite-free space by hosts of parasitic cowbirds. *Oikos*, **118**, 464-470. 10.1111/j.1600-0706.2008.17000.x

Forstmeier, W. (2002). Benefits of early arrival at breeding grounds vary between males. *Journal of Animal Ecology*, **71**, 1-9. 10.1046/j.0021-8790.2001.00569.x

Fretwell, S. D., & Lucas, H. L. J. (1969). On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheoretica*, **19**, 16-36.

Germain, R. R., Schuster, R., Delmore, K. E., & Arcese, P. (2015). Habitat preference facilitates successful early breeding in an open-cup nesting songbird. *Functional Ecology*, **29**, 1522-1532. 10.1111/1365-2435.12461

González-Prieto, A. M., & Hobson, K. A. 2013. Environmental conditions on wintering grounds and during migration influence spring nutritional condition and arrival phenology of Neo-tropical migrants at a northern stopover site. *Journal of Ornithology*, **154**, 1067-1078. 10.1007/s10336-013-0975-y

Hahn, D. C., Sedgwick, J. A., Painter, I. S., & Casna, N. J. (1999). A spatial and genetic analysis of cowbird host selection. *Studies in Avian Biology*, **18**, 204-217.

Hasselquist, D. (1998). Polygyny in great reed warblers: a long-term study of factors contributing to male fitness. *Ecology*, **79**, 2376-2390. 10.2307/176829

Hawlena, D., Saltz, D., Abramsky, Z., & Bouskila, A. (2010). Ecological trap for desert lizards caused by anthropogenic changes in habitat structure that favor predator activity. *Conservation Biology*, **24**, 803-809. 10.1111/j.1523-1739.2010.01477.x

Higgins, K. F., Kirsch, L. M., & Ball, I. J. (1969). A cable-chain device for locating duck nests. *Journal of Wildlife Management*, **33**, 1009-1011. 10.2307/3799339

Hoover, J. P., & Reetz, M. J. (2006). Brood parasitism increases provisioning rate, and reduces offspring recruitment and adult return rates, in a cowbird host. *Oecologia*, **149**, 165-173. 10.1007/s00442-006-0424-1

Hovick, T. J., & Miller, J. R. (2013). Broad-scale heterogeneity influences nest selection by brown-headed cowbirds. *Landscape Ecology*, **28**, 1493-1503. 10.1007/s10980-013-9896-7

Jones, T. M., Ward, M. P., Benson, T. J., & Brawn, J. D. (2017). Variation in nestling body condition and wing development predict cause-specific mortality in fledgling dickcissels. *Journal of Avian Biology*, **48**, 439-447. 10.1111/jav.01143

Joos, C. J., Thompson, F. R., III, & Faaborg, J. (2014). The role of territory settlement, individual quality, and nesting initiation on productivity of Bell's vireos *Vireo bellii bellii*. *Journal of Avian Biology*, **45**, 584-590. 10.1111/jav.00400

Lamb, C. T., Mowat, G., McLellan, B. N., Nielsen, S. E., & Boutin, S. (2017). Forbidden fruit: human settlement and abundant fruit create an ecological trap for an apex omnivore. *Journal of Animal Ecology*, **86**, 55-65. 10.1111/1365-2656.12589

Littell, R. C., Milliken, G. A., Stroup, W. W., Wolfinger, R. D., & Schanbenberger, O. 2006. SAS for mixed models. 2 edition. SAS Institute Inc., Cary, NC, USA.

Lloyd, J. D., & Martin, T. E. (2005). Reproductive success of chestnut-collared longspurs in native and exotic grassland. *Condor*, **107**, 363-374. 10.1650/7701

Lokemoen, J. T., & Koford, R. R. (1996). Using candlers to determine the incubation stage of passerine eggs. *Journal of Field Ornithology*, **67**, 660-668.

Maresh Nelson, S. B., Coon, J. J., Duchardt, C. J., Miller, J. R., Debinski, D. M., & Schacht, W. H. (2018). Contrasting impacts of invasive plants and human-altered landscape context on nest survival and brood parasitism of a grassland bird. *Landscape Ecology*, **33**, 1799-1813. 10.1007/s10980-018-0703-3

Martin, P. R., & Martin, T. E. (2001). Ecological and fitness consequences of species coexistence: a removal experiment with wood warblers. *Ecology*, **82**, 189-206. 10.1890/0012-9658(2001)082[0189:eafcos]2.0.co;2

Martin, T. E., & Geupel, G. R. (1993). Nest-monitoring plots - methods for locating nests and monitoring success. *Journal of Field Ornithology*, **64**, 507-519.

Mazerolle, D. F., Dufour, K. W., Hobson, K. A., & den Haan, H. E. 2005. Effects of large-scale climatic fluctuations on survival and production of young in a Neotropical migrant song-bird, the yellow warbler *Dendroica petechia. Journal of Avian Biology*, **36**, 155-163. 10.1111/j.0908-8857.2005.03289.x

McLoughlin, P. D., Gaillard, J. M., Boyce, M. S., Bonenfant, C., Messier, F., Duncan, P., . . . Klein, F. (2007). Lifetime reproductive success and composition of the home range in a large herbivore. *Ecology*, **88**, 3192-3201. 10.1890/06-1974.1

Mosser, A., Fryxell, J. M., Eberly, L., & Packer, C. (2009). Serengeti real estate: density vs. fitness-based indicators of lion habitat quality. *Ecology Letters*, **12**, 1050-1060. 10.1111/j.1461-0248.2009.01359.x

National Climatic Data Center. National Oceanic and Atmospheric Administration. https://www.ncdc.noaa.gov/data-access. Website last accessed on 08 March, 2019.

Orians, G. H. (1969). On the evolution of mating systems in birds and mammals. *American Naturalist*, **103**, 589-603. 10.1086/282628

Orians, G. H., & Wittenberger, J. F. (1991). Spatial and temporal scales in habitat selection. *American Naturalist*, **137**, 29-49.

Ralph, C. J., Geupel, G. R., Pyle, P., Martin, T. E., DeSante, D. F., & Mila, B. (1996). Manual of field methods for monitoring landbirds. *General Technical Report - Pacific Southwest Research Station, USDA Forest Service*, 44 pp.

Remeš, V. (2003). Effects of exotic habitat on nesting success, territory density, and settlement patterns in the blackcap (*Sylvia atricapilla*). *Conservation Biology*, **17**, 1127-1133. 10.1046/j.1523-1739.2003.01611.x

Ricklefs, R. E. (1969). An analysis of nesting mortality in birds. *Smithsonian Contributions to Zoology*, 1-48.

Robertson, B. A., & Hutto, R. L. (2006). A framework for understanding ecological traps and an evaluation of existing evidence. *Ecology*, **87**, 1075-1085. 10.1890/0012-9658(2006)87[1075:affuet]2.0.co;2

Schlaepfer, M. A., Runge, M. C., & Sherman, P. W. (2002). Ecological and evolutionary traps. *Trends in Ecology & Evolution*, **17**, 474-480. 10.1016/s0169-5347(02)02580-6

Sergio, F., & Newton, I. (2003). Occupancy as a measure of territory quality. *Journal of Animal Ecology*, **72**, 857-865. 10.1046/j.1365-2656.2003.00758.x

Shaffer, T. L., & Thompson, F. R., III. (2007). Making meaningful estimates of nest survival with model-based methods. *Studies in Avian Biology*, **34**, 84-95.

Sousa, B. F., & Westneat, D. F. (2013a). Positive association between social and extra-pair mating in a polygynous songbird, the dickcissel (*Spiza americana*). *Behavioral Ecology and Sociobiology*, **67**, 243-255. 10.1007/s00265-012-1444-y

Sousa, B. F., & Westneat, D. F. (2013b). Variance in mating success does not produce strong sexual selection in a polygynous songbird. *Behavioral Ecology*, **24**, 1381-1389. 10.1093/beheco/art077

Suedkamp Wells, K. M., Ryan, M. R., Millspaugh, J. J., Thompson, F. R., III, & Hubbard, M. W. (2007). Survival of postfledging grassland birds in Missouri. *Condor*, **109**, 781-794.

Tarwater, C. E., Germain, R. R., & Arcese, P. (2018). Examination of context-dependent effects of natal traits on lifetime reproductive success using a long-term study of a temperate songbird. *Auk*, **135**, 609-621. 10.1642/auk-17-177.1

Temple, S. A. 2002. Dickcissel (*Spiza americana*).*in* A. Poole, editor. The Birds of North America Online. Cornell Lab of Ornithology, Ithaca.

Tewksbury, J. J., Garner, L., Garner, S., Lloyd, J. D., Saab, V., & Martin, T. E. (2006). Tests of landscape influence: nest predation and brood parasitism in fragmented ecosystems. *Ecology*, **87**, 759-768. 10.1890/04-1790

Uboni, A., Smith, D. W., Stahler, D. R., & Vucetich, J. A. (2017). Selecting habitat to what purpose? The advantage of exploring the habitat-fitness relationship. *Ecosphere*, **8**, 10.1002/ecs2.1705

Van Horne, B. (1983). Density as a misleading indicator of habitat quality. *Journal of Wildlife Management*, **47**, 893-901.

Vitz, A. C., & Rodewald, A. D. (2011). Influence of condition and habitat use on survival of post-fledgling songbirds. *Condor*, **113**, 400-411. 10.1525/cond.2011.100023

Walk, J. W., Wentworth, K., Kershner, E. L., Bollinger, E. K., & Warner, R. E. (2004). Renesting decisions and annual fecundity of female dickcissels (*Spiza americana*) in Illinois. *Auk*, **121**, 1250-1261. 10.1642/0004-8038(2004)121[1250:rdaafo]2.0.co;2

Zimmerman, J. L. (1966). Polygyny in the dickcissel. *Auk*, **83**, 534-546.

Zimmerman, J. L. (1971). The territory and its density dependent effect in *Spiza americana*. *Auk*, **88**, 591-612. 10.2307/4083752

Zimmerman, J. L., Finck, E. J. (1989). Philopatry and correlates of territorial fidelity in male dickcissels. *North American Bird Bander*, **14**, 83-85.

Zuckerberg, B., Ribic, C. A., McCauley, L. A. 2018. Effects of temperature and precipitation on grassland bird nesting success as mediated by patch size. Conservation Biology, 32, 872-882. 10.1111/cobi.13089

TABLES

Table 2.1. Analyses of adaptive habitat selection by male and female dickcissels. Each row summarizes one of seven analyses of whether habitat preferences at territory and patch scales predict individual reproductive success.

Analysis	**Unit of Replication**	**Territory / Patch Preference Metrics (Fixed Effects)**	**Reproductive Metrics (Response Variables)**
(A) Male habitat preferences and mate attraction	Territory	Settlement rank / Maximum territory density in the patch containing the territory	Territory polygyny level[a]
(B) Male habitat preferences and brood parasitism	Nest	Settlement rank of the territory / Maximum territory density in the patch where the nest was built	Nest parasitized? (Y/N)[b]
(C) Female habitat preferences and brood parasitism	Nest	Polygyny level in the territory / Nest-to-territory ratio in the patch where the nest was built	Nest parasitized? (Y/N)[b]
(D) Male habitat preferences and fledgling production	Territory	Settlement rank / Maximum territory density in the patch containing the territory	Territory productivity[c]
(E) Female habitat preferences and fledgling production	Nest	Polygyny level in the territory / Nest-to-territory ratio in the patch where the nest was built	Nest productivity[a,d]
(F) Male habitat preferences and nestling body condition	Nestling	Settlement rank of the territory / Maximum territory density in the patch where the nestlings were reared	Nestling condition[e]
(G) Female habitat preferences and nestling body condition	Nestling	Polygyny level in the territory / Nest-to-territory ratio in the patch where the nestlings were reared	Nestling condition[e]

[a] Modeled with a Poisson distribution.

[b] Modeled with a binomial distribution. Only nests that survived to incubation were included in these analyses. Cowbirds typically parasitize nests during the laying phase, so nests that did not survive to incubation did not have an equal opportunity to be parasitized.

[c] Modeled with a negative binomial distribution.

[d] Only nests that survived to fledging were included in this analysis.

[e] Modeled with a Gaussian distribution.

Table 2.2. AIC tables comparing territory- and patch-scale habitat preferences of male and female dickcissels to reproductive metrics. Sub-tables correspond to analyses in Table 2.1. Only base models—which include supported random effects and covariates—and more highly ranked models are shown. See Appendix D for complete AIC tables.

Model	**# Parameters**	**Deviance**	**ΔAIC_c**	**Model weight (ω)**
(A) Male habitat preferences and territory polygyny levels[a]				
Settlement Rank × Year	6	354.10	0	0.500
Max. Territory Density	4	359.89	1.42	0.236
Base Model (Tenure)	3	362.81	2.22	0.158
(B) Male habitat preferences and cowbird parasitism[b]				
Max. Territory Density	4	202.70	0	0.445
Base Model (Initiation Date)	3	204.84	0.05	0.434
(C) Female habitat preferences and cowbird parasitism[b]				
Nest-to-Territory Ratio	4	201.55	0	0.518
Base Model (Initiation Date)	3	204.84	1.21	0.283
(D) Male habitat preferences and territory productivity[c]				
Settlement Rank × Year	7	373.29	0	0.860
Max. Territory Density	5	383.37	5.72	0.049
Base Model (Total Nests)	4	385.54	5.75	0.049
(E) Female habitat preferences and nest productivity[d]				
Nest-to-Territory Ratio	2	225.31	0	0.411
Base Model (No Covariates)	1	227.69	0.25	0.363
(F) Male habitat preferences and nestling body condition[e]				
Settlement Rank	4	562.66	0	0.675
Settlement Rank × Year	6	560.33	1.97	0.252
Base Model (Time of Day)	3	570.37	5.60	0.041
(G) Female habitat preferences and nestling body condition[e]				
Territory Polygyny Level	4	565.70	0	0.449
Nest-to-Territory Ratio	4	567.23	1.52	0.210
Base Model (Time of Day)	3	563.41	2.00	0.165

[a] Models include territory tenure as a covariate and ‘Pasture × Year’ as a random variable.
[b] Models include nest initiation date as a covariate and ‘Pasture’ as a random variable.
[c] Models include the total number of nests built on the territory as a covariate and ‘Pasture × Year’ as a random variable.
[d] Models include no random variables or covariates.
[e] Models include time of nestling measurement as a covariate and ‘NestID’ as a random variable.

FIGURES

Figure 2.1. Map of study sites. The Grand River Grasslands region is outlined in the inset. Study pastures and patches within pastures are shown in the main figure.

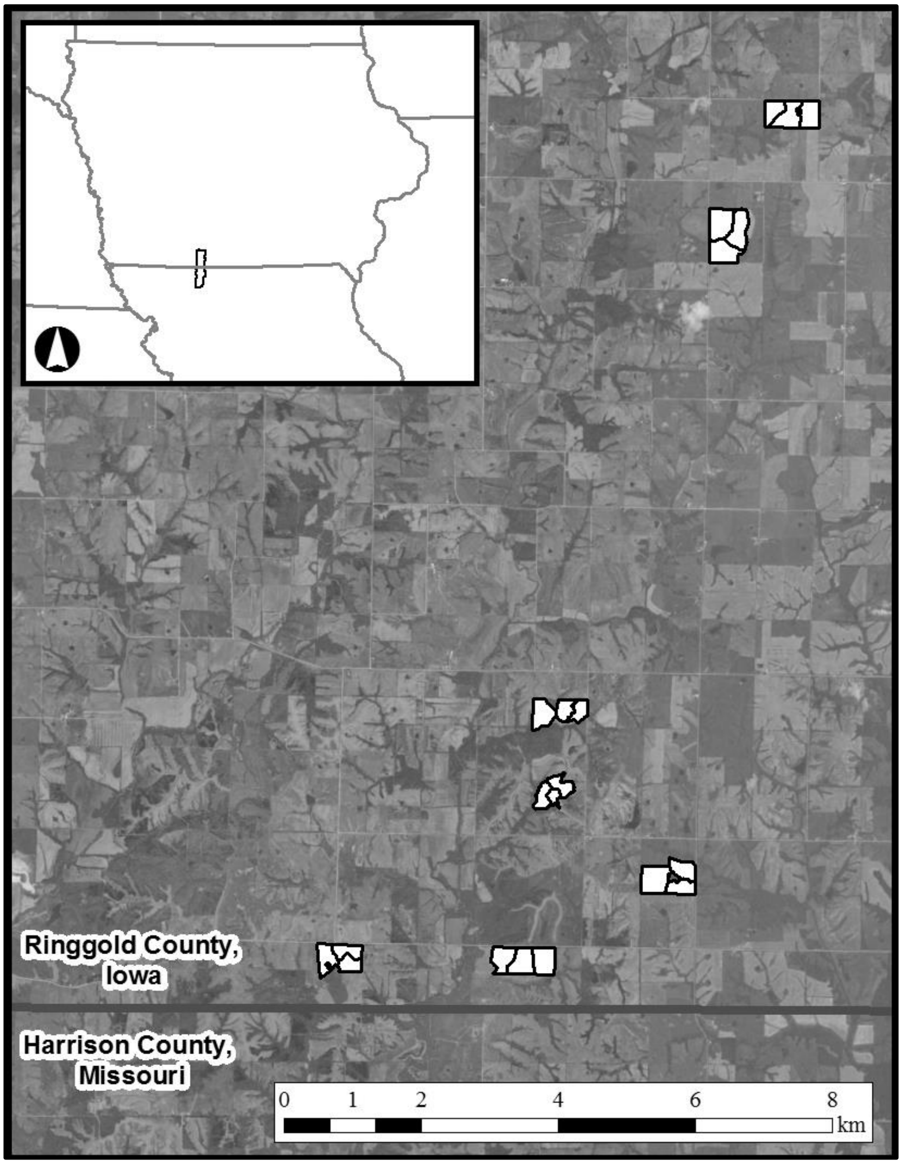


Figure 2.2. Densities of dickcissel territories (dashed) and nests (solid) in 2014 (black) and 2015 (grey), across all study pastures in Ringgold County, IA. Daily density estimates were calculated as the total number of known territories and nests on each day, divided by the total area surveyed each year (2014: 6 pastures, 171.8 ha; 2015: 7 pastures, 206.8 ha). Territory density estimates have been smoothed between survey dates.

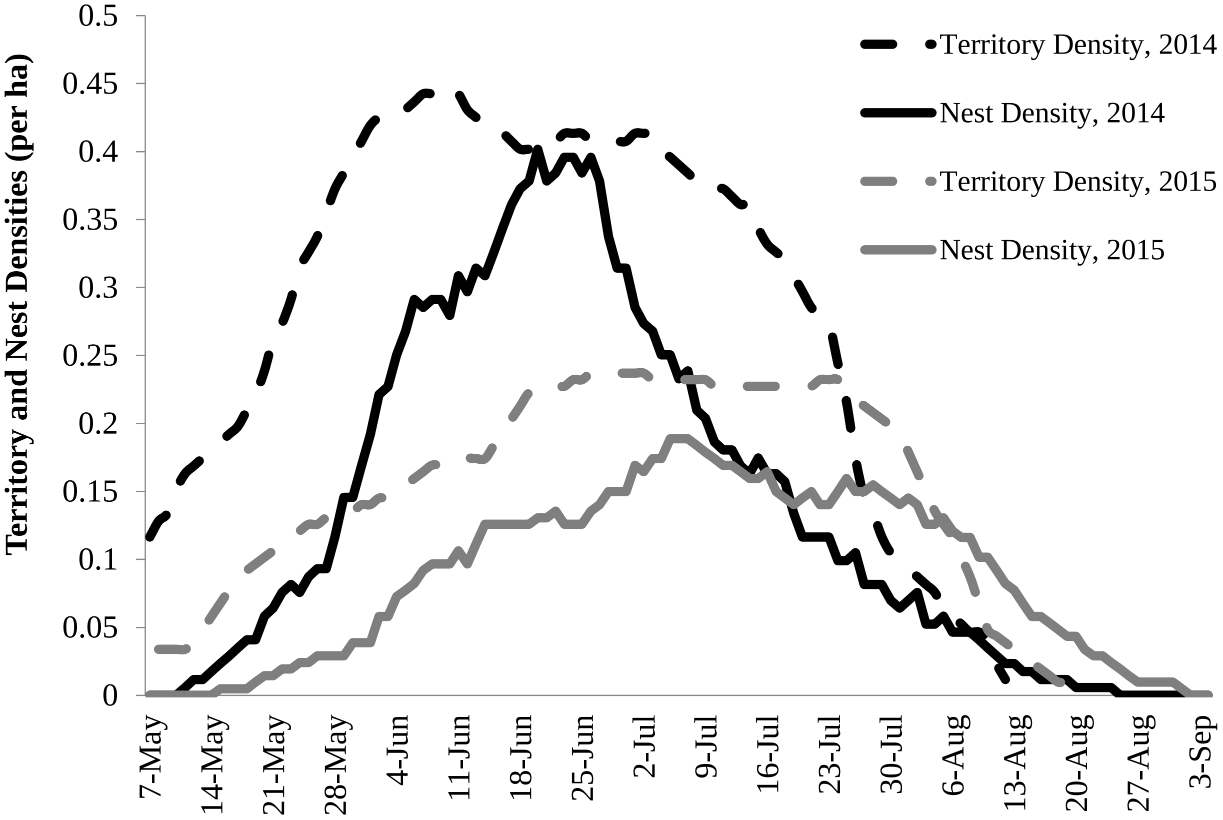


Figure 2.3. Distribution of territory polygyny levels in 2014 (black) and 2015 (grey). The number of territories in which zero, one, two, three, or four females nested concurrently is shown.

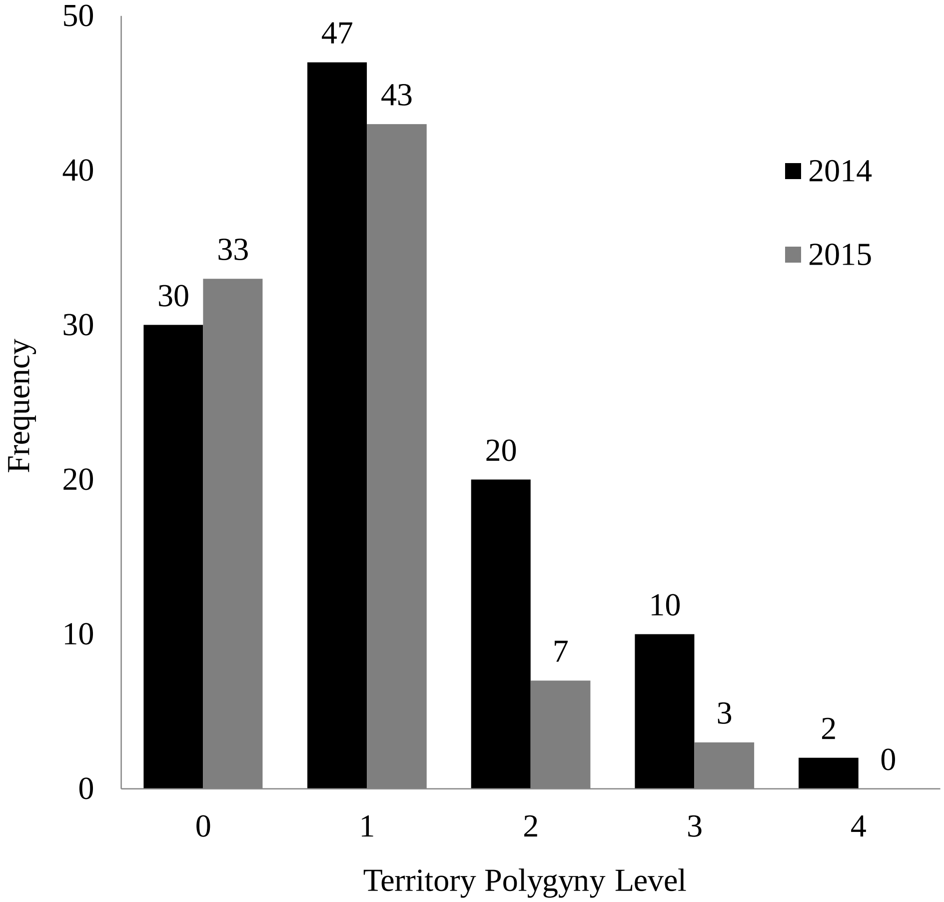


Figure 2.4. Territory polygyny level predicted (A) as a function of territory settlement rank in 2014 (dashed) and 2015 (solid), and (B) as a function of patch territory density. Estimates are for a territory defended for the average tenure of 45 days. Error bars represent 85% confidence intervals. See Appendix E for the number of territories with each settlement rank in each year.

(A)

(B)

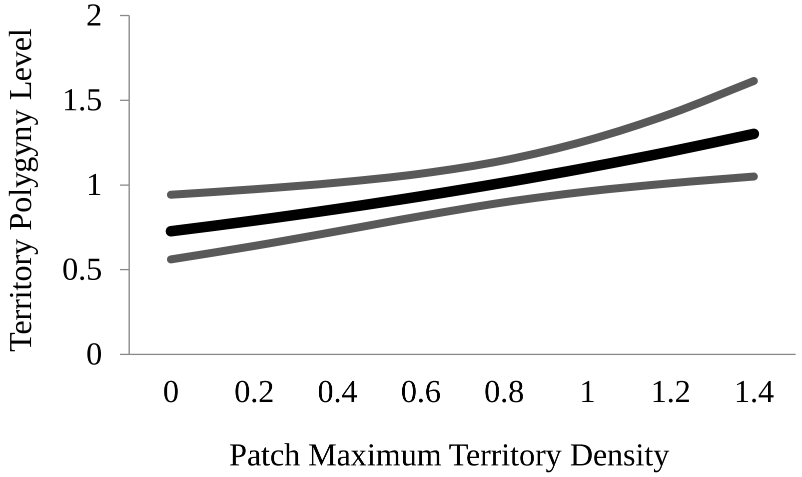


Figure 2.5. Probability that a nest will be parasitized by brown-headed cowbirds predicted as a function of (A) maximum territory density and (B) nest-to-territory ratio in the patch where the nest is built. Estimates are for a nest initiated on the average initiation date (23 June). Error bars represent 85% confidence intervals.

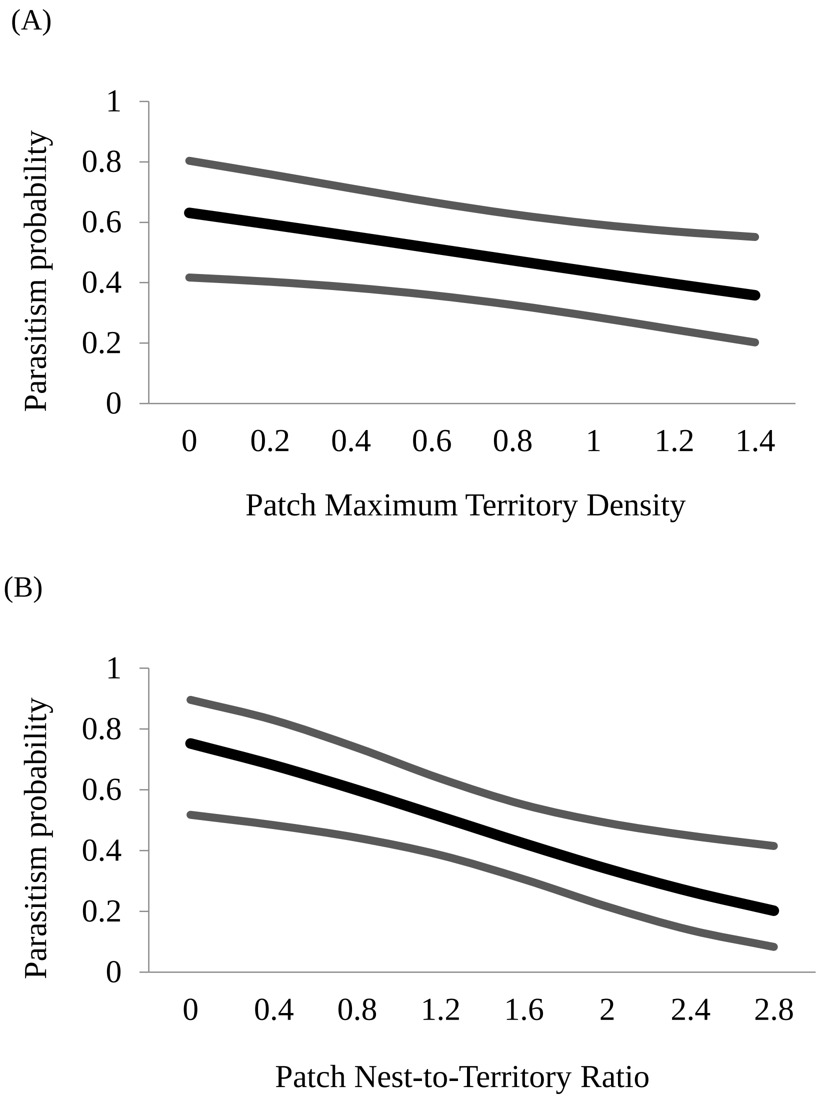
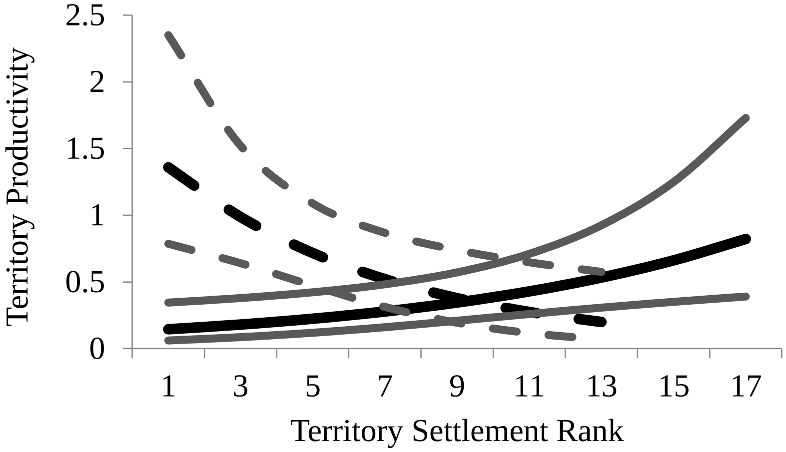


Figure 2.6. Territory productivity—the total number of dickcissel fledglings produced from a territory during its tenure—predicted (A) as a function of territory settlement rank in 2014 (dashed) and 2015 (solid), and (B) as a function of maximum patch territory density. Estimates are for a territory in which exactly one nest is built. Error bars represent 85% confidence intervals. See Appendix E for the number of territories with each settlement rank in each year.

(A)



(B)

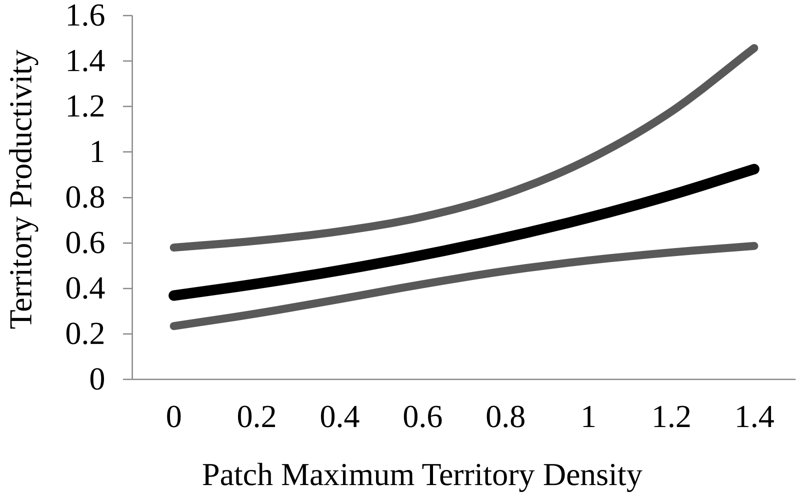


Figure 2.7. Nest productivity—the number of dickcissels predicted to fledge from a nest that produced at least one fledgling—predicted as a function of the nest-to-territory ratio in the patch where the nest is built. Error bars represent 85% confidence intervals.

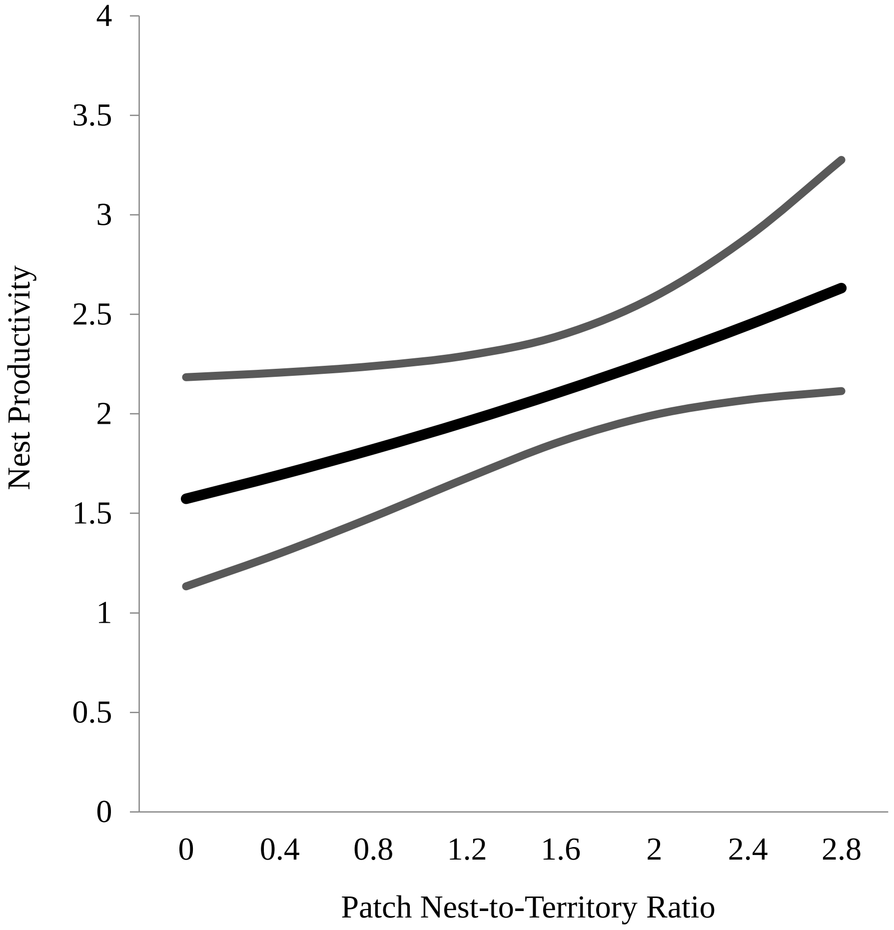
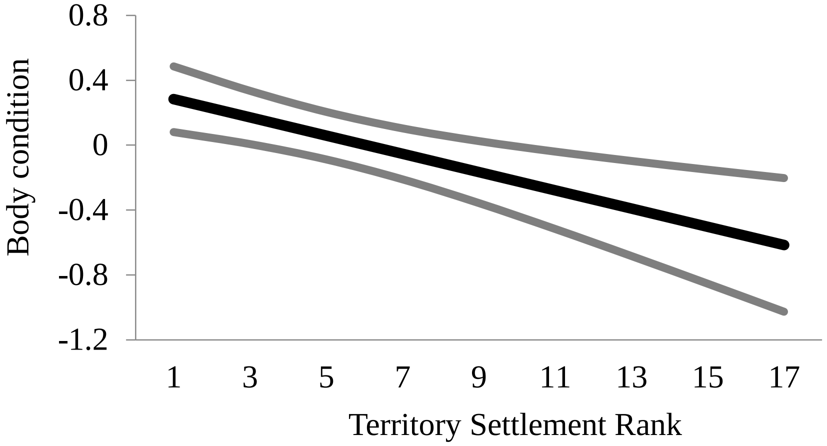


Figure 2.8. Nestling body condition predicted as a function of (A) territory settlement rank, (B) territory polygyny level, and (C) nest-to-territory ratio in the patch where the nestling is reared. Error bars represent 85% confidence intervals.

