Ecological and economic implications of plant diversity and grazing in pasture systems

By

Adrian Pierre-Frederic Monroe

A Dissertation
Submitted to the Faculty of
Mississippi State University
in Partial Fulfillment of the Requirements
for the Degree of Doctor of Philosophy
in Forest Resources
in the Department of Wildlife, Fisheries, and Aquaculture

Mississippi State, Mississippi

August 2014
Ecological and economic implications of plant diversity and grazing in pasture systems

By

Adrian Pierre-Frederic Monroe

Approved:

__________________________
Samuel Keith Riffell
(Co-Major Professor)

__________________________
James A. Martin
(Co-Major Professor)

__________________________
L. Wes Burger
(Committee Member)

__________________________
Kristine O. Evans
(Committee Member)

__________________________
Eric D. Dibble
(Graduate Coordinator)

__________________________
George M. Hopper
Dean
College of Forest Resources
Converting exotic forages to native warm-season grasses (NWSG) such as big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*), and Indian grass (*Sorghastrum nutans*) offers a sustainable alternative because NWSG may yield comparative livestock gains with less fertilizer, as well as offer habitat for arthropods and declining grassland bird species such as Dickcissels (*Spiza americana*). In the Southeastern United States, the predominant forage species are exotics such as bermudagrass (*Cynodon dactylon*) and tall fescue (*Schedonorus arundinaceus*), so NWSG conversion could substantially improve sustainability and wildlife habitat on private lands in the region. In 2011 and 2012, I studied response of Dickcissels and arthropods to forage origin, diversity, and grazing at the Mississippi State University Prairie Research Unit in Monroe Co., MS, USA. Four treatments were established among 12 pastures representing a gradient in management intensity, including a grazed bermudagrass and tall fescue mix (GMEP), grazed Indian grass monoculture (GINP), grazed mixed native pasture (GMNP), and a non-grazed mixed native pasture (NMNP).
Grazed treatments were stocked with steers from May through August each year. I also evaluated the economic implications of each grazing system.

In general, there was a positive response to native grasses among Dickcissels and arthropods and a negative effect from grazing. Dickcissel productivity (fledgling ha⁻¹) was highest in NMNP and lowest in GMEP, whereas productivity was intermediate and similar among grazed native pastures. This pattern was attributable to availability of suitable nest sites because nest survival and brood size did not vary by treatment. Several arthropod taxa responded positively to greater vegetation density in NMNP, but communities were largely similar among grazed pastures irrespective of forage origin or diversity, suggesting little short-term response to NWSG. In spite of unfavorable growing conditions due to drought, cattle grazing NWSG consistently outperformed conspecifics in GMEP, with 45–72% higher average daily gain. Partial budget analysis indicated that NWSG pastures yielded up to 36% marginal rates of return despite establishment costs. These results suggest NWSG conversion can benefit tall grass specialists such as Dickcissels while offering a competitive alternative to exotic forages, resulting in net benefits for both conservationists and producers.
DEDICATION

To my friends, family, and Kira Newcomb. I am forever grateful for your patience, love, and support.
ACKNOWLEDGEMENTS

I first would like to thank my advisors, Drs. Sam Riffell and James Martin, for offering me this amazing opportunity and supporting me throughout my dissertation. They deserve great credit for working so well together yet maintaining their own unique approach toward research and advising, and I have learned so much during this time. I am also grateful that they encouraged me to pursue my own research interests, and I hope they have benefited from this adventure as well. I thank Drs. Wes Burger and Kristine Evans for serving on my committee. Their comments, critiques, and discussions have been invaluable in completing this dissertation.

Many current and former graduate students graciously volunteered their time to help collect data for my project, including James Callicutt, Kelsey Drey, Kristine Evans, Jim Feaga, David Fishman, Zac Loman, Mark McConnell, and Kira Newcomb. Also many thanks to Tara Conkling for help with fieldwork and sharing technicians for two field seasons. Most of my data could not have been collected without assistance from field technicians, including Whit Batton, Candice Bogan, Justin Burger, Amber Clark, Shana Easley, Kati Fleming, Taylor Guthrie, Lindsay Latino, Beverley McKinley, Evan O’Donnell, Matt Thornton, and Anna Tisdale, and several students from Wildlife Techniques class. I would also like to thank David Cross and Jian Chen for assistance with identifying fire ant species and breeding systems. Dr. Elizabeth Holcomb provided advice on insect sampling, and JoVonn Hill and Terry Schiefer helped with ant and insect
identification. Drs. Keith Coble and John Michael Riley offered guidance on my economics analysis. Finally, I am indebted to WFA staff for their assistance with technician hiring and payroll.

Funding was provided by the USDA NRCS Agricultural Wildlife Conservation Center, the Mississippi Agricultural and Forestry Experiment Station (MAFES), and a Southern Sustainable Agriculture Research & Education (SARE) graduate student grant. The Forest and Wildlife Research Center and the College of Forest Resources at Mississippi State University provided additional support.
TABLE OF CONTENTS

DEDICATION .................................................................................................................... ii

ACKNOWLEDGEMENTS ................................................................................................ iii

LIST OF TABLES ........................................................................................................ viii

LIST OF FIGURES ...................................................................................................... x

CHAPTER

I. GENERAL INTRODUCTION ................................................................................... 1

II. ESTIMATING AVIAN NEST DENSITY USING CAPTURE-RECAPTURE MODELS ......... 4

   Introduction ............................................................................................................ 4

   Methods .................................................................................................................. 6

      Nest Searching and Monitoring .................................................................. 7

      Nest Attendance Modeling ........................................................................... 8

      Nest Density Modeling .................................................................................. 9

      Simulation Study ............................................................................................ 14

   Results ................................................................................................................... 15

      Nest Attendance Modeling ........................................................................... 15

      Field Study ....................................................................................................... 16

      Simulation Results ........................................................................................... 17

   Discussion ............................................................................................................. 18

III. TESTING HYPOTHESES ABOUT NEST SITE SELECTION AND BREEDING SUCCESS OF AN OBLIGATE GRASSLAND BIRD IN NATIVE AND EXOTIC GRAZING SYSTEMS .......... 31

   Introduction ........................................................................................................... 31

   Methods ................................................................................................................ 33

      Study Area ....................................................................................................... 33

      Vegetation Sampling ....................................................................................... 35

      Nest Searching and Monitoring .................................................................. 36

      Measuring Nestling Condition ..................................................................... 37

      Arthropod Sampling ....................................................................................... 38