(A)



(B)

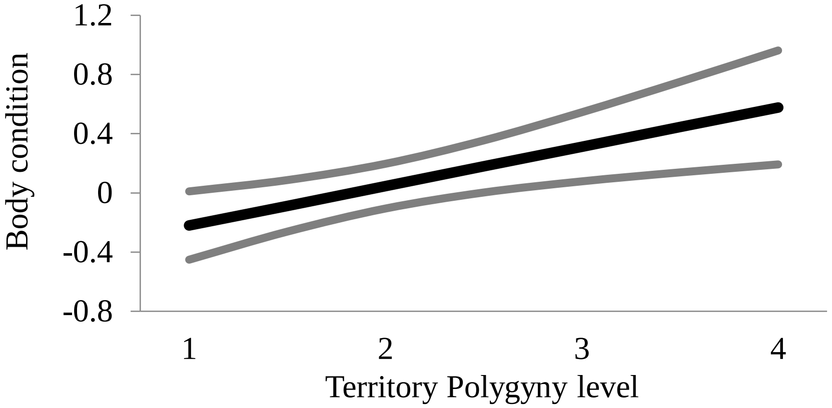
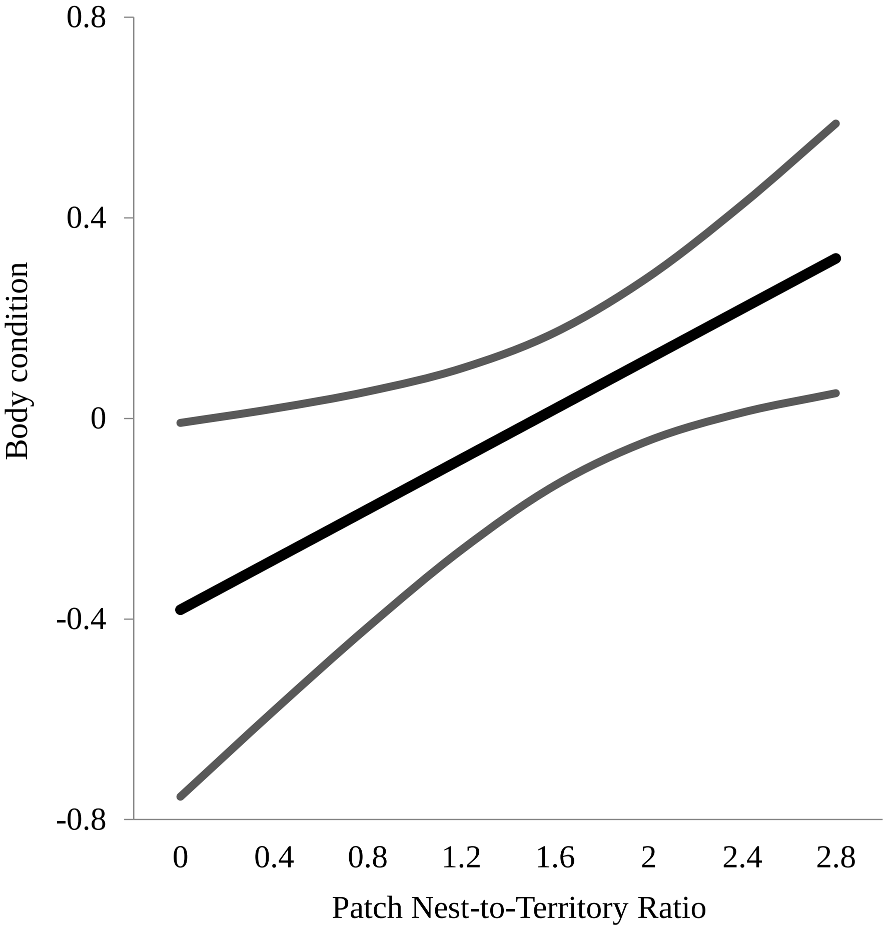


Figure 2.8 continued…

(C)



CHAPTER 3 – DOES VEGETATION MEDIATE ADAPTIVE HABITAT SELECTION BY A GRASSLAND BIRD?[2]

ABSTRACT

Animals are predicted to improve fitness by preferring high-quality patches, but the mechanisms enabling adaptive habitat selection are poorly understood. One possibility is that vegetation mediates fitness (e.g., via effects on predators or food availability) and animals judge habitat quality using vegetation cues. Testing this hypothesis requires measuring vegetation and habitat preferences at several spatial scales, and evaluating multiple reproductive metrics. We used this approach in southern Iowa from 2014-2015, studying the dickcissel (*Spiza americana*), a grassland songbird that prefers habitats associated with high offspring body condition and infrequent brood parasitism by brown-headed cowbirds (*Molothrus ater*). To assess whether dickcissels chose high-quality habitats using plant cues, we assessed whether vegetation features predicted male and female habitat preferences and compared these features to mate attraction, parasitism, fledgling production, and offspring condition. We found limited evidence that vegetation mediated adaptive habitat selection. Cowbird parasitism declined with increasing woodland in the landscape, offspring condition declined with forb cover in patches, and fledgling production declined with invasive tall fescue (*Schedonorus arundinaceus*) cover in patches—but none of these variables influenced preferences. Moreover, although males preferred dense foliage and heterogeneous litter, neither variable affected reproduction. The only indication that vegetation mediated adaptive habitat selection was that females preferred bare ground in territories, which increased territory fledgling productivity. Most preferences for vegetation were decoupled from fitness, raising questions about the origins of these mismatches and suggesting some species may rely on personal experience or social information for adaptive habitat selection.

---

[2] Authors: *S. B. Maresh Nelson, J. J. Coon, and J. R. Miller.*

INTRODUCTION

A frequent prediction of evolutionary ecology is that animals should exhibit adaptive habitat selection, preferentially settling in habitats where they achieve relatively high fitness (Clark & Shutler, 1999; Chalfoun & Schmidt, 2012). This prediction is based on the presumption that animals capable of identifying high-quality habitats will pass this ability to their young, eventually fixing the behavior in the population (Jaenike & Holt, 1991). While this prediction fails in some cases—such as when historically high-quality habitats become ecological traps (e.g., Robertson & Hutto, 2007; Lamb et al., 2017)—animals frequently achieve high fitness in preferred habitats (Chalfoun & Martin, 2007; McLoughlin et al., 2007; Uboni et al. 2017). The mechanisms enabling adaptive habitat selection, however, are often poorly understood.

Several mechanisms may underlie adaptive habitat selection. Animals may improve fitness by preferentially returning to areas where they have previously been successful (Switzer, 1997; Chalfoun & Martin, 2010) or by using public information (Danchin et al., 2004) to select habitats where conspecifics have succeeded (Forstmeier, 2002; Kelly & Ward, 2017). Animals might also sample direct cues of habitat quality, such as predator and parasite abundance (Forsman & Martin, 2009; Buxton et al., 2017) or prey abundance (Orians & Wittenberger, 1991). However, these direct cues may be difficult for animals to assess due to effort required to gather information, low detectability of predators, or phenological mismatches between habitat selection and peak prey availability.

Instead, animals may rely on proximate vegetation cues as indirect indicators of habitat quality. An expansive body of research has focused on understanding relationships between habitat selection and vegetation, with a longstanding focus on birds (e.g., MacArthur et al., 1966;

Wiens, 1969; Cody, 1981), and evidence shows that vegetation can indirectly impact avian fitness. Plant composition and structure at fine spatial scales mediate nest exposure (Latif et al., 2012), olfactory dynamics (Fogarty et al., 2017), and predator habitat selection (Klug et al., 2010). At broad scales, land cover and edge effects can mediate nest survival and brood parasitism (e.g., by brown-headed cowbirds *Molothrus ater*) via changes in predator and parasite distributions (Chalfoun et al., 2002; Benson et al., 2013; Chiavacci et al., 2018). Furthermore, plant species composition, density, and leaf litter may impact access to arthropods, a food source critical for raising robust offspring (Osborne et al., 2012; Germain et al., 2015).

These linkages suggest that birds may experience pressure to select habitats containing vegetation features that confer fitness benefits (Clark & Shutler, 1999). At the same time, different vegetation features may affect alternative components of avian fitness (e.g., predation, foraging) in different ways, and impacts may vary across spatial scales (Chalfoun & Martin, 2007; Bloom et al., 2013). If this variability is not explicitly considered, key relationships between vegetation, habitat preferences, and fitness may be overlooked.

In this study, we assessed whether a polygynous grassland bird—the dickcissel (*Spiza americana*)—uses vegetation cues to engage in adaptive habitat selection. We measured vegetation and habitat preferences of male and female birds at two spatial scales (territories and broader patches in which they were embedded) and quantified five reproductive metrics (polygyny, cowbird parasitism, nest productivity, territory productivity, and offspring body condition). We have previously found that territories preferred by male and female dickcissels produce nestlings in favorable body condition, while preferred patches are associated with low parasitism risk (Chapter 2). We also demonstrated that in 2014, males preferred territories where they mated with more females and produced more offspring, but males in *less*-preferred territories were more successful in these respects in 2015. Our current aim is to determine whether vegetation cues mediated any of these relationships.

Vegetation might facilitate adaptive habitat selection by dickcissels, given the multiple ways plant composition and structure can influence their distributions and reproduction (reviewed in Dechant et al., 2003). Male dickcissels tend to quickly occupy territories and patches with more forb cover and tall, dense vegetation, and these territories often achieve relatively high levels of polygyny and nest success (Zimmerman, 1971; Harmeson, 1974). At a finer scale, increasing cover of the common invasive grass tall fescue (*Schedonorus arundinaceus*) at dickcissel nest sites in our study region is associated with reduced nest success and increased cowbird parasitism (Maresh Nelson et al., 2018). Tall fescue cover may also affect food availability, given its association with low arthropod biomass (Rudgers & Clay, 2008) and slow arthropod growth (Jokela et al., 2016). These impacts—along with other reported effects of vegetation on dickcissel breeding ecology (Dechant et al., 2003)—indicate that vegetation could be a strong mediating force in adaptive habitat selection.

METHODS

STUDY AREA

We assessed whether vegetation mediated adaptive habitat selection by dickcissels on seven grassland pastures (17.6-41.1 ha in area) in 2014-2015. Pastures were located in the Grand River Grasslands of Ringgold County, Iowa, U.S.A. (Miller et al., 2012; Fig. 2.1). Each pasture was subdivided into three patches (21 patches, 3.5-15.6 ha) treated with divergent management regimes and representing variable plant and avian communities (Appendix B; Duchardt et al., 2016). We considered these patches as distinct replicates in this study.

TERRITORY MAPPING

We mapped dickcissel territories every 3-7 d ($\bar{x}$±SD = 4.9±1.4 d) from 7 May-13 August in 2014 and 8 May-22 August in 2015 (18-23 surveys per pasture per year; Sousa & Westneat, 2013; Joos et al., 2014). Surveys were conducted between 0500-1300 h, and not during precipitation or high wind. To reduce bias, we varied survey routes and pasture survey order (Bibby et al., 2000).

We carried out mapping surveys by completely traversing each study site, conducting focal observations of encountered males (length: $\bar{x}$±SD = 9.4±6.1 min) and recording all perches they used (3.4±1.8 perches per focal observation) with a GPS (Joos et al., 2014). We improved territory mapping by luring as many male dickcissels into mist nets as possible using playbacks, then fitting them with a USGS band and a unique combination of three color-bands. During surveys, observers recorded band combinations and the shape of male throat markings to identify individuals. Each GPS point was assigned to a territory based on band combinations and throat markings of the associated male, as well as perch proximity and simultaneous sightings of other males (Bibby et al., 2000). We constructed territory boundaries using ArcMap 10.5 (ESRI, Redlands, CA, USA), drawing boundaries as minimum convex polygons (Remeš, 2003) around all points where a given territory-owner sang or was seen with a female (28.7±17.6 perches recorded per territory). We only considered a male to hold a territory if observed in ≥2 surveys. Points recorded in different surveys were only considered to be in the same territory if at least one was within 30 m of a location used by the same male in another survey. Tenure of each territory was calculated as the number of days between the territory-owner's first detection and the day after its last detection.

NEST SEARCHING

We searched for dickcissel nests in territories throughout each breeding season, attempting to find every nest built on our study sites. We located nests by observing adult behaviors (Martin & Geupel, 1993), dragging a rope through vegetation (Higgins et al., 1969), and watching for incidental flushes. We recorded nest positions with a GPS and visited them every 1-3 days (Ralph et al., 1996), recording date, time, and nest contents. We weighed and measured the tarsus lengths of nestlings 4-6 days after hatching. Nests found empty before chicks were seven-days old were considered depredated, while nests were considered successful when at least one dickcissel fledged. We confirmed fledging based on parental alarm calls and provisioning.

We assigned each nest to a territory based on location and interactions between the mother and nearby males, and thereby calculated territory productivity (the total number of dickcissels fledged from a given territory throughout its tenure). We determined territory polygyny levels based on the maximum number of nests simultaneously active on a given territory (Orians & Wittenberger, 1991; Sousa & Westneat, 2013). To do this, we determined the initiation date (date first egg was laid) and end date (date of fledging or failure) of each nest. We calculated initiation dates using age estimates from egg-candling and chick development (Lokemoen & Koford, 1996; Temple, 2002) and by assuming one egg laid per day, 12-day incubation periods, and 9-day nestling phases (Sousa & Westneat, 2013; Chapter 2).

In some cases (22 of 193 territories), we deemed it likely that we had failed to find a nest in a territory, as we saw parents feeding fledglings or observed a female in ≥2 surveys far from any known nests. We added one to the polygyny level of these territories to avoid underestimation. Moreover, when we saw parents provisioning nestlings in these territories (seven), we added two fledglings (the median number produced from successful nests) to territory productivity.

VEGETATION MEASUREMENTS

We measured vegetation structure and composition within territories, patches, and surrounding landscapes to explore whether vegetation mediates adaptive habitat selection. We chose vegetation variables based on *a priori* hypotheses of effects on dickcissel habitat selection and fitness (Table 3.1; Dechant et al., 2003; Fisher & Davis, 2010).

We measured vegetation in as many territories as possible at the end of each breeding season, from 30 July-23 August in 2014 and 1-15 September in 2015. We used ArcMap to generate a random point at least 5 m inside each territory and drew a 48-m line transect along a random bearing from this point, such that the entire transect fell inside the territory (24-m transects when 48 m did not fit). We measured vegetation in five 0.5-m^2 quadrats placed every 12 m (or every 6 m, for 24-m transects) along this line (Fig 3.1; modified from Misenhelter & Rotenberry, 2000; Harrison & Green, 2010). In each quadrat, we visually estimated the percent cover of all cool-season grasses combined, the invasive cool-season grass tall fescue (*Schedonorus arundinaceus*) in particular, and of warm-season grasses, forbs, woody plants, standing dead vegetation, litter, and bare ground. We recorded cover estimates as the midpoints of the intervals 0%, 1-5%, 6-25%, 26-50%, 51-75%, 76-95%, or 96-100% (Daubenmire, 1959). At each quadrat, we used a Robel pole to record maximum plant height and estimate vegetation density (the tallest vertical decimeter interval at least 50% obstructed when viewed from 1 m above and 4 m away in each cardinal direction; Robel et al., 1970). Finally, we measured litter depth at three points per quadrat. We calculated averages across the five quadrats to obtain territory-scale estimates for each variable, and we calculated the coefficients of variation (CV) for litter depth and Robel height in each territory (we used CV instead of standard deviation because the latter scales with the mean, leading to issues with multicollinearity; Fraterrigo & Rusak, 2008).

We note that territory vegetation was measured at the end of the breeding season, and thus may have differed from vegetation when birds were selecting habitat. However, our data suggest that relative differences in vegetation at the end of the season reflect differences existing at the beginning of the season. From May-August 2016, we resampled vegetation every month in 63 permanent 0.5-m^2 plots marked on our 7 pastures (3 per patch). On average, quadrats with low levels or high levels of any given vegetation component in May (relative to other quadrats) still exhibited relatively low or high levels, respectively, of those components in August—even if absolute estimates changed over the season (see Appendix F for details and data). The only exceptions to this pattern were seen with maximum vegetation height and CV of Robel height (relative values in May 2016 did not predict relative values in August 2016), so we excluded these variables from our analyses.

In addition to measuring territory-scale vegetation, we measured patch-scale vegetation in July of 2014 and 2015. We placed 30 0.5-m^2 quadrats along previously established line transects in each patch of each pasture (Fig 3.1; Duchardt et al., 2016) and quantified the same variables measured at the territory scale in each quadrat. To derive patch-scale values of variables, we calculated average percent-cover across all 30 quadrats and the average and standard deviation of all Robel and litter-depth estimates.

We quantified land cover within 1000 m of each patch using an aerial orthophoto of Ringgold County from summer 2014 (Iowa Geographic Map Server; Maresh Nelson et al., 2018). We digitized land cover as herbaceous, woodland, row-crop, water, or impervious surface using ArcMap. Classifications of crop versus herbaceous cover were verified using the 2014 National Cropland Data Layer (USDA 2017). To understand the scale at which landscape context had the strongest influences on habitat selection and fitness, we then generated 250-m-, 500-m-, and 1000-m-radius buffers around each patch and calculated the percent of total area within each buffer comprised of herbaceous, row-crop, and woodland cover. Finally, we measured the smallest distance between the centroid of each territory and the nearest patch of woodland as proximity to wooded edges can influence risk of detection by cowbirds and some nest predators (Benson et al., 2013). See Appendix G for averages and ranges of all estimated vegetation metrics.

DATA ANALYSIS

We quantified male habitat preferences at the territory scale assuming territories selected earlier in the season were more highly preferred (Robertson & Hutto, 2006). We assigned each territory a settlement rank based on the relative order in which it was established (Joos et al., 2014). If multiple territories were established in the same location in a given year (overlap >50%), we assigned the later-settled territories the same rank as the first overlapping territory. To avoid pseudoreplication, we only included the overlapping territory with the longest tenure in our analyses.

We quantified male preferences at the patch scale as the maximum territory density recorded on each patch each year (Remeš, 2003; Chalfoun & Martin, 2007). This variable was correlated with ordinal date of first territory establishment on the patch (GLM: $F_{1,\,31} = 12.53$, $p = 0.001$, $R^2 = 0.288$, $\beta_{\text{First Territory Date}} = -0.008 \pm 0.002$ SE). Female preferences at the territory scale were based on territory polygyny levels (see above). Territories where more females nested were assumed more preferred. Last, we quantified female preferences at the patch scale as total nests built on the patch divided by total territories established on the patch per year (nest-to-territory ratios; Zimmerman, 1971). This variable was correlated with ordinal date of first nest initiation on the patch (GLM: $F_{1,\,27} = 7.03$, $p = 0.013$, $R^2 = 0.207$, $\beta_{\text{First Nest Date}} = -0.012 \pm 0.004$ SE).

We documented five metrics of reproductive success. First, territory polygyny levels—identical to our metric of female territory preference—indicated male reproductive success since polygyny often leads to increased fledgling production (Sousa & Westneat, 2013). Frequency of cowbird parasitism (presence or absence of cowbirds in nests) indicated reproductive success of both males and females. Total dickcissel young fledged from all nests in a given territory (territory productivity) served as a direct measure of offspring production by defending males. This was a less direct measure of offspring production by females, however, because multiple mothers may contribute to territory productivity in polygynous territories. We considered the number of dickcissel fledglings produced from individual successful nests (nest productivity) a more direct estimate of female productivity (Benson et al., 2010). Finally, we quantified offspring body condition for each nestling as its residual from a linear regression of nestling mass versus tarsus length across all nestlings (Vitz & Rodewald, 2011). Dickcissel chicks with higher mass adjusted for tarsus length have greater post-fledging survivial (Jones et al., 2017).

All analyses were performed in PROC GLIMMIX (SAS Institute, Cary, NC, USA). Four analyses tested whether vegetation at the territory, patch, or landscape scales influenced male or female habitat preferences, and another four analyses tested whether vegetation affected reproduction. We used a binomial distribution for analyses of cowbird parasitism, and for each other response variable we chose the best distribution—Gaussian, negative binomial, or Poisson—based on which yielded the lowest AIC score and a Pearson chi-squared/df ratio <1.2 (to avoid issues with overdispersion, Littell et al., 2006). We chose whether to include ‘Pasture’, ‘Year’, or

‘Pasture × Year’ as random effects using likelihood-ratio tests. We included ‘NestID’ as a random variable in analyses of nestling condition.

In each analysis, we created a set of candidate models including one univariate model for each territory, patch, and landscape vegetation variable (except we did not include territory vegetation models in analyses of patch-scale habitat preferences). We excluded some vegetation variables (litter cover, patch standing dead vegetation, land cover measured within 500 m of patches) due to redundancy with other variables ($|r|\geq 0.7$; Dormann et al., 2013). All candidate models included appropriate random variables, as well as covariate fixed effects selected in prior work to account for variables influencing habitat preference and fitness unrelated to vegetation (e.g., nest initiation date, territory tenure length, number of nests built in a territory, etc.; Chapter 2). We did not include territory size as a covariate in our analyses because we have previously found this variable does not influence dickcissel fitness or habitat preference (Chapter 2). Each candidate set included a base model with only random variables and covariates. We compared candidate models in each set using an information-theoretic approach. We considered models supported if their Akaike weight was greater than the weight of the respective base model and contributed to the cumulative top 90% of their set’s model weight (Burnham and Anderson 1998: 127).

In several analyses, more than one model contributed to the top 90% model set. To refine identification of vegetation variables influencing each habitat preference and reproductive metric, we conducted a second stage of model selection. Whereas Stage 1 consisted of only univariate models, Stage 2 included additive or interactive combinations of variables selected in Stage 1. We again considered Stage-2 models supported if they contributed to the cumulative top 90% of model weights and had Akaike weight greater than the respective base model. Since this process selected multiple top models containing the same parameters, we used model averaging to calculate weighted slope parameters and predicted values of response variables across the observed ranges of variation of selected vegetation variables (Shaffer and Thompson 2007).

We interpreted our results by comparing vegetation features that influenced habitat preferences to features influencing reproduction. If a given feature was preferred by male or female dickcissels *and* improved their reproduction, we considered this evidence for vegetation-mediated adaptive habitat selection. If preferred vegetation was associated with reduced reproductive success, we considered this potential evidence of a vegetation-mediated ecological trap.

RESULTS

DATA STRUCTURE

Data from one pasture (3 patches) in 2014 were excluded because dickcissels vacated it after a June storm. We mapped 107 territories on the other 6 pastures that year (2014 territory size: $\bar{x}$±SD = 0.75±0.91 ha; median = 0.51 ha). We excluded 24 territories from analyses, where males displaced or encroached on other males' territories, and excluded another 3 where we did not measure vegetation (thus, 80 territories from 2014 were included in analyses). That year we found 149 nests (46 successful) and measured 140 nestlings. We estimated there were seven unfound nests based on repeated observations of females in territories with no known nests. Three of these unfound nests appeared to produce fledglings based on observing provisioning. Sixty-five of the 129 nests that survived to incubation (50.4%) were parasitized.

We mapped 86 territories across all 7 pastures in 2015 (2015 territory size: $\bar{x}$±SD = 1.01±0.84 ha; median = 0.87 ha). We excluded 13 territories from analyses based on male displacement, and another 18 where we did not measure vegetation (thus, 56 territories from 2015 were included in analyses). That year we found 59 nests (13 successful) and measured 42 nestlings. We estimated there were 15 unfound nests, four of which produced fledglings. Nineteen of the 52 nests that survived to incubation (36.5%) were parasitized.

VEGETATION, HABITAT PREFERENCES, AND REPRODUCTIVE SUCCESS

Dickcissel habitat preferences and fitness were independently related to vegetation composition and structure in multiple ways (Tables 3.2 & 3.3). Analyses of territory settlement ranks and maximum patch territory densities showed males preferred patches with heterogeneous litter depth and high vegetation density. Territories in patches with these characteristics were established early in the season (Patch Litter Depth CV: $\beta = -0.0896$, SE = 0.0401, Fig 3.2A; Patch Avg. Robel: $\beta = -0.1732$, SE = 0.0418, Fig 3.2B), and patches with denser vegetation were settled at relatively high densities ($\beta = 0.0564$, SE = 0.0338, Fig 3.2C).

Territories with more bare ground and less standing dead vegetation cover attained high levels of polygyny (Bare Ground: $\beta = 0.0077$, SE = 0.0038, Fig 3.3A; SDV: $\beta = -0.0083$, SE = 0.0048, Fig 3.3B). These patterns indicate that not only did females prefer territories with these characteristics, but also males defending territories with these characteristics were more successful in attracting mates. Although Stage 1 of this analysis suggested polygyny levels may decrease with increasing row-crop cover in the landscape, Stage 2 showed these were uninformative parameters (Arnold 2010). Analysis of female patch-scale preferences supported no relationships between vegetation and nest-to-territory ratios.

Vegetation affected several components of fitness. Nests in landscapes with higher levels of woodland cover within 250 m were less likely to be parasitized ($\beta = -10.47$, SE = 1.77, Fig 3.4), suggesting that both males and females experienced enhanced reproduction there. In contrast, increasing woody cover in territories was weakly associated with reduced nest productivity

(Woody Cover: β = -0.0567, SE = 0.0351, Fig 3.5). We also found negative effects on nestling body condition of territory vegetation density (β = -0.0746, SE = 0.0466, Fig 3.6A) and patch forb cover (β = -0.0092, SE = 0.0127, Fig 3.6B).

The most complex influence of vegetation was on the number of fledglings produced from individual territories. Territory productivity increased with cool-season grass cover in territories, but decreased with tall fescue cover at the patch scale (Territory CSG: β = 0.0251, SE = 0.0067, Fig 3.7A; Patch Tall fescue: β = -0.0409, SE = 0.0103, Fig 3.7B). Moreover, we identified an interaction showing that the positive effect of territory-scale cool-season grass cover decreased with increasing patch-scale tall fescue cover (Territory CSG: β = 0.0272, SE = 0.0079; Patch Tall fescue: β = -0.0258, SE = 0.0306; CSG × Tall fescue: β = -0.0002, SE = 0.0004, Fig 3.7C). Several weaker effects also emerged: territory productivity increased with bare ground in territories (β = 0.0127, SE = 0.0070, Fig 3.7D) and decreased with increasing row-crop cover within 250 m (β = -2.5360, SE = 1.8537, Fig 3.7E) and 1000 m (β = -3.1559, SE = 1.8308, Fig 3.7F) of patches. Although Stage 1 indicated that patch-scale cool-season grass cover was associated with reduced productivity and patch-scale warm-season grass and bare ground cover were associated with increased productivity, we did not include these metrics in Stage 2 since they were correlated with more highly supported variables.

DISCUSSION

Male and female dickcissels preferred specific vegetation features, but the features they preferred had little impact on fitness—even while other vegetation features clearly affected reproductive success (Table 3.3). These results suggest that most vegetation cues we measured did not enable adaptive habitat selection, at least at the scale of territories and grassland patches.

The only exception was that increasing bare ground in territories was associated with both greater polygyny levels (female territory preferences) *and* slightly greater territory productivity (reproductive success). This indicates an adaptive female preference for bare ground. It is important to note a caveat here, though. By definition of polygyny, multiple females nested on preferred territories, so we do not know that high fledgling production from these territories benefitted each female. If *nest* productivity had increased with bare ground, the conclusion would be more definitive—but it did not. Caveat aside, females responded to this cue, raising the question of why bare ground improved productivity. At nest-site scales, bare ground can reduce nest survival due to poor concealment (Davis, 2005), but at broader scales, high levels of bare ground may discourage some nest predators—such as snakes, which avoid recently burned areas with lots of bare ground—from foraging nearby (Lyons et al., 2015). Moreover, bare ground can increase avian foraging efficiency due to improved access to arthropods (Doxon & Carroll, 2010; Osborne 2010). This might increase chick survival to fledging, and thus territory productivity.

Other vegetation components also clearly influenced reproduction. Woodland cover in landscapes reduced cowbird parasitism; forb cover at patch scales and Robel height in territories reduced nestling condition; woody cover in territories reduced nest productivity; cool-season grasses had mixed effects on territory productivity; and row-crop cover in landscapes reduced territory productivity. However, none of these areas were preferred by dickcissels. So why could dickcissels not use these cues to select high-quality habitats?

One hypothesis is that relationships of some vegetation features with reproduction have arisen too recently. For example, extensive cultivation of corn and soybeans in the Midwest only began in the nineteenth century (Warner, 1994), so birds may not yet view crop fields as a landscape feature to avoid. Similarly, the dominant cool-season grasses in the Grand River Grasslands—including not only smooth brome (*Bromus inermis*), Kentucky bluegrass (*Poa pratensis*), and orchard grass (*Dactylis glomerata*), which improved fledgling production, but also tall fescue, which was detrimental—were introduced to the U.S. from Eurasia in recent centuries for cattle forage (Barnes, 1995; Ellis-Felege et al., 2013). Historically, tallgrass prairies were dominated by warm-season grasses, which differ from the non-native cool-season species in physical structure and growth phenology. Birds may not have had enough time to evolve appropriate preferences regarding non-native grasses—let alone to specific species.

This explanation echoes reports that anthropogenic changes create ecological traps, such that previously reliable cues now lead animals to poor-quality habitats (Robertson & Hutto, 2007; Hale & Swearer, 2016). Essentially, human activity can scramble animals' abilities to rely on evolved preferences for vegetation cues. Even if animals are not attracted to poor habitats *per se*, they may still experience 'equal-preference traps' (sensu Robertson & Hutto, 2006), wherein they at least do not avoid unfavorable areas. Our results support this situation, since dickcissels did not avoid features like row-crop fields and invasive tall fescue despite their negative relationship with reproductive success.

An alternative, though not mutually exclusive, hypothesis for why vegetation preferences did not correspond with fitness impacts is that effects of vegetation may be too variable among regions for preferences to consistently benefit reproduction. Species like dickcissels, which use a wide variety of grassland habitats within their broad geographic range (Dechant et al., 2003), may be particularly affected by such variation. To illustrate, territory forb cover in Kansas is associated with high polygyny levels in dickcissels (Zimmerman 1971; Harmeson 1974), but we did not observe this pattern in Iowa. This may explain why we found no preference for forbs, contradicting other studies (Zimmerman, 1966; Harmeson, 1974; Finck, 1984; Delisle &

Savidge, 1997). A potential reason for this discrepancy is that dickcissels in our study region used a wide variety of nest substrates, including forbs (e.g., musk thistle *Carduus nutans*, heath aster *Symphyotrichum ericoides*), low shrubs (e.g., buckbrush *Symphoricarpos orbiculatus*, osage orange *Maclura pomifera*), and warm-season bunchgrasses (e.g., big bluestem *Andropogon gerardii*, indiangrass *Sorghastrum nutans*). Since previous authors have attributed preference for forbs to the nest sites they afford, dickcissels may not have needed to gravitate towards forbs in the Grand River Grasslands. Other nest substrates were available.

Cowbird parasitism provides another example of vegetation having inconsistent effects on fitness among regions. Parasitism rates were low in patches with high woodland cover within 250 m, a pattern other authors have attributed to cowbirds preferentially parasitizing woodland-breeding hosts (Pietz et al., 2009; Hovick et al., 2013). This pattern may not be universal, however, since parasitism of dickcissel nests is unrelated to woodland cover around grassland patches in the Flint Hills of Kansas (Jensen & Cully, 2005). This may result from regional differences in total tree cover, as the Great Plains typically has less extensive woodlands than the central Midwest, and may thus harbor fewer alternative cowbird hosts (Hovick & Miller, 2013). We note though that Jensen & Cully (2005) only measured woodland cover within 5-10 km of patches—much broader scales than we examined in our study. Further work should examine the geographic consistency of scale-dependent effects, and also whether regional variation in cowbird parasitism might counteract natural selection for dickcissels to prefer wooded areas.

Parasitism also illustrates another hypothesis to explain poor congruence between vegetation preferences and fitness: tradeoffs among components of reproduction. Even if parasitism consistently declines with local woodland cover, this benefit may be offset in some regions by increased nest predation risk. Proximity of nests to woodland edges is sometimes associated with high levels of nest loss (Johnson & Temple, 1990; Winter et al., 2000), and woodland cover in landscapes can increase predation rates by particular predator species (Chiavacci et al. 2018). Even though these impacts are geographically variable (Benson et al., 2013), they may be common enough to prevent the evolution of preference for woodland-dominated landscapes.

Regardless of why vegetation cues did not enable adaptive habitat selection, the fact remains that dickcissels *did* prefer high-quality habitats. In 2014-2015, both sexes preferred territories where nestling condition was high and patches where parasitism was low. In 2014, males preferred territories that achieved high polygyny levels and produced many fledglings (Chapter 2). What other mechanisms besides vegetation cues might have enabled these behaviors?

Dickcissels may have relied on direct cues of habitat quality, such as abundance of nest predators or cowbirds. Use of the latter cue has been demonstrated in migratory birds in Montana, which settle at lower densities in forests where experimenters broadcast cowbird vocalizations than in forests where playbacks are absent (Forsman & Martin, 2009). Other experiments using playbacks (Emmering & Schmidt, 2011) and predator removals (Fontaine & Martin, 2006) indicate that birds select habitat based on predator abundance as well, although to our knowledge these behaviors have not been examined in grassland species.

Another direct cue birds could use is arthropod abundance and size—perhaps particularly important for improving offspring condition. Several studies of grassland birds (Flanders et al., 2006; Nocera et al., 2009) and other species (Orians & Wittenberger, 1991) have found that avian abundances and habitat preferences are related to insect numbers. However, use of these cues may be limited if arthropods emerge after birds have settled.

Even if they are unable to use proximate habitat cues, birds may rely on personal information or social information to select high-quality habitats (Danchin et al., 2004; Piper, 2011).

For instance, some birds return more frequently to territories and patches where they have previously succeeded (Bollinger & Gavin, 1989; Switzer et al., 1997; Chalfoun & Martin, 2010), and multiple studies have found species preferring areas where conspecifics have been successful (Forstmeier, 2002; Doligez et al., 2004; Betts et al. 2008; Kelly et al., 2017). These findings suggest birds may not need to prospect for proximate cues indicating habitat quality at the start of the breeding season, and instead may rely on experience to choose high-quality habitats.

While it is unclear whether these mechanisms facilitated adaptive habitat selection in our system, our research demonstrates the limitations of studying vegetation cues. Multiple authors have shown that birds prefer to place their nests in specific vegetation features, but these features rarely improve nest success (reviewed in Chalfoun & Schmidt, 2012). Our results expand on this pattern, showing that vegetation preferred in territories and patches can have little bearing on fitness—even when considering multiple components of reproduction. We are not claiming that animal preferences for vegetation never improve fitness (Clark & Shutler, 1999; Chalfoun & Martin, 2007; Quinlan & Green, 2012), but our results indicate that an exclusive focus on adaptive responses to vegetation may be misplaced. We suggest that future studies on adaptive habitat selection via plant cues focus on guiding restoration and conservation. For example, assessments of whether anthropogenic activities (e.g., management, invasive plant introductions) create ecological traps can provide information to avoid attracting animals to poor-quality habitats (Lloyd & Martin, 2005; Robertson & Hutto, 2007; Yoon & Read, 2016). Studies without an applied purpose, however, may find that focusing solely on vegetation cues reveals little about how animals engage in adaptive habitat selection.

Our study highlights these points. The finding that tall fescue reduces dickcissel productivity supports the idea that controlling this invasive grass may benefit grassland wildlife (Coley et al., 1995; Osborne et al. 2012; Lyons et al. 2015; Jokela et al, 2016; Chapter 4, Maresh Nelson et al., 2018). Even so, our study could not discern how dickcissels selected high-quality habitats since we did not examine mechanisms other than responses to vegetation cues. We suggest that future studies be more holistic, examining proximate cues as well as social and personal information (e.g., Nocera et al., 2009). This approach may more successfully illuminate the complex suites of behaviors enabling adaptive habitat selection.

LITERATURE CITED

Arnold, T. W. (2010). Uninformative parameters and model selection using Akaike's Information Criterion. *Journal of Wildlife Management*, **74**, 1175-1178. 10.2193/2009-367

Barnes, T. G., Madison, L. A., Sole, J. D., & Lacki, M. J. (1995). An assessment of habitat quality for northern bobwhite in tall fescue-dominated fields. *Wildlife Society Bulletin*, **23**, 231-237.

Benson, T. J., Anich, N. M., Brown, J. D., & Bednarz, J. C. (2010). Habitat and landscape effects on brood parasitism, nest survival, and fledgling production in Swainson's warblers. *Journal of Wildlife Management*, **74**, 81-93. 10.2193/2008-442

Benson, T. J., Chiavacci, S. J., & Ward, M. P. (2013). Patch size and edge proximity are useful predictors of brood parasitism but not nest survival of grassland birds. *Ecological Applications*, **23**, 879-887.

Betts, M. G., Hadley, A. S., Rodenhouse, N., & Nocera, J. J. (2008). Social information trumps vegetation structure in breeding-site selection by a migrant songbird. *Proceedings of the Royal Society B-Biological Sciences*, **275**, 2257-2263. 10.1098/rspb.2008.0217

Bibby, C. J., Burgess, N. D., & Hill, D. A. 2000. Bird census techniques. 2nd edition. Academic Press, Inc., London.

Bloom, P. M., Clark, R. G., Howerter, D. W., & Armstrong, L. M. (2013). Multi-scale habitat selection affects offspring survival in a precocial species. *Oecologia*, **173**, 1249-1259. 10.1007/s00442-013-2698-4

Bollinger, E. K., & Gavin, T. A. (1989). The effects of site quality on breeding-site fidelity in bobolinks. *Auk*, **106**, 584-594.

Burnham, K. P., & Anderson, D. R. (1998). Model selection and inference: a practical information-theoretic approach. Springer, New York, NY.

Buxton, V. L., Ward, M. P., & Sperry, J. H. (2017). Frog breeding pond selection in response to predators and conspecific cues. *Ethology*, **123**, 397-404. 10.1111/eth.12608

Chalfoun, A. D., & Martin, T. E. (2007). Assessments of habitat preferences and quality depend on spatial scale and metrics of fitness. *Journal of Applied Ecology*, **44**, 983-992. 10.1111/j.1365-2664.2007.01352.x

Chalfoun, A. D., & Martin, T. E. (2010). Facultative nest patch shifts in response to nest predation risk in the Brewer's sparrow: a "win-stay, lose-switch" strategy? *Oecologia*, **163**, 885-892. 10.1007/s00442-010-1679-0

Chalfoun, A. D., & Schmidt, K. A. (2012). Adaptive breeding-habitat selection: is it for the birds? *Auk*, **129**, 589-599. 10.1525/auk.2012.129.4.589

Chalfoun, A. D., Thompson, F. R., & Ratnaswamy, M. J. (2002). Nest predators and fragmentation: a review and meta-analysis. *Conservation Biology*, **16**, 306-318. 10.1046/j.1523-1739.2002.00308.x

Chiavacci, S. J., Benson, T. J., & Ward, M. P. (2018). Linking landscape composition to predator-specific nest predation requires examining multiple landscape scales. *Journal of Applied Ecology*, **55**, 2082-2092. 10.1111/1365-2664.13090

Clark, R. G., & Shutler, D. (1999). Avian habitat selection: pattern from process in nest-site use by ducks? *Ecology*, **80**, 272-287. 10.1890/0012-9658(1999)080[0272:ahspfp]2.0.co;2

Cody, M. L. (1981). Habitat selection in birds - the roles of vegetation structure, competitors, and productivity. *Bioscience*, **31**, 107-113. 10.2307/1308252

Coley, A. B., Fribourg, H. A., Pelton, M. R., & Gwinn, K. D. (1995). Effects of tall fescue endophyte infestation on relative abundance of small mammals. *Journal of Environmental Quality*, **24**, 472-475. 10.2134/jeq1995.00472425002400030012x

Danchin, E., Giraldeau, L. A., Valone, T. J., & Wagner, R. H. (2004). Public information: from nosy neighbors to cultural evolution. *Science*, **305**, 487-491. 10.1126/science.1098254

Daubenmire, R. (1959). A canopy-coverage method of vegetational analysis. *Northwest Science*, **33**, 43-64.