   Statistical Analysis ............................................................................................. 39
Nest and Pasture Vegetation ................................................................. 39
Nest Survival and Productivity ............................................................ 40
Food Limitation Hypothesis ................................................................. 43
Results .................................................................................................. 43
  Pasture Vegetation ........................................................................... 43
  Nest Site Vegetation ........................................................................ 44
  Nest Survival .................................................................................... 45
  Nestling Condition ........................................................................... 47
Discussion ............................................................................................ 47
  Implications for NWSG Conversion in Grazing Systems ................. 51

IV. ARTHROPOD COMMUNITY RESPONSE TO IMPORTED FIRE
    ANTS AND CONVERSION OF EXOTIC GRASS PASTURE
    TO NATIVE WARM-SEASON GRASS .......................................... 61

  Introduction ....................................................................................... 61
  Methods ............................................................................................. 64
    Study Area ...................................................................................... 64
    Vegetation Sampling ....................................................................... 65
    Arthropod Sampling ....................................................................... 66
    Fire Ant Surveys ............................................................................ 66
  Statistical Analysis ........................................................................... 69
    Arthropod Community .................................................................. 69
    Imported Fire Ants ........................................................................ 71
  Results ................................................................................................ 74
    Arthropod Community Response to NWSG Conversion and IFA .... 75
    Fire Ant Response to NWSG Conversion ........................................ 76
      Activity ....................................................................................... 76
      Abundance .................................................................................. 77
      Mound density ............................................................................ 78
  Discussion .......................................................................................... 78

V. ECONOMIC AND CONSERVATION IMPLICATIONS OF
    CONVERTING EXOTIC FORAGES TO NATIVE WARM-
    SEASON GRASS ............................................................................ 95

  Introduction ....................................................................................... 95
  Methods and Analysis ........................................................................ 98
    Study Site and Experiment ............................................................ 98
    Average Daily Gain Analysis ......................................................... 99
    Relative Profitability Analysis ....................................................... 100
    Wildlife Response ......................................................................... 103
  Results ................................................................................................ 104
    Average Daily Gain Analysis ......................................................... 104
    Partial Budget Analysis ................................................................ 105
  Discussion .......................................................................................... 106
2.1 Model selection results based on Akaike’s Information Criterion corrected for small sample sizes (AICc) for female Dickcissel (Spiza americana) nest attendance at the Mississippi State University Prairie Research Unit in Prairie, MS, USA, 2011–2012...........................................................................................................23

2.2 Stage- and treatment-specific estimates of female Dickcissel nest attendance probability, after model-averaging. I also report mean and variance (on the logit scale) of estimates used as informative priors in the JS nest density model...............................................................24

2.3 Summary statistics of stage- and treatment-specific survival (ϕ) and detection (p) probabilities estimated by the JS nest density model.............................................................................................................25

2.4 Summary statistics for stage-specific mean and variance hyper-parameters for entry (γ) and survival (ϕ) estimated by the multi-state JS model for Dickcissel nest density, on the probability scale.................................................................................................26

3.1 Vegetation parameters measured at nest sites used for pair-wise combinations in nest survival models based on results from previous studies of nesting Dickcissels (Spiza americana)........................................52

3.2 Mean (SE) nest site vegetation estimates by treatment, and their factor loadings, for the first two dimensions of Canonical Analysis of Principal Coordinates (CAP) ordination for Dickcissel nests and paired random points at the Mississippi State University Prairie Research Unit in Monroe Co., MS, USA, 2011–2012...............................53

3.3 Mean (SE) number of Dickcissel eggs per nest and number of fledglings per successful nest by treatment..................................................54

3.4 A priori candidate set of nest survival models for Dickcissels ranked by Deviance Information Criterion (DIC).........................................................54

3.5 Mean, standard deviation, and 95% credible intervals (CrI) of parameter estimates for six models for Dickcissel nest survival........................................55
4.1 Treatment\textsuperscript{a} mean estimates (SE) for vegetation measurements at Mississippi State University Prairie Research Unit, 2011-2012. ...........84

4.2 Correlation ($r^2$) of vegetation, imported fire ant (IFA) indices, and survey month and year with arthropod ordination axes from nonmetric multidimensional scaling (NMDS). ...........................................85

4.3 Mean, standard deviation, and 95% credible intervals (CrI) for parameter estimates from distance sampling model of IFA mound density. ........................................................................................................86

5.1 Rate and cost of items for establishment of GINP and GMNP at the Mississippi State University Prairie Research Unit in Prairie, MS, USA. ........................................................................................................113

5.2 Mean average daily gain (kg d\textsuperscript{-1}, and 95% CI) for steer estimated from linear mixed models by year, removal month, and treatment\textsuperscript{a}. ..............114

5.3 Costs and revenue ($ ha\textsuperscript{-1}) from partial enterprise budgets used to calculate marginal rate of return for conversion of GMEP to GINP or GMNP........................................................................................................114

5.4 Sensitivity analysis\textsuperscript{a} of marginal rate of return from conversion of GMEP to GINP and GMNP. ........................................................................................................114
LIST OF FIGURES

2.1 Relative number of active nests (●) and active nests estimated by the JS
    nest density model (▲; and 95% CrI) from bi-weekly searches
    for Dickcissel nests at the Mississippi State University Prairie
    Research Unit in Prairie, MS, USA........................................................27

2.2 Mean Dickcissel nest density (and 95% CrI) estimated by treatment
    from relative abundance (●), relative abundance with incidental
    nests (■), and the JS nest density model (▲)..................................28

2.3 Mean posterior transition probability estimates\textsuperscript{a} (survival) for analysis
    of simulated datasets from 4 scenarios using the multi-state
    Jolly-Seber model...................................................................................29

2.4 Mean posterior nest abundance estimates from analysis of simulated
    datasets from 4 scenarios using the multi-state Jolly-Seber
    model, compared with known (true) abundance and observed
    (relative) abundance for each dataset. ..................................................30

3.1 Distribution of treatments\textsuperscript{a} and vegetation sampling transects at the
    Mississippi State University Prairie Research Unit in Monroe
    Co., MS, USA, 2011–2012. .................................................................56

3.2 Treatment\textsuperscript{a} mean estimates (± SE) of pasture vegetation structure and
    composition\textsuperscript{b}, from June to July in 2011 (●) and 2012 (▲). ........57

3.3 Treatment-specific\textsuperscript{a} dispersion ellipses from Canonical Analysis of
    Principal Coordinates (CAP) ordination of Dickcissel nest sites
    (solid line) and paired random points (dashed line) based on
    vegetation and fire ant covariates\textsuperscript{b}.............................................58

3.4 Proportional use of nesting substrates by treatment\textsuperscript{a} for Dickcissels at
    the Mississippi State University Prairie Research Unit in Monroe
    Co., MS, USA, 2011–2012. .................................................................59