Davis, S. K. (2005). Nest-site selection patterns and the influence of vegetation on nest survival of mixed-grass prairie passerines. *Condor*, **107**, 605-616. 10.1650/0010-5422(2005)107[0605:nspati]2.0.co;2

Dechant, J. A., Sondreal, M. L., Johnson, D. H., Igl, L. D., Goldade, C. M., Zimmerman, A. L., & Euliss, B. R. (2003). Effects of management practices on grassland birds: dickcissel. *Northern Prairie Wildlife Research Center*.

Delisle, J. M., & Savidge, J. A. (1997). Avian use and vegetation characteristics of Conservation Reserve Program fields. *Journal of Wildlife Management*, **61**, 318-325. 10.2307/3802587

Doligez, B., Pärt, T., & Danchin, E. (2004). Prospecting in the collared flycatcher: gathering public information for future breeding habitat selection? *Animal Behaviour*, **67**, 457-466. 10.1016/j.anbehav.2003.03.010

Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., . . . Lautenbach, S. (2013). Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, **36**, 27-46. doi:10.1111/j.1600-0587.2012.07348.x

Doxon, E. D., & Carroll, J. P. (2010). Feeding ecology of ring-necked pheasant and northern bobwhite chicks in Conservation Reserve Program fields. *Journal of Wildlife Management*, **74**, 249-256. 10.2193/2008-522

Duchardt, C. J., Miller, J. R., Debinski, D. M., & Engle, D. M. (2016). Adapting the fire-grazing interaction to small pastures in a fragmented landscape for grassland bird conservation. *Rangeland Ecology & Management*, **69**, 300-309. 10.1016/j.rama.2016.03.005

Ellis-Felege, S. N., Dixon, C. S., & Wilson, S. D. (2013). Impacts and management of invasive cool-season grasses in the Northern Great Plains: challenges and opportunities for wildlife. *Wildlife Society Bulletin*, **37**, 510-516. 10.1002/wsb.321

Emmering, Q. C., & Schmidt, K. A. (2011). Nesting songbirds assess spatial heterogeneity of predatory chipmunks by eavesdropping on their vocalizations. *Journal of Animal Ecology*, **80**, 1305-1312. 10.1111/j.1365-2656.2011.01869.x

Finck, E. J. (1984). Male dickcissel behavior in primary and secondary habitats. *Wilson Bulletin*, **96**, 672-680.

Fisher, R. J., & Davis, S. K. (2010). From Wiens to Robel: a review of grassland-bird habitat selection. *Journal of Wildlife Management*, **74**, 265-273. 10.2193/2009-020

Flanders, A. A., Kuvlesky, W. P., Ruthven, D. C., Zaiglin, R. E., Bingham, R. L., Fulbright, T. E., . . . Brennan, L. A. (2006). Effects of invasive exotic grasses on South Texas rangeland breeding birds. *Auk*, **123**, 171-182. 10.1642/0004-8038(2006)123[0171:eoiego]2.0.co;2

Fogarty, D. T., Elmore, R. D., Fuhlendorf, S. D., & Loss, S. R. (2017). Influence of olfactory and visual cover on nest site selection and nest success for grassland-nesting birds. *Ecology and Evolution*, **7**, 6247-6258. 10.1002/ece3.3195

Fontaine, J. J., & Martin, T. E. (2006). Habitat selection responses of parents to offspring predation risk: an experimental test. *American Naturalist*, **168**, 811-818. 10.1086/508297

Forsman, J. T., & Martin, T. E. (2009). Habitat selection for parasite-free space by hosts of parasitic cowbirds. *Oikos*, **118**, 464-470. 10.1111/j.1600-0706.2008.17000.x

Forstmeier, W. (2002). Benefits of early arrival at breeding grounds vary between males. *Journal of Animal Ecology*, **71**, 1-9. 10.1046/j.0021-8790.2001.00569.x

Fraterrigo, J. M., & Rusak, J. A. (2008). Disturbance-driven changes in the variability of ecological patterns and processes. *Ecology Letters*, **11**, 756-770. 10.1111/j.1461-0248.2008.01191.x

Fretwell, S. D., & Lucas, H. L. J. (1969). On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheoretica*, **19**, 16-36.

Germain, R. R., Schuster, R., Delmore, K. E., & Arcese, P. (2015). Habitat preference facilitates successful early breeding in an open-cup nesting songbird. *Functional Ecology*, **29**, 1522-1532. 10.1111/1365-2435.12461

Hale, R., & Swearer, S. E. 2016. Ecological traps: current evidence and future directions. Proceedings of the Royal Society B-Biological Sciences, **283**, 20152647. 10.1098/rspb.2015.2647

Harmeson, J. P. (1974). Breeding ecology of the dickcissel. *Auk*, **91**, 348-359.

Harrison, M. L., & Green, D. J. (2010). Vegetation influences patch occupancy but not settlement and dispersal decisions in a declining migratory songbird. *Canadian Journal of Zoology*, **88**, 148-160. 10.1139/z09-125

Higgins, K. F., Kirsch, L. M., & Ball, I. J. (1969). A cable-chain device for locating duck nests. *Journal of Wildlife Management*, **33**, 1009-1011. 10.2307/3799339

Hovick, T. J., & Miller, J. R. (2013). Broad-scale heterogeneity influences nest selection by brown-headed cowbirds. *Landscape Ecology*, **28**, 1493-1503. 10.1007/s10980-013-9896-7

Hovick, T. J., Miller, J. R., Dinsmore, S. J., Engle, D. M., Debinski, D. M., & Fuhlendorf, S. D. (2012). Effects of fire and grazing on grasshopper sparrow nest survival. *Journal of Wildlife Management*, **76**, 19-27. 10.1002/jwmg.243

Jaenike, J., & Holt, R. D. (1991). Genetic-variation for habitat preference - evidence and explanations. *American Naturalist*, **137**, S67-S90. 10.1086/285140

Jensen, W. E., & Cully, J. F. (2005). Geographic variation in brown-headed cowbird (*Molothrus ater*) parasitism on dickcissels (*Spiza americana*) in Great Plains tallgrass prairie. *Auk*, **122**, 648-660. 10.1642/0004-8038(2005)122[0648:gvibcm]2.0.co;2

Johnson, R. G., & Temple, S. A. (1990). Nest predation and brood parasitism of tallgrass prairie birds. *Journal of Wildlife Management*, **54**, 106-111. 10.2307/3808909

Jokela, K. J., Debinski, D. M., & Mcculley, R. L. (2015). Effects of tall fescue and its fungal endophyte on the development and survival of tawny-edged skippers (Lepidoptera: Hesperiidae). *Environmental Entomology*, **pii**, 1-10.

Jones, T. M., Ward, M. P., Benson, T. J., & Brawn, J. D. (2017). Variation in nestling body condition and wing development predict cause-specific mortality in fledgling dickcissels. *Journal of Avian Biology*, **48**, 439-447. 10.1111/jav.01143

Joos, C. J., Thompson, F. R., III, & Faaborg, J. (2014). The role of territory settlement, individual quality, and nesting initiation on productivity of Bell's vireos *Vireo bellii bellii*. *Journal of Avian Biology*, **45**, 584-590. 10.1111/jav.00400

Kelly, J. K., & Ward, M. P. (2017). Do songbirds attend to song categories when selecting breeding habitat? A case study with a wood warbler. *Behaviour*, **154**, 1123-1144. 10.1163/1568539x-00003461

Klug, P. E., Jackrel, S. L., & With, K. A. (2010). Linking snake habitat use to nest predation risk in grassland birds: the dangers of shrub cover. *Oecologia*, **162**, 803-813. 10.1007/s00442-009-1549-9

Lamb, C. T., Mowat, G., McLellan, B. N., Nielsen, S. E., & Boutin, S. (2017). Forbidden fruit: human settlement and abundant fruit create an ecological trap for an apex omnivore. *Journal of Animal Ecology*, **86**, 55-65. 10.1111/1365-2656.12589

Latif, Q. S., Heath, S. K., & Rotenberry, J. T. (2012). How avian nest site selection responds to predation risk: testing an adaptive peak hypothesis. *Journal of Animal Ecology*, **81**, 127-138. 10.1111/j.1365-2656.2011.01895.x

Littell, R. C., Milliken, G. A., Stroup, W. W., Wolfinger, R. D., & Schanbenberger, O. 2006. SAS for mixed models. 2 edition. SAS Institute Inc., Cary, NC, USA.

Lloyd, J. D., & Martin, T. E. (2005). Reproductive success of chestnut-collared longspurs in native and exotic grassland. *Condor*, **107**, 363-374. 10.1650/7701

Lokemoen, J. T., & Koford, R. R. (1996). Using candlers to determine the incubation stage of passerine eggs. *Journal of Field Ornithology*, **67**, 660-668.

Lyons, T. P., Miller, J. R., Debinski, D. M., & Engle, D. M. (2015). Predator identity influences the effect of habitat management on nest predation. *Ecological Applications*, **25**, 1596-1605. 10.1890/14-1641.1

MacArthur, R., Recher, H., & Cody, M. (1966). On relation between habitat selection and species diversity. *American Naturalist*, **100**, 319-&. 10.1086/282425

Maresh Nelson, S. B., Coon, J. J., Duchardt, C. J., Miller, J. R., Debinski, D. M., & Schacht, W. H. (2018). Contrasting impacts of invasive plants and human-altered landscape context on nest survival and brood parasitism of a grassland bird. *Landscape Ecology*, **33**, 1799-1813. 10.1007/s10980-018-0703-3

Martin, T. E., & Geupel, G. R. (1993). Nest-monitoring plots - methods for locating nests and monitoring success. *Journal of Field Ornithology*, **64**, 507-519.

McLoughlin, P. D., Gaillard, J. M., Boyce, M. S., Bonenfant, C., Messier, F., Duncan, P., . . . Klein, F. (2007). Lifetime reproductive success and composition of the home range in a large herbivore. *Ecology*, **88**, 3192-3201. 10.1890/06-1974.1

Miller, J. R., Morton, L. W., Engle, D. M., Debinski, D. M., & Harr, R. N. (2012). Nature reserves as catalysts for landscape change. *Frontiers in Ecology and the Environment*, **10**, 144-152. 10.1890/100227

Misenhelter, M. D., & Rotenberry, J. T. (2000). Choices and consequences of habitat occupancy and nest site selection in sage sparrows. *Ecology*, **81**, 2892-2901. 10.1890/0012-9658(2000)081[2892:cacoho]2.0.co;2

Nocera, J. J., Forbes, G. J., & Giraldeau, L.-A. (2009). Aggregations from using inadvertent social information: a form of ideal habitat selection. *Ecography*, **32**, 143-152. 10.1111/j.1600-0587.2008.05614.x

Orians, G. H., & Wittenberger, J. F. (1991). Spatial and temporal scales in habitat selection. *American Naturalist*, **137**, 29-49.

Osborne, D. C. 2010. Response of avian, arthropod, and vegetation communities to mid-contract management in Conservation Reserve Program tall fescue monocultures. Southern Illinois University, Carbondale, Southern Illinois University, Carbondale.

Osborne, D. C., Sparling, D. W., & Hopkins, R. L., II. (2012). Influence of conservation reserve program mid-contract management and landscape composition on northern bobwhite in tall fescue monocultures. *Journal of Wildlife Management*, **76**, 566-574. 10.1002/jwmg.258

Patten, M. A., Shochat, E., Reinking, D. L., Wolfe, D. H., & Sherrod, S. K. (2006). Habitat edge, land management, and rates of brood parasitism in tallgrass prairie. *Ecological Applications*, **16**, 687-695. 10.1890/1051-0761(2006)016[0687:helmar]2.0.co;2

Pietz, P. J., Buhl, D. A., Shaffer, J. A., Winter, M., & Johnson, D. H. (2009). Influence of trees in the landscape on parasitism rates of grassland passerine nests in Southeastern North Dakota. *Condor*, **111**, 36-42. 10.1525/cond.2009.080012

Piper, W. H. (2011). Making habitat selection more "familiar": a review. *Behavioral Ecology and Sociobiology*, **65**, 1329-1351. 10.1007/s00265-011-1195-1

Quinlan, S. P., & Green, D. J. (2012). Riparian habitat disturbed by reservoir management does not function as an ecological trap for the yellow warbler (*Setophaga petechia*). *Canadian Journal of Zoology*, **90**, 320-328. 10.1139/z11-138

Ralph, C. J., Geupel, G. R., Pyle, P., Martin, T. E., DeSante, D. F., & Mila, B. (1996). Manual of field methods for monitoring landbirds. *General Technical Report - Pacific Southwest Research Station, USDA Forest Service*, 44 pp.

Remeš, V. (2003). Effects of exotic habitat on nesting success, territory density, and settlement patterns in the blackcap (*Sylvia atricapilla*). *Conservation Biology*, **17**, 1127-1133. 10.1046/j.1523-1739.2003.01611.x

Robel, R. J., Briggs, J. N., Dayton, A. D., & Hulbert, L. C. (1970). Relationships between visual obstruction measurements and weight of grassland vegetation. *Journal of Range Management*, **23**, 295-297. 10.2307/3896225

Robertson, B. A., & Hutto, R. L. (2006). A framework for understanding ecological traps and an evaluation of existing evidence. *Ecology*, **87**, 1075-1085. 10.1890/0012-9658(2006)87[1075:affuet]2.0.co;2

Robertson, B. A., & Hutto, R. L. (2007). Is selectively harvested forest an ecological trap for olive-sided flycatchers? *Condor*, **109**, 109-121. 10.1650/0010-5422(2007)109[109:ishfae]2.0.co;2

Rudgers, J. A., & Clay, K. (2008). An invasive plant-fungal mutualism reduces arthropod diversity. *Ecology Letters*, **11**, 831-840. 10.1111/j.1461-0248.2008.01201.x

Sousa, B. F., & Westneat, D. F. (2013). Positive association between social and extra-pair mating in a polygynous songbird, the dickcissel (*Spiza americana*). *Behavioral Ecology and Sociobiology*, **67**, 243-255. 10.1007/s00265-012-1444-y

Switzer, P. V. (1997). Past reproductive success affects future habitat selection. *Behavioral Ecology and Sociobiology*, **40**, 307-312. 10.1007/s002650050346

Temple, S. A. 2002. Dickcissel (*Spiza americana*).*in* A. Poole, editor. The Birds of North America Online. Cornell Lab of Ornithology, Ithaca.

Uboni, A., Smith, D. W., Stahler, D. R., & Vucetich, J. A. (2017). Selecting habitat to what purpose? The advantage of exploring the habitat-fitness relationship. *Ecosphere*, **8**, 10.1002/ecs2.1705

Vitz, A. C., & Rodewald, A. D. (2011). Influence of condition and habitat use on survival of post-fledgling songbirds. *Condor*, **113**, 400-411. 10.1525/cond.2011.100023

Warner, R. E. (1994). Agricultural land-use and grassland habitat in Illinois - future-shock for Midwestern birds. *Conservation Biology*, **8**, 147-156. 10.1046/j.1523-1739.1994.08010147.x

Wiens, J. A. (1969). An approach to the study of ecological relationships among grassland birds. *Ornithological Monographs*, **No. 8**, 1-93.

Winter, M., Johnson, D. H., & Faaborg, J. (2000). Evidence for edge effects on multiple levels in tallgrass prairie. *Condor*, **102**, 256-266. 10.1650/0010-5422(2000)102[0256:efeeom]2.0.co;2

Yoon, S., & Read, Q. (2016). Consequences of exotic host use: impacts on Lepidoptera and a test of the ecological trap hypothesis. *Oecologia*, **181**, 985-996. 10.1007/s00442-016-3560-2

Zimmerman, J. L. (1971). The territory and its density dependent effect in *Spiza americana*. *Auk*, **88**, 591-612. 10.2307/4083752

TABLES

Table 3.1. Ecological justifications for including each metric of plant structure and composition in our assessments of whether vegetation mediates relationships between habitat selection and reproductive success.

Variable	**Hypotheses and justifications**
Cool-season grasses	Cool-season grasses (including tall fescue) have been linked to reduced nest success of grasshopper sparrows in our study region (Hovick et al., 2012). These grasses may provide poor nest concealment (increasing risk of predation by visual predators) or reduce air turbulence (increasing risk of predation by olfactory predators).
Tall Fescue	Tall fescue has been specifically linked to reduced nest success of dickcissels and grasshopper sparrows in our study region (Lyons et al., 2015; Maresh Nelson et al., 2018). This grass may provide poor nest concealment (increasing risk of predation by visual predators), reduce air turbulence (increasing risk of predation by olfactory predators), or reduce arthropod biomass
Warm-season grasses	Warm-season grasses provide tall, structurally variable cover, which may increase nest concealment and air turbulence.
Forbs	Forb cover is frequently associated with increased dickcissel abundances in patches and has been linked to increase polygyny levels (Zimmerman, 1971; Dechant et al., 2003).
Woody plants	Woody cover near nests may increase cowbird parasitism (Patten et al., 2006) or predation risk by snakes (Klug et al., 2010).
Litter cover	Leaf litter may decrease birds’ abilities to access arthropods, or may provide cover for small nest predators.
Bare ground	Bare ground may increase birds’ abilities to access arthropods.
Standing dead vegetation	Standing dead vegetation may be a salient visual cue in the early summer when territories are being established, or decrease birds’ abilities to access arthropods.
Litter depth (Avg)	Increasing litter depth may decrease access to arthropods, or may provide cover for small nest predators.
Litter depth (CV)	Increasing heterogeneity of litter depth may provide a balance of habitat for arthropods and accessibility for birds feeding on them, or provide nest sites in litter clumps.
Robel height (Avg)	Increasing vegetation density could improve nest concealment and disrupt odor detection (Fogarty et al., 2017).

Table 3.1 continued…

Variable	**Hypotheses and justifications**
Robel height (CV)	Increasing heterogeneity of vegetation density could reduce predator search efficiency.
Maximum plant height	Increasing vegetation height could improve nest concealment and disrupt odor detection (Fogarty et al., 2017).
Herbaceous cover	Decreasing herbaceous cover in the landscape may alter the abundance or foraging behaviors of grassland-dependent nest predators (e.g., badgers, racers).
Row-crop cover	Row-crop fields produce limited food during the summer, causing omnivores to forage more in grasslands when crops are prevalent in the landscape; or crop edges may support higher abundances of mesocarnivores (Chalfoun et al., 2002).
Woodland cover	Cowbirds may prefer to parasitize woodland birds, so parasitism may be less common when tree cover is prevalent in the landscape (Maresh Nelson et al., 2018), or fragmented woodlands could support higher abundances of mesocarnivores (Chalfoun et al., 2002).
Distance to Woods [c]	Proximity to woods may increase predation and parasitism (Benson et al., 2013).

Table 3.2. AIC comparisons of models examining relationships between vegetation metrics and (A) territory settlement rank, (B) maximum patch territory density, (C) territory polygyny level, (D) patch nests-to-territory ratios, (E) brood parasitism risk, (F) nest productivity, (G) territory productivity, and (H) nestling body condition. Only base models and supported candidate models (i.e., models in the 90% cumulative model-weight set and with ΔAIC_c less than the base model) are shown. See Appendix H for complete AIC tables.

Model	k	Deviance	ΔAIC_c	Model weight (ω)
(A) Territory Settlement Rank[a,b]				
Stage 1: Univariate vegetation models				
Patch_AvgRobel	5	675.86	0.00	0.680
Patch_AvgLitterDepth	5	677.83	1.97	0.254
Base	4	689.02	11.00	0.003
Stage 2: Refining selected variables				
Patch_AvgRobel + Patch_AvgLitterDepth	6	671.20	0.00	0.714
Patch_AvgRobel	5	675.86	2.47	0.208
Patch_AvgLitterDepth	5	677.83	4.44	0.078
Base	4	689.02	13.47	0.001
(B) Maximum Patch Territory Density[a]				
Stage 1: Univariate vegetation models				
Patch_AvgRobel	5	29.86	1.40	0.114
Base	4	32.37	1.41	0.114
(C) Territory Polygyny Level[c]				
Stage 1: Univariate vegetation models				
Terr_Bare	4	329.18	0.00	0.158
Terr_SDV	4	329.79	0.48	0.124
Patch_Bare	4	330.57	1.39	0.079
Crop250	4	330.93	1.74	0.066
Crop1000	4	331.39	2.21	0.052
Base	3	333.66	2.36	0.049
Stage 2: Refining selected variables[c]				
Terr_Bare + Terr_SDV	5	326.79	0.00	0.220
Terr_Bare	4	329.18	0.39	0.181
Terr_Bare + Terr_SDV + Crop250	6	325.45	0.81	0.147
Terr_SDV	4	329.79	0.87	0.143
Terr_Bare + Terr_SDV + Crop1000	6	326.56	1.92	0.084
Crop250	4	330.93	2.13	0.076

Table 3.2 continued…

Model	**k**	**Deviance**	**ΔAIC_c**	**Model weight (ω)**
Crop1000	4	331.39	2.60	0.060
Base	3	333.66	2.75	0.056
(D) Nest-to-territory Ratio[d]				
Stage 1: Univariate vegetation models				
Base	4	47.89	0	0.154
(E) Brood Parasitism Risk[e]				
Stage 1: Univariate vegetation models[a]				
Woodland250	5	193.79	0.00	0.921
Base	4	207.24	11.45	0.003
(F) Nest Productivity[f]				
Stage 1: Univariate vegetation models				
Terr_Woody	3	199.16	0	0.129
Base	2	202.25	0.89	0.083
(G) Territory Productivity[g]				
Stage 1: Univariate vegetation models				
Terr_CSG	5	363.09	0.00	0.177
Patch_Fescue	5	363.92	0.83	0.117
Terr_Bare	5	364.58	1.49	0.084
Patch_CSG	5	364.75	1.66	0.077
Crop1000	5	364.80	1.71	0.075
Patch_WSG	5	365.93	2.84	0.043
Crop250	5	366.07	2.98	0.040
Patch_Bare	5	366.31	3.22	0.035
Base	4	368.52	3.27	0.034
Stage 2: Refining selected variables				
Terr_CSG + Patch_Fescue + Terr_Bare	7	346.79	0.00	0.215
Terr_CSG + Patch_Fescue + Crop1000	7	347.05	0.26	0.189
Terr_CSG + Patch_Fescue + Terr_Bare + Crop250	8	345.75	1.22	0.117
Terr_CSG + Patch_Fescue + Terr_Bare + Crop1000	8	346.00	1.47	0.103
Terr_CSG × Patch_Fescue + Terr_Bare	8	346.59	2.06	0.077
Terr_CSG + Patch_Fescue + Crop250	7	349.03	2.24	0.070
Terr_CSG × Patch_Fescue + Crop1000	8	346.98	2.45	0.063
Terr_CSG + Patch_Fescue	6	351.73	2.72	0.055
Terr_CSG × Patch_Fescue + Crop250	8	347.89	3.36	0.040
Base	4	368.52	15.16	0.000

Table 3.2 continued…

Model	k	Deviance	ΔAIC$_c$	Model weight (ω)
(H) Nestling Body Condition[h]				
Stage 1: Univariate vegetation models				
Patch_Forbs	5	566.36	0.00	0.150
Terr_AvgRobel	5	566.58	0.22	0.134
Base	4	570.37	1.90	0.058
Stage 2: Refining selected variables				
Patch_Forbs	5	566.36	0.00	0.337
Patch_AvgRobel	5	566.58	0.22	0.302
Patch_Forbs + Patch_AvgRobel	6	564.98	0.76	0.231
Base	4	570.37	1.90	0.130

[a] All models included ‘PastureID × Year’ as a random variable.

[b] All models included ‘Year’ as a covariate.

[c] No models included ‘Patch_Bare’ due to high correlation with ‘Terr_Bare’.

[d] All models included ‘PastureID × Year’ as a random variable. Stage 2 not conducted because no variables were selected in Stage 1.

[e] All models included ‘PastureID’ as a random variable and ‘Nest Initiation Date’ as a covariate. Bare ground and litter depth were not included in this model set due to a lack of *a priori* hypotheses suggesting these variables might influence parasitism. Stage 2 not conducted since only one model was supported in Stage 1.

[f] All models included ‘#BHCO Fledged’ as a covariate.

[g] All models included ‘PastureID × Year’ as a random variable and ‘Total Nests’ as a covariate. No models in Stage 2 included ‘Patch_CSG’ or ‘Patch_WSG’ due to high correlation with ‘Patch_Fescue’, or ‘Patch_Bare’ due to high correlation with ‘Terr_Bare’.

[h] All models included ‘NestID’ as a random variable and ‘Time of Day’ as a covariate.

Table 3.3. Summary of how habitat preferences and reproductive success of dickcissels were influenced by each component of vegetation structure and composition measured at territory, patch, and landscape scales. For each habitat preference metric, we show whether dickcissels preferred or avoided territories (settlement rank, ♂; polygyny level, ♀) and patches (maximum territory density, ♂; nest-to-territory (N-T) ratio, ♀) with increasing levels of the vegetation component. For each metric of fitness, we indicate whether male or female reproductive success was improved or reduced with increasing levels of the vegetation component.

Habitat variables	**Habitat preference metrics**				**Reproductive metrics**			
	Territory Settlement Rank	Max. Territory Density	Territory Polygyny Level	N-T Ratio	Cowbird Parasitism	Nest Productivity	Territory Productivity	Nestling Body Condition
Territory-scale								
Avg. of Robel height	=	NA	=	NA	=	=	=	Reduced (♂♀)
Avg. of litter depth	=	NA	=	NA	=	=	=	=
CV of litter depth	=	NA	=	NA	=	=	=	=
Standing dead	=	NA	Avoided (♀)	NA	=	=	=	=
Bare ground	=	NA	Preferred (♀)	NA	=	=	Improved (♂♀)	=
Warm-season grass	=	NA	=	NA	=	=	=	=
Cool-season grass	=	NA	=	NA	=	=	Improved (♂♀)	=
Tall fescue	=	NA	=	NA	=	=	=	=
Forb	=	NA	=	NA	=	=	=	=
Woody	=	NA	=	NA	=	Reduced (♂♀)	=	=
Dist. to tree edge	=	NA	=	NA	=	=	=	=
Patch-scale								
Avg. of Robel height	Preferred (♂)	Preferred (♂)	=	=	=	=	=	=
Avg. of litter depth	Preferred (♂)	=	=	=	=	=	=	=
CV of litter depth	=	=	=	=	=	=	=	=
Bare ground	=	=	=	=	=	=	=	=

Table 3.3 continued…

	Territory Settlement Rank	Max. Territory Density	Territory Polygyny Level	N-T Ratio	Cowbird Parasitism	Nest Productivity	Territory Productivity	Nestling Body Condition
Patch-scale								
Warm-season grass	=	=	=	=	=	=	Improved (♂♀)	=
Cool-season grass	=	=	=	=	=	=	Reduced (♂♀)	=
Tall fescue	=	=	=	=	=	=	Reduced (♂♀)	=
Forb	=	=	=	=	=	=	=	Reduced (♂♀)
Woody	=	=	=	=	=	=	=	=
Landscape-scale								
Herb 250m	=	=	=	=	=	=	=	=
Herb 1000m	=	=	=	=	=	=	=	=
Crop 250m	=	=	=	=	=	=	Reduced (♂♀)	=
Crop 1000m	=	=	=	=	=	=	Reduced (♂♀)	=
Woodland 250m	=	=	=	=	Improved (♂♀)	=	=	=
Woodland 1000m	=	=	=	=	=	=	=	=

FIGURES

Figure 3.1. Schematic of the patch- and territory-scale vegetation sampling design on study pastures. Each pasture was comprised of three patches, and we measured vegetation in 30 0.5-m^2 quadrats per patch. Quadrats (squares) were placed 25 m to either side of 1-3 line transects in each patch. We measured vegetation in 5 0.5-m^2 quadrats per territory (shaded polygon), placing quadrats 12 m apart along a 48-m line transect randomly placed within the territory boundaries.

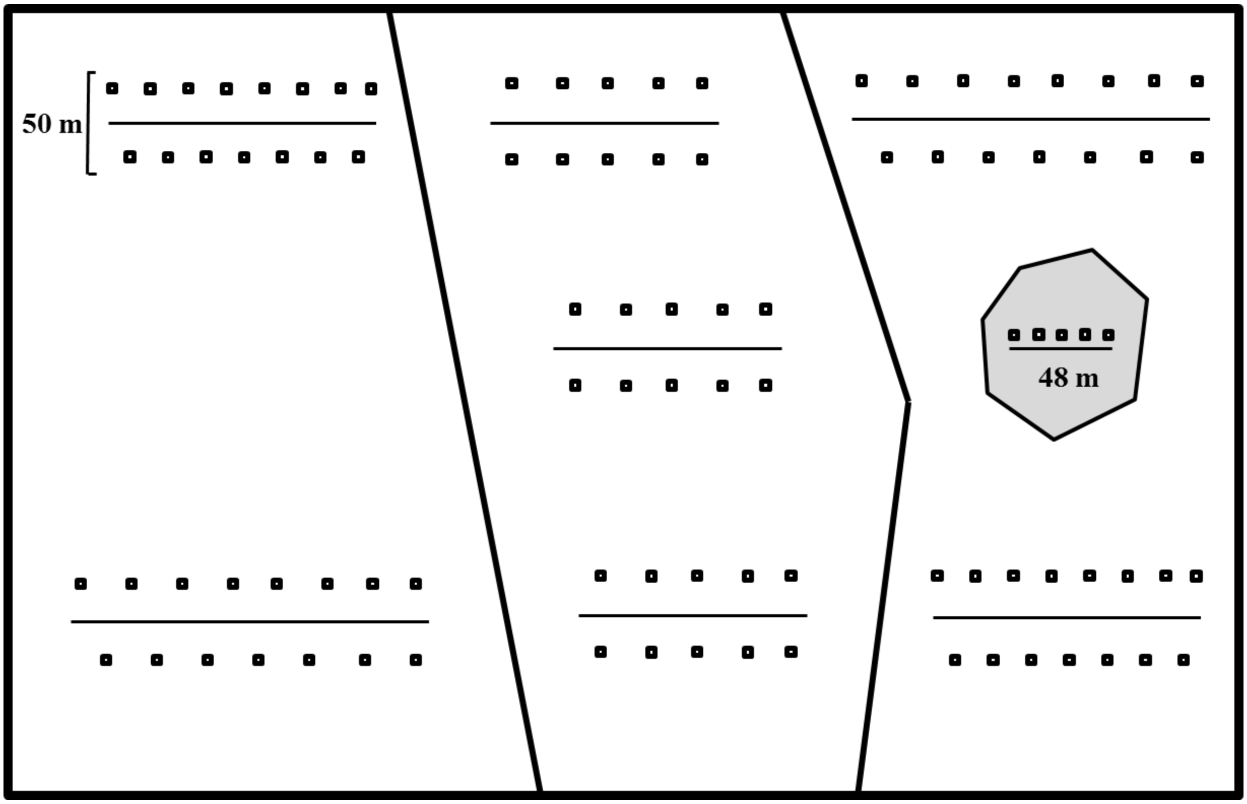


Figure 3.2. Influence of (A) average patch-scale litter depth on territory settlement rank, and of average patch-scale Robel height on (B) territory settlement rank and (C) maximum patch territory density. Error bars represent 85% confidence intervals.

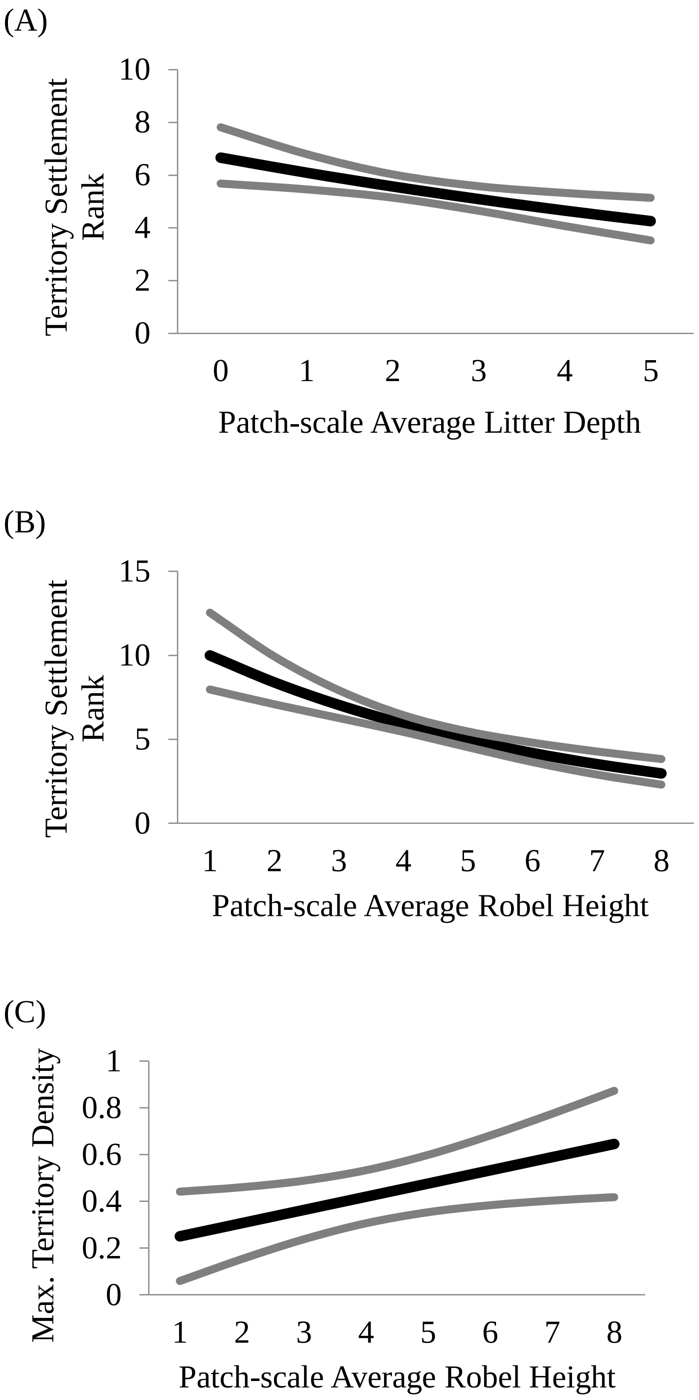
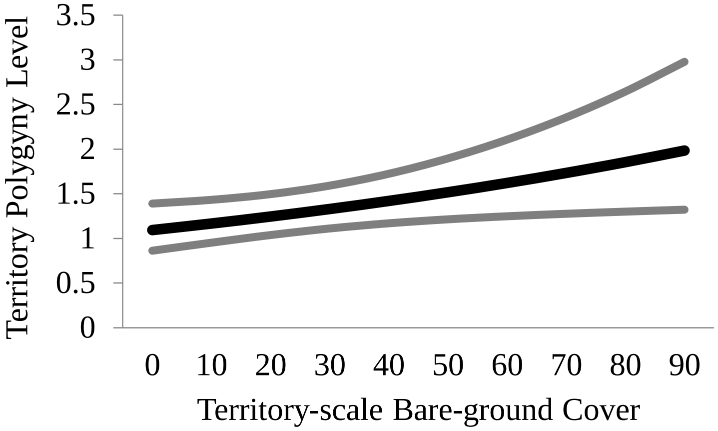


Figure 3.3. Influence of (A) territory-scale bare-ground cover and (B) territory-scale standing dead vegetation cover on territory polygyny levels. Error bars represent 85% confidence intervals.

(A)



(B)

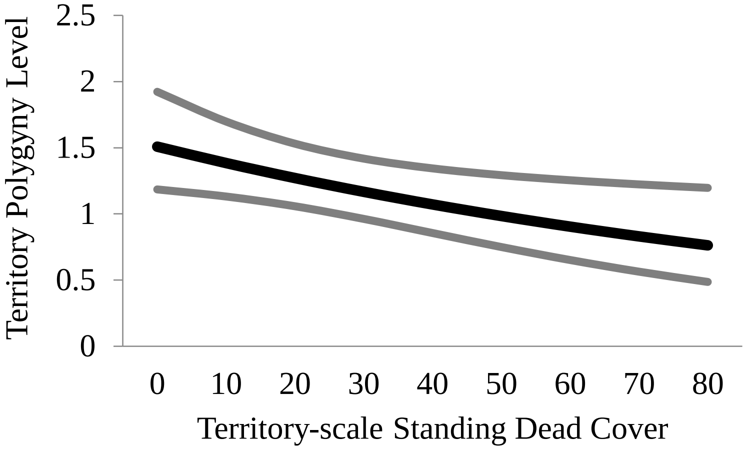


Figure 3.4. Influence of woodland cover within 250 m of patches on the likelihood of nests being parasitzed by brown-headed cowbirds. Error bars represent 85% confidence intervals.