3.5 Mean Dickcissel productivity (and 95% CrI) by treatment\textsuperscript{a} in 2011 and
    2012.................................................................................................60
4.1 Mean bermudagrass (*Cynodon dactylon*) coverage (and 95% CI)\textsuperscript{a} by treatment\textsuperscript{b} and year, measured at the MSU Prairie Research Unit in Prairie, MS, USA, 2011–2012. ..........................................................87

4.2 Ordination plot\textsuperscript{a} from non-metric multidimensional scaling (NMDS) of eight Orders (a), and dispersion ellipses (95% CI) for arthropod Orders grouped by treatment in June (b) and in July (c). .........................88

4.3 Mixed effects regression\textsuperscript{a} of Orthoptera biomass against four vegetation parameters correlated with arthropod community ordination. .................89

4.4 Mixed effects regression\textsuperscript{a} of Coleoptera biomass against four vegetation parameters correlated with arthropod community ordination. .............90

4.5 Mixed effects regression\textsuperscript{a} of Hemiptera biomass against four vegetation parameters correlated with arthropod community ordination. ...............91

4.6 Mixed effects regression\textsuperscript{a} of Araneae biomass against four vegetation parameters correlated with arthropod community ordination. .............92

4.7 Interaction plots for mean IFA occurrence (± SE) by treatment\textsuperscript{a} measured from 36 vials per pasture. .................................................................93

4.8 Mean IFA mound density (and 95% CrI) by treatment\textsuperscript{a} estimated from pastures. .........................................................................................................94

5.1 Price paid in May (1999–2013) and price received in January (2000–2014) for steers reported by NASS (a), and corresponding marginal rate of return for converting GMEP to GINP (b) and GMNP (c), given 2011 partial budget values at the Mississippi State University Research Unit in Monroe Co., MS, USA, 2011–2012. .....................................................................................................115

5.2 Mean estimates of Dickcissel productivity (and 95% CrI) by treatment (Chapter 3). ...........................................................................................................116
CHAPTER I
GENERAL INTRODUCTION

During the 20th century, agricultural intensification played a predominant role in meeting food demand for a growing global human population, increasing per hectare productivity primarily through greater inputs of fertilizer and pesticides (Tilman et al. 2001). However, greater productivity has also come at a cost to biological diversity due to reductions in structural and compositional diversity of local vegetation (e.g., Donald et al. 2001, Fuhlendorf and Engle 2001, Benton et al. 2002, Kleijn et al. 2009) and increases in nonpoint source pollution (e.g., Stout et al. 2000, Tilman et al. 2002, Eickhout et al. 2006). Given the projected further global population growth through 2050 (UNDESA 2013), developing and implementing sustainable agricultural practices is essential to preventing further biodiversity loss (Tilman et al. 2002).

In North America, intensive management of grazing lands is common (Fuhlendorf and Engle 2001, Toombs and Roberts 2009). Monocultures of exotic forages are also established throughout the Southern United States (Barnes et al. 2013, Fulbright et al. 2013) and managed with heavy grazing and large inputs of nitrogen fertilizer (Monson and Burton 1982, Burns et al. 1984, Phillips and Coleman 1995). Such management likely reduces suitability of grasslands for many native wildlife species (e.g., Fuhlendorf and Engle 2001, Kruess and Tscharntke 2002, Dennis et al. 2008). For example, abundance and diversity of arthropods often decrease with low plant diversity (e.g.,
Murdoch et al. 1972, Southwood et al. 1979, Siemann et al. 1998, Woodcock et al. 2009) and heavy grazing (Gibson et al. 1992a, Dennis et al. 1998, Kruess and Tscharntke 2002, Dennis et al. 2008). Grassland bird species in North America also experienced widespread population declines (Sauer and Link 2011), and intensive management of exotic forages can limit availability of prey items and suitable nest sites, particularly for tall structure specialists (e.g., Flanders et al. 2006, Hickman et al. 2006, Fuhlendorf et al. 2006).

There is increasing interest in replacing exotic grasses with native warm-season grasses (NWSG) because they offer several benefits for livestock and wildlife (Taylor 2000, Giuliano and Daves 2002, Harper et al. 2007). For example, cattle may perform better when grazing NWSG than exotic grasses due to structural and forage quality (Burns et al. 1984, Burns et al. 1991). Native grasses also require fewer fertilizer inputs because they can be adapted to local growing conditions (Jung et al. 1988), and NWSG pastures are generally taller and not grazed as intensively as exotic pasture, offering more suitable nesting habitat for grassland birds (Hughes et al. 1999, Giuliano and Daves 2002). Furthermore, cattle production on native grasses is often more profitable due to higher production costs of intensively-managed exotic forages (Phillips and Coleman 1995, Coleman et al. 2001, Gillen and Berg 2001).

In the Southeastern United States, exotic forages such as bermudagrass (*Cynodon dactylon*) and tall fescue (*Schedonorus arudinaceus*) are established across millions of hectares (Barnes et al. 2013), so incorporating NWSG into beef production systems has enormous potential for improving sustainability and conserving biodiversity on private lands (Pimentel et al. 1992). Still, uncertainty among landowners regarding opportunity
cost and risks of establishment and maintenance present barriers to adopting NWSG in contemporary grazing management (Taylor 2000, Doll and Jackson 2009). Characterizing the response of wildlife and economic implications of converting exotic forages to NWSG is necessary for producers and conservationists to make informed decisions regarding NWSG conversion. Therefore my research objectives are to:

1. evaluate potential mechanisms by which NWSG conversion affects nest site suitability and productivity for Dickcissels;
2. characterize arthropod community response to NWSG conversion; and
3. quantify the relative benefit of NWSG conversion for producers regarding profit and Dickcissel productivity.
CHAPTER II
ESTIMATING AVIAN NEST DENSITY USING CAPTURE-RECAPTURE MODELS