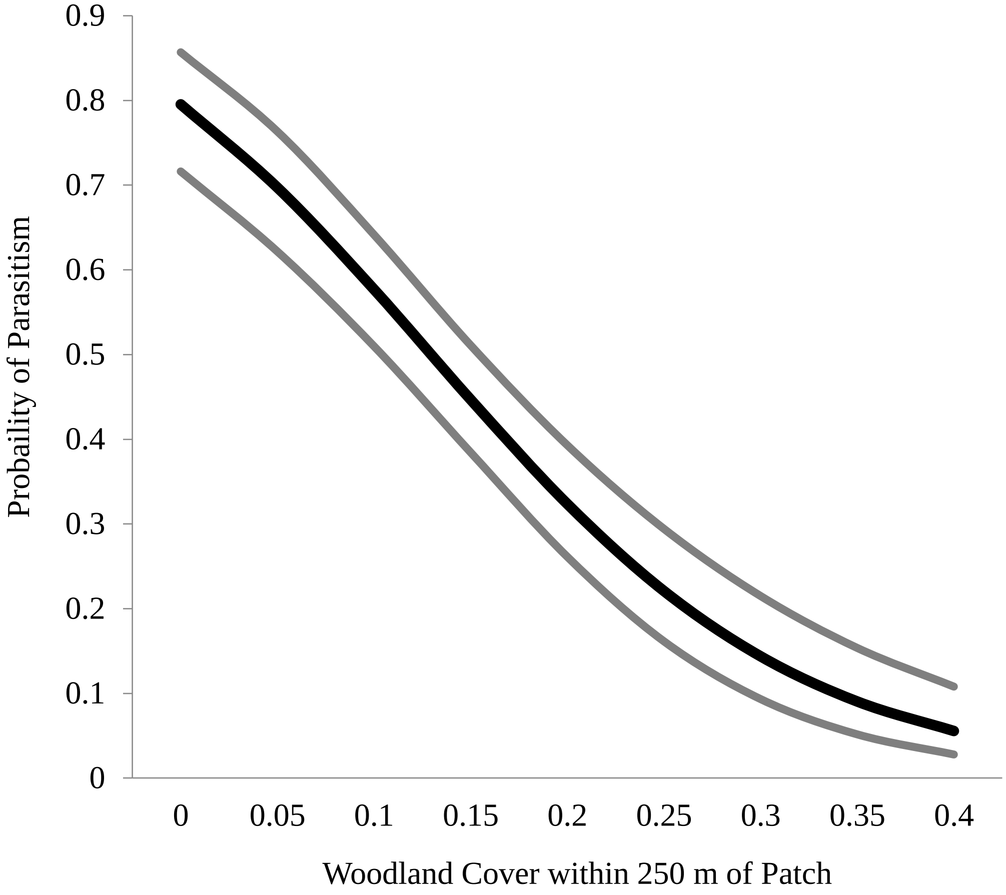


Figure 3.5. Influence of territory-scale woody plant cover on the number of dickcissel fledglings produced from successful nests. Error bars represent 85% confidence intervals.

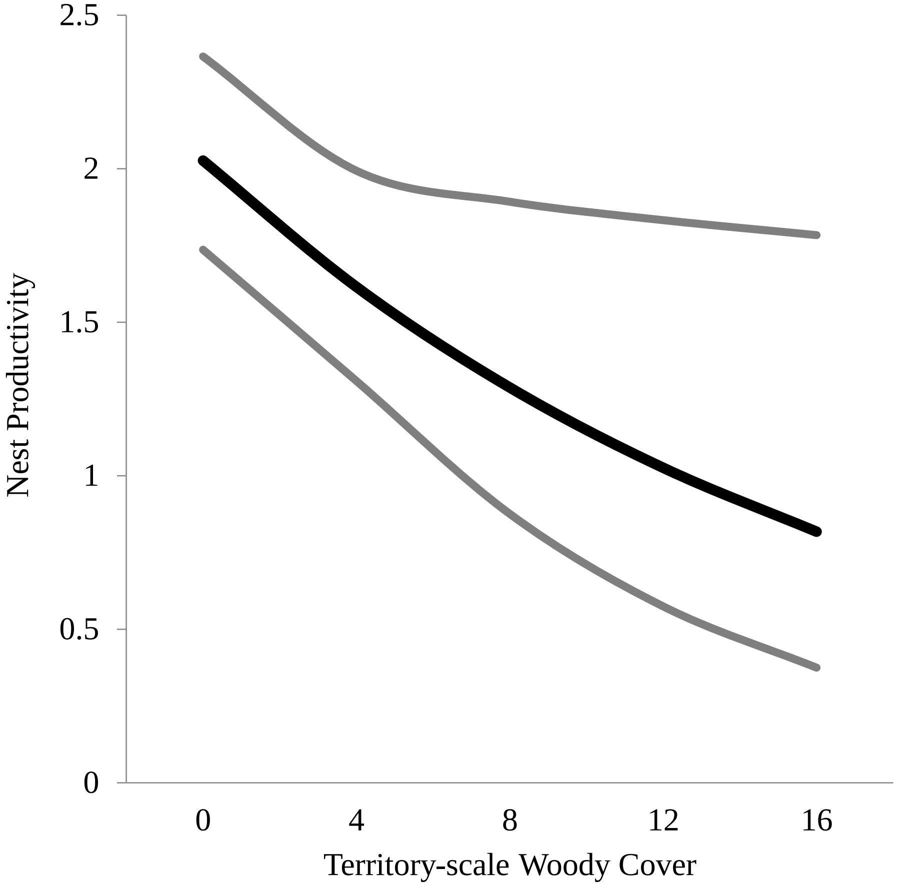
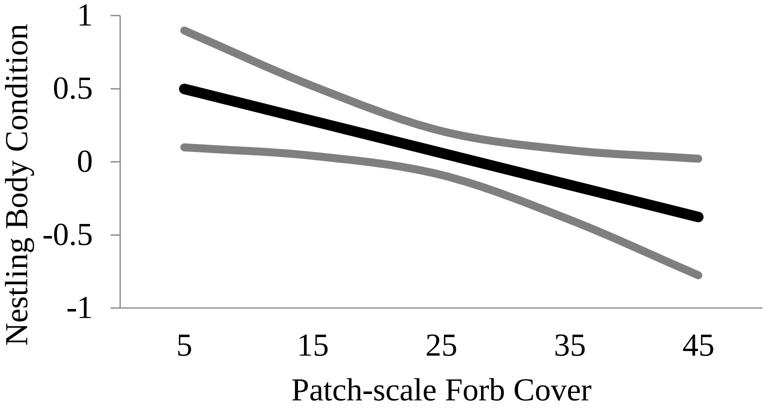


Figure 3.6. Influence of (A) patch-scale forb cover and (B) territory-scale Robel height on nestling body condition. Error bars represent 85% confidence intervals.

(A)



(B)

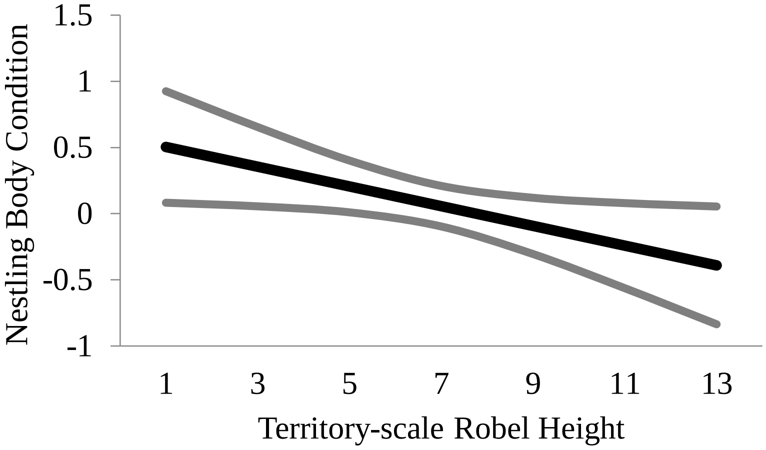
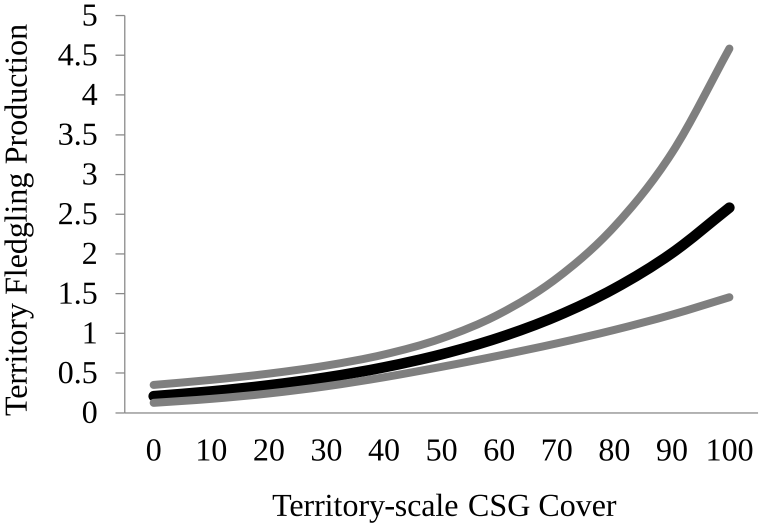


Figure 3.7. Influence on territory fledgling production of (A) territory-scale cool-season grass cover, (B) patch-scale tall fescue cover, (C) the interaction between those two variables, (D) territory-scale bare ground cover, (E) row-crop cover within 250 m of patches, and (F) row-crop cover within 1000 m of patches. Error bars represent 85% confidence intervals.

(A)



(B)

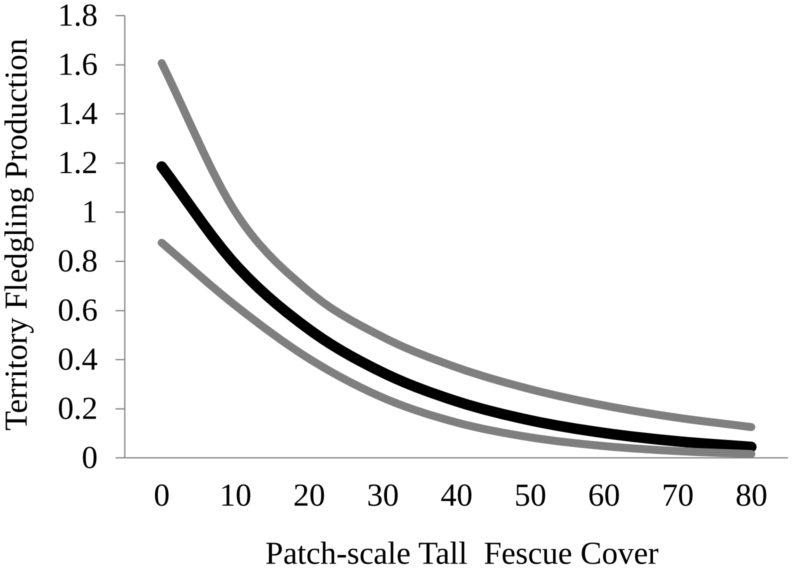
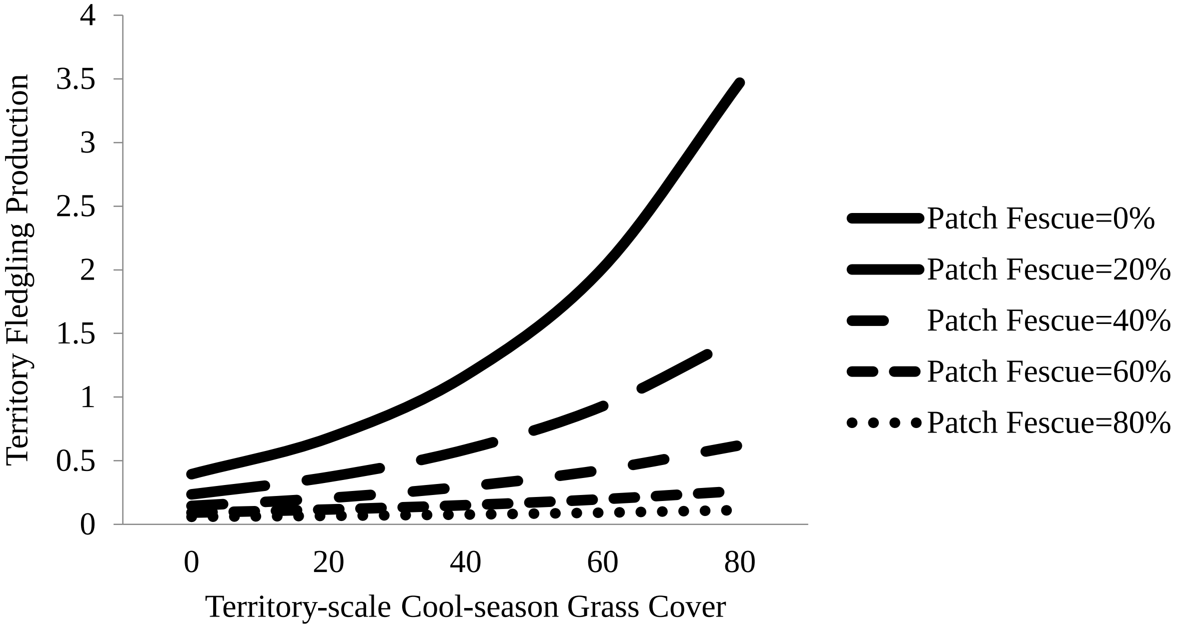


Figure 3.7 continued…

(C)



(D)

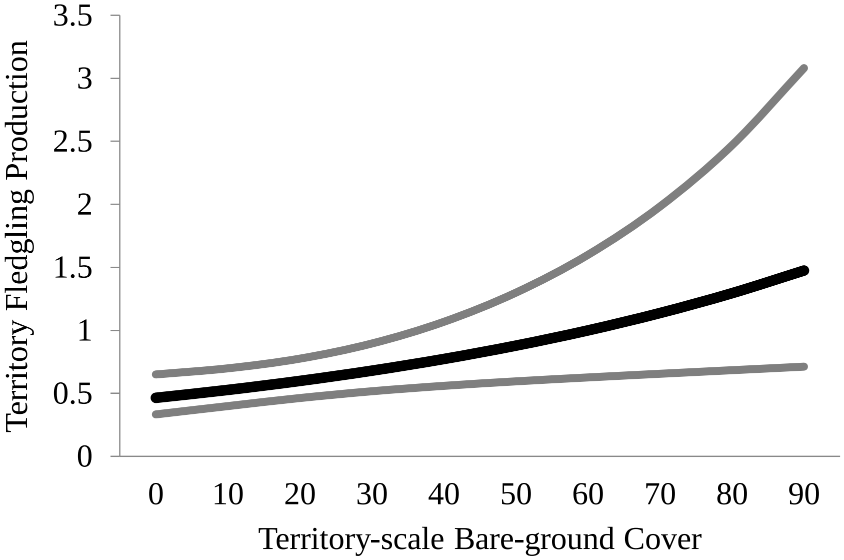
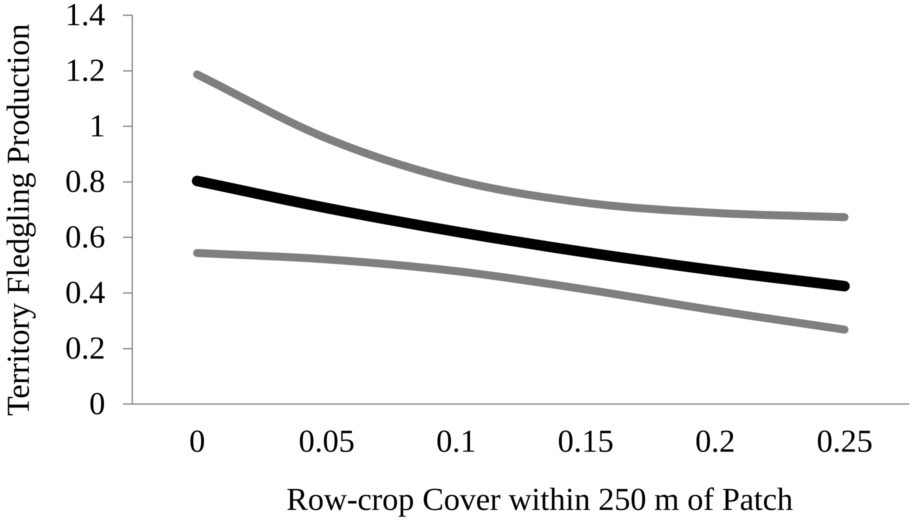
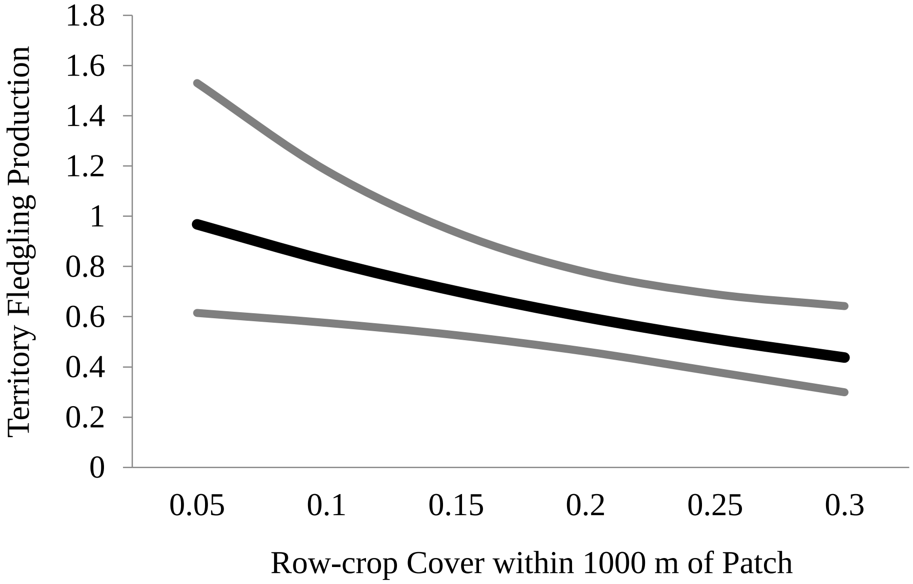


Figure 3.7 continued…

(E)



(F)



CHAPTER 4 – CONTRASTING IMPACTS OF INVASIVE PLANTS AND HUMAN-ALTERED LANDSCAPE CONTEXT ON NEST SURVIVAL AND BROOD PARASITISM OF A GRASSLAND BIRD[3]

ABSTRACT

Context Humans have altered grasslands in recent decades through crop conversion, woody encroachment, and plant invasions. Concurrently, grassland birds have experienced range-wide declines. Studies have reported effects of plant invasions and land conversion on nest ecology, but few have assessed relative impacts of these changes.

Objectives We compared impacts of invasive plants and landscape context on nest survival of a grassland songbird, the dickcissel (*Spiza americana*). We also compared effects on parasitism by brown-headed cowbirds (*Molothrus ater*) and tested whether parasitism affects survival.

Methods From 2013-2016, we monitored 477 dickcissel nests. We measured nest-site vegetation (including woody plants, tall fescue *Schedonorus arundinaceus*, and other invasive grasses) and measured landscape context at broad scales.

Results Nest survival declined with increasing tall fescue cover at nest sites, and parasitism was more common at nests with greater fescue and woody cover. Some evidence suggested a negative effect of row-crop cover within 1000 m on nest survival, but no landscape patterns unambiguously affected survival. Woodland cover and wooded-edge prevalence were associated with

---

[3] *Reprinted with permission from Springer Nature: Maresh Nelson SB, Coon JJ, Duchardt CJ, Miller JR, Debinski DM, Schacht WS. 2018. Contrasting impacts of invasive plants and human-altered landscape context on nest survival and brood parasitism of a grassland bird. Landscape Ecology 33 (10) 1799-1813. doi:10.1007/s10980-018-0703-3.*

reduced parasitism risk. Parasitized nests had smaller clutches, failed more frequently, and produced fewer fledglings than non-parasitized nests.

Conclusions Determining the impacts of invasive plants and other anthropogenic changes on grassland birds will aid in prioritizing management to improve habitat quality. Our results indicate that optimizing landscape context around habitats may not affect dickcissel nest survival strongly, except perhaps through effects on parasitism. In contrast, controlling tall fescue and shrubs within grasslands could benefit birds by increasing nest success and reducing parasitism.

INTRODUCTION

North American grasslands have undergone far-reaching changes in land use and land cover in the last century, with profound consequences for native wildlife. In the Central U.S., for example, grassland ecosystems have been converted to row-crop agriculture (Samson & Knopf, 1994; Warner, 1994), transformed by woody plant encroachment due to fire suppression and heavy grazing (Briggs et al., 2005; Engle et al., 2008), and invaded by exotic grasses that alter plant and arthropod communities (Flanders et al., 2006; McGranahan et al., 2012). In the same period, more than half of all grassland bird species in North America have undergone range-wide population declines (Peterjohn & Sauer, 1999; Sauer et al., 2017).

Changes in land cover have diminished grassland bird populations in part through habitat loss (Coppedge et al., 2001; Murphy, 2003), but avian declines are also a product of low offspring production in remaining habitats (Schmidt & Whelan, 1999; Fletcher et al., 2006). Learning how changes in land use and cover affect grassland birds thus requires examining how these changes alter nest survival and brood parasitism by brown-headed cowbirds (*Molothrus ater*), which reduce host fitness through egg removal and competition for parental care (Sealy, 1992).

Multiple studies have investigated how landscape context (Herkert et al., 2003; Ribic et al., 2012; Hovick & Miller, 2013) and plant invasions (Lloyd & Martin, 2005; Grant et al., 2006; Nelson et al., 2017) independently influence avian nest survival and parasitism, but we know very little about the relative importance of these factors. Moreover, our understanding of the spatial scales at which invasive plants and land-use change most strongly affect avian reproduction is limited (Chiavacci et al., 2018). This uncertainty complicates conservation. Invasive plants almost inevitably emerge in grassland reserves and restorations, and controlling them requires substantial investment of time and funds (Rowe, 2010). Because those resources could otherwise be put towards land-acquisition planning and additional restorations, illuminating the relative conservation value of invasive plant control, grassland expansion, and landscape optimization will improve decision-making (e.g., Pyke, 2011; Rosenberg et al., 2016).

At broad spatial scales, grassland losses and proliferating wooded edges can intensify nest predation by increasing predator abundance or search efficiency (Chalfoun et al., 2002; Simonsen & Fontaine, 2016), although such increases are inconsistent (Grant et al., 2006; Benson et al., 2013). In contrast, nests near wooded edges are consistently at high risk of parasitism (Benson et al., 2013), though tree cover in the landscape may mitigate this if cowbirds prefer to parasitize woodland hosts (Pietz et al., 2009; Hovick & Miller, 2013). Relative to these factors, few data exist on the effects of row-crop cover. Crops can increase predator abundances (Pedlar et al., 1997; Chalfoun et al., 2002), but may not increase nest loss (Cottam et al., 2009).

At fine spatial scales, invasive grasses and shrubs can increase predation and parasitism by providing homogeneous nest cover or creating perches for cowbirds (Lloyd & Martin, 2005; Patten et al., 2006; Hovick et al., 2012). Moreover, invasive grasses often support relatively few arthropod prey (Flanders et al., 2006; George et al., 2013), and some—such as the widespread forage grass tall fescue (*Schedonorus arundinaceus*)—decrease arthropod growth rates by providing poor diets for folivores (Jokela et al., 2016). These trophic effects may increase predation by heightening demands on parental activity to provision nestlings (Martin et al., 2000).

Our goal in this study was to compare the impacts of invasive plants at fine spatial scales and landscape patterns reflecting land conversion at broad spatial scales on the survival and parasitism of dickcissel (*Spiza americana*) nests in a U.S. grassland. We also examined whether cowbirds reduce the number of dickcissel young fledged to discern whether reducing parasitism could benefit populations. We chose to study dickcissels, a grassland bird declining in much of its range (Sauer et al., 2017), because landscape context and invasions affect their distributions (Herkert et al., 2003; Osborne & Sparling, 2013). Dickcissels also share habitat with other declining birds preyed upon by similar predators (Ribic et al., 2012), so revealing impacts on this species will lend insight into the broader avian community.

We first predicted that nests in microsites with high invasive grass cover, and tall fescue cover in particular, would experience high nest-predation rates due to poor concealment and limited food availability (Flanders et al., 2006; Hovick et al., 2012; Jokela et al., 2016). We also expected that woody plants at nest sites would increase predation and parasitism due to their use by snakes and cowbirds (Patten et al., 2006; Klug et al., 2010). We then predicted that nests in landscapes with little grassland cover but high prevalence of crops and wooded-edges would face intense predation and parasitism due to concentration into small patches with high predator and cowbird abundance (Chalfoun et al., 2002; Simonsen & Fontaine, 2016). Finally, although proximity to wooded edges could increase parasitism, we predicted that woodland cover in the landscape would reduce parasitism by supporting alternative cowbird hosts (Pietz et al., 2009).

METHODS

STUDY SYSTEM

We investigated dickcissel nest survival and parasitism from 2013-2016 on 15 study pastures (14-41.1 ha in area) in Ringgold County, Iowa, USA. One pasture is privately owned and the others are managed by the Iowa Department of Natural Resources. The pastures are within the Grand River Grasslands, a region spanning the Iowa-Missouri border that represents a prime opportunity to restore tallgrass praire in a working landscape (Miller et al., 2012). The dominant land use in the Grand River Grasslands is cattle grazing, but record-high commodity prices from 2006-2011 recently resulted in a loss of grazed and ungrazed grasslands and an increase in row-crop acreage (Wright & Wimberly, 2013). Also, though woodlands have long been present in the region, their extent is expanding as species like eastern redcedar (*Juniperus virginiana*) and Osage-orange (*Maclura pomifera*) encroach in unburned grasslands (Harr et al., 2014). Our pastures reflect a gradient of these landscape conditions, with row-crop cover within 1000 m of nests ranging from 1-66% and woodland cover ranging from 2-44% (Appendix I).

In addition to woody plants, the region harbors invasive herbaceous plants. Tall fescue is one of the most abundant of these species, occurring in all but one of our pastures and ranging from 0 to 63% cover within them (unpublished data). Other invasive grasses like Kentucky bluegrass (*Poa pratensis*), smooth brome (*Bromus inermis*), and orchard grass (*Dactylis glomerata*) are also widespread. Common native plants (e.g., Indiangrass *Sorghastrum nutans*, big bluestem *Andropogon gerardii*, goldenrods *Solidago* spp.) are mostly warm-season species.

Management varied across study pastures, including cattle-grazing, spring-burning, and glyphosate herbicide sprayed in November 2014 to control tall fescue (Appendix J). We chose this diverse mixture of pastures to identify variables influencing reproduction over a broad array of conditions. Due to logistical constraints we did not monitor all 15 pastures each year: we monitored 10 in 2013, 7 in 2014, 8 in 2015, and 6 in 2016 (dates in Appendix J).

DATA COLLECTION

We located dickcissel nests from May to August, 2013-2016. We searched for nests in 2013 primarily by dragging a 30-m rope over study pastures (Higgins et al., 1969). Whenever a bird flushed nearby, we searched the area for a nest. We conducted 2-4 complete drags (average=3.6) per pasture. From 2014-2016, we primarily searched for nests by observing adult dickcissel behavior (Martin & Geupel, 1993).We found nests through incidental flushes in all years.

We recorded nest positions with a GPS and tied flagging 2.5 m to the north and south to aid relocation. We aged eggs by candling (Lokemoen & Koford, 1996) and nestlings based on development (Temple, 2002). We visited nests every 1-3 days (Ralph et al., 1996), noting nest stage (laying, incubation, or nestling) and nest contents each time. Nests were considered depredated if all contents disappeared before chicks reached day 7—the earliest age of force fledging (hatch day=day 1). We confirmed fledging based on parental behavior.

To understand how invasive plants influence nest survival and parasitism at a fine spatial scale, we measured percent-cover of woody plants, tall fescue, and all cool-season grasses combined (including tall fescue) in five 0.5-m^2 quadrats around each nest within 21 days of nests fledging or failing. We also measured warm-season grass, forb, and litter cover within those quadrats to assess whether other plant components influenced reproduction. One quadrat was centered on the nest cup, and the other four were placed randomly 1-5 m from the cup in each cardinal direction (Hovick et al., 2012; Lyons et al., 2015). We visually estimated percent-cover and recorded estimates as the midpoints of the intervals 0%, 1-5%, 6-25%, 26-50%, 51-75%, 76-

95%, or 96-100% (Daubenmire, 1959). At each quadrat, we estimated vegetation density, using a Robel pole to record the highest vertical decimeter interval at least 50% obstructed when viewed at 1 m off the ground and 4 m in each cardinal direction (Robel et al., 1970). We calculated average cover estimates for each vegetation variable across all five quadrats and calculated the average and standard deviation of all Robel readings (averages and ranges in Appendix I).

To measure landscape context altered by human activity (i.e., grassland, crop, and woodland cover; wooded-edge prevalence and proximity), we categorized land cover within 1000 m of study pastures using a 2014 orthophoto of Ringgold County (Iowa Geographic Map Server). Using ArcMap 10.4.1 (ESRI, Redlands, CA) we digitized land cover as either herbaceous (prairie, cattle pastures, and hayfields), cropland (corn and soybean fields), woodland (forests and dense shrublands), water (farm ponds and creeks), or impervious surface (roads and buildings). We used the 2014 National Cropland Data Layer to verify classifications of crops versus herbaceous cover (USDA, 2017). We measured the distance from each nest to the nearest wooded edge. We then created 250 m-, 500 m-, and 1000 m-radius buffers around every nest and calculated percent-cover of herbaceous, cropland, and woodland cover—as well as the length of wooded edges—within each (averages and ranges in Appendix I). These distances were chosen to understand the scale at which landscape context had the strongest influence. The 250-m buffers (~19.6 ha) are similar in area to the home ranges of some small nest predators (e.g., snakes; Klug et al., 2011); the 500-m buffers (~78.5 ha) are similar to the home-ranges of some medium-sized predators (e.g., raccoons *Procyon lotor*; Beasley et al., 2007); and the 1000-m buffers (~314.1 ha) are well within the extent of cowbird home-ranges (Patten et al., 2006).

DATA ANALYSES

We estimated daily nest survival probabilities using the logistic exposure method (Shaffer, 2004). Each interval between two sequential visits to a nest was considered one replicate, and the response variable was whether the nest survived that interval. Nests were considered to have survived an interval if at least one viable dickcissel offspring remained in the nest afterwards (Hovick et al., 2012). We did not consider nests to have survived if only cowbird offspring remained; from the perspective of dickcissel fitness, these nests were effectively depredated through egg removal by cowbirds or a combination of egg removal and secondary depredation. We related nest survival to explanatory variables using PROC GLIMMIX (Littell et al., 2006) in SAS 9.4 (SAS Institute Inc., Cary, NC) to accommodate the binomial distribution of the response. We included ‘PastureID’ as a random variable in every model to account for potential non-independence among nests on the same pastures. We evaluated dispersion in the data based on ratios of Pearson chi-squared statistics to degrees of freedom (Littell et al., 2006). No adjustments were required.

To evaluate support for variables influencing nest survival, we compared multiple models using an information-theoretic approach (Burnham & Anderson, 1998). The explanatory variables each fell into one of three groups: temporal, nest contents, and habitat variables. We therefore compared candidate models through a three-stage process that allowed for variable selection across these groups without creating an overly large model set (Benson et al., 2010a).

In the first stage, we evaluated temporal models. This stage controlled for variation in survival within and among seasons (Nest Visit Date and Year variables, respectively), potentially due to changes in predator abundance and activity (Borgmann et al., 2013). In the second stage of analysis, we compared nest-contents models. This stage controlled for differences in survival between the laying, incubation, and nestling stage (Nest Stage variable) and between nests containing different numbers of chicks (#Chicks variable). We also tested our prediction that parasitized nests have lower survival (Parasitism variable) and examined whether this effect only manifests in specific nest stages by including an interaction between Parasitism and Nest Stage.

In the final stage of analysis, we examined habitat models addressing our predictions that nest survival is negatively correlated with (a) invasive grass and woody plant cover within 5 m of nests, and (b) land cover patterns reflecting land conversion at broad spatial scales (250-1000 m). Because we directly compared the fit of all invasive plant and land cover models, this analysis allowed us to conclude which variables warrant the greatest conservation attention. We also tested whether other nest-site vegetation components—vegetation density (mean and variability of Robel height), forbs, warm-season grasses, and litter cover—influenced nest success. These variables frequently affect grassland bird reproduction (Fisher & Davis, 2010).

At all three stages of the model selection process, we ranked the relative fit of candidate models using AIC adjusted for small samples (AIC_c) and compared them to a stage-specific base model. We considered models to be highly supported if they had Akaike weight (ω_i) greater than the stage-specific base model and contributed to the cumulative top 90% of their respective stage weights (Burnham & Anderson 1998: 127). In the first stage, the base model was a random effects-only model. In subsequent stages, all variables from highly-supported models identified in previous stages (except uninformative variables; Arnold, 2010) were included in every candidate model in the new set—including the new base model. Thus, each stage carried forward the important explanatory variables from previous stages and could then contribute additional, well-supported variables. We avoided issues associated with multicollinearity by calculating Pearson's correlation coefficients among explanatory variables and ensuring that no highly correlated variables (i.e., $|r| > 0.7$) were included in the same models (Dormann et al., 2013).

We computed parameter estimates for selected variables and predicted values of daily nest survival across each variable's observed range of values, holding other variables at their averages (Shaffer & Thompson, 2007). We generated 85% confidence intervals around slopes and predicted values (85% because AIC model selection tends to select variables with slopes excluding zero at this confidence level; Arnold, 2010). Finally, we computed an overall predicted fledging probability for a nest with a 4-day laying phase, 12-day incubation phase, and 9-day nestling phase (calculated as: average laying-phase daily survival probability raised to the 4th power × average incubation-phase daily survival probability raised to the 12th power × average nestling-phase daily survival probability raised to the 9th power). We calculated a 95% confidence interval for this estimate using the delta method (Powell, 2007).

We next estimated the probability of nests being parasitized by cowbirds, again using PROC GLIMMIX and including 'PastureID' as a random variable. Each nest constituted one replicate, and we modelled the response variable with a binomial distribution. We excluded nests depredated before the incubation phase from this analysis; cowbirds typically parasitize nests during laying (Sealy, 1992), so nests that did not survive the entire laying phase had less time in which to be parasitized and were thus incomparable to other nests. We judged the first day of each nest's incubation phase by back-calculating from our estimates of nest age, assuming 12-day incubation and 9-day nestling phases (Temple, 2002). We then estimated nest initiation dates by assuming a laying phase equal in days to the maximum number of host eggs or nestlings seen in the nest (dickcissels lay one egg per day; Temple, 2002) and including a correction factor to account for egg removal by cowbirds. We assumed that one host egg was removed for every 1-2 cowbird offspring in the nest (i.e., we added one day to the laying-phase length of a nest with 1-2 cowbirds, two days for nests with 3-4 cowbirds, etc.).

To evaluate support for variables influencing parasitism, we again took an information-theoretic approach. We followed a two-stage process, first controlling for temporal variation (i.e., changes in parasitism risk within and between seasons; Initiation Date and Year variables, respectively) and then comparing the effects of invasive plants and landscape context on parasitism risk. Not all habitat variables included in the nest survival analysis were used in the parasitism analysis. Specifically, we did not predict that row-crop cover in the landscape or litter cover at nest sites would influence parasitism risk, so these variables were not included in candidate models. Instead, we considered that since cowbirds follow grazing ungulates (Patten et al., 2006), presence of cattle in a pasture could increase parasitism risk. We thus included 'Cattle' in the candidate set for parasitism, assigning this binary variable based on whether nests were built in grazed pastures (Appendix I). In pastures where cattle were stocked for only part of the season, we assigned this variable based on whether cattle were present during the nest's laying phase. Model selection criteria were identical to those used in the nest survival analysis. We again derived slope estimates and calculated parasitism probabilities across the range of observed values of each highly supported explanatory variable. No highly correlated variables were included together in candidate models or in the final model.

Our final goal was to examine the effects of cowbird parasitism on reproduction. As mentioned, we tested whether parasitism reduces nest survival in our logistic exposure analysis. Furthermore, we conducted an ANOVA and Scheffé's post-hoc test to examine whether dickcissel clutch sizes were greater in unparasitized nests versus nests with either one or multiple cowbird eggs. We also conducted a t-test to determine whether more dickcissel young fledged from successful nests that had or had not been parasitized.

RESULTS

We found 527 dickcissel nests; 499 contained viable eggs or nestlings, and we measured vegetation at 477 of those nests. Vegetation was not measured at some nests due to mowing by managers shortly after the nest cycle. Henceforth, we only consider these 477 nests. Cowbirds parasitized 254 nests (53.3%). Parasitized nests often contained just one cowbird egg or nestling (n=104), though some had two (n=83), three (n=42), four (n=22), five (n=2), or even six (n=1). Non-parasitized nests that survived to incubation (n=204) contained $\bar{x} = 3.71 \pm 0.73$ [SD] dickcissel eggs, while similar nests with one cowbird egg (n=95) contained 3.02 ± 1.10 dickcissel eggs, and nests with multiple cowbird eggs (n=149) contained 2.46 ± 1.07 dickcissel eggs. These means all differed from one another, indicating that cowbirds reduced host clutch size, and more so with greater parasitism intensity (ANOVA and Scheffé's post-hoc test: $F_{2,\,445} = 77.43$, $p<0.001$).