Introduction
Assessing habitat quality is important for avian conservation and management because resource availability can influence density, reproduction, and survival, and thus population trajectory (Johnson 2007). Collecting multiple metrics may also be necessary due to potential negative correlations between abundance and survival or productivity (Van Horne 1983, Bock and Jones 2004). Nest searching and monitoring is commonly used to quantify nest survival rates, an index of individual fitness, but studies may overlook relationships at the population level without also measuring density (Johnson 2007). For example, members of a territorial species may exclude conspecifics from areas with high quality resources (ideal despotic distribution; Fretwell 1972), thereby increasing per capita reproductive success but reducing productivity per hectare due to low nest density. In addition, quantifying nest density may be useful because bird surveys can disproportionately detect displaying males (Mayfield 1981) and may not be indicative of pairing status or fecundity (Rappole et al. 1993, Pagen et al. 2002). Nest density estimates may also reveal a more direct association between individuals and locations than bird surveys that can include floaters (nonbreeding individuals). Finally, nest density may be more informative than adult abundance for polygynous species when territory quality is related to harem size (Zimmerman 1982, Searcy and Yasukawa 1983).
Grassland-obligate bird populations in North America have exhibited precipitous declines (Sauer and Link 2011), necessitating continued study of bird response to management and conservation programs (Vickery and Herkert 2001). However, obtaining unbiased estimates of nest density remains elusive. Previous grassland bird studies typically compared nest densities using relative or apparent indices (e.g., Churchwell et al. 2008, Conover et al. 2011b, Hatchett et al. 2013). As with other survey methods, nest detectability is rarely 100%, so relative indices may confound variation in true abundance with variation in detectability (Royle and Dorazio 2008). For example, nest search methods such as rope drags rely on flushing incubating females to reveal nest locations (Gloutney et al. 1993, Winter et al. 2003), but female nest attendance may vary with nest site vegetation and nest stage (Winter et al. 2003, Giovanni et al. 2011, Powell et al. 2012), potentially biasing estimates of relative nest density compared to the true population. Site-level differences in survival rates could further complicate nest density comparisons because nests with low survival will be less represented than nests with higher survival (Heisey et al. 2007).

Robust survey methods for estimating abundance such as N-mixture models assume population closure (Royle 2004) and therefore are inappropriate for modeling abundance of nests that initiate and fail throughout a season. Previous attempts to account for detectability in nest density estimates also did not incorporate estimates of survival and recruitment, and thus remained relative measures of density (Smith et al. 2009, Giovanni et al. 2011). I present an alternative approach using a novel application of the Jolly-Seber (JS) capture-recapture model (Jolly 1965, Seber 1965) to obtain unbiased estimates of nest densities by modeling detectability, survival, and new nest construction.
I apply this method to the Dickcissel (*Spiza americana*), a tallgrass specialist and Neotropical migrant (Temple 2002) nesting in cattle production systems in Mississippi. I used the JS model to compare nest densities in native and exotic grass pastures, and grazed and non-grazed treatments. I also compare estimates to relative measures of nest density, and illustrate the use of prior knowledge of female nest attendance to enhance detectability estimates in a Bayesian framework. Finally, I assessed accuracy of the JS model with simulated datasets of known abundance generated from different levels of detectability and survival.

**Methods**

In 2011 and 2012, we conducted nest searches in 12 pastures (range = 6.4–10.5 ha) at Mississippi State University's Prairie Research Unit in Monroe Co., Mississippi, USA (N 33°47', W 88°38'). Pastures were assigned to one of 4 treatments, and each treatment was replicated 3 times. One treatment consisted of a grazed exotic grass mix of bermudagrass (*Cynodon dactylon*) and tall fescue (*Schedonorus arundinaceus*) (hereafter, grazed mixed exotic pasture, or GMEP). The remaining treatments were native grass stands established in 2008. Native grass treatments included grazed Indian grass monoculture (*Sorghastrum nutans*) (hereafter, grazed Indian grass native pasture, or GINP), grazed native warm-season grass mix of big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*), and Indian grass (hereafter, grazed mixed native pasture, or GMNP), and a non-grazed mixed native pasture treatment (hereafter, NMNP). During each study year, native treatments were prescribed burned in spring, and grazed treatments were stocked with fall-born steers from mid-May until September at 2.7 head ha⁻¹.
Nest Searching and Monitoring

From mid-May through July each year, I used a rope-drag method (Winter et al. 2003) to search each pasture for nests once every 2 weeks (5 searches in 2011, 6 in 2012). Beginning at one corner, 3 observers systematically traversed the entire pasture dragging a 30-m rope, and noted flush locations of incubating females. The rope was weighted at 2-m intervals with 0.6-L bottles filled with several rocks (noisemakers) and was extended between 2 observers with a third observer positioned in-between to spot flushing females. I searched pastures with equal effort by dropping surveyor flags at regular intervals during each pass and collecting these on the return, ensuring pastures were covered evenly and without overlap (Winter et al. 2003). Nest searching typically occurred from sunrise through mid-day, and I alternated the order in which we searched pastures within a day to minimize potential temporal biases in nest attendance by females (Winter et al. 2003, Davis and Holmes 2012). I recorded nest locations with a Global Positioning System (GPS) device and applied spray paint to vegetation 5 m north of nests (Winter et al. 2003).

I checked nests every 2–4 days and increased nest visits to every 1–2 days near anticipated fledge dates to ensure an accurate determination of nest fate. Nest age and stage were estimated by noting whether eggs felt warm (indicating incubation), by egg candling (Lokemoen and Koford 1996), or with voucher photos of nestling development. I similarly monitored nests found opportunistically, outside of search events (hereafter, incidental nests; \( n = 58 \)).
**Nest Attendance Modeling**

Females of some species may remain on the nest despite use of the rope drag method (Giovanni et al. 2011), and thus detection probability may be <1 for this method. To test if female Dickcissels fail to flush from the rope drag method, I conducted trials by dragging a rope over a subset of known nests to determine whether females remained on the nest. Of the 43 active nests tested in 2011 and 21 nests in 2012, all trials induced the female to flush, indicating that the rope drag method was effective, given female attendance.

I used logistic regression and the package *lme4* (Bates et al. 2013) in R (version 3.0.2, R Development Core Team 2014) to evaluate factors that may influence female nest attendance and to derive informative priors for detectability to supplement the JS nest density model. I restricted modeling to active nests, and therefore probability of female attendance should be >0 for all nests. Attendance was then modeled from the encounter history of flushing females during the initial discovery of nests and subsequent nest checks, and I included a random effect of nest to account for correlation among repeated visits to the same nest. I began by constructing models with covariates for attendance due to treatment, nest stage, treatment + stage, and treatment × stage because I predicted that nest stage would have the greatest influence on female attendance, and because I was primarily interested in effects of treatment in this study. I created additional univariate models with effects of time (min since sunrise), date, and year to evaluate their support compared with stage and treatment. Nest attendance may also vary with vegetation density (Giovanni et al. 2011), so at each nest I measured visual obstruction with a Robel pole (Robel et al. 1970), and visually estimated overhead
concealment to the nearest 5% with a 6.5 cm diameter ball placed in the nest cup. I then created univariate models for each parameter. I compared support among models to that of a null (intercept-only) model using Akaike's Information Criterion corrected for small sample sizes (AICc; Burnham and Anderson 2010). I report AIC differences (ΔAICc) and Akaike weights (wi), which denotes the relative support of one model given the other models in the candidate set. I considered models competitive if they ranked <2 AICc units from the top model and >2 AICc units above the null. I used model-averaged parameter estimates and unconditional standard errors for our informative priors, estimated with the R package AICcmodavg (Mazerolle 2013).

**Nest Density Modeling**

I first computed relative nest density estimates (nests ha⁻¹) only from nests found during search events, and used a Bayesian approach to estimate mean density by treatment and year. Nest density (excluding incidentals) in each pasture p during year k was modeled from a normal distribution as \( y_{p,k} \sim N(\mu_{j,k}, \sigma^2) \), with mean nest density for treatment j and year k assumed to be normally distributed (\( \mu_{j,k} \sim N[0,1000] \)), and with an inverse-gamma prior for variance (\( \sigma^{-2} \sim \text{Gamma}[0.1,0.1] \)). I similarly modeled mean nest density while including incidental nests. I fit both models using JAGS (version 3.4.0; Plummer 2003) and the package R2jags (Su and Yajima 2013) in R. I ran models for 50,000 iterations after burning the first 5,000, and thinned by 10 from 3 parallel chains. Convergence was assessed by visually examining the chains, and with the \( \hat{R} \) statistic, which compares within and between variations of parallel chains (Gelman et al. 2014).
In the JS model, new nest construction (recruitment) is modeled as a random process of individuals entering the study from a latent superpopulation (with abundance \( N_s \)) because, unlike other capture-recapture models, estimates of detection and survival are not conditioned on first capture (Jolly 1965, Seber 1965). I used the multi-state formulation of JS (Royle and Dorazio 2012, Kéry and Schaub 2012), which permits accounting for stage-specific differences in survival and detection probability. In this model, \( B_t \) new individuals enter the study population during time interval \( t \) with probability \( \gamma_t \), and \( N_s \) individuals enter by the end of the season (after \( T \) time intervals):
\[
N_s = \sum_{t=1}^{T} B_t.
\]
For data augmentation, I appended an arbitrarily large number of encounter histories for nests that I did not detect to the \( n \) encounter histories observed in our study (Royle and Dorazio 2012, Kéry and Schaub 2012). The model then estimates the number of individuals from the augmented set that enters the study but remains unobserved \((N_s - n)\). Once entered, each individual then survives from \( t \) to \( t + 1 \) with probability \( \phi \), and is detected with probability \( p \).

I designed state transition and observation matrices to account for stage-specific differences in entry, survival, and detectability of individual nests in the population, and I based my model on 2-week time intervals to match the schedule of our nest searching. In the state transition matrix, I modeled a unique entry probability parameter for each pasture \( p \) in time interval \( t \) and year \( k \) for the lay, incubation, and nestling stages \((\gamma_{1,pk}, \gamma_{2,pk}, \text{ and } \gamma_{3,pk}, \text{ respectively})\). I used a multinomial logit link to ensure that stage-specific entry probabilities sum to <1 (Kéry and Schaub 2012). In reality, a nest can only enter the population at the lay stage, but because nest search events were separated by 2-week intervals it was possible that a nest had not yet initiated at \( t \) but was found on or after
hatch day at \( t + 1 \), and therefore in the model this nest entered at the nestling stage. I modeled a pasture-specific entry probability for each stage on the logit scale, with stage-specific covariates for pasture (\( gamp \)), and linear effects of time interval (\( \alpha_1 \)) and year (\( \alpha_2 \)):

\[
\text{logit} \left( \gamma_{1,ptk} \right) = gamp_{1,p} + \alpha_1 Time_t + \alpha_2 Year_k
\]

\[
\text{logit} \left( \gamma_{2,ptk} \right) = gamp_{2,p} + \alpha_1 Time_t + \alpha_2 Year_k
\]

(2.1)

\[
\text{logit} \left( \gamma_{3,ptk} \right) = gamp_{3,p} + \alpha_1 Time_t + \alpha_2 Year_k
\]

For survival, nests could not persist in the same nest stage from one time interval to the next, so \( \phi \) was fixed at 0. However, a nest in treatment \( j \) could survive from lay to incubation stage (\( \phi_{1,j} \)), lay to nestling stage (\( \phi_{2,j} \)), or incubation to nestling stage (\( \phi_{3,j} \)), and therefore I estimated individual survival parameters for each transition. The probability of a nest in the lay stage becoming inactive before the following interval was thus \( 1 - \phi_{1,j} - \phi_{2,j} \), again constrained by a multinomial logit link. The probability of becoming inactive (fledge or fail) after the incubation stage is simply \( 1 - \phi_{3,j} \). Finally, once nests reached the nestling stage in time \( t \), they became inactive by \( t + 1 \), and remained inactive, so \( \phi \) was fixed at 1 for both transitions. The state transition matrix was thus:

\[
\begin{array}{cccccc}
\text{Not entered} & \text{Not entered} & \text{Lay} & \text{Incubation} & \text{Nestling} & \text{Inactive} \\
1 - \gamma_{1,ptk} - \gamma_{2,ptk} - \gamma_{3,ptk} & \gamma_{1,ptk} & \gamma_{2,ptk} & \gamma_{3,ptk} & 0 \\
0 & 0 & \phi_{1,j} & \phi_{2,j} & 1 - \phi_{1,j} - \phi_{2,j} \\
0 & 0 & 0 & \phi_{3,j} & 1 - \phi_{3,j} \\
0 & 0 & 0 & 0 & 1 \\
0 & 0 & 0 & 0 & 1 \\
\end{array}
\]

Pastures varied in number of nests entering in each stage, which could make estimating pasture-specific entry probabilities difficult for pastures with few nests. I
therefore specified population-level hyper-parameters ($\mu_\gamma$ and $\sigma_\gamma^2$), from which were drawn pasture-specific covariates for entry probability, e.g., $g_{\gamma_{1,p}} \sim N(\mu_{\gamma_{1}}, \sigma_{\gamma_{1}}^2)$.

Therefore, covariates with little information from the data shrink their estimates toward a population mean and variance, and I assumed that entry probabilities for each stage functioned similarly in the broader population but could vary by pasture. This assumption is reasonable given the highly localized distribution of my study pastures compared with the regional distribution of Dickcissels (Temple 2002), so processes of migration and colonization are likely similar among the study pastures. I similarly modeled treatment-specific survival estimates as drawn from population-level hyper-parameters ($\mu_\phi$ and $\sigma_\phi^2$).