Dickcissel chicks fledged from 140 nests (29.4%). Of these, 89 produced only dickcissels (2.92 ± 1.20 per nest), while 51 produced both dickcissel (1.86 ± 0.82) and cowbird (1.47 ± 0.89) fledglings. More dickcissels fledged from successful nests without cowbirds (t-test: $t_{133} = 6.36$, $p<0.001$). Of the 337 failed nests, 291 (86.4%) were fully depredated by predators, 25 (7.5%) were abandoned (10 perhaps due to observer-induced stress), 16 (4.8%) produced only cowbirds (1.94 ± 0.82), 3 failed during storms, cattle trampled 1, and 1 fell from its substrate.

We included 465 nests with complete habitat data in the nest survival analysis; the others contained only cowbirds at discovery. We conducted 2057 sequential visits to these nests, cumulatively representing 4866 exposure days. Only 448 nests with complete habitat data were included in the analysis of parasitism risk; the other 29 failed during the laying phase.

NEST SURVIVAL

The best temporal model included the interaction between year and nest visit date (Table 4.1). Nest survival decreased over the season in some years, but increased in others (Fig K.1 in Appendix K). Stage 2 supported an interaction between nest stage and parasitism: nest survival was lower overall in the nestling phase relative to incubation, but parasitized nests in the nestling phase had lower survival than both non-parasitized nests in the nestling phase and parasitized and non-parasitized nests in other phases (Fig 4.1). Comparing the impacts of invasive plants and landscape context, an effect of tall fescue at nest sites clearly had the most support (ω=0.78); survival decreased with tall fescue cover (β = -0.008, SE = 0.003; Fig 4.2A). The only other variable with support at this stage was row-crop cover within 1000 m of nests, and evidence for this effect was weak (ω=0.03). Predicted probabilities showed that cropland reduces nest survival (β = -0.011, SE = 0.006), though the confidence interval for this effect included zero (Fig 4.2B).

The overall best model for daily nest survival probability therefore included Year × Nest Visit Date, Nest Stage × Parasitism, tall fescue cover at the nest site, and row-crop cover within 1000 m. The area under the ROC curve for this model was 0.650 (95% CI: 0.618, 0.683), indicating a reasonable prediction accuracy. Averaging across all years and parasitism statuses, and holding tall fescue and row-crop cover at their average observed values, this model predicts a daily nest survival probability of 0.9364 in the laying phase, 0.9478 in the incubation phase, and 0.8952 in the nestling phase. Extrapolated over the full nest cycle, this equates to a predicted fledging probability of 0.1476 (95% CI: 0.0972, 0.1980).

COWBIRD PARASITISM

The best temporal model for parasitism included year and initiation date (Table 4.2). Parasitism varied among years and declined over the season (β = -0.040, SE = 0.007; Figs K.2 and K.3 in Appendix K). A year-by-initiation-date interaction was also supported, revealing different rates of decline among years (Fig K.4 in Appendix K). Annual differences were minor, however, so we only carried the main effects forward. Among the invasive plant and landscape context variables examined, woodland cover within 500 m of nests received the most support (ω=0.53). Increasing woodland was linked to reduced parasitism (β = -0.071, SE = 0.018; Fig 4.3A). Below this effect, two invasive plant metrics, woody cover and tall fescue cover, were in the top 90% model set. Parasitism increased with both variables (woody: β = 0.031, SE = 0.013, Fig 4.4A; tall fescue: β = 0.015, SE = 0.006, Fig 4.4B). Finally, wooded edge within 500 m of nests, woodland cover within 250 m, and wooded edge within 1000 m also received support. However, these variables were correlated ($r > 0.7$), so we could not include all in the final model. To select the most important variables, we compared the AIC_c scores of models containing all combinations of the landscape metrics and found that woodland cover and wooded edge within 500 m (Fig 4.3B) achieved the best balance of parsimony and model fit.

The overall best model for the probability of cowbirds parasitizing a nest therefore included initiation date, year, woodland cover and prevalence of wooded edges within 500 m of the nest, and woody cover and tall fescue cover at the nest site. The area under the ROC curve for this model was 0.783 (95% CI: 0.741, 0.825), indicating high accuracy.

DISCUSSION

With many grassland birds in steep decline and their habitats primarily situated in human-dominated landscapes, it is urgent that we understand how anthropogenic changes influence avian reproduction (Fletcher et al., 2006; Sauer et al., 2017). Focusing on dickcissels, our study provides a direct comparison between the impacts of multiple invasive plants at a fine spatial scale and human-facilitated changes in land cover at broad scales. Our results clarify that these factors have unequal effects on nest survival and cowbird parasitism. For one, increasing prevalence of the invasive grass tall fescue at nest sites was associated with reduced nest survival, while evidence for an effect of landscape context on survival was limited to a tentative negative effect of row-crop cover within 1000 m of nests. In contrast, the strongest effects on parasitism occurred at a broad spatial scale, with increasing woodland cover and edge prevalence within 500 m of nests associated with low parasitism risk. Secondarily, parasitism increased with tall fescue and woody plant cover at nest sites. Together, these results suggest that row-crops and woody encroachment around dickcissel habitats at broad scales do not strongly erode habitat quality, having marginal effects on nest survival or even mitigating parasitism. In contrast, invasive plants can exacerbate predation and parasitism. Thus, management of invasions within grasslands may benefit reproduction more than optimizing landscape context around reserves.

Three caveats should be noted. First, if nest predators differ among bird species (Cox et al., 2012), habitat-mediated impacts on predation may not be identical between dickcissels and other grassland birds. Information on these issues is sparse, however, so we suggest that future studies identifying predators of multiple bird species report how many nests of each bird are depredated by each predator. As a second caveat, relationships between habitat and predation may differ between regions due to geographic variation in predator communities or interactions between landscape composition and predator densities and behaviors (DeGregorio et al., 2016; Chiavacci et al., 2018). In applying our results to other regions, it is thus important to consider how local predator communities may interact with local habitats. For example, our study region—the Grand River Grasslands—contains moderately large grassland patches compared to many Midwestern regions (Miller et al., 2012). Stronger relationships between landscape context and nest predation may be observed in more highly fragmented grasslands (Herkert et al., 2003; but see Renfrew et al., 2005). As a final caveat, even though changes in landscape context may not reduce nest survival, they can still affect avian populations. Grassland birds often respond to land cover when selecting habitat, sometimes avoiding landscapes with limited grassland cover, so we caution not to assume that processes like woodland expansion have no conservation relevance (Coppedge et al., 2001; Grant et al., 2004; Shahan et al., 2017).

Before reflecting on individual habitat variables, it is worth noting that nest survival and parasitism varied within and among seasons. Parasitism consistently declined within seasons, potentially due to reduced cowbird activity (Benson et al., 2010a). Nest survival, in contrast, increased during some years but decreased in others. This variability is likely a product of annual differences in nest predator communities or activity patterns (Borgmann et al., 2013). Managers seeking to improve habitat quality should be cognizant of temporal variation, as it could obscure assessments of avian reproduction conducted over limited timeframes. Moreover, it is essential to account for such variation in determining the effects of individual habitat variables.

Our finding that tall fescue increases nest predation is consistent with research on grasshopper sparrows (*Ammodramus savannarum*) in the Grand River Grasslands (Lyons et al., 2015) and northern bobwhites in south-central Illinois (Osborne et al., 2012), but conflicts with a study showing that grassland bird nests built in tall fescue-dominated microsites do not have particularly low survival (Galligan et al., 2006). Our results may be more robust than those of Galligan et al. (2006), given our larger sample size (477 vs. 47-264 nests) and the fact that we used a continuous metric of tall fescue cover rather than a qualitative metric of dominance, but the effects of invasive plants on avian ecology do often depend on interplays between local predators and habitats (Nelson et al., 2017). Our results and those of Lyons et al. (2015) indicate that tall fescue increases nest predation in the Grand River Grasslands, and potentially in nearby areas of southern Iowa and northern Missouri. However, further research is needed to reveal the generalizability and mechanisms of these effects.

Tall fescue's effects on nest survival and parasitism could be driven by several factors. First, fescue provides minimal structural heterogeneity (Osborne & Sparling, 2013), which may reduce effort required for predators and cowbirds to search through complex vegetation (Nelson et al., 2017). Low heterogeneity could also reduce air turbulence in plant canopies, increasing detectability of odor plumes (Conover, 2007: 183-187). This might explain why olfactory predators (e.g., raccoons, striped skunks *Mephitis mephitis*) frequently depredate grasshopper sparrow nests in sites with high tall fescue cover (Lyons et al., 2015). However, our results indicated no effects on nest success and parasitism of either Robel height or heterogeneity (StDev Robel), suggesting that these mechanisms may not be at work. Alternatively, tall fescue may provide a poor diet for arthropods, reducing their abundance or biomass near nests (Kirfman et al., 1986; Jokela et al., 2016). If birds compensate by increasing provisioning rates to nestlings or foraging farther from nests (Britschgi et al., 2006), increased visual cues could attract predators (Martin et al., 2000). We present no data on arthropods or provisioning, but this hypothesis is supported indirectly by the fact that dickcissel nests were depredated more frequently in the nestling phase. Moreover, in our study region, predation of grasshopper sparrow nests by garter snakes (*Tham-*

nophis spp.) and eastern racers (*Coluber constrictor*) increases with tall fescue cover near nests (Lyons et al., 2015). These snakes are known to depredate nests almost exclusively during the day, when visual cues are more readily available (DeGregorio et al., 2014), and garter snakes use both visual and olfactory cues to detect prey (Chiszar et al., 1981). These patterns lend plausibility to a visually mediated effect of tall fescue on predation.

Aside from tall fescue, the only habitat variable influencing survival was corn and soybean cover within 1000 m of nests. There was high model-selection uncertainty for this effect, but the reduction in survival associated with increasing crop cover was consistent with our expectations because nest predators are often abundant along agricultural edges (Pedlar et al., 1997; Dijak & Thompson, 2000; Chalfoun et al., 2002). This pattern may also arise because crop fields provide abundant forage for omnivorous predators in autumn, and may thus support abundant omnivore populations (Cottam et al., 2009). However, crops are unavailable in the summer, potentially increasing nest predation by forcing those omnivores to forage in grasslands.

Contrary to tall fescue and crops, we were surprised by the lack of relationship between woody plants and nest survival. We predicted that woody cover near nests would reduce survival due to snake predation (Klug et al., 2010) and that wooded edges in the landscape would reduce survival due to elevated predator abundance (Dijak & Thompson, 2000; Chalfoun et al., 2002). It may be that predation by some predators increased near shrubs and edges, but not strongly enough to alter overall predation rates (Renfrew & Ribic, 2003; Benson et al., 2010b). Alternatively, dominant dickcissel nest predators in our region may not respond to woody cover.

In contrast to effects on nest predation, we observed strong declines in parasitism with increasing tree cover and wooded-edge prevalence within 500 m of nests—a pattern consistent with previous studies of grassland bird reproduction (Pietz et al., 2009; Hovick & Miller, 2013).

This is unlikely a product of low cowbird abundance, since cowbirds do not avoid landscapes with high tree cover (Grant et al., 2004; Cox et al., 2012). Authors have instead suggested that when woodlands are present in the landscape, cowbirds prefer to parasitize woodland-breeding hosts rather than grassland hosts (Pietz et al., 2009; Hovick & Miller, 2013). This hypothesis is supported by studies monitoring nests across multiple habitats that have observed higher parasitism rates in forests and woodland edges versus in grasslands (Hahn & Hatfield, 1995; Strausberger & Ashley, 1997). However, it would be particularly notable if this mechanism also causes woodland cover to reduce parasitism of dickcissel nests, since dickcissels are highly preferred cowbird hosts—even relative to some woodland birds (Rivers et al., 2010). If this pattern indeed resulted from cowbird host-switching, that might also explain why parasitism increased with shrub cover at nest sites: cowbirds may search for woodland hosts in shrub patches within grasslands and incidentally discover grassland bird nests nearby.

Habitat-mediated effects on parasitism have consequences for avian reproduction. As in previous studies, parasitized nests contained fewer dickcissel eggs than non-parasitized nests and fewer dickcissels fledged from parasitized nests (Benson et al., 2010a; Hovick & Miller, 2013). Moreover, although survival of parasitized and non-parasitized nests was similar during laying and incubation, parasitized nests were more likely to fail in the nestling phase. This pattern has also been observed in American redstarts (*Setophaga ruticilla*; Hannon et al., 2009) and may occur because cowbird chicks beg frequently and loudly, increasing auditory cues for predators (Dearborn, 1999). Extreme begging may also stimulate host parents to increase provisioning rates, intensifying visual cues (Dearborn et al., 1998). Irrespective of mechanisms, these negative effects indicate that reducing parasitism may aid grassland birds.

As North American grasslands continue to be transformed by invasive plants, plowed, and fragmented, wildlife managers face difficult choices. Conservation and restoration budgets are usually tight, and managers often need to decide whether to devote resources to invasive plant control, land purchases, or additional restorations (Rowe et al., 2010). Moreover, when acquiring new lands, managers sometimes consider the conservation value of alternative land parcels, a choice that may be influenced by landscape context (Snyder et al., 2007). Our study provides guidance in decision-making by identifying site-level and landscape factors that should be targeted to increase habitat quality. First, because woodland cover in the landscape mitigates parasitism risk and row-crop cover appears to reduce nest survival, it would be wise for conservation managers to prioritize purchasing grasslands in landscapes with limited crop cover—or to restore nearby crop fields to grassland—rather than avoid acquiring sites near woodlands. Second, although woody cover at broad scales may not be problematic, our results suggest that controlling shrub cover within grasslands could reduce cowbird parasitism.

Finally, our finding that tall fescue exacerbates nest predation and parasitism indicates that replacing tracts of tall fescue with heterogeneous vegetation should be a priority. However, conflicting results from another region (Galligan et al., 2006) caution that fescue may not be universally harmful. We suggest that managers use adaptive management to assess the benefits of controlling tall fescue, experimentally reducing fescue in some areas (e.g., by applying herbicide in the fall, when many native grasses and forbs are dormant) while monitoring avian communities and nest survival in treated and untreated areas (Osborne et al., 2012; Osborne & Sparling, 2013). If herbicide is used, this may have non-target effects (e.g., secondary invasions; Matthews et al., 2017) and impacts may vary among bird species or over time. Regardless of effects on nest success, if managers increase habitat heterogeneity at appropriate scales, this may still serve the valuable goal of increasing avian diversity (Duchardt et al., 2016).

LITERATURE CITED

Arnold, T. W. (2010). Uninformative parameters and model selection using Akaike's Information Criterion. *Journal of Wildlife Management*, **74**,1175-1178.

Beasley, J. C., DeVault, T. L., Rhodes, O. E. (2007). Home-range attributes of raccoons in a fragmented agricultural region of northern Indiana. *Journal of Wildlife Management*, **71**, 844-850.

Benson, T. J., Anich, N. M., Brown, J. D., Bednarz, J. C. (2010a). Habitat and landscape effects on brood parasitism, nest survival, and fledgling production in Swainson's warblers. *Journal of Wildlife Management*, **74**, 81-93.

Benson, T. J., Brown, J. D., Bednarz, J. C. (2010b). Identifying predators clarifies predictors of nest success in a temperate passerine. *Journal of Animal Ecology*, **79**, 225-234.

Benson, T. J., Chiavacci, S. J., Ward, M. P. (2013). Patch size and edge proximity are useful predictors of brood parasitism but not nest survival of grassland birds. *Ecological Applications*, **23**, 879-887.

Borgmann, K. L., Conway, C. J., Morrison, M. L. (2013). Breeding phenology of birds: mechanisms underlying seasonal declines in the risk of nest predation. *PLoS ONE* (art. e65909).

Briggs, J. M., Knapp, A. K., Blair, J. M., Heisler, J. L., Hoch, G. A., Lett, M. S., McCarron, J. K. (2005). An ecosystem in transition: causes and consequences of the conversion of mesic grassland to shrubland. *BioScience*, **55**, 243-254.

Britschgi, A., Spaar, R., Arlettaz, R. (2006). Impact of grassland farming intensification on the breeding ecology of an indicator insectivorous passerine, the whinchat *Saxicola rubetra*: lessons for overall alpine meadowland management. *Biological Conservation*, **130**, 193-205.

Burnham, K. P., & Anderson, D. R. (1998). Model selection and inference: a practical information-theoretic approach. Springer, New York, NY.

Chalfoun, A. D., Ratnaswamy, M. J., Thompson, F. R. (2002). Songbird nest predators in forest-pasture edge and forest interior in a fragmented landscape. *Ecological Applications*, **12**, 858-867.

Chiavacci, S. J., Benson, T. J., Ward, M. P. (2018). Linking landscape composition to predator-specific nest predation requires examining multiple landscape scales. *Journal of Applied Ecology*, **55**, 2082-2092.

Chiszar, D., Taylor, S. V., Radcliffe, C. W., Smith, H. M., O'Connell, B. (1981). Effects of chemical and visual stimuli upon chemosensory searching by garter snakes and rattlesnakes. *Journal of Herpetology*, **15**, 415-424.

Conover, M. R. (2007). Predator-prey dynamics: the role of olfaction. Boca Raton, FL, USA: CRC Press.

Coppedge, B. R., Engle, D. M., Masters, R. E., Gregory, M. S. (2001). Avian response to landscape change in fragmented southern great plains grasslands. *Ecological Applications*, **11**, 47-59.

Cottam, M. R., Robinson, S. K., Heske, E. J., Brawn, J. D., Rowe, K. C. (2009). Use of landscape metrics to predict avian nest survival in a fragmented midwestern forest landscape. *Biological Conservation*, **142**, 2464-2475.

Cox, W. A., Thompson, F. R. III, Faaborg, J. (2012). Species and temporal factors affect predator-specific rates of nest predation for forest songbirds in the Midwest. *Auk*, **129**, 147-155.

Daubenmire, R. (1959). A canopy-coverage method of vegetational analysis. *Northwest Science*, **33**, 43-64.

Dearborn, D. C. (1999). Brown-headed cowbird nestling vocalizations and risk of nest predation. *Auk*, **116**, 448-457.

Dearborn, D. C., Anders, A. D., Thompson, F. R., Faaborg, J. (1998). Effects of cowbird parasitism on parental provisioning and nestling food acquisition and growth. *Condor*, **100**, 326-334.

DeGregorio, B. A., Chiavacci, S. J., Benson, T. J., Sperry, J. H., Weatherhead, P. J. (2016). Nest predators of North American birds: continental patterns and implications. *BioScience*, **66**, 655-665.

DeGregorio, B. A., Chiavacci, S. J., Weatherhead, P. J., Wilson, J. D., Benson, T. J., Sperry, J. H. (2014). Snake predation on North American bird nests: culprits, patterns and future directions. *Journal of Avian Biology*, **45**, 325-333.

Dijak, W. D., Thompson, F. R. (2000). Landscape and edge effects on the distribution of mammalian predators in Missouri. *Journal of Wildlife Management*, **64**, 209-216.

Dormann, C. F., Elith, J., Bacher, S., et al. (2013). Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, **36**, 27-46.

Duchardt, C. J., Miller, J. R., Debinski, D. M., Engle, D. M. (2016). Adapting the fire-grazing interaction to small pastures in a fragmented landscape for grassland bird conservation. *Rangeland Ecology and Management*, **69**, 300-309.

Engle, D. M., Coppedge, B. R., Fuhlendorf, S. D. (2008). From the Dust Bowl to the Green Glacier: human activity and environmental change in Great Plains grasslands. Pp. 253-271 in Van Auken OW, ed. Western North American Juniperus Communities. New York, NY, USA: Springer.

Fisher, R. J., Davis, S. K. (2010). From Wiens to Robel: a review of grassland-bird habitat selection. *Journal of Wildlife Management*, **74**, 265-273.

Flanders, A. A., Kuvlesky, W. P., Ruthven, D. C., Zaiglin, R. E., Bingham, R. L., Fulbright, T. E., Hernandez, F., Brennan, L. A. (2006). Effects of invasive exotic grasses on South Texas rangeland breeding birds. *Auk*, **123**, 171-182.

Fletcher, R. J., Koford, R. R., Seaman, D. A. (2006). Critical demographic parameters for declining songbirds breeding in restored grasslands. *Journal of Wildlife Management*, **70**, 145-157.

Galligan, E. W., DeVault, T. L., Lima, S. L. (2006). Nesting success of grassland and savanna birds on reclaimed surface coal mines of the Midwestern United States. *Wilson Journal of Ornithology*, **118**, 537-546.

George, A. D., O'Connell, T. J., Hickman, K. R., Leslie, D. M. Jr. (2013). Food availability in exotic grasslands: a potential mechanism for depauperate breeding assemblages. *Wilson Journal of Ornithology*, **125**, 526-533.

Grant, T. A., Madden, E., Berkey, G. B. (2004). Tree and shrub invasion in northern mixed-grass prairie: implications for breeding grassland birds. *Wildlife Society Bulletin*, **32**, 807-818.

Grant, T. A., Madden, E., Shaffer, T. L., Pietz, P. J., Berkey, G. B., Kadrmas, N. J. (2006). Nest survival of clay-colored and vesper sparrows in relation to woodland edge in mixed-grass prairies. *Journal of Wildlife Management*, **70**, 691-701.

Hahn, D. C., Hatfield, J. S. (1995). Parasitism at the landscape scale: cowbirds prefer forests. *Conservation Biology*, **9**, 1415-1424.

Hannon, S. J., Wilson, S., McCallum, C. A. (2009). Does cowbird parasitism increase predation risk to American redstart nests? *Oikos*, **118**, 1035-1043.

Harr, R. N., Morton, L. W., Rusk, S. R., Engle, D. M., Miller, J. R., Debinski, D. M. (2014). Landowners' perceptions of risk in grassland management: woody plant encroachment and prescribed fire. *Ecology and Society*, **19**, art. 41.

Herkert, J. R., Reinking, D. L., Wiedenfeld, D. A., et al. (2003). Effects of prairie fragmentation on the nest success of breeding birds in the midcontinental United States. *Conservation Biology*, **17**, 587-594.

Higgins, K. F., Kirsch, L. M., Ball, I. J. (1969). A cable-chain device for locating duck nests. *Journal of Wildlife Management*, **33**, 1009-1011.

Hovick, T. J., Miller, J. R. (2013). Broad-scale heterogeneity influences nest selection by brown-headed cowbirds. *Landscape Ecology*, **28**, 1493-1503.

Hovick, T. J., Miller, J. R., Dinsmore, S. J., Engle, D. M., Debinski, D. M., Fuhlendorf, S. D. (2012). Effects of fire and grazing on grasshopper sparrow nest survival. *Journal of Wildlife Management*, **76**, 19-27.

Jokela, K. J., Debinski, D. M., McCulley, R. L. (2016). Effects of tall fescue and its fungal endophyte on the development and survival of tawny-edged skippers (Lepidoptera: Hesperiidae). *Environmental Entomology*, **45**, 142-149.

Kirfman, G. W., Brandenburg, R. L., Garner, G. B. (1986). Relationship between insect abundance and endophyte infestation level in tall fescue in Missouri. *Journal of the Kansas Entomological Society*, **59**, 552-554.

Klug, P. E., Jackrel, S. L., With, K. A. (2010). Linking snake habitat use to nest predation risk in grassland birds: the dangers of shrub cover. *Oecologia*, **162**, 803-813.

Klug, P. E., Fill, J., With, K. A. (2011). Spatial ecology of eastern yellow-bellied racer (*Coluber constrictor flaviventris*) and great plains rat snake (*Pantherophis emoryi*) in a contiguous tallgrass-prairie landscape. *Herpetologica*, **67**, 428-439.

Littell, R. C., Milliken, G. A., Stroup, W. W., Wolfinger, R. D., Schabenberger, O. (2006). SAS for mixed models. 2nd ed. Cary, NC, USA: SAS Institute Inc.

Lloyd, J. D., Martin, T. E. (2005). Reproductive success of chestnut-collared longspurs in native and exotic grassland. *Condor*, **107**, 363-374.

Lokemoen, J. T., Koford, R. R. (1996). Using candlers to determine the incubation stage of passerine eggs. *Journal of Field Ornithology*, **67**, 660-668.

Lyons, T. P., Miller, J. R., Debinski, D. M., Engle, D. M. (2015). Predator identity influences the effect of habitat management on nest predation. *Ecological Applications*, **25**, 1596-1605.

Martin, T. E., Geupel, G. R. (1993). Nest-monitoring plots - methods for locating nests and monitoring success. *Journal of Field Ornithology*, **64**, 507-519.

Martin, T. E., Scott, J., Menge, C. (2000). Nest predation increases with parental activity: separating nest site and parental activity effects. *Proceedings of the Royal Society B-Biological Sciences*, **267**, 2287-2293.

Matthews, J. W., Molano-Flores, B., Elis, J., Marcum, P. B., Handel, W., Zylka, J., Phillipe, L. R. (2017). Impacts of management and antecedent site conditionon restoration outcomes in a sand prairie. *Restoration Ecology*, **25**, 972-981.

McGranahan, D. A., Engle, D. M., Wilsey, B. J., Fuhlendorf, S. D., Miller, J. R., Debinski, D. M. (2012). Grazing and an invasive grass confound spatial pattern of exotic and native grassland plant species richness. *Basic and Applied Ecology*, **13**, 654-662.

Miller, J. R., Morton, L. W., Engle, D. M., Debinski, D. M., Harr, R. N. (2012). Nature reserves as catalysts for landscape change. *Frontiers in Ecology and the Environment*, **10**, 144-152.

Murphy, M. T. (2003). Avian population trends within the evolving agricultural landscape of eastern and central United States. *Auk*, **120**, 20-34.

Nelson, S. B., Coon, J. J., Duchardt, C. J., Fischer, J. D., Halsey, S. J., Kranz, A. J., Parker, C. M., Schneider, S. C., Swartz, T. M., Miller, J. R. (2017). Patterns and mechanisms of invasive plant impacts on North American birds: a systematic review. *Biological Invasions*, **19**, 1547-1563.

Osborne, D. C., Sparling, D. W., Hopkins, R. L. II (2012). Influence of Conservation Reserve Program mid-contract management and landscape composition on northern bobwhite in tall fescue monocultures. *Journal of Wildlife Management*, **76**, 566-574.

Osborne, D. C., Sparling, D. W. (2013). Multi-scale associations of grassland birds in response to cost-share management of conservation reserve program fields in Illinois. *Journal of Wildlife Management*, **77**, 920-930.

Patten, M. A., Shochat, E., Reinking, D. L., Wolfe, D. H., Sherrod, S. K. (2006). Habitat edge, land management, and rates of brood parasitism in tallgrass prairie. *Ecological Applications*, **16**, 687-695.

Pedlar, J. H., Fahrig, L., Merriam, H. G. (1997). Raccoon habitat use at 2 spatial scales. *Journal of Wildlife Management*, **61**, 102-112.

Peterjohn, B. G., Sauer, J. R. (1999). Population status of North American grassland birds from the North American Breeding Bird Survey, 1966-1996. *Studies in Avian Biology*, **19**, 27-44.

Pietz, P. J., Buhl, D. A., Shaffer, J. A., Winter, M., Johnson, D. H. (2009). Influence of trees in the landscape on parasitism rates of grassland passerine nests in Southeastern North Dakota. *Condor*, **111**, 36-42.

Powell, L. (2007). Approximating variance of demographic parameters using the delta method: a reference for avian biologists. *Condor*, **109**, 949-954.

Pyke, D. A. (2011). Restoring and rehabilitating sagebrush habitats. *Studies in Avian Biology*, **38**, 531-548.

Ralph, C. J., Geupel, G. R., Pyle, P., Martin, T. E., DeSante, D. F., & Mila, B. (1996). Manual of field methods for monitoring landbirds. *General Technical Report - Pacific Southwest Research Station, USDA Forest Service*, 44 pp.

Renfrew, R. B., Ribic, C. A. (2003). Grassland passerine nest predators near pasture edges identified on videotape. *Auk*, **120**, 371-383.

Renfrew, R. B., Ribic, C. A., Nack, J. L. (2005). Edge avoidance by nesting grassland birds: a futile strategy in a fragmented landscape. *Auk*, **122**, 618-636.

Ribic, C. A., Guzy, M. J., Anderson, T. J., Sample, D. W., Nack, J. L. (2012). Bird productivity and nest predation in agricultural grasslands. *Studies in Avian Biology*, **43**, 119-134.

Rivers, J. W., Jensen, W. E., Kosciuch, K. L., Rothstein, S. I. (2010). Community-level patterns of host use by the brown-headed cowbird (*Molothrus ater*), a generalist brood parasite. *Auk*, **127**, 263-273.

Robel, R. J., Briggs, J. N., Dayton, A. D., Hulbert, L. C. (1970). Relationships between visual obstruction measurements and weight of grassland vegetation. *Journal of Range Management*, **23**, 295-297.

Rosenberg, K. V., Kennedy, J. A., Dettmers, R. et al. (2016). Partners in Flight Landbird Conservation Plan: 2016 Revision for Canada and Continental United States. Partners in Flight Science Committee. 119 pp.

Rowe, H. I. (2010). Tricks of the trade: techniques and opinions from 38 experts in tallgrass prairie restoration. *Restoration Ecology*, **18**, 253-262.

Samson, F., Knopf, F. (1994). Prairie conservation in North America. *BioScience*, **44**, 418-421.

Sauer, J. R., Niven, D. K., Hines, J. E., Ziolkowski, D. J., Pardieck, K. L., Fallon, J. E., Link, W. A. (2017). The North American Breeding Bird Survey, results and analysis 1966-2015. Version 2.07.2017. Laurel, MD, USA: USGS Patuxent Wildlife Research Center.

Schmidt, K. A., Whelan, C. J. (1999). The relative impacts of nest predation and brood parasitism on seasonal fecundity in songbirds. *Conservation Biology*, **13**, 46-57.

Sealy, S. G. (1992). Removal of yellow warbler eggs in association with cowbird parasitism. *Condor*, **94**, 40-54.

Shaffer, T. L. (2004). A unified approach to analyzing nest success. *Auk*, **121**, 526-540.

Shaffer, T. L., Thompson, F. R., III (2007). Making meaningful estimates of nest survival with model-based methods. *Studies in Avian Biology*, **34**, 84-95.

Shahan, J. L., Goodwin, B. J., Rundquist, B. C. (2017). Grassland songbird occurrence on remnant prairie patches is primarily determined by landscape characteristics. *Landscape Ecology*, **32**, 971-988.

Simonsen, V. L., Fontaine, J. J. (2016). Landscape context influences nest survival in a Midwest grassland. *Journal of Wildlife Management*, **80**, 877-883.

Snyder, S. A., Miller, J. R., Skibbe, A. M., Haight, R. G. (2007). Habitat acquisition strategies for grassland birds in an urbanizing landscape. *Environmental Management*, **40**, 981-992.

Strausberger, B. M., Ashley, M. V. (1997). Community-wide patterns of parasitism of a host "generalist" brood-parasitic cowbird. *Oecologia*, **112**, 254-262.

Temple, S. A. (2002). Dickcissel (*Spiza americana*); in Poole A, ed. The Birds of North America Online. Ithaca: Cornell Lab of Ornithology.

Warner, R. E. (1994). Agricultural land use and grassland habitat in Illinois: future shock for Midwestern birds? *Conservation Biology*, **8**, 147-156.

Wright, C. K., Wimberly, M. C. (2013). Recent land use change in the Western Corn Belt threatens grasslands and wetlands. *Proceedings of the National Academy of Sciences of the United States of America*, **110**, 4134-4139.

TABLES

Table 4.1. Models examining the factors that influence daily nest survival probabilities of dickcissel nests in Ringgold County, IA, ranked by AIC_c values. All models in all stages include 'PastureID' as a random variable.

Model	k^a	Deviance	ΔAIC_c	Model weight (ω)
Stage 1: Temporal variables				
Year × Nest Visit Date[b]	9	1749.64	0.00[c]	0.90
Nest Visit Date	3	1770.19	5.58	0.05
Nest Visit Date + Nest Visit Date^2	4	1765.62	5.91	0.05
Year + Nest Visit Date	6	1769.58	13.89	0.00
Intercept-only Model	2	1777.90	14.17	0.00
Year	5	1776.12	18.43	0.00
Stage 2: Nest-contents[d]				
Stage × Parasitism[e]	14	1706.98	0.00[c]	0.93
Nest Stage[f]	11	1718.20	5.15	0.07
Parasitism	10	1747.19	32.12	0.00
Stage 2 Base Model	9	1749.64	32.56	0.00
#Chicks[g]	10	1749.62	34.55	0.00
Stage 3: Nest-site and landscape variables[h]				
Tall Fescue	15	1697.15	0.00[c]	0.78
1000 m Crop Cover	15	1704.05	6.92	0.03
Stage 3 Base Model	14	1706.98	7.80	0.02
StDev Robel	15	1705.03	7.87	0.02
Avg Robel	15	1702.99	8.06	0.01
Cool-season grasses	15	1705.20	8.06	0.01
500 m Crop Cover	15	1735.44	8.09	0.01
1000 m Herb Cover	15	1705.26	8.11	0.01
Warm-season grasses	15	1705.75	8.60	0.01
250 m Crop Cover	15	1705.77	8.66	0.01
500 m Herb Cover	15	1705.87	8.72	0.01
500 m Woodland Cover	15	1706.19	9.05	0.01
250 m Herb Cover	15	1706.22	9.07	0.01
Wood (nest site)	15	1706.29	9.17	0.01
Forbs	15	1706.49	9.34	0.01
250 m Woodland Cover	15	1706.53	9.38	0.01
1000 m Woodland Cover	15	1706.74	9.60	0.01
Distance to Woods	15	1706.79	9.65	0.01

Table 4.1. continued…

Model	k[a]	Deviance	ΔAIC_c	Model weight (ω)
250 m Wooded-edge Length	15	1706.86	9.75	0.01
Stage 3 continued…				
Litter Cover	15	1706.95	9.80	0.00
1000 m Wooded-edge Length	15	1706.96	9.82	0.00
500 m Wooded-edge Length	15	1706.97	9.83	0.00

---

[a] Number of parameters in the model.

[b] Nest visit date: date of the end of the interval over which nest survival was recorded.

[c] Minimum AIC_c values: 1767.71 (Stage 1); 1735.15 (Stage 2); 1727.35 (Stage 3).

[d] The Stage 2 base model included Year × Nest Visit Date. All other models in this stage expanded upon this base model with the variables listed in the model name.

[e] Parasitism: whether the nest contained any cowbirds on the visit when survival was recorded.

[f] Nest stage: whether the nest was in the laying, incubation, or nestling phase at the beginning of the interval over which survival was recorded.

[g] #Chicks: number of dickcissel and/or cowbird chicks in the nest at the beginning of the interval over which survival was recorded.

[h] The Stage 3 base model included Year × Nest Visit Date + Stage × Parasitism. All other models in this stage expanded upon this base model with the variables listed in the model name.

Table 4.2. Models examining the factors that influence the probability of dickcissel nests being parasitized by brown-headed cowbirds, ranked by AIC$_c$ values. All models in both stages include 'PastureID' as a random variable.

Model	k^a	Deviance	ΔAIC$_c$	Model weight (ω)
Stage 1: Temporal variables				
Year + Initiation Date	6	527.02	0.00[b]	0.73
Year × Initiation Date	9	522.79	1.99	0.27
Initiation Date	3	548.40	15.25	0.00
Year	5	562.59	33.52	0.00
Intercept-only Model	2	582.61	47.42	0.00
Stage 2: Nest-site and landscape variables[c]				
500 m Woodland Cover	7	517.12	0.00[b]	0.53
Wood (nest site)	7	520.06	2.94	0.12
Tall Fescue	7	520.94	3.82	0.08
500 m Wooded-edge Length	7	521.29	4.17	0.07
250 m Woodland Cover	7	521.42	4.31	0.06
1000 m Wooded-edge Length	7	522.43	5.31	0.04
1000 m Woodland Cover	7	523.84	6.72	0.02
250 m Wooded-edge Length	7	524.62	7.50	0.01
Stage 2 Base Model	6	527.02	7.84	0.01
Cattle	7	525.44	8.33	0.01
StDev Robel	7	525.70	8.58	0.01
Distance to Woods	7	525.77	8.65	0.01
Forbs	7	526.01	8.89	0.01
500 m Herb Cover	7	526.17	9.06	0.01
Warm-season Grasses	7	526.39	9.27	0.01
Cool-season Grasses	7	526.43	9.31	0.00
1000 m Herb Cover	7	526.59	9.47	0.00
250 m Herb Cover	7	526.82	9.71	0.00
Avg Robel	7	526.85	9.74	0.00

[a] Number of parameters in the model.

[b] Minimum AIC$_c$ values: 540.04 (Stage 1); 532.20 (Stage 2).

[c] The Stage 2 base model included Year + Initiation Date. All other models in this stage expanded upon this base model with the variables listed in the model name.

FIGURES

Figure 4.1. Daily survival probability for non-parasitized (dark) and parasitized (light) dickcissel nests in different stages of the nesting cycle. Bars represent 85% confidence intervals.