I evaluated the response of model estimates to two different priors for hyper-parameter means, including a standard uninformative normal prior on the logit scale ($\mu \sim N[0,1000]$) and a weakly-informative uniform prior ($\text{logit}[\mu] \sim U[0,1]$) appropriate for parameters with limited data (Lunn et al. 2013). The model converged with normal and uniform priors for both sets of parameters, and density estimates were generally similar among models. However, estimates of $\mu_\gamma$ tended to be near 0 (i.e. <0.015) due to the large number of augmented individuals and using the normal prior for $\mu_\gamma$ reduced mean estimates of $N_s$ by ~5 nests in 2011, suggesting the uniform prior discouraged estimates of $\mu_\gamma$ near 0. Conversely, estimates of $\mu_\phi$ and $\sigma_\phi^2$ were more variable with the normal prior for $\mu_\phi$, likely due to a paucity of samples in the lay stage needed to estimate the first two transition probabilities. I found convergence and subsequent simulation results were improved by specifying the normal prior for $\mu_\gamma$ and the uniform prior for $\mu_\phi$, and therefore I used this parameterization for the final model.
For the detection matrix, I estimated one parameter for each nesting stage and treatment ($p_{1,j}$, $p_{2,j}$, and $p_{3,j}$ for lay, incubation, and nestling stages in treatment $j$, respectively). Correspondingly, the probability of missing an active nest is $1 - p$. I fixed the probability of “not entered” and inactive nests remaining undetected at 1. This yields:

<table>
<thead>
<tr>
<th></th>
<th>Seen lay</th>
<th>Seen inc.</th>
<th>Seen nes.</th>
<th>Not seen</th>
</tr>
</thead>
<tbody>
<tr>
<td>Not entered</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Lay</td>
<td>$p_{1,j}$</td>
<td>0</td>
<td>0</td>
<td>$1 - p_{1,j}$</td>
</tr>
<tr>
<td>Incubation</td>
<td>0</td>
<td>$p_{2,j}$</td>
<td>0</td>
<td>$1 - p_{2,j}$</td>
</tr>
<tr>
<td>Nestling</td>
<td>0</td>
<td>0</td>
<td>$p_{3,j}$</td>
<td>$1 - p_{3,j}$</td>
</tr>
<tr>
<td>Inactive</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
</tr>
</tbody>
</table>

I allowed detectability to vary by treatment and assumed $p$ was constant over time and year (see Nest Attendance Modeling). Achieving convergence was difficult during initial attempts to model nest density using uninformative priors for detectability. However, one benefit of using a Bayesian approach is the ability to incorporate prior knowledge in models using informative priors (Martin et al. 2005, McCarthy and Masters 2005). I therefore used empirically derived estimates of mean and variance in detectability for each treatment and stage from modeling female nest attendance. I supplied these estimates as priors in the JS model on the logit scale, e.g.,

$$\text{logit}(p_{1,j}) \sim N(\mu_{p,1,j}, \sigma_{p,1,j}^2).$$

I restricted the JS nest density analysis to nests found during bi-weekly nest searching events because nests found incidentally likely differed in detectability from nests found by rope-drag, and because length of time intervals varied considerably among incidental nests found within each 2-week period. I back-dated nest stages for when nests were active but undetected and supplied nest stages in the latent state $z$ matrix (Kéry and
Schaub 2012). Nest searchers were sometimes aware of nests detected during previous
nest search events, so I supplied NAs to the encounter history for detected nests in
subsequent search events until nests became inactive to avoid bias in detectability. In
addition, we performed one fewer search event the first year than the second (5 in 2011, 6
in 2012), so to compare total superpopulations between years I specified NAs in the
encounter history for the missing 6th search event in 2011, allowing the model to predict
the number of nests, given the model and the data. Finally, I computed nest densities by
treatment and year as a derived parameter by dividing pasture-specific superpopulation
estimates by the searchable area in each pasture and then averaging densities among
pastures in each treatment.

I fit the JS nest density model using R2jags in R. I ran the model on 3 parallel
chains for 150,000 iterations, burning the first 50,000 and thinning by 10. I used 95%
credible intervals (CrI) to compare nest densities among treatments, and between the JS
model and the relative nest density models.

Simulation Study

I evaluated accuracy and precision of the model by simulating datasets and
comparing estimates generated from the JS model with known values of $N_s$, $p$, and $\phi$. I
simulated data with low $p$ ($p_1 = 0.4$, $p_2 = 0.6$, $p_3 = 0.1$), high $p$ ($p_1 = 0.6$, $p_2 = 0.8$, $p_3 =
0.3$), low $\phi$ ($\phi_1 = 0.1$, $\phi_2 = 0.4$, $\phi_3 = 0.2$) and high $\phi$ ($\phi_1 = 0.3$, $\phi_2 = 0.6$, $\phi_3 = 0.4$), and
created 4 scenarios with all combinations of $p$ and $\phi$ (i.e., low $\phi$ and low $p$, low $\phi$ and
high $p$, high $\phi$ and low $p$, and high $p$ and high $\phi$). I also assumed that $p$ and $\phi$ were
constant over the 6 2-week time intervals. To mimic my study system, the simulation
began with 2000 individual nests in the “not entered” state at $t = 0$. From $t = 1−6$, I used estimates of entry probability ($\mu_r$) and linear effect of time ($\alpha_t$) from the field study to simulate entry of individuals in each stage over time. I then simulated stage transitions and encounter histories for each individual at each time interval based on my proposed state and observation matrices (Kéry and Schaub 2012), generating 100 datasets for each scenario. This resulted ~229 individuals on average included in the latent superpopulation (range: 186–270), of which 101–223 individuals were observed, depending on the simulation scenario. Although I supplied each analysis with a latent $z$ matrix, the matrix included only individuals that were observed at least once, and therefore known but unobserved individuals could not influence estimates of $N_s$, $p$, and $\phi$. Similar to the field study, using uninformative priors for $p$ led to few models converging, so I specified informative priors for $p$ at each stage. I used the JS model to acquire mean posterior estimates for $N_s$ and $\phi$ from each dataset, sampling for 100,000 iterations after burning the first 50,000, and thinning by 10 from 3 parallel chains. All models included a linear effect of time on entry probability. I also computed root mean squared error (RMSE) to evaluate variance and bias in observed and estimated abundance relative to the true $N_s$.

Results

Nest Attendance Modeling

Including incidental nests, I found 208 nests over 2 years ($n = 85$ and 123 in 2011 and 2012, respectively). Of these nests, 63 in 2011 and 87 in 2012 were found during nest search events. Based on 748 nest visits, female nest attendance was best predicted by nest stage (Table 2.1). An additive effect of treatment with nest stage was competitive, but the
stage × treatment model was not well supported ($\Delta AIC_c = 9.98$, $w_i < 0.01$). All other univariate models, including treatment, were also not well supported ($\Delta AIC_c > 140.00$, $w_i < 0.01$). After model-averaging the 2 competitive models, confidence intervals indicated that female nest attendance was highest during incubation, lowest during the nestling stage, and intermediate at the lay stage (Table 2.2). Confidence intervals overlapped among treatments, although attendance tended to be higher for GMEP.

**Field Study**

The JS nest density model indicated a greater superpopulation in 2012 ($N_s = 129.7$, 95% CrI: 113, 148) than in 2011 ($N_s = 100.1$, 95% CrI: 86, 118), reflected in a positive mean estimate of year on entry probability ($\alpha_2 = 0.25$, 95% CrI: –0.10, 0.60). Probability of entry declined over time ($\alpha_1 = –0.60$, 95% CrI: –0.82, –0.39), and number of active nests decreased seasonally, especially during the second year (Fig. 2.1). After back-dating nests under observation, the relative number of active nests were consistently less than number of active nests estimated by the JS model (Fig. 2.1). In 2011, the JS model indicated greater nest densities for NMNP than for GMEP, whereas densities among grazed treatments were intermediate and similar (Fig. 2.2). In 2012, nest density in NMNP was higher than all other treatments. Estimates from the JS model were also more precise than estimates from models of relative nest density, and mean estimates from the JS model were consistently greater than relative estimates, except when incidentals were included. However, including incidental nests in relative nest density estimates also resulted in wider credible intervals.

Estimates of stage- and treatment-specific detectability parameters were similar to estimates derived from female nest attendance modeling (Table 2.2), including relatively
high detection at the incubation stage and lower detectability at the lay and nestling stages (Table 2.3). However, credible intervals for \( p \) and \( \phi \) overlapped among treatments in each stage and transition. Among estimates of \( \mu_\gamma \), entry probability tended to be highest for the incubation stage, lowest for the nestling stage, and intermediate for the lay stage (Table 2.4). Estimates of \( \mu_\phi \) were also higher for the lay to nestling transition state, though credible intervals overlapped among transitions.

**Simulation Results**

The JS model tended to overestimate \( \phi \) for the first 2 transitions (\( \phi_1 \) and \( \phi_2 \)), particularly among high \( \phi \) scenarios (Fig. 2.3). Conversely, \( \phi_3 \) was estimated accurately in all scenarios, suggesting that the small sample of individuals in the lay stage contributed to difficulties in estimating transition probability to incubation and nestling stages. Nest abundance was estimated near known true abundances in all 4 scenarios (Fig. 2.4), suggesting that any inaccuracy in estimates of \( \phi \) from the lay stage did not have a strong effect on estimates of \( N_s \). However, estimates of \( N_s \) tended to be less accurate for high \( \phi \) low \( p \) scenario (RMSE = 15.7), and even less accurate for low \( \phi \) low \( p \) scenario (RMSE = 16.9). Accuracy in \( N_s \) estimates improved when \( p \) was high (RMSE = 8.1 and 8.7 for low and high \( \phi \), respectively). Relative abundance consistently underestimated true abundance, especially among low \( p \) scenarios (RMSE = 103.5 and 95.8 for low and high \( \phi \), respectively). Our simulations therefore illustrate the importance of accounting for detectability because increases in \( p \) led to greater estimates of relative abundance despite similar true abundance among scenarios.
Discussion

My results indicate that the JS model provided greater and more precise estimates of Dickcissel nest densities compared with indices of relative density. The JS model estimated a greater superpopulation in 2012 than 2011 (albeit with uncertainty from slightly overlapping credible intervals), though with 2 years of data it is unclear whether estimates reflect a broader annual trend. However, my results are consistent with previous studies of Dickcissels in recently established herbaceous buffers (Conover et al. 2011a, 2011b), and it is possible that as stands mature they provide more nest sites for this species until nest sites are fully saturated or competition reduces reproductive success. I cannot estimate the size of the female Dickcissel population based on nest abundance because females can re-nest up to 3 times in a season (Temple 2002), and I did not band females so individuals could not be identified. However, in a radio-telemetry study >60% of female Dickcissels emigrated from the study site following nest failure (Walk et al. 2004), suggesting that many if not most nests in my study were constructed by new females. The JS model also estimated greater nest densities in NMNP than in GMEP, whereas this trend was obscured among relative estimates due to high variability. Dickcissels construct nests in tall and dense vegetation (Zimmerman 1971, Winter 1999), and nest density and rates of polygyny increase with nest site availability (Zimmerman 1971, Zimmerman 1982), suggesting that non-grazed native grass pastures provided more nest sites and supported greater nest densities than grazed exotic grass pastures.

Including incidental nests in relative nest density models sometimes yielded mean density estimates similar to estimates from the JS model. However, these relative density estimates were also more variable, likely because many incidental nests were found
during repeated visits to pastures for nest checks. As a result, pastures with greater nest densities led to greater discovery of incidental nests, whereas pastures with few nests were seldom visited, and thus few incidental nests were found. This pattern was best illustrated in the NMNP treatment in 2012, where in one pasture I found 27 nests from nest searching and 21 incidentals, compared to another pasture with one nest from nest searching and zero incidentals. Consequently, researchers that use relative nest densities may be faced with the choice of either using only nests found during search events, and thus underestimating the true population size (poor accuracy), or including incidental nests and increasing the variance in estimates (poor precision).

Reduced female nest attendance during the nestling stage is consistent with other studies (Smith et al. 2009, Giovanni et al. 2011, Powell et al. 2012), as females typically spend more time off the nest foraging. I found some support for variation in nest attendance by treatment, which may reflect differences among treatments in ambient temperature (Conway and Martin 2000) or predation risk (Martin et al. 2000). However, estimates were more similar among treatments after model-averaging. There also was support relative to the null for effects of date and time on nest attendance, but these models were much less competitive compared with nest stage, and thus were not used to model nest density. Using nest attendance estimates as informative priors in my analysis is controversial because some argue that this introduces an element of subjectivity when we aim to make objective inferences on study systems (Dennis 1996). Nevertheless, informative priors were used successfully in previous studies to increase precision in parameter estimates when data were sparse (e.g., Martin et al. 2005, McCarthy and Masters 2005), and specifically to improve detection probability estimates (Giovanini et
al. 2013). Given the 2-week intervals between surveys in my protocol, obtaining the same
detectability estimates directly from the model would require a larger sample of nests in
each stage and treatment, more repeated visits, or assumptions of constant detection
among stages and treatments and thus overlook true ecological processes. Our study also
highlights the benefit of collecting ancillary data, such as female presence during nest
visits, which could be useful for modeling detection probability because I was able to
derive informative priors from the same study population used in the nest density
analysis, and therefore likely to capture ecological processes relevant to this population.