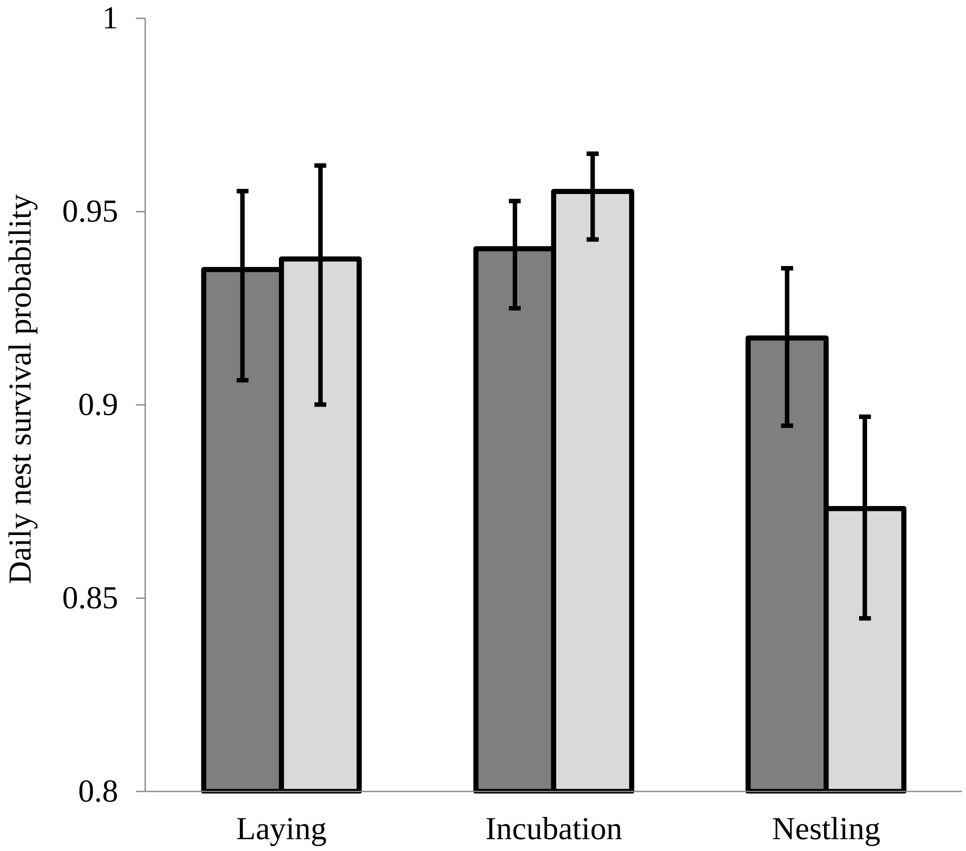
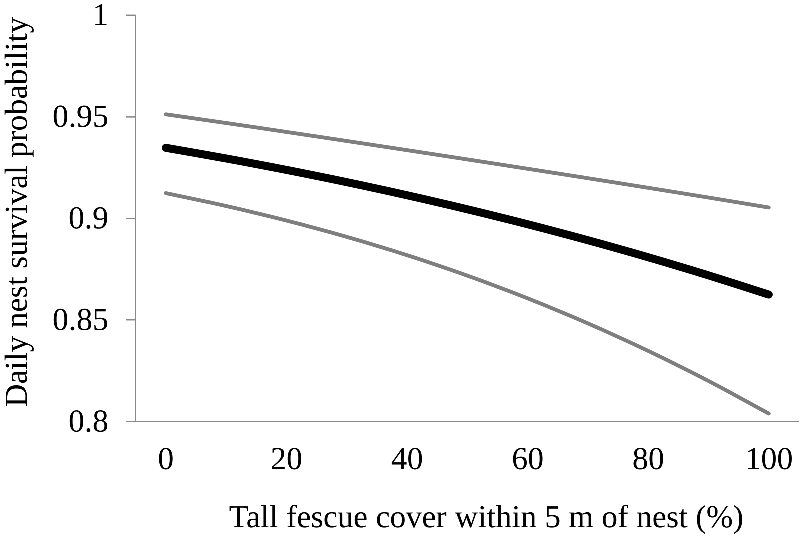


Figure 4.2. Daily nest survival probability as a function of (A) tall fescue cover within 5 m of dickcissel nests, and (B) row-crop cover within 1000 m of nests. Grey lines represent 85% confidence intervals.

(A)



(B)

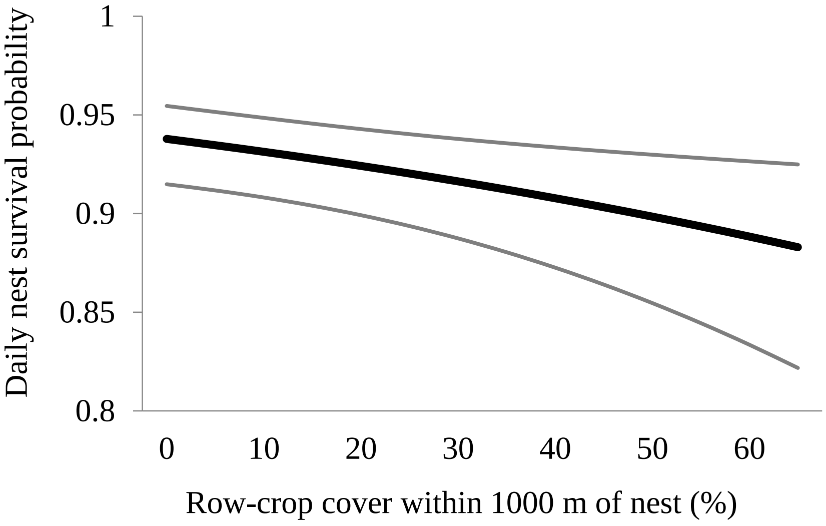
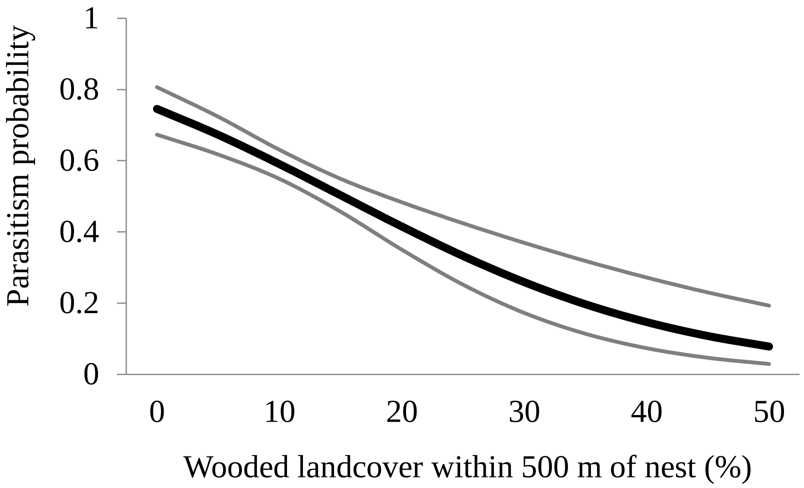


Figure 4.3. Cowbird parasitism risk as a function of (A) woodland cover and (B) wooded-edge length within 500 m of nests. Grey lines represent 85% confidence intervals.

(A)



(B)

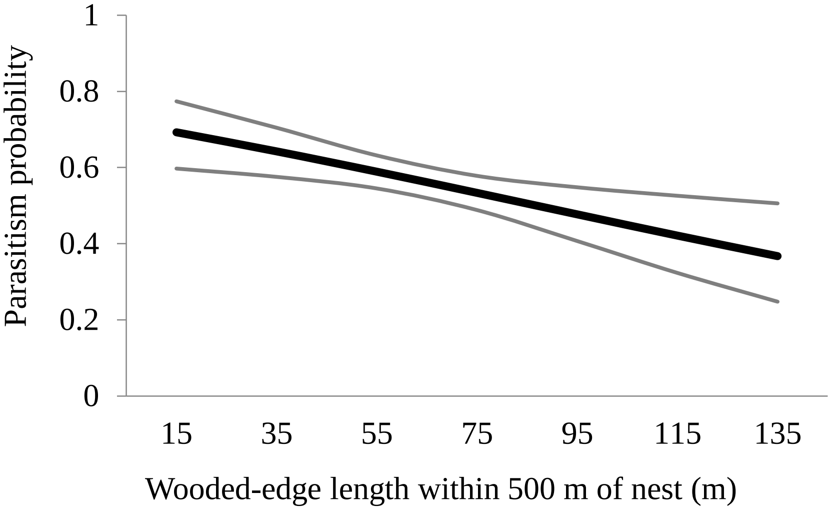
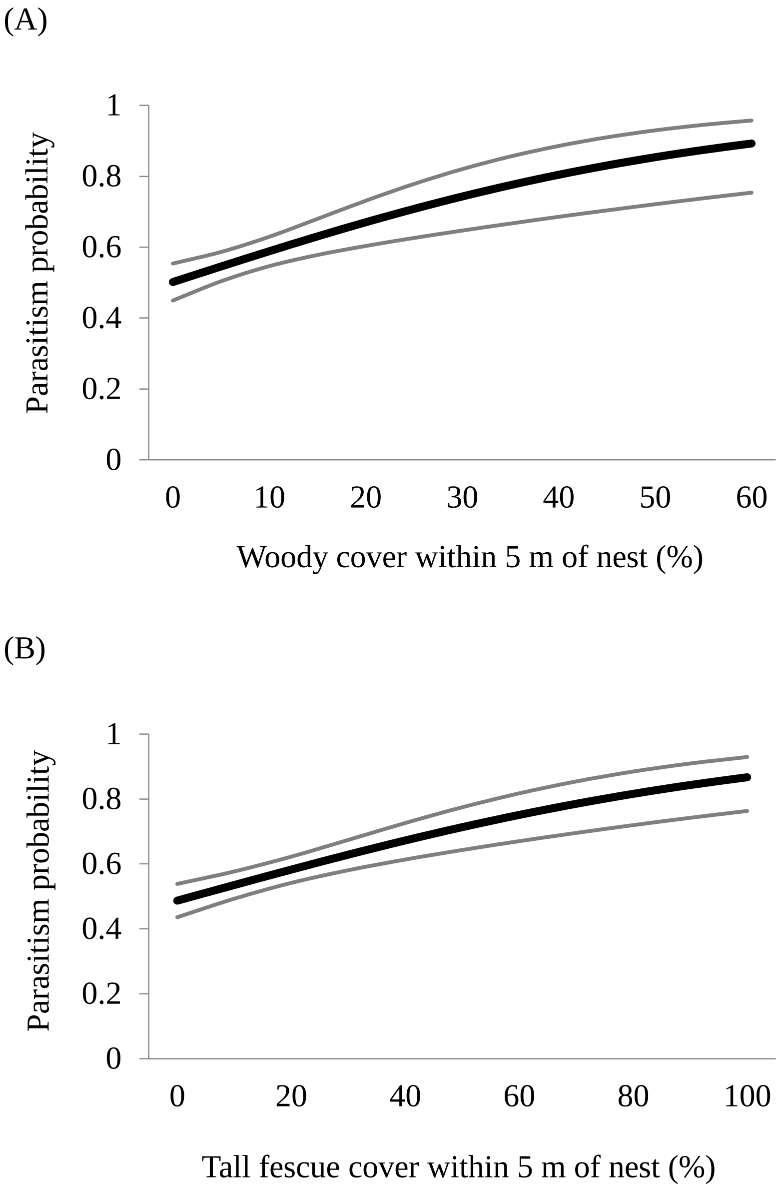


Figure 4.4. Cowbird parasitism risk as a function of (A) woody cover and (B) tall fescue cover within 5 m of nests. Grey lines represent 85% confidence intervals.



CHAPTER 5 – SUMMARY

I began my doctoral research with what I had thought might be a straightforward question: do dickcissel habitat preferences improve their reproductive success? It may indeed be that animals often engage in adaptive habitat selection, but my studies have shown there is no guarantee that the ways they do so are simple. Reflecting on my results, I am struck that the answer to my question is one ecologists have been delivering since the inception of ecology. It depends.

It depends on whether you are considering a male or female dickcissel. Males face strong competition for mates: a sizable portion of males will attract no mates, whilst another portion will pair with multiple females (Fig 2.3). Males are thus under pressure to acquire the territories most attractive to females. Perhaps that is why males settled quickly in territories that produced offspring in excellent body condition: females tended to settle polygynously there. Males would derive a twofold advantage from acquiring these habitats: enhanced offspring quality *and* increased polygyny, which increases fledgling production. For females, however, the advantage may only lie in increased offspring condition (and the enhanced post-fledging survival that often comes with it). It makes sense that females should prefer these habitats; afterall, dickcissels rarely lay another clutch after producing a successful brood, so post-fledging survival is crucial.

Whether habitat preferences improve fitness depends not only on sex, but also on temporally variable factors. Ecological conditions change over time, and stochasticity sometimes demands its due. For instance, unlike in 2014, male dickcissels settling early in 2015 found the tables against them. Not only were females in short supply for most of May (Fig 2.2), but males lucky enough to attract mates were met with high nest predation rates in the early season.

These patterns represent unusual and even novel observations. Many authors have suggested it may be difficult for birds to develop effective habitat-selection strategies to improve nest success because microhabitats avoided by one type of predator are often used by others. Few authors though have suggested that between-year variability in predator communities as a limiting factor. However, in each year of my study (2013-2016), nest survival rates exhibited distinct within-season trends in nest survival—in some years survival was higher earlier, in some years later (Appendix K)—suggesting that early occupancy of preferred areas may not always be beneficial. On top of this, perhaps the most unique element of the between-year variability I observed was that variation in conspecific population sizes, and thus mate availability, disrupted adaptive habitat selection. To my knowledge, no other authors have reported this.

Returning again to my original question, adaptive habitat selection depends on the spatial scale under consideration. Patterns in brood parasitism demonstrate this clearly. Whether or not dickcissels exhibited habitat preferences among territories, they had no impact on parasitism. In contrast, at broad scales, birds congregated early and in high densities in patches with low parasitism rates. This pattern drives home the importance of measuring preferences at scales relevant to the fitness components measured. Brown-headed cowbirds have large and overlapping home-ranges, such that dickcissels may not be able to find individual territories with lower parasitism risk than neighboring territories. But among larger patches, parasitism may vary as a function of local cowbird abundance and woodland cover in the landscape (Fig 4.3).

A lesson from these collective results is that our judgements of whether animals exhibit adaptive habitat selection frequently depend on the metrics of fitness examined. Although I did not identify any clear trade-offs among dickcissel reproductive metrics, it is clear that I would have missed interesting relationships and complexity if I had measured fewer parameters. Each fitness metric showed unique, scale-dependent associations with habitat preferences.

Doubtless, because I did not measure still *more* parameters (e.g., post-fledging survival, adult survival, migratory and overwintering processes), there were many relevant patterns I could not elucidate. Similarly, because my study lasted just two years, I could not assess relationships between lifetime fitness and habitat selection. These would be fascinating areas to explore in the future. Indeed, just as I argued at the beginning of this dissertation for a multi-scale, multi-fitness-metric approach, if birds did not fly so far or GPS transmitters cost so much, I would advocate as vociferously for a consistent emphasis on full-annual-cycle research and lifetime monitoring of birds. This would not only monumentally expand our comprehension of adaptive habitat selection, but would also provide valuable knowledge for conservation.

In this dissertation, however, I am content to contribute to conservation by increasing awareness of how invasive plants and other anthropogenic habitat changes impact grassland birds. In particular, I showed that increasing cover of the invasive grass tall fescue at broad and fine spatial scales reduced dickcissel nest success and productivity. These results build on a handful of prior studies indicating that tall fescue is detrimental to wildlife—and to breeding grassland birds in particular (Coley et al., 1995; Osborne et al., 2012; Osborne & Sparling, 2013; Lyons et al., 2015; Jokela et al., 2016). Although another study found no effect of tall fescue on nest success (Galligan et al., 2006) and it is always important to bear in mind that impacts of even the same invasive species can vary over time and space (Nelson et al., 2017), our findings strengthen the case for controlling tall fescue to improve habitat for grassland wildlife. It is heartening then, as my colleague Jaime Coon's upcoming dissertation will address, that there may be opportunities to collaborate on efforts to control tall fescue with private landowners who see it as a threat to their cattle operations (Stuedemann & Hoveland, 1988; Coon et al., 2018).

Controlling tall fescue might be especially important because my research indicates that dickcissels do not avoid areas with large amounts of this grass, in spite of its negative impacts on fitness. This situation is consistent with the idea that tall fescue creates an equal-preference ecological trap—a novel finding. This result was just one of many showing that, on average, dickcissels did not identify high-quality habitats based on vegetation features. We discussed several reasons for why this might be in Chapter 3 and highlighted that dickcissels must rely on alternative behavioral mechanisms to engage in adaptive habitat selection. Future work might, for example, focus on how birds respond to arthropod abundance, or whether they are more likely to return to territories and patches where they or their neighbors successfully reproduced.

Such studies would be well served to consider my results. First, fitness manifests in many forms, so researchers should measure multiple metrics. Second, fitness metrics should be matched with relevant spatial scales. Finally, authors should consider how temporally variable conditions might alter their conclusions. Following these guidelines should greatly improve our ability to understand the nuanced ways in which animals engage in adaptive habitat selection.

LITERATURE CITED

Coley, A. B., Fribourg, H. A., Pelton, M. R., & Gwinn, K. D. (1995). Effects of tall fescue endophyte infestation on relative abundance of small mammals. *Journal of Environmental Quality*, **24**, 472-475. 10.2134/jeq1995.00472425002400030012x

Coon, J. J., Morton, L. W., & Miller, J. R. 2018. A survey of landowners in the Grand River Grasslands: Managing wildlife, cattle, and non-native plants. Report 2018-03, University of Illinois at Urbana-Champaign Department of Natural Resources and Environmental Sciences, Urbana, IL.

Galligan, E. W., DeVault, T. L., & Lima, S. L. (2006). Nesting success of grassland and savanna birds on reclaimed surface coal mines of the Midwestern United States. *Wilson Journal of Ornithology*, **118**, 537-546. 10.1676/05-086.1

Jokela, K. J., Debinski, D. M., & Mcculley, R. L. (2016). Effects of tall fescue and its fungal endophyte on the development and survival of tawny-edged skippers (Lepidoptera: Hesperiidae). *Environmental Entomology,* **pii**, 1-10.

Lyons, T. P., Miller, J. R., Debinski, D. M., & Engle, D. M. (2015). Predator identity influences the effect of habitat management on nest predation. *Ecological Applications*, **25**, 1596-1605. 10.1890/14-1641.1

Nelson, S. B., Coon, J. J., Duchardt, C. J., Fischer, J. D., Halsey, S. J., Kranz, A. J., . . . Miller, J. R. (2017). Patterns and mechanisms of invasive plant impacts on North American birds: a systematic review. *Biological Invasions*, 1-17. 10.1007/s10530-017-1377-5

Osborne, D. C., & Sparling, D. W. (2013). Multi-scale associations of grassland birds in response to cost-share management of conservation reserve program fields in Illinois. *Journal of Wildlife Management*, **77**, 920-930. 10.1002/jwmg.553

Osborne, D. C., Sparling, D. W., & Hopkins, R. L., II. (2012). Influence of conservation reserve program mid-contract management and landscape composition on northern bobwhite in tall fescue monocultures. *Journal of Wildlife Management*, **76**, 566-574. 10.1002/jwmg.258

Stuedemann, J. A., & Hoveland, C. S. (1988). Fescue endophyte: history and impact on animal agriculture. *Journal of Production Agriculture*, **1**, 39-44. 10.2134/jpa1988.0039

APPENDIX A – ANNUAL CLIMATE DATA

Table A.1. Monthly (May-August) climate data from 2014-2015 in our study region. Temperatures are in ^{o}C and precipitation is in inches. Data were collected at the nearest weather station, in Lamoni, IA, USA. Data were obtained from the National Climatic Data Center (National Oceanic and Atmospheric Administration).

Year	**Month**	**Avg. Temp.**	**Avg. Daily High Temp.**	**Avg. Daily Low Temp.**	**Precipitation**
2014	May	16.6	22.6	10.6	3.7
	June	22.1	27.4	16.7	10.9
	July	21.7	27.2	16.1	3.4
	August	23.6	28.3	18.9	10.8
	May-August	21.0	26. 4	15.6	28.8
2015	May	16.5	21.7	11.3	6.8
	June	22.8	28.2	17.5	5.9
	July	24.4	29.9	18.9	10.0
	August	22.7	28.4	17.0	4.7
	May-August	21.6	27.1	16.2	27.4

APPENDIX B – PASTURE DESCRIPTIONS (CHAPTERS 2 & 3)

Table B.1. Study pastures in Ringgold County, IA where we collected data on dickcissel (*Spiza americana*) habitat preferences and reproductive success from 2014-2015. Pastures were managed with prescribed burning, cattle grazing, and glyphosate herbicide.

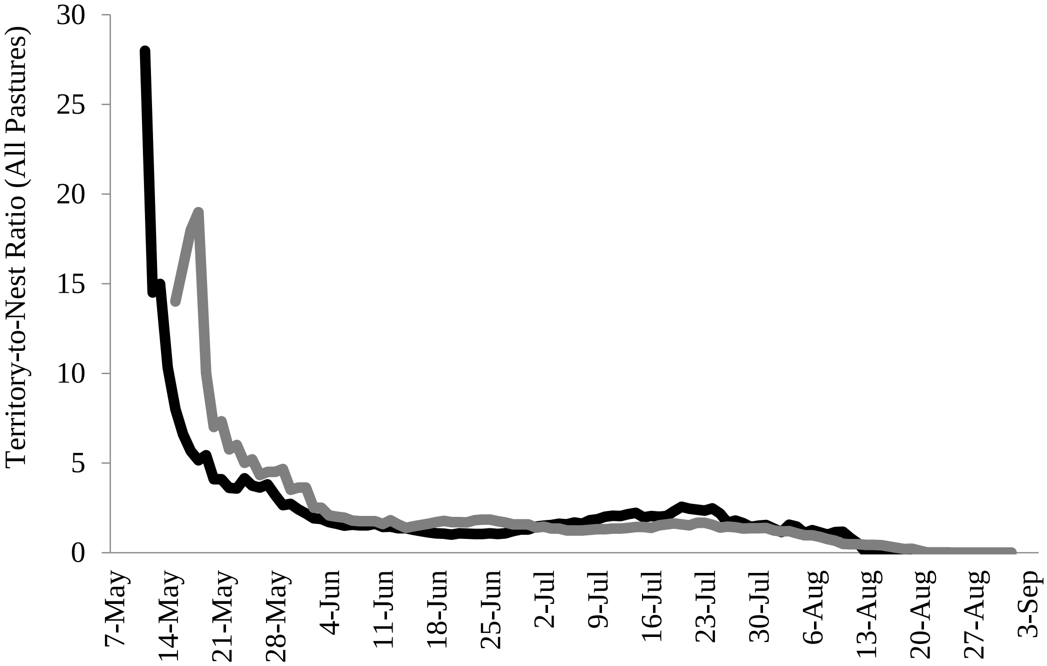
Pasture	**Pasture Area (Ha)**	**Area of Patches in Pasture (Ha)**	**Burn History**	**Stocked with Cattle?**	**Glyphosate Treatment?**
PYN	24.50	6.95 + 7.85 + 9.70	One patch burned each year[a]	Yes	None
KLN	30.78	8.18 + 10.64 + 11.96	One patch burned each year[a]	Yes	None
STE	33.15	8.31 + 9.26 + 15.58	Burned in spring 2012	Yes	None
LTR[b]	34.99	10.84 + 11.96 + 12.19	Burned in spring 2012 and 2015	Yes	Two patches sprayed in fall 2014
KLT	41.06	13.15 + 13.21 + 14.70	Burned in spring 2012	No	None
RNR	24.69	6.37 + 6.97 + 11.35	Burned in spring 2012	No	None
RIN	17.58	3.45 + 6.84 + 7.29	Burned in spring 2012	No	None

[a] Pastures managed with patch-burn grazing since 2007; burned patches were rotated each year so the entire pasture was burned over 3-year cycles.

[b] Data collected on LTR in 2014 were excluded from analyses due to an intense June storm that altered vegetation, killed nesting birds, and precipitated a mass exodus of territorial males. 2015 data were included in analyses.

APPENDIX C – ANNUAL MALE-TO-FEMALE RATIOS

Figure C.1. Ratio of dickcissel territories to nests in 2014 (black) and 2015 (grey) across all study pastures in Ringgold County, IA. Ratios were calculated by dividing the number of territories known to exist each day by the number of nests known to be active each day. Territory counts were smoothed between survey dates before calculating ratios. This ratio was uncalculable before 11 May (2014) and before 15 May (2015); even though there were territories established before those dates, no nests had yet been built. The fact that the line begins later in 2015 thus reflects that the male-to-female ratio in early May was lower in 2014 versus 2015.



APPENDIX D – FULL AIC TABLES (CHAPTER 2)

AIC tables for analyses of adaptive habitat selection by dickcissels (*Spiza americana*). Tables A-G correspond to the analyses summarized in Table 2.1. Stage 1 of model selection determined covariates to include in subsequent models. Stage 2 then examined whether male or female habitat preferences at the territory and patch scales predicted reproductive metrics. Data were collected in 2014 and 2015 in Ringgold County, IA.

We quantified male preferences at the territory scale by ranking territories by the relative order in which they were first observed. Territories established in the same location (>50% spatial overlap) were assigned the settlement rank of the earliest-established territory among them. We quantified female preferences at the territory scale based on territory polygyny levels, determined by the maximum number of simultaneously active nests on each territory. We estimated male preferences at the patch scale based on maximum territory densities on each patch each year. We estimated female habitat preferences at the patch scale by dividing the total number of nests on each patch each year by the total number of territories recorded there.

Table D.1. Models examining whether male habitat preferences at the territory and patch scales predict territory polygyny levels. All models included ‘Pasture × Year’ as a random variable.

Model	# parameters	Deviance	ΔAIC_c	Model weight (ω)
Stage 1: Covariates				
Tenure[a]	3	362.81	0.00	1.000
Territory Area (Ha)	3	390.58	27.78	0.000
Intercept-only Model	2	392.89	28.01	0.000
Stage 2: Habitat preferences[b]				
Settlement Rank × Year	6	354.10	0.00	0.500
Maximum Territory Density	4	359.89	1.50	0.236
Base Model (Tenure)	3	362.81	2.30	0.158
Settlement Rank	4	362.47	4.08	0.065

Table D.1. continued…

Model	# parameters	Deviance	ΔAIC_c	Model weight (ω)
Max. Territory Density × Year	6	359.12	5.02	0.041

[a] Number of days for which the territory was defended.
[b] All models in this stage include ‘Tenure’ as a covariate.

Table D.2. Models examining whether male habitat preferences at the territory and patch scales predict the probability of nests in those territories or patches being parasitized by brown-headed cowbirds (*Molothrus ater*). All models included ‘Pasture’ as a random variable.

Model	# parameters	Deviance	ΔAIC_c	Model weight (ω)
Stage 1: Covariates				
Initiation Date	3	204.84	0.00	0.986
Random Effects-only Model	2	216.20	9.29	0.009
Year	3	215.58	10.73	0.005
Stage 2: Habitat preferences[a]				
Maximum Territory Density	4	202.7	0.00	0.445
Base Model (Initiation Date)	3	204.84	0.05	0.434
Max. Territory Density × Year	6	202.54	4.10	0.057
Settlement Rank	4	206.80	4.10	0.057
Settlement Rank × Year	6	206.74	8.29	0.007

[a] All models in this stage include ‘Initiation Date’ as a covariate.

Table D.3. Models examining whether female habitat preferences at the territory and patch scales predict the probability of nests in those territories or patches being parasitized by brown-headed cowbirds. All models included ‘Pasture’ as a random variable.

Model	# parameters	Deviance	ΔAIC_c	Model weight (ω)
Stage 1: Covariates (See Table D.2, Stage 1)				
Stage 2: Habitat preferences [a]				
Nest-to-territory Ratio	4	201.55	0.00	0.518
Base Model (Initiation Date)	3	204.84	1.21	0.283
Nest-to-territory Ratio × Year	6	200.39	3.10	0.110
Territory Polygyny Level	4	205.65	4.10	0.067

Table D.3. continued…

Model	# parameters	Deviance	ΔAIC_c	Model weight (ω)
Territory Polygyny Level × Year	6	203.52	6.24	0.023

[a] All models in this stage include 'Initiation Date' as a covariate.

Table D.4. Models examining whether male habitat preferences at the territory and patch scales predict territory productivity. All models included 'Pasture × Year' as a random variable.

Model	# parameters	Deviance	ΔAIC_c	Model weight (ω)
Stage 1: Covariates				
Total Nests[a]	4	385.54	0.00	0.968
Tenure[b]	4	392.50	6.96	0.030
Territory Area (Ha)	4	398.08	12.55	0.002
Random Effects-only Model	3	401.69	14.05	0.001
Stage 2: Habitat preferences[c]				
Settlement Rank × Year	7	373.29	0.00	0.860
Maximum Territory Density	5	383.37	5.72	0.049
Base Model (Total Nests)	4	385.54	5.75	0.049
Settlement Rank	7	380.64	7.35	0.022
Max. Territory Density × Year	5	385.16	7.51	0.020

[a] Total number of nests built on the territory during its tenure.
[b] Number of days for which the territory was defended.
[c] All models in this stage include 'Total Nests' as a covariate.

Table D.5. Models examining whether female habitat preferences at the territory and patch scales predict nest productivity in those territories or patches. No random variables were included.

Model	# parameters	Deviance	ΔAIC_c	Model weight (ω)
Stage 1: Covariates				
Intercept-only Model	1	227.69	0	0.504
Year	2	227.66	2.1	0.177
Nest Initiation Date	2	227.69	2.13	0.174
Nest Initiation Date × Year	4	223.57	2.49	0.145
Stage 2: Habitat preferences				
Nest-to-territory Ratio	2	225.31	0	0.411

Table D.5. continued…

Model	**# parameters**	**Deviance**	**ΔAIC_c**	**Model weight (ω)**
Intercept-only Model	1	227.69	0.25	0.363
Territory Polygyny Level	2	227.69	2.38	0.125
Nest-to-territory Ratio × Year	4	224.53	3.7	0.065
Territory Polygyny Level × Year	4	225.64	4.81	0.037

Table D.6. Models examining whether male habitat preferences at the territory and patch scales predict the body condition of nestlings reared in those territories or patches. Condition was calculated for each nestling as residual mass from a linear regression of mass and tarsus length. All models included 'NestID' as a random variable.

Model	**# parameters**	**Deviance**	**ΔAIC_c**	**Model weight (ω)**
Stage 1: Covariates				
Time of Day[a]	3	570.37	0.00	0.998
#BHCO Chicks[b]	2	585.32	14.94	0.001
Random Effects-only Model	3	587.68	15.22	0.000
Nestling Age[c]	3	586.85	16.47	0.000
Ordinal Date[d]	3	587.15	16.78	0.000
Year	3	587.43	17.05	0.000
#Chicks[e]	3	587.67	17.30	0.000
Stage 2: Habitat preferences[f]				
Settlement Rank	4	562.66	0.00	0.675
Settlement Rank × Year	6	560.33	1.97	0.252
Base Model (Time of Day)	3	570.37	5.60	0.041
Maximum Territory Density	4	567.97	6.47	0.027
Max. Territory Density × Year	6	567.88	9.53	0.006

[a] Time of day nestlings were measured.

[b] Maximum number of brown-headed cowbird chicks observed in the nest.

[c] Age of nestlings when measured.

[d] Ordinal date on which nestlings were measured.

[e] Total number of chicks (dickcissels and cowbirds) observed in the nest.

[f] All models in this stage include 'Time of Day' as a covariate.

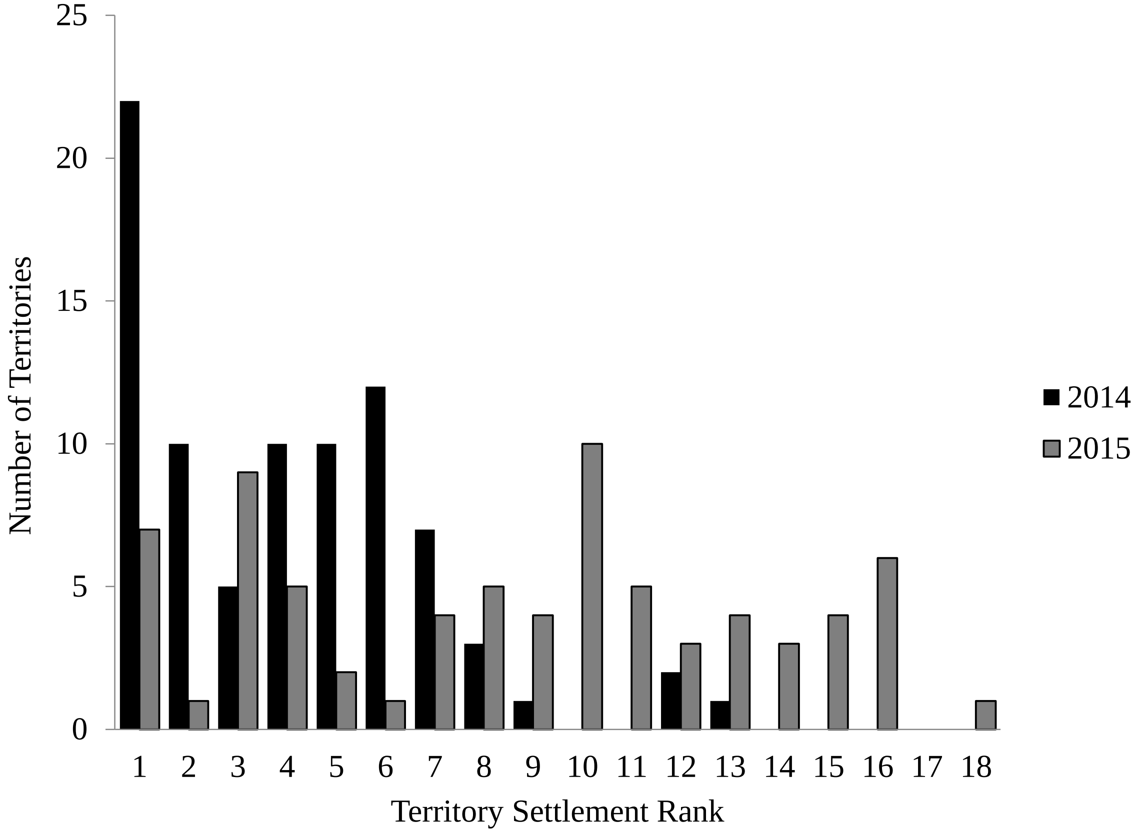
Table D.7. Models examining whether female habitat preferences at the territory and patch scales predict the body condition of nestlings reared in those territories or patches. Condition was calculated for each nestling as residual mass from a linear regression of mass and tarsus length. All models included ‘NestID’ as a random variable.

Model	**# parameters**	**Deviance**	**ΔAIC_c**	**Model weight (ω)**
Stage 1: Covariates (See Table D.6, Stage 1)				
Stage 2: Habitat preferences[a]				
Territory Polygyny Level	4	565.70	0.00	0.449
Nest-to-territory Ratio	4	567.23	1.52	0.210
Base Model (Time of Day)	3	563.41	2.00	0.165
Territory Polygyny Level × Year	6	570.37	2.55	0.125
Nest-to-territory Ratio × Year	6	565.78	4.37	0.050

[a] All models in this stage include ‘Time of Day’ as a covariate.

APPENDIX E – TERRITORY SETTLEMENT RANK HISTOGRAMS

Figure E.1. Histogram of the number of dickcissel territories per year assigned each settlement rank. These figures only include territories used in our analyses, and thus do not include territories excluded due to >50% spatial overlap with other territories (when multiple territores overlapped >50% we only included the territory with the longest tenure).



APPENDIX F – REPEATED VEGETATION MEASURES IN PERMANENT PLOTS

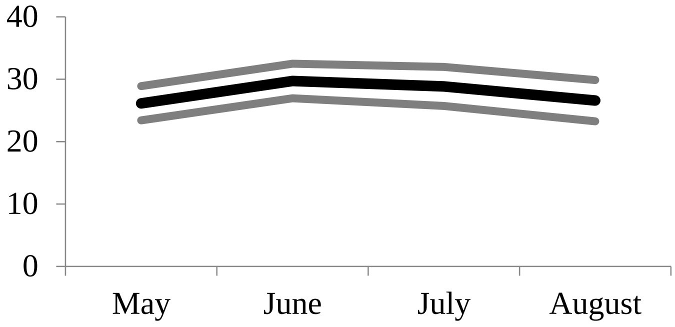
In the summer of 2016, I gathered vegetation data to assess whether my decision to estimate vegetation structure and composition in dickcissel territories and study patches late in the breeding seasons of 2014 and 2015 meant that my vegetation measurements did not actually reflect vegetation at the time dickcissels were making their settlement decisions. Specifically, in mid-May 2016, I haphazardly placed and permanently marked 3 0.5-m^2 plots at least 100 m apart on each of my study patches, yielding 63 permanent vegetation sampling plots (7 pastures × 3 patches/pasture ×3 plots/patch = 63 plots). I then collected estimates for all the same quadrat-level vegetation components I collected in my territory- and patch-scale vegetation measurements (e.g., percent cover of plant functional groups, Robel height, litter depth; see Appendix G) in exactly the same locations each month of the 2016 breeding season (May-August; four independent estimates per permanent plot).

Vegetation estimates were conducted in the same way as described in Chapter 3 of this dissertation. Accordingly, percent cover estimates were recorded as the midpoints of the intervals 0% (0), 1-5% (3), 6-25% (16), 26-50% (38), 51-75% (63), 76-95% (86), or 96-100% (98). Robel height was measured (in decimeters) at each quadrat from each cardinal direction, and a quadrat-level estimate was obtained by averaging across these four readings. Litter depth was measured to the nearest 0.25 cm at three points in each quadrat and these readings were averaged to obtain a quadrat-level estimate.

In ‘Panel A’ of each of the figures below, I show the values of each vegetation component in each month, averaged across all 63 quadrats, to display changes in absolute estimates over time. In ‘Panel B’ of each figure, I then show how vegetation estimates at the beginning of the breeding season (i.e., in May) predict estimates in each other month. In these graphs, I have displayed the trajectory of vegetation change separately for quadrats with differing May conditions. Thus, for graphs relating to percent-cover estimates, there is a separate trajectory averaging all plots with a value in May of ‘0-1’, of ‘3’, of ‘16’, of ‘38’, of ‘63’, of ‘86’, and of ‘98’. A similar method is used to show how Robel height and litter depth in May predict those variables' values later in the season. The legend in each graph indicates how many quadrats had each vegetation estimate in May.

Figure F.1. Average percent cover of cool-season grasses within quadrats in May, June, July, and August, shown across (A) all quadrats, with standard errors, and (B) quadrats with differing starting (i.e., May) values.

(A)



(B)

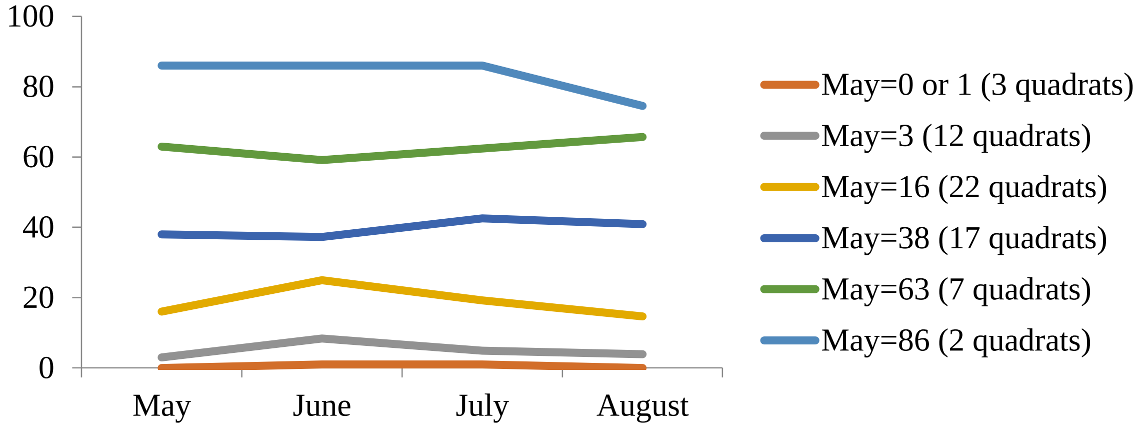
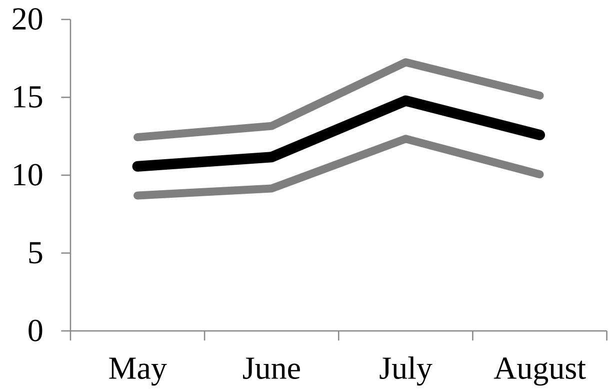


Figure F.2. Average percent cover of tall fescue (*Schedonorus arundinaceus*) within quadrats in May, June, July, and August, shown across (A) all quadrats, with standard errors, and (B) quadrats with differing starting (i.e., May) values.

(A)



(B)

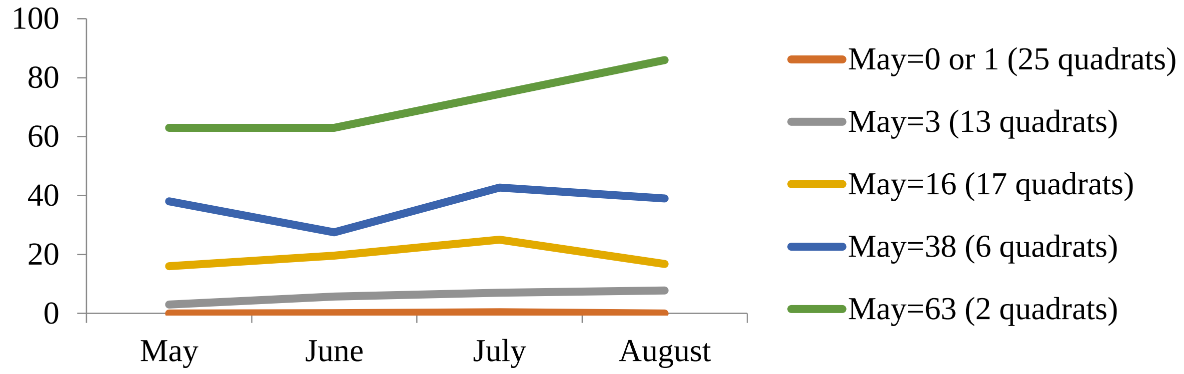
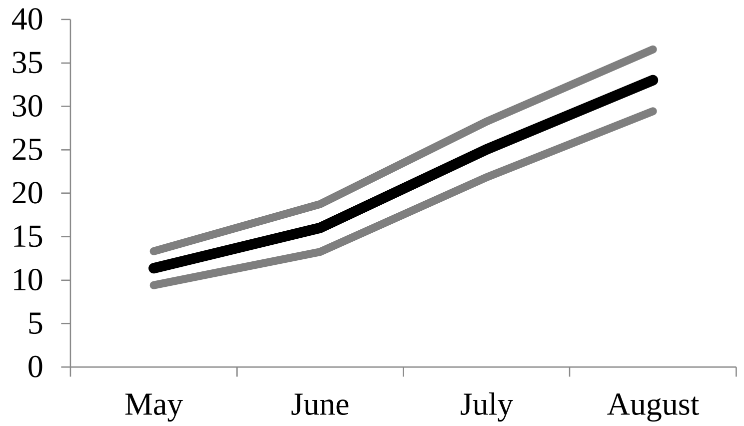


Figure F.3. Average percent cover of warm-season grasses within quadrats in May, June, July, and August, shown across (A) all quadrats, with standard errors, and (B) quadrats with differing starting (i.e., May) values.

(A)



(B)

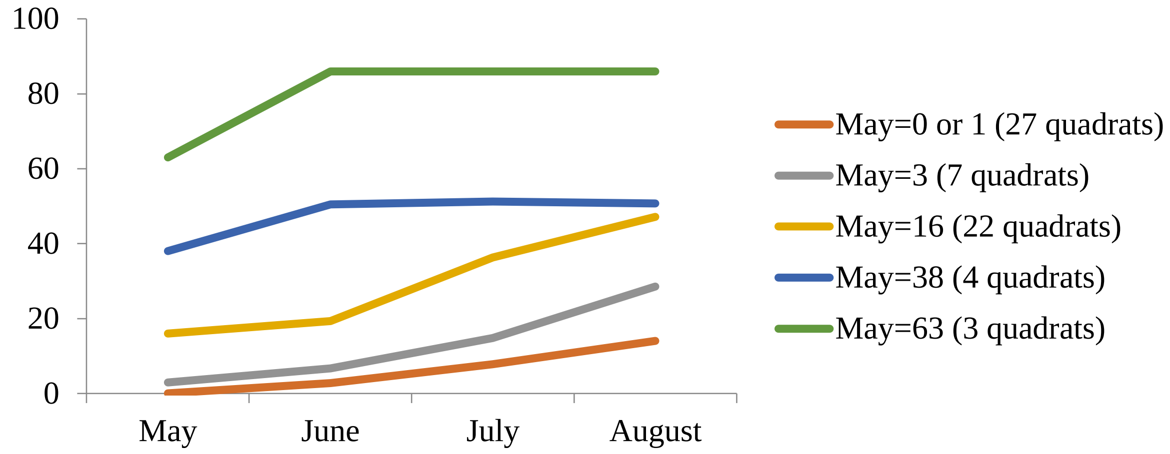
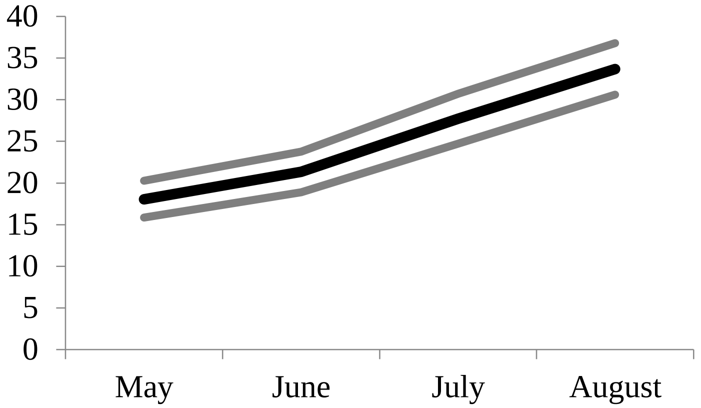


Figure F.4. Average percent cover of forbs within quadrats in May, June, July, and August, shown across (A) all quadrats, with standard errors, and (B) quadrats with differing starting (i.e., May) values.

(A)



(B)

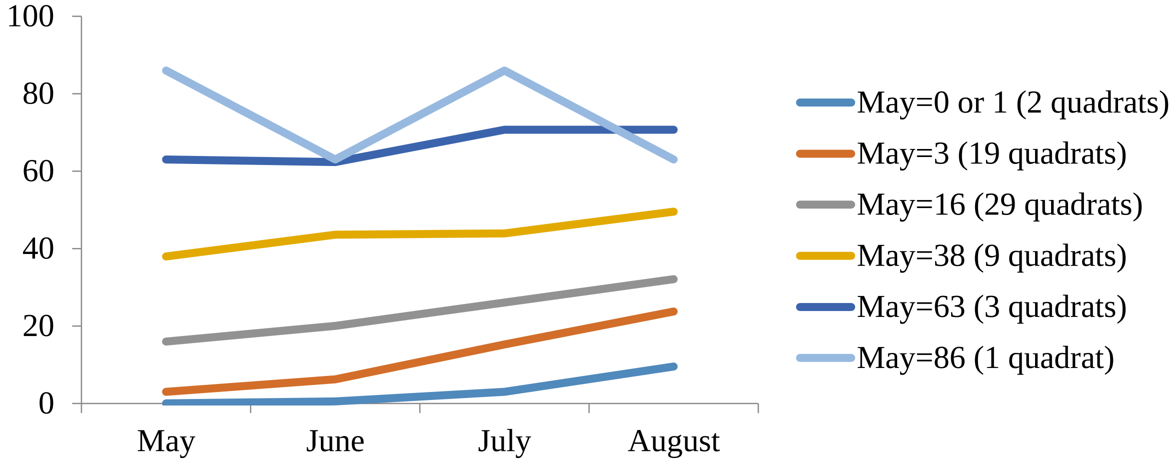
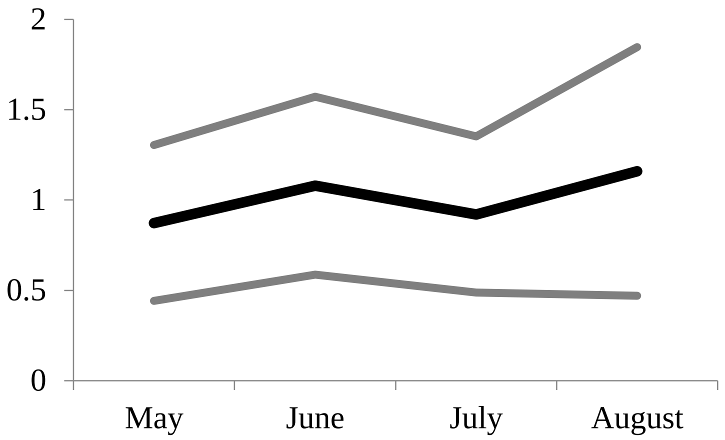


Figure F.5. Average percent cover of woody plants within quadrats in May, June, July, and August, shown across (A) all quadrats, with standard errors, and (B) quadrats with differing starting (i.e., May) values.

(A)



(B)

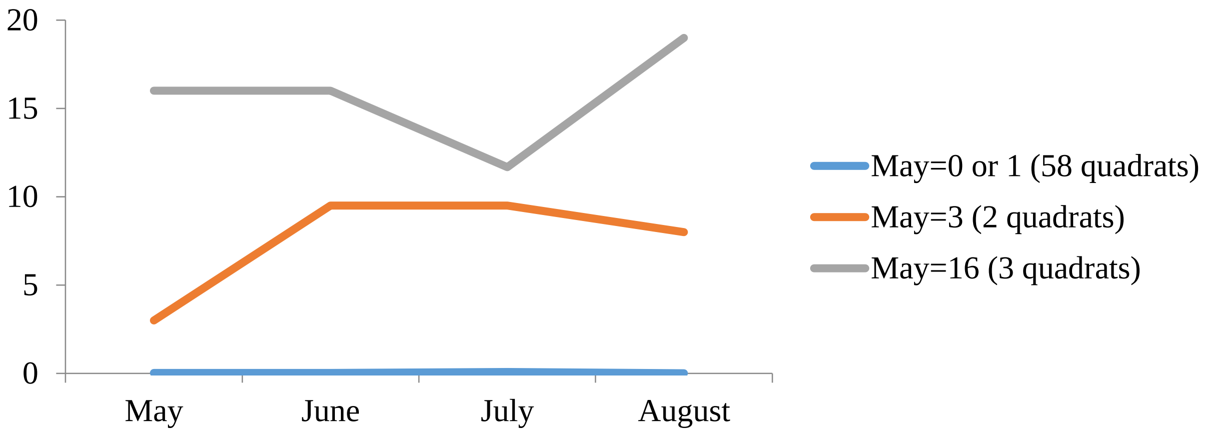


Figure F.6. Average percent cover of standing dead vegetation within quadrats in May, June, July, and August, shown across (A) all quadrats, with standard errors, and (B) quadrats with differing starting (i.e., May) values.

(A)

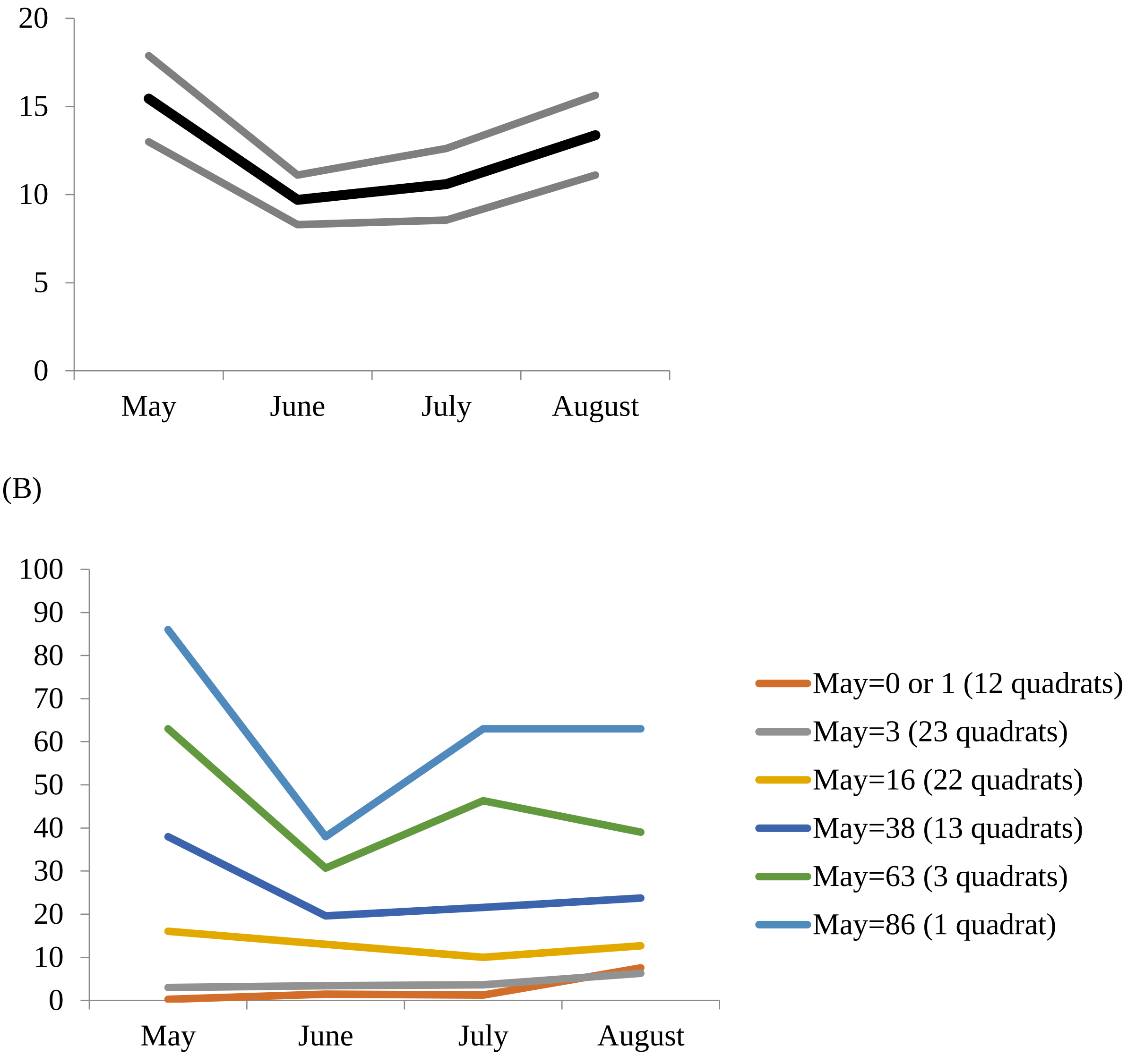
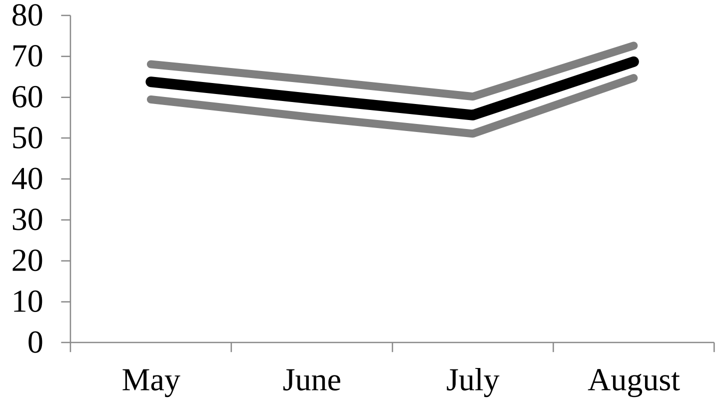


Figure F.7. Average percent cover of litter within quadrats in May, June, July, and August, shown across (A) all quadrats, with standard errors, and (B) quadrats with differing starting (i.e., May) values.

(A)



(B)

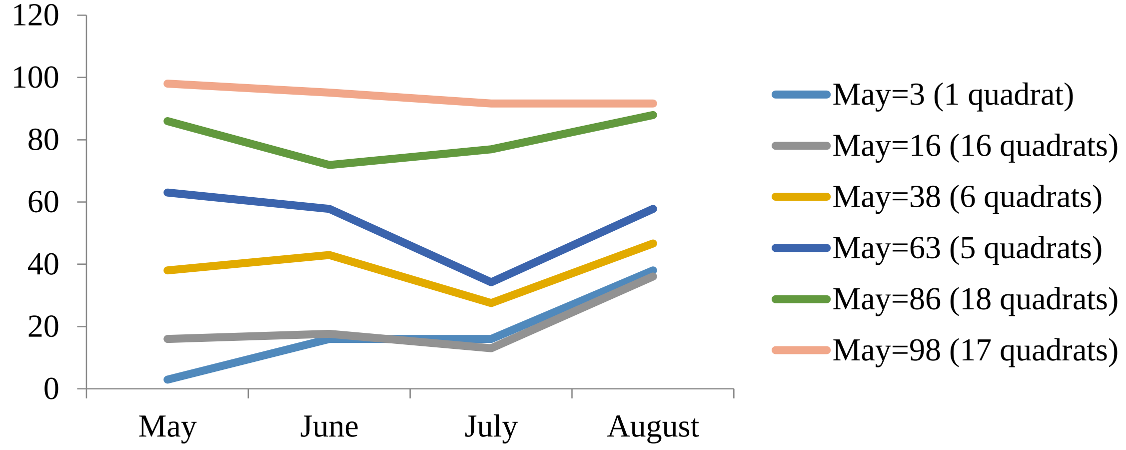
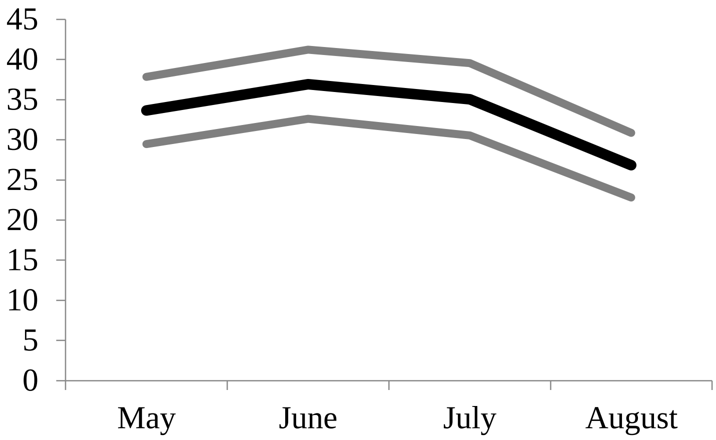


Figure F.8. Average percent cover of bare ground within quadrats in May, June, July, and August, shown across (A) all quadrats, with standard errors, and (B) quadrats with differing starting (i.e., May) values.

(A)



(B)

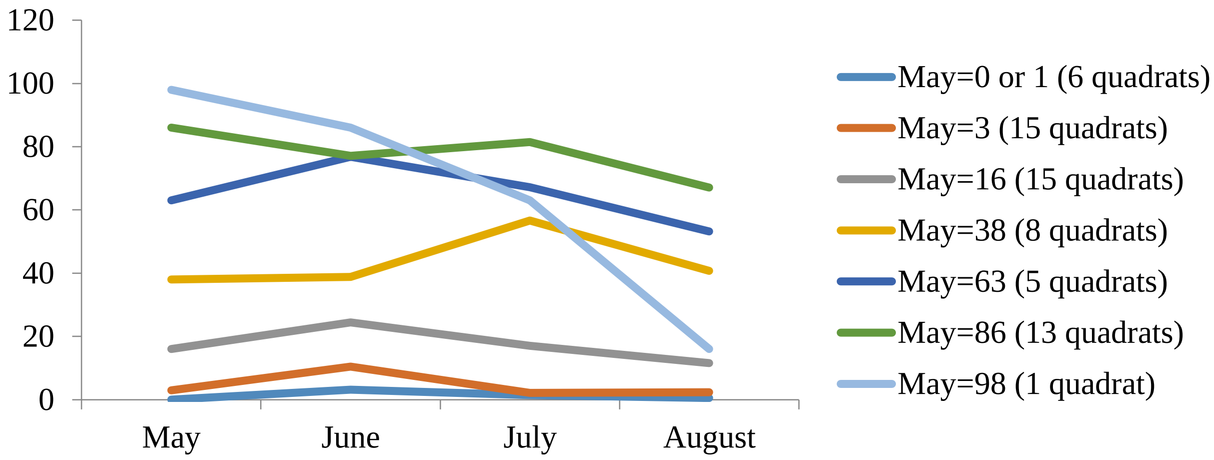
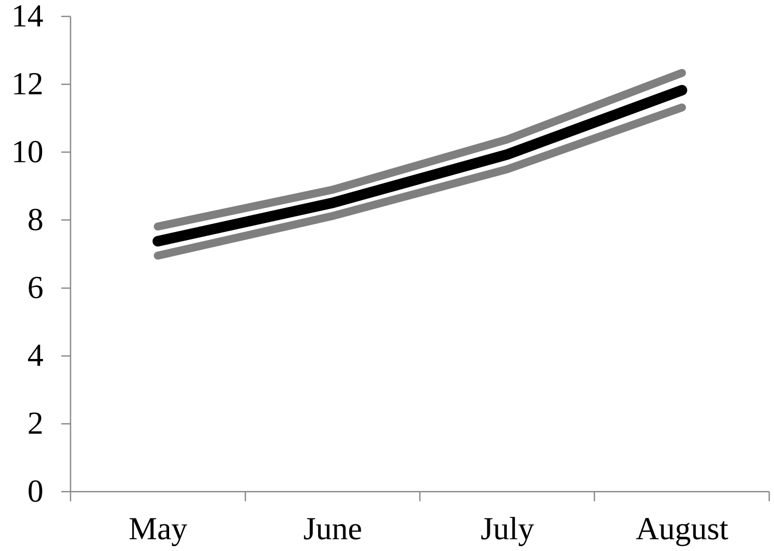


Figure F.9. Average maximum height of vegetation within quadrats in May, June, July, and August, shown across (A) all quadrats, with standard errors, and (B) quadrats with differing starting (i.e., May) values.

(A)



(B)

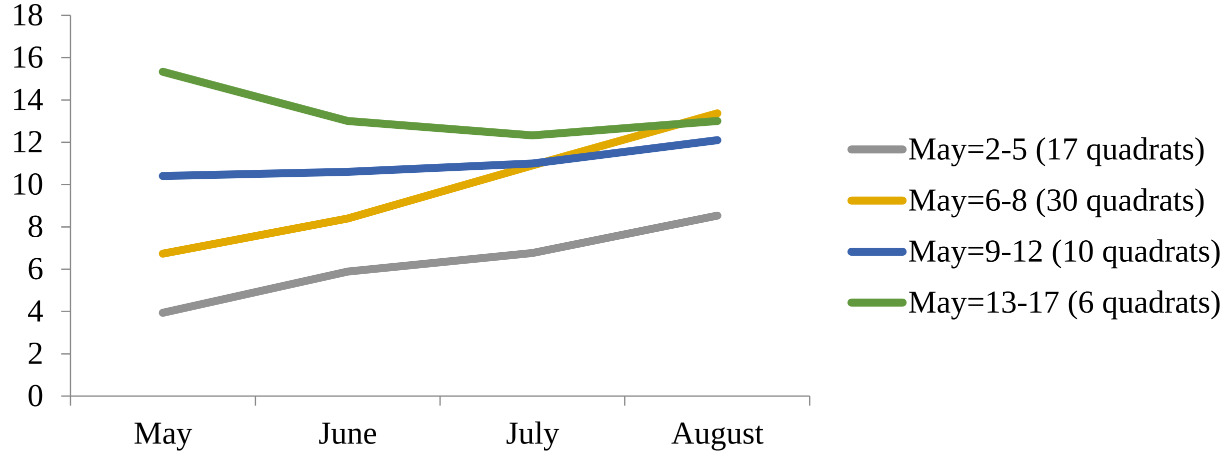
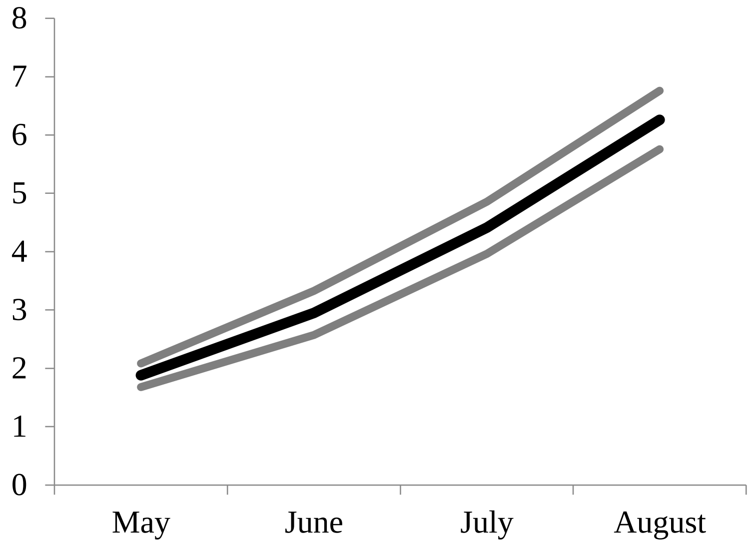


Figure F.10. Average Robel height within quadrats in May, June, July, and August, shown across (A) all quadrats, with standard errors, and (B) quadrats with differing starting (i.e., May) values.

(A)



(B)

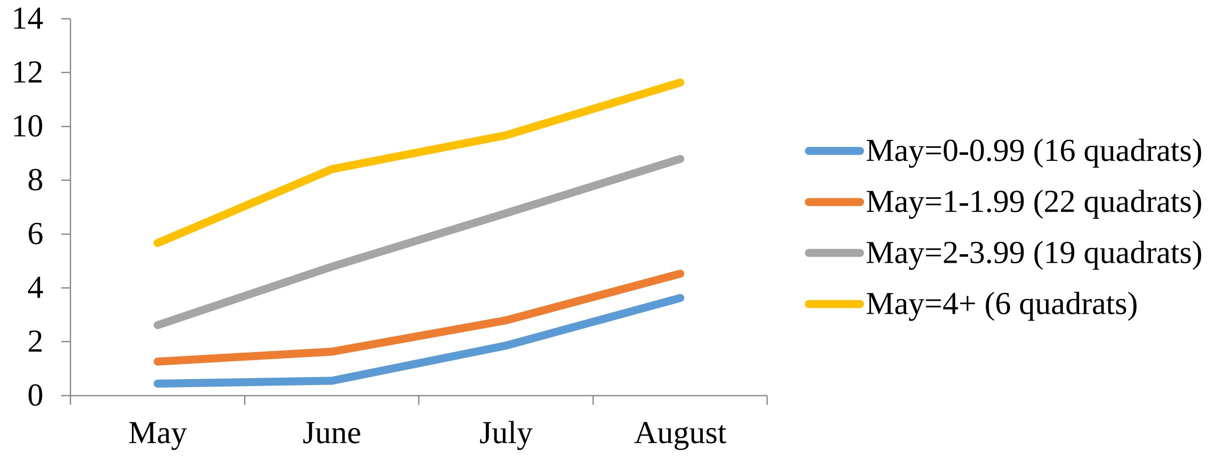
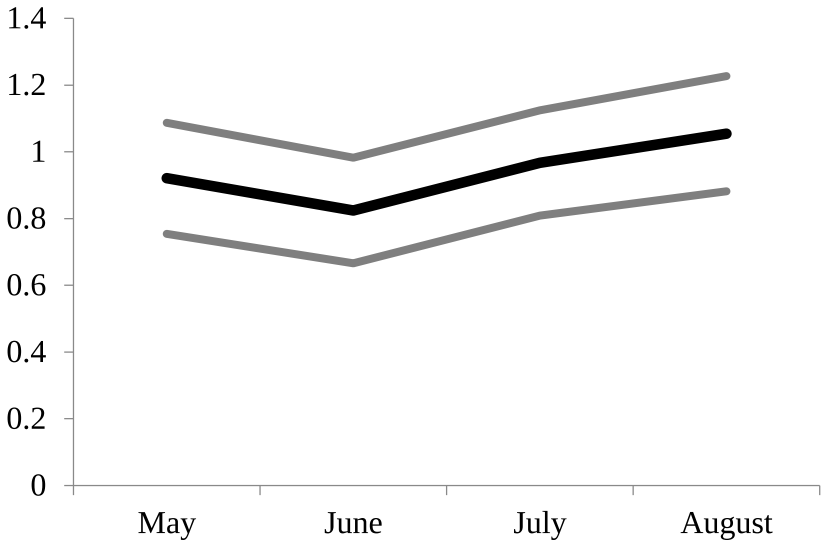


Figure F.11. Average litter depth within quadrats in May, June, July, and August, shown across (A) all quadrats, with standard errors, and (B) quadrats with differing starting (i.e., May) values.

(A)



(B)

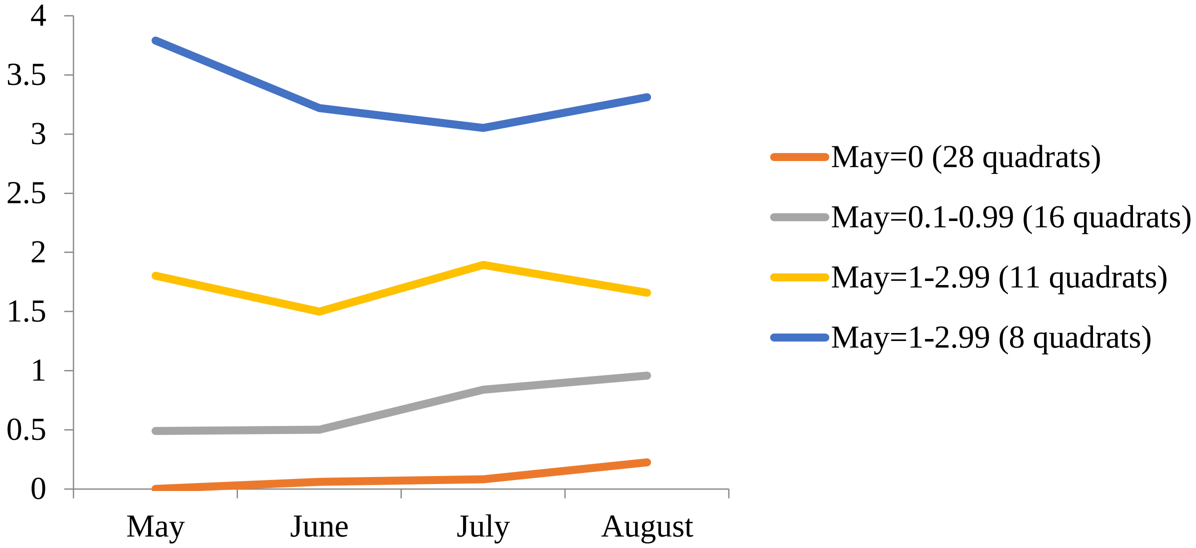
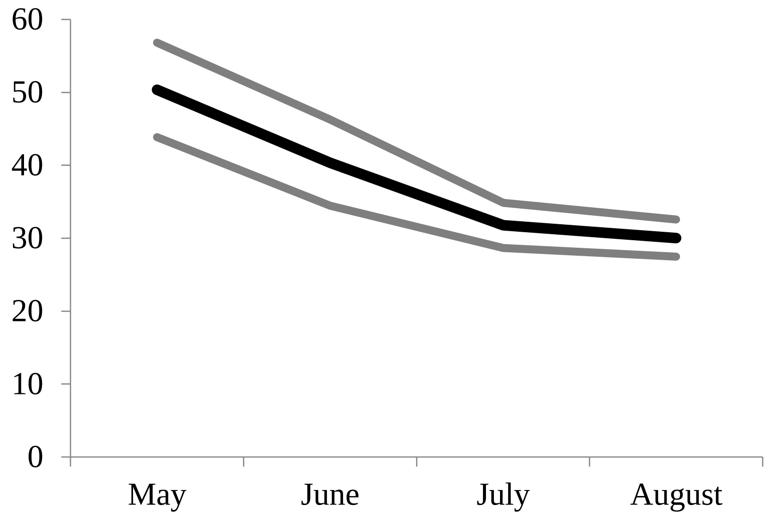


Figure F.12. Average CV of Robel height within quadrats in May, June, July, and August, shown across (A) all quadrats, with standard errors, and (B) quadrats with differing starting (i.e., May) values.

(A)



(B)

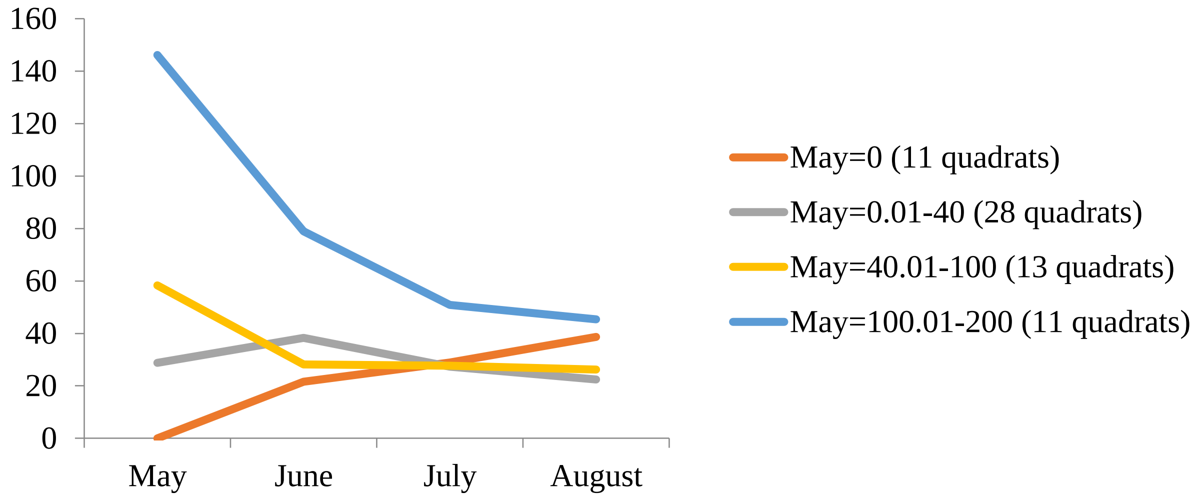
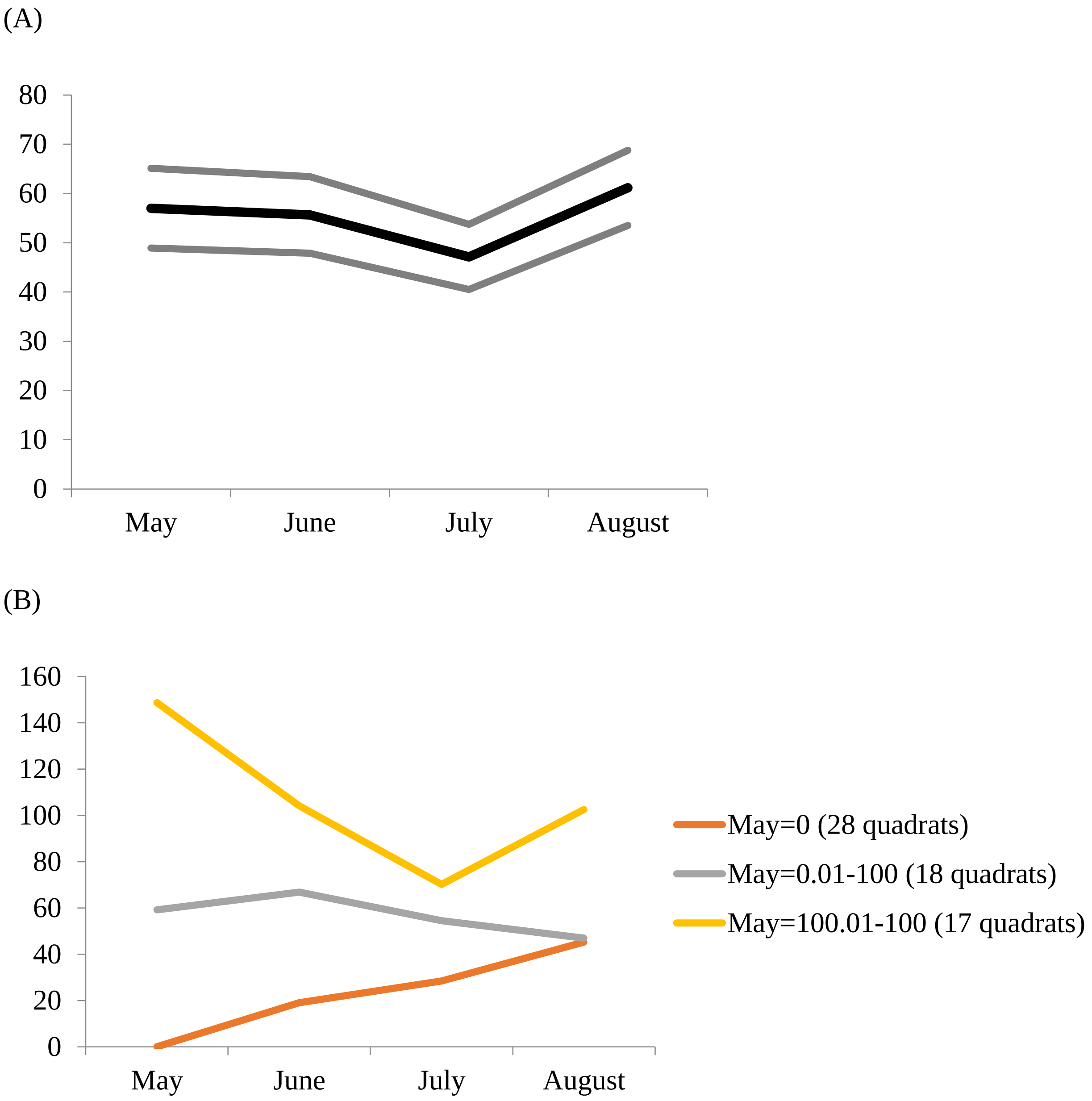


Figure F.13. Average CV of litter depth within quadrats in May, June, July, and August, shown across (A) all quadrats, with standard errors, and (B) quadrats with differing starting (i.e., May) values.



APPENDIX G – DESCRIPTION OF EXPLANATORY VARIABLES (CHAPTER 3)

Table G.1. Metrics examined for relationships to dickcissel habitat preferences and reproductive success. Observed ranges, averages, and standard deviations are given.

Variable	Description	Range	Avg. (SD)
Model Covariates			
Year	2014 or 2015	—	—
Nest Initiation Date[a]	Ordinal date of first egg laying	134-222	174.2 (20.5)
Time of Day[b]	Time of day when nestling mass and tarsus length were measured	5.75-20.3	13.16 (3.29)
Total Nests[c]	Number of nests built in the territory throughout the given breeding season	0-6	1.49 (1.26)
Territory Tenure[d]	Days from when a territory was first observed to the day after it was last observed	6-99	48.06 (23.56)
#BHCO Fledged[e]	Number of cowbirds fledged from the nest	0-4	0.57 (0.95)
Territory-scale vegetation variables, averaged across five quadrats per territory			
Terr_CSG	% cover of cool-season graminoids, including tall fescue	0-95.6	39.75 (27.33)
Terr_Fescue	% cover of tall fescue	0-90.8	19.85 (27.46)
Terr_WSG	% cover of warm-season grasses	0-95.6	25.96 (22.04)
Terr_Forbs	% cover of forbs	5-76.8	30.24 (16.72)
Terr_Wood	% cover of woody plants	0-28.4	2.88 (5.29)
Terr_StandingDead	% cover of standing dead vegetation	1-79	23.14 (17.45)
Terr_Bare	% cover of bare ground	0-86	17.19 (18.78)
Terr_LitterCover	% cover of litter cover	5.6-98	82.07 (21.37)
Terr_AvgLitterDepth	Average of litter depth measurements (cm)	0-8.1	2.94 (2.15)
Terr_CVLitterDepth	Coefficient of variation of litter depth measurements (cm)	0-223.61	75.75 (41.01)
Terr_AvgRobel	Average of visual obstruction readings (dm)	1.55-13	6.27 (2.61)
Terr_CVRobel	Coefficient of variation of visual obstruction readings (dm)	7.72-65.74	28.26 (11.38)
Terr_MaxHeight	Height of tallest vegetation (dm)	7-19.6	12.34 (2.87)
Terr_DistanceToWoods	Minimum distance from territory centroid to the nearest woodland patch	0-390.62	98.84 (71.50)
Patch-scale vegetation variables, averaged across 30 quadrats per patch			
Patch_CSG	% cover of cool-season graminoids, including tall fescue	12.3-86.4	40.06 (22.61)

Table G.1 continued…

Variable	**Description**	**Range**	**Avg. (SD)**
Patch_Fescue	% cover of tall fescue	0-73.83	17.92 (21.19)
Patch_WSG	% cover of warm-season grasses	2.97-61.2	25.18 (15.51)
Patch_Forbs	% cover of forbs	6.37-42.4	23.59 (8.99)
Patch_Wood	% cover of woody plants	0-9.3	3.00 (2.48)
Patch_StandingDead	% cover of standing dead vegetation	0.3-46.83	18.62 (13.82)
Patch_ Bare	% cover of bare ground	3.3-74.33	21.41 (19.48)
Patch_LitterCover	% cover of litter cover	13.3-95.6	71.85 (23.33)
Patch_AvgLitterDepth	Average of litter depth measurements (cm)	0-4.94	2.34 (1.69)
Patch_CVLitterDepth	Coefficient of variation of litter depth measurements (cm)	0-538.52	143.35 (134.70)
Patch_AvgRobel	Visual obstruction (dm), four readings per quadrat (Robel et al. 1970)	1.46-7.5	4.50 (1.59)
Patch_CVRobel	Coefficient of variation of visual obstruction readings (dm)	29.75-61.84	43.98 (9.62)
Patch_MaxHeight	Height of tallest vegetation (dm)	5.03-13	9.65 (1.76)
Landscape-scale vegetation variables, measured within 250 and 1000 m of each patch			
Landscape_Herb1000	% herbaceous cover within 1000 m	0.47-0.71	0.59 (0.07)
Landscape_Herb250	% herbaceous cover within 250 m	0.53-0.90	0.72 (0.09)
Landscape_Crop1000	% row-crop cover within 1000 m	0.04-0.32	0.22 (0.08)
Landscape_Crop250	% row-crop cover within 250 m	0-0.27	0.12 (0.08)
Landscape_Woodland1000	% wooded cover within 1000 m	0.04-0.40	0.17 (0.12)
Landscape_Woodland250	% wooded cover within 250 m	0-0.42	0.14 (0.10)

[a] Covariate in analyses of cowbird parasitism rates.
[b] Covariate in analyses of nestling body condition.
[c] Covariate in analyses of territory productivity.
[d] Covariate in analyses of territory polygyny levels.
[e] Covariate in analyses of nest productivity.

APPENDIX H – FULL AIC TABLES (CHAPTER 3)

Complete AIC tables for analyses of vegetation as a mediating mechanism of adaptive habitat selection by dickcissels (*Spiza americana*). Data were collected in 2014 and 2015 in Ringgold County, IA. There is one table below for each comparison of vegetation variables (measured at territory, patch, and landscape scales) to dickcissel habitat preferences and reproductive success. Models are ranked by their AIC_c values. In each analysis, Stage 1 compares univariate vegetation models to a base model (random variables and covariates only). Stage 2 then compares additive and interactive combinations of variables in models (a) with ΔAIC_c smaller than the base model and (b) included in the cumulative top 90% confidence set of Stage 1. Vegetation metrics correlated at |r| > 0.7 were never included in the same models.

Table H.1. Models examining whether vegetation metrics mediate male habitat preference at the territory scale, measured based on territory settlement ranks. All models contain ‘PastureID × Year’ as a random variable and ‘Year’ as a covariate.

Model	**k**	**Deviance**	**ΔAIC_c**	**Model weight (ω)**
Stage 1: Univariate vegetation models				
Patch_AvgRobel	5	675.86	0.00	0.680
Patch_AvgLitterDepth	5	677.83	1.97	0.254
Terr_DistanceToTrees	5	683.83	7.97	0.013
Terr_Forbs	5	685.57	9.71	0.006
Patch_Bare	5	685.28	9.42	0.005
Patch_CSG	5	686.28	10.42	0.004
Terr_StandingDead	5	686.39	10.53	0.004
Patch_Fescue	5	686.40	10.54	0.003
Base	4	689.02	11.00	0.003
Crop1000	5	687.08	11.22	0.002
Terr_LitterDepthCV	5	687.18	11.32	0.002
Terr_Fescue	5	687.32	11.46	0.002
Crop250	5	687.49	11.63	0.002

Table H.1 continued…

Model	k	Deviance	ΔAIC_c	Model weight (ω)
Terr_LitterDepthAvg	5	687.55	11.69	0.002
Terr_Bare	5	687.59	11.73	0.002
Patch_Forbs	5	687.74	11.88	0.002
Terr_AvgRobel	5	687.89	12.03	0.002
Terr_CSG	5	688.14	12.28	0.001
Herb1000	5	688.37	12.51	0.001
Herb250	5	688.39	12.53	0.001
Woodland250	5	688.46	12.60	0.001
Patch_WSG	5	688.45	12.60	0.001
Terr_Woody	5	688.63	12.77	0.001
Woodland1000	5	688.65	12.79	0.001
Terr_WSG	5	688.81	12.95	0.001
Patch_Woody	5	688.84	12.98	0.001
Patch_LitterDepthCV	5	689.02	13.16	0.001
Stage 2: Refining selected variables				
Patch_AvgRobel + Patch_AvgLitterDepth	6	671.20	0.00	0.714
Patch_AvgRobel	5	675.86	2.47	0.208
Patch_AvgLitterDepth	5	677.83	4.44	0.078
Base	4	690.02	13.47	0.001

Table H.2. Models examining whether patch- or landscape-scale vegetation mediate male habitat preference at the patch scale, measured based on maximum patch territory densities. All models contain 'PastureID × Year' as a random variable. Stage 2 not conducted since only one model was selected in Stage 1.

Model	k	Deviance	ΔAIC_c	Model weight (ω)
Stage 1: Univariate vegetation models[a]				
Patch_AvgRobel	5	29.86	0	0.114
Base	4	32.37	0.01	0.114
Patch_AvgLitterDepth	4	30.32	0.46	0.091
Patch_Woody	5	30.37	0.51	0.088

Table H.2 continued…

Model	k	Deviance	ΔAIC_c	Model weight (ω)
Patch_Bare	5	30.69	0.82	0.076
Patch_Fescue	5	30.69	0.82	0.076
Patch_WSG	5	31.16	1.3	0.060
Crop1000	5	31.24	1.38	0.057
Patch_CSG	5	31.44	1.58	0.052
Crop250	5	31.50	1.64	0.050
Herb1000	5	31.50	1.64	0.050
Woodland250	5	32.13	2.27	0.037
Herb250	5	32.20	2.33	0.036
Patch_Forbs	5	32.30	2.44	0.034
Woodland1000	5	32.32	2.46	0.033
Patch_LitterDepthCV	5	32.35	2.49	0.033

Table H.3. Models examining whether vegetation metrics mediate female habitat preference at the territory scale and male success in attracting mates—both measured based on territory polygyny levels. All models contain 'Territory Tenure' as a covariate.

Model	k	Deviance	ΔAIC_c	Model weight (ω)
Stage 1: Univariate vegetation models				
Terr_Bare	4	329.18	0.00	0.158
Terr_SDV	4	329.79	0.48	0.124
Patch_Bare	4	330.57	1.39	0.079
Crop250	4	330.93	1.74	0.066
Crop1000	4	331.39	2.21	0.052
Base	3	333.66	2.36	0.049
Woodland250	4	332.00	2.82	0.039
Terr_LitterDepthAvg	4	332.02	2.84	0.038
Woodland1000	4	332.39	3.20	0.032
Patch_LitterDepthAvg	4	332.49	3.31	0.030
Patch_Forbs	4	332.72	3.53	0.027
Terr_Dist_to_tree	4	332.78	3.60	0.026
Terr_Woody	4	332.88	3.69	0.025
Patch_Fescue	4	333.27	4.08	0.021
Patch_Woody	4	333.27	4.09	0.020

Table H.3 continued…

Model	k	Deviance	ΔAIC_c	Model weight (ω)
Terr_CSG	4	333.31	4.13	0.020
Terr_LitterDepthCV	4	333.50	4.32	0.018
Terr_Fescue	4	333.51	4.33	0.018
Patch_CSG	4	333.51	4.33	0.018
Patch_LitterDepthCV	4	333.53	4.34	0.018
Herb250	4	333.54	4.36	0.018
Terr_WSG	4	333.55	4.37	0.018
Terr_AvgRobel	4	333.61	4.42	0.017
Terr_Forbs	4	333.63	4.44	0.017
Patch_AvgRobel	4	333.65	4.46	0.017
Patch_WSG	4	333.65	4.47	0.017
Herb1000	4	333.66	4.48	0.017
Stage 2: Refining selected variables				
Terr_Bare + Terr_SDV	5	326.79	0.00	0.220
Terr_Bare	4	329.18	0.39	0.181
Terr_Bare + Terr_SDV + Crop250	6	325.45	0.81	0.147
Terr_SDV	4	329.79	0.87	0.143
Terr_Bare + Terr_SDV + Crop1000	6	326.56	1.92	0.084
Crop250	4	330.93	2.13	0.076
Crop1000	4	331.39	2.60	0.060
Base	3	333.66	2.75	0.056
Crop250 + Crop1000	5	330.49	3.85	0.032

Table H.4. Models examining whether patch- or landscape-scale vegetation mediate female habitat preference at the patch scale, measured based on nest-to-territory ratios in patches. All models contain ‘PastureID × Year’ as a random variable and ‘Year’ as a covariate. Stage 2 was not performed because Stage 1 supported no vegetation variables.

Model	k	Deviance	ΔAIC_c	Model weight (ω)
Stage 1: Univariate vegetation models				
Base	4	47.89	0	0.154
Patch_Woody	5	57.46	0.14	0.144

Table H.4 continued…

Model	k	Deviance	ΔAIC_c	Model weight (ω)
Patch_Fescue	5	46.19	1.09	0.089
Patch_Forbs	5	46.33	1.23	0.083
Herb1000	5	46.43	1.34	0.079
Crop1000	5	46.48	1.39	0.077
Patch_CSG	5	47.42	2.32	0.048
Patch_Bare	5	47.42	2.33	0.048
Patch_AvgRobel	5	47.7	2.6	0.042
Woodland250	5	47.74	2.64	0.041
Crop250	5	47.83	2.73	0.039
Patch_WSG	5	47.85	2.75	0.039
Patch_LitterDepthCV	5	47.88	2.78	0.038
Herb250	5	47.87	2.78	0.038
Woodland1000	5	47.88	2.78	0.038

Table H.5. Models examining whether vegetation metrics mediated brood parasitism by brown-headed cowbirds (*Molothrus ater*). All models contain ‘PastureID’ as a random variable and ‘Nest Initiation Date’ as a covariate. Stage 2 was not performed because Stage 1 supported only one vegetation variable.

Model	k	Deviance	ΔAIC_c	Model weight (ω)
Stage 1: Univariate vegetation models[a]				
Woodland250	5	193.79	0	0.921
Terr_WSG	5	201.96	8.26	0.015
Patch_CSG	5	202.98	9.29	0.009
Crop1000	5	203.23	9.53	0.008
Woodland1000	5	203.38	9.69	0.007
Patch_Fescue	5	203.74	10.05	0.006
Terr_SDV	5	204.34	10.65	0.004
Crop250	5	204.61	10.92	0.004
Patch_Forbs	5	204.70	11.01	0.004
Patch_AvgRobel	5	205.05	11.35	0.003
Base	4	207.24	11.45	0.003
Terr_Fescue	5	205.45	11.76	0.003

Table H.5 continued…

Model	k	Deviance	ΔAIC_c	Model weight (ω)
Terr_Dist_to_tree	5	205.91	12.22	0.002
Patch_WSG	5	206.05	12.36	0.002
Terr_AvgRobel	5	206.60	12.90	0.001
Terr_Forbs	5	206.84	13.15	0.001
Terr_CSG	5	206.92	13.23	0.001
Herb250	5	207.10	13.41	0.001
Herb1000	5	207.17	13.48	0.001
Terr_Woody	5	207.19	13.50	0.001
Patch_Woody	5	207.21	13.52	0.001
Patch_SDV	5	207.25	13.56	0.001

[a] Bare ground and liter depth were not included in this model set due to a lack of *a priori* hypotheses suggesting these variables might influence parasitism.

Table H.6. Models examining whether vegetation metrics mediated nest productivity (the number of dickcissel young fledged from successful nests). All models contain '#BHCO Fledged' as a covariate. Stage 2 not conducted since only one model was selected in Stage 1.

Model	k	Deviance	ΔAIC_c	Model weight (ω)
Stage 1: Univariate vegetation models				
Terr_Woody	3	199.16	0.00	0.129
Base	2	202.25	0.89	0.083
Terr_Fescue	3	200.91	1.76	0.053
Patch_Fescue	3	201.09	1.94	0.049
Patch_LitterDepthCV	3	201.29	2.13	0.044
Patch_CSG	3	201.88	2.73	0.033
Terr_AvgRobel	3	201.92	2.77	0.032
Patch_Forbs	3	201.96	2.80	0.032
Patch_AvgRobel	3	201.99	2.83	0.031
Crop250	3	202.01	2.85	0.031
Terr_CSG	3	202.02	2.86	0.031
Terr_Forbs	3	202.08	2.92	0.030
Herb1000	3	202.13	2.97	0.029
Herb250	3	202.14	2.98	0.029
Terr_SDV	3	202.16	3.00	0.029

Table H.6 continued…

Model	k	Deviance	ΔAIC_c	Model weight (ω)
Terr_Bare	3	202.15	3.00	0.029
Terr_WSG	3	202.17	3.01	0.029
Terr_LitterDepthAvg	3	202.20	3.04	0.028
Terr_LitterDepthCV	3	202.19	3.04	0.028
Patch_Woody	3	202.22	3.06	0.028
Crop1000	3	202.22	3.07	0.028
Terr_Dist_to_tree	3	202.22	3.07	0.028
Woodland250	3	202.25	3.09	0.027
Patch_LitterDepthAvg	3	202.24	3.09	0.027
Woodland1000	3	202.25	3.09	0.027
Patch_Bare	3	202.25	3.09	0.027
Patch_WSG	3	202.25	3.09	0.027

Table H.7. Models examining whether vegetation metrics mediated territory productivity (the total number of dickcissel young fledged from each territory). All models contain ‘PastureID × Year’ as a random variable and ‘Total Nests’ as a covariate.

Model	k	Deviance	ΔAIC_c	Model weight (ω)
Stage 1: Univariate vegetation models				
Terr_CSG	5	363.09	0	0.177
Patch_Fescue	5	363.92	0.83	0.117
Terr_Bare	5	364.58	1.49	0.084
Patch_CSG	5	364.75	1.66	0.077
Crop1000	5	364.80	1.71	0.075
Patch_WSG	5	365.93	2.84	0.043
Crop250	5	366.07	2.98	0.040
Patch_Bare	5	366.31	3.22	0.035
Base	4	368.52	3.27	0.034
Woodland250	5	366.7	3.46	0.031
Terr_AvgRobel	5	366.76	3.67	0.028
Woodland1000	5	366.85	3.76	0.027
Terr_Fescue	5	367.05	3.97	0.024
Terr_SDV	5	367.5	4.41	0.019
Terr_WSG	5	367.63	4.55	0.018

Table H.7 continued…

Model	k	Deviance	ΔAIC_c	Model weight (ω)
Terr_Woody	5	367.7	4.62	0.018
Herb250	5	367.79	4.7	0.017
Patch_LitterDepthAvg	5	367.87	4.78	0.016
Patch_Forbs	5	367.9	4.82	0.016
Herb1000	5	368.06	4.98	0.015
Terr_LitDepCV	5	368.07	4.98	0.015
Patch_RobelAvg	5	368.22	5.13	0.014
Patch_Woody	5	368.33	5.24	0.013
Terr_Forbs	5	368.36	5.27	0.013
Terr_Dist_to_tree	5	368.43	5.34	0.012
Terr_LitterDepthAvg	5	368.48	5.4	0.012
Patch_LitterDepthCV	5	368.5	5.42	0.012
Stage 2: Refining selected variables				
Terr_CSG + Patch_Fescue + Terr_Bare	7	346.79	0	0.215
Terr_CSG + Patch_Fescue + Crop1000	7	347.05	0.26	0.189
Terr_CSG + Patch_Fescue + Terr_Bare + Crop250	8	345.75	1.22	0.117
Terr_CSG + Patch_Fescue + Terr_Bare + Crop1000	8	346	1.47	0.103
Terr_CSG × Patch_Fescue + Terr_Bare	8	346.59	2.06	0.077
Terr_CSG + Patch_Fescue + Crop250	7	349.03	2.24	0.070
Terr_CSG × Patch_Fescue + Crop1000	8	346.98	2.45	0.063
Terr_CSG + Patch_Fescue	6	351.73	2.72	0.055
Terr_CSG × Patch_Fescue + Crop250	8	347.89	3.36	0.040
Terr_CSG × Patch_Fescue	7	350.4	3.61	0.035
Terr_CSG × Patch_Fescue + Terr_Bare + Crop1000	9	345.97	3.73	0.033
Terr_CSG + Terr_Bare	6	360.38	11.37	0.001
Terr_CSG	5	363.09	11.89	0.001
Patch_Fescue	5	363.92	12.72	0.000
Patch_Fescue + Crop250 + Crop1000	7	359.98	13.19	0.000
Terr_Bare × Patch_Fescue	7	360.15	13.36	0.000
Terr_Bare	5	364.58	13.38	0.000

Table H.7 continued…

Model	k	Deviance	ΔAIC_c	Model weight (ω)
Crop1000	5	364.8	13.60	0.000
Terr_Bare + Crop250	6	363.07	14.06	0.000
Terr_Bare + Crop1000	6	363.64	14.63	0.000
Crop250	5	366.07	14.87	0.000
Base	4	368.52	15.16	0.000
Crop250 + Crop1000	6	364.46	15.45	0.000

Table H.8. Models examining whether vegetation metrics mediated nestling body condition. All models contain 'NestID' as a random variable and 'Time of Day' as a covariate.

Model	k	Deviance	ΔAIC_c	Model weight (ω)
Stage 1: Univariate vegetation models				
Patch_Forbs	5	566.36	0	0.150
Terr_AvgRobel	5	566.58	0.22	0.134
Base	4	570.37	1.9	0.058
Patch_LitterDepthCV	5	568.43	2.07	0.053
Terr_Forbs	5	568.44	2.08	0.053
Herb250	5	568.76	2.4	0.045
Terr_CSG	5	568.83	2.47	0.044
Patch_LitterDepthAvg	5	569.13	2.78	0.033
Woodland250	5	569.4	3.04	0.033
Terr_Woody	5	569.5	3.14	0.031
Terr_Dist_to_tree	5	569.67	3.31	0.029
Crop1000	5	569.95	3.59	0.025
Patch_CSG	5	569.99	3.63	0.024
Herb1000	5	569.99	3.63	0.024
Terr_WSG	5	570.04	3.69	0.024
Patch_Woody	5	570.06	3.7	0.024
Terr_Fescue	5	570.08	3.72	0.023
Terr_SDV	5	570.14	3.78	0.023
Patch_AvgRobel	5	570.15	3.8	0.022
Patch_Fescue	5	570.22	3.86	0.022
Terr_Bare	5	570.23	3.87	0.022
Patch_WSG	5	570.27	3.91	0.021
Terr_LitterDepthCV	5	570.31	3.95	0.021

Table H.8 continued…

Model	k	Deviance	ΔAIC_c	Model weight (ω)
Patch_Bare	5	570.31	3.95	0.021
Crop250	5	570.33	3.97	0.021
Woodland1000	5	570.37	4.01	0.020
Stage 2: Refining selected variables				
Patch_Forbs	5	566.36	0	0.337
Patch_AvgRobel	5	566.58	0.22	0.302
Patch_Forbs + Patch_AvgRobel	6	564.98	0.76	0.231
Base	4	570.37	1.9	0.130

APPENDIX I – DESCRIPTION OF EXPLANATORY VARIABLES (CHAPTER 4)

Table I.1. Explanatory variables examined for effects on daily nest survival and cowbird parasitism probabilities for dickcissel nests during the 2013-2016 breeding seasons in Ringgold County, IA, USA. Observed ranges, averages, and standard deviations are given.

Variable	**Description**	**Range**	**Avg. (SD)**
Temporal variables			
Year	2013, 2014, 2015, or 2016	--	--
Nest Visit Date[a]	Ordinal date of end of the visit interval	139-244	187.9 (19.2)
Initiation Date[b]	Ordinal date first egg was laid in the given nest	133-222	173.5 (18.6)
Nest contents variables			
Nest Stage[a]	Whether the nest was in the laying, incubation, or nestling stage in the given visit interval	--	--
Parasitism[a]	Whether the nest contained any cowbird eggs or chicks during the given visit interval	--	--
#Chicks[a]	Number of chicks (dickcissel and cowbird) in the nest at the end of the given visit interval	0-6	0.94 (1.2)
Nest-site vegetation variables within 5 m of the nest			
Cool-season grasses	% cover of cool-season graminoids, including tall fescue	0-95.6	37.2 (26.9)
Tall Fescue	% cover of tall fescue	0-93.2	15.2 (23)
Warm-season grasses	% cover of warm-season grasses	0-95.6	23.1 (25.3)
Forbs	% cover of non-legume forbs	0.4-93.2	37.8 (20.3)
Wood (nest site)	% cover of woody plants	0-60.2	6.8 (9.9)
Litter Cover[a]	% cover of litter	2.2-98	78.6 (22.6)
Avg Robel	Visual obstruction, averaged across 20 readings (dm; Robel et al. 1970)	1.3-15	6.7 (2.7)
StDev Robel	Standard deviation of 20 visual obstruction readings (dm)	0.5-6	2.1 (1.1)

Table I.1 continued…

Variable	Description	Range	Avg. (SD)
Landscape variables			
1000 m Herb Cover	% cover of herbaceous land cover within 1000 m of the nest	27.3-92.7	62.7 (9)
500 m Herb Cover	% cover of herbaceous land cover within 500 m of the nest	29.2-96.5	73.8 (12.5)
250 m Herb Cover	% cover of herbaceous land cover within 250 m of the nest	43-98.9	82.2 (11.9)
1000 m Crop Cover[a]	% cover of row-crop land cover within 1000 m of the nest	0.9-65.9	16.9 (10.8)
500 m Crop Cover[a]	% cover of row-crop land cover within 500 m of the nest	0-66.2	11.9 (12.2)
250 m Crop Cover[a]	% cover of row-crop land cover within 250 m of the nest	0-49.7	8.1 (10.6)
1000 m Woodland Cover	% cover of wooded land cover within 1000 m of the nest	2.4-44.2	17.6 (11.8)
500 m Woodland Cover	% cover of wooded land cover within 500 m of the nest	0.5-51.9	11.7 (9.1)
250 m Woodland Cover	% cover of wooded land cover within 250 m of the nest	0-32	3.3 (7.9)
1000 m Wooded-edge Length	Length of wooded edges within 1000 m of the nest (m)	23.1-115.7	76 (26.6)
500 m Wooded-edge Length	Length of wooded edges within 500 m of the nest (m)	9.2-138.8	65.3 (30.4)
250 m Wooded-edge Length	Length of wooded edges within 250 m of the nest (m)	0-174.6	56 (44.1)
Distance to Woods	Minimum distance to the nearest wooded edge (m)	4.8-382.1	111.8 (65.2)
Cattle[b]	Nest in a study site stocked with cattle? In pastures stocked for only part of the season, this variable was assigned based on whether cattle were present during the nest's laying phase.	--	--

[a] Variable only included in analysis of daily nest survival.

[b] Variable only included in analysis of cowbird parasitism probability.

APPENDIX J – PASTURE DESCRIPTIONS (CHAPTER 4)

Table J.1. Study pastures where we monitored dickcissel (*Spiza americana*) nests in Ringgold County, IA, USA from 2013-2016. Pastures were managed with prescribed burning, cattle grazing, and glyphosate applied to control tall fescue. We located nests from 10 June-18 August in 2013, 16 May-12 August in 2014, 25 May-22 August in 2015, and 23 May-7 August in 2016. Below, CSG=cool-season grasses and NWSG=native warm-season grasses.

Pasture code	**Area (ha)**	**Management regime**			**Years monitored**	**Dominant vegetation**
		Burn schedule	**Cattle?**	**Herbicide**		
GIL	27.8	Burned every 3-5 yrs	Yes[a]	2/3 sprayed in fall 2014	2013, 2016	Tall fescue, other CSG, and shrubs
235N	25.3	Burned every 3-5 yrs	Yes	Sprayed in 2011	2013	Mixed CSG, NWSG, and forbs
PYW	17.1	Burned every 3-5 yrs	Yes	None	2013	Mixed CSG, NWSG, and forbs
RIS	31.4	1/3 burned each yr[a]	Yes	None	2013	Mixed CSG, NWSG, and forbs
PYS	21.6	1/3 burned each yr[a]	Yes	None	2013	Mixed CSG, NWSG, and forbs
PYN	24.5	1/3 burned each yr[a]	Yes[a]	None	2013-2015	Mixed CSG, NWSG, and forbs
KLN	31.3	1/3 burned each yr[a]	Yes[a]	None	2013-2015	Mixed CSG, NWSG, and forbs
STE	34.8	Burned every 3-5 yrs	Yes	None	2013-2015	Tall fescue and other CSG
LTR	35.0	Burned every 3-5 yrs	Yes[a]	2/3 sprayed in fall 2014	2013-2016	Mixed CSG, NWSG, and forbs
KLT	41.1	Burned every 3-5 yrs	No	None	2013-2016	NWSG and forbs
RNR	24.8	Burned every 3-5 yrs	No	None	2014-2015	Mixed CSG, NWSG, and forbs
RIN	15.4	Burned every 3-5 yrs	No	None	2014-2015	NWSG and forbs
RIE	30.1	Burned every 3-5 yrs	No	Parts sprayed annually	2015-2016	Mixed CSG, NWSG, and forbs
RC2	14.7	Not burned	No	2/3 sprayed in fall 2014	2016	Mixed CSG, NWSG, and forbs
BSH	14.0	Not burned	No	2/3 sprayed in fall 2014	2016	Tall fescue and forbs

[a] In all years and on all grazed (‘Yes’) pastures, cattle were stocked in mid-April. From 2014-2016 on these pastures, however, cattle were removed on 1 July. Cattle were stocked till mid-September on all other grazed pastures.

[b] Burned areas were rotated so the entire pasture was burned over three-year cycles.

APPENDIX K – TEMPORAL VARIATION IN NEST SURVIVAL AND PARASITISM

Supported relationships between temporal variables (e.g., annual and within-season effects) and dickcissel nest survival (Figure I1) and brood parasitism (Figure I2-I4).

Figure K.1. Changes in dickcissel daily nest survival probability within the breeding season vary among years in Ringgold County, IA. Confidence intervals are not shown, for clarity.

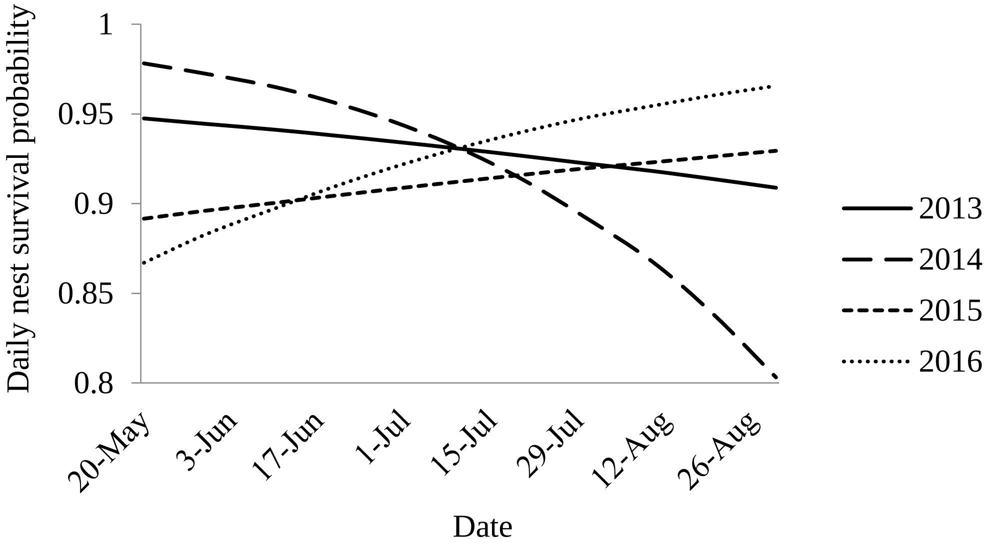


Figure K.2. Risk of parasitism by brown-headed cowbirds in dickcissel nests in Ringgold County, IA, in each year from 2013-2016. Bars represent 85% confidence intervals.

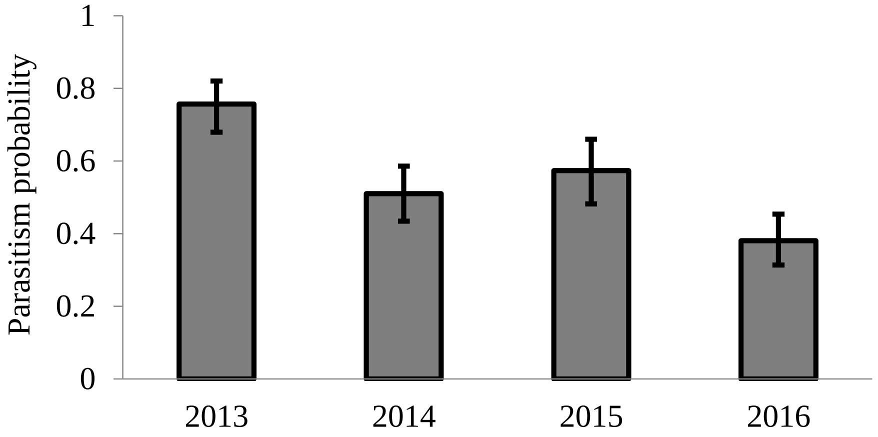
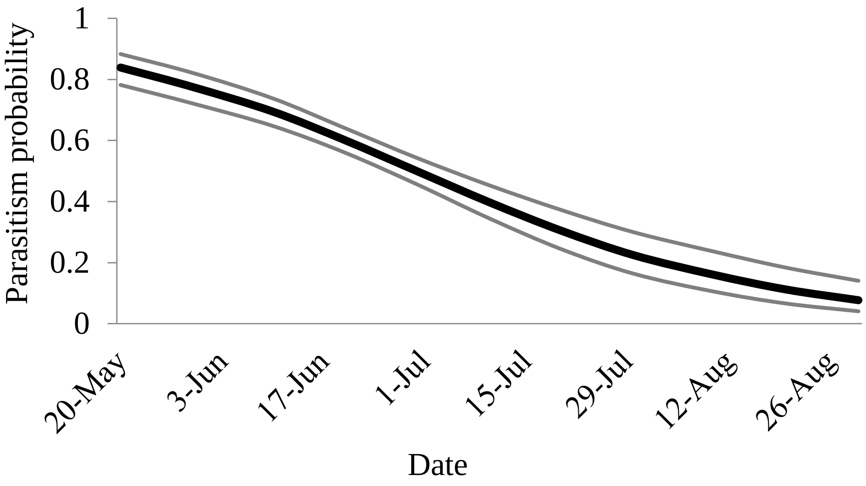


Figure K.3. Parasitism risk declines over the breeding season. Grey lines represent 85% confidence intervals.



β = -0.040 ± 0.007 (SE)

Figure K.4. The rate of decline in parasitism over the breeding season is not entirely consistent among years, but it is broadly similar. Confidence intervals are not shown, for clarity.