Overlap in survival and detectability parameter estimates among treatments in the
JS model suggests that nest density estimates in my field study were largely driven by
pasture-specific entry probability, informed by the number of nests found during each
search event. The biological significance of entry probability and survival parameters is
unclear in this case, as they could also be a result of our nest searching protocol. For
example, lower entry probability at the nestling stage reflects the unlikely situation of
nests not yet initiated during the previous nest search event being subsequently found
with nestlings 2 weeks later. Similarly, lower survival for nests in the lay to incubation
transition ($\phi_{1,j}$) compared with the lay to nestling transition ($\phi_{2,j}$) seems unlikely from a
biological standpoint because survival was shown to decrease with nest age for
Dickcissels (Churchwell et al. 2008). Rather, nests found in the lay stage are more likely
found with nestlings after 2 weeks than in the incubation stage (if still active). Based on
my simulation study I still argue that accounting for differences in survival and
detectability is important to avoid biasing nest density estimates. However, for
researchers interested in formally evaluating nest survival rates I recommend using
regular nest checks and models such as logistic exposure (Shaffer 2004), rather than rely on the JS nest density model for inferences on survival parameters.

The multi-state JS nest density model is broadly applicable to studies examining effects of management on avian demographics, and it requires few additional resources if researchers are monitoring nests to estimate survival. It could also yield estimates of per hectare productivity when combined with data on brood size and fledging rates. However, it may not be appropriate for certain search methods such as behavioral observations or “haphazard” walking (Winter et al. 2003) unless search effort is accounted for in the model. Failure to standardize effort could confound abundance estimates and prevent meaningful comparisons among study sites. Researchers should also consider that the source of variation in detectability might differ by search method and nest stage. For example, using behavioral observations of adults to find nests may be more effective later in the day and nesting cycle because adults spend more time off the nest (Winter et al. 2003). I also suggest that researchers modify their protocol to facilitate modeling nest density. For example, characterizing nest stage is clearly important given its relationship to female nest attendance, and thus detectability. Researchers may also wish to accurately age nests, because back-dating can improve estimates of stage transition probabilities and can determine whether nests were active but missed during previous search events. In addition, I recommend using shorter intervals between nest search events as this may improve estimates of detectability and survival, though shortening intervals may also require modifying the state transition matrix to accommodate persistence in stages across time intervals. Finally, in my field study I did not note whether known nests were detected during subsequent search events, instead
supplying NAs in the encounter history (but not in the latent \( z \) matrix) to avoid biasing estimates of detection probability. Future studies may instead use nest searchers that are naïve to the location of known nests to further improve parameter estimates.
Table 2.1 Model selection results based on Akaike’s Information Criterion corrected for small sample sizes ($\text{AIC}_c$) for female Dickcissel ($\text{Spiza americana}$) nest attendance at the Mississippi State University Prairie Research Unit in Prairie, MS, USA, 2011–2012.

<table>
<thead>
<tr>
<th>Model</th>
<th>$K^a$</th>
<th>$\Delta\text{AIC}_c^b$</th>
<th>$w_i^c$</th>
<th>Deviance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stage</td>
<td>4</td>
<td>0</td>
<td>0.65</td>
<td>868.45</td>
</tr>
<tr>
<td>Stage + Treatment</td>
<td>7</td>
<td>1.27</td>
<td>0.35</td>
<td>863.62</td>
</tr>
<tr>
<td>Stage $\times$ Treatment</td>
<td>13</td>
<td>9.98</td>
<td>0.00</td>
<td>859.98</td>
</tr>
<tr>
<td>Date</td>
<td>3</td>
<td>142.21</td>
<td>0.00</td>
<td>1012.68</td>
</tr>
<tr>
<td>Time</td>
<td>3</td>
<td>145.88</td>
<td>0.00</td>
<td>1016.35</td>
</tr>
<tr>
<td>Treatment</td>
<td>5</td>
<td>150.42</td>
<td>0.00</td>
<td>1016.85</td>
</tr>
<tr>
<td>Null (intercept-only)</td>
<td>2</td>
<td>154.67</td>
<td>0.00</td>
<td>1027.16</td>
</tr>
<tr>
<td>VOR</td>
<td>3</td>
<td>154.95</td>
<td>0.00</td>
<td>1025.42</td>
</tr>
<tr>
<td>Year</td>
<td>3</td>
<td>155.19</td>
<td>0.00</td>
<td>1025.66</td>
</tr>
<tr>
<td>Concealment</td>
<td>3</td>
<td>156.66</td>
<td>0.00</td>
<td>1027.13</td>
</tr>
</tbody>
</table>

$^a$Parameter count.

$^b$$\text{AIC}_c$ differences, min. $\Delta\text{AIC}_c = 876.50$.

$^c$Akaike weights.
Table 2.2  Stage- and treatment-specific estimates of female Dickcissel nest attendance probability, after model-averaging. I also report mean and variance (on the logit scale) of estimates used as informative priors in the JS nest density model.

<table>
<thead>
<tr>
<th>State</th>
<th>Treatment</th>
<th>Est.</th>
<th>Lower</th>
<th>Upper</th>
<th>logit(μ)</th>
<th>logit(σ²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lay</td>
<td>GMEP</td>
<td>0.57</td>
<td>0.36</td>
<td>0.75</td>
<td>0.27</td>
<td>0.18</td>
</tr>
<tr>
<td></td>
<td>GINP</td>
<td>0.48</td>
<td>0.27</td>
<td>0.70</td>
<td>–0.09</td>
<td>0.22</td>
</tr>
<tr>
<td></td>
<td>GMNP</td>
<td>0.43</td>
<td>0.24</td>
<td>0.64</td>
<td>–0.30</td>
<td>0.20</td>
</tr>
<tr>
<td></td>
<td>NMNP</td>
<td>0.44</td>
<td>0.26</td>
<td>0.64</td>
<td>–0.24</td>
<td>0.17</td>
</tr>
<tr>
<td>Incubation</td>
<td>GMEP</td>
<td>0.80</td>
<td>0.72</td>
<td>0.87</td>
<td>1.41</td>
<td>0.05</td>
</tr>
<tr>
<td></td>
<td>GINP</td>
<td>0.74</td>
<td>0.63</td>
<td>0.83</td>
<td>1.06</td>
<td>0.07</td>
</tr>
<tr>
<td></td>
<td>GMNP</td>
<td>0.70</td>
<td>0.61</td>
<td>0.78</td>
<td>0.84</td>
<td>0.04</td>
</tr>
<tr>
<td></td>
<td>NMNP</td>
<td>0.71</td>
<td>0.65</td>
<td>0.77</td>
<td>0.90</td>
<td>0.02</td>
</tr>
<tr>
<td>Nestling</td>
<td>GMEP</td>
<td>0.34</td>
<td>0.24</td>
<td>0.45</td>
<td>–0.68</td>
<td>0.06</td>
</tr>
<tr>
<td></td>
<td>GINP</td>
<td>0.26</td>
<td>0.17</td>
<td>0.38</td>
<td>–1.03</td>
<td>0.05</td>
</tr>
<tr>
<td></td>
<td>GMNP</td>
<td>0.22</td>
<td>0.16</td>
<td>0.31</td>
<td>–1.25</td>
<td>0.08</td>
</tr>
<tr>
<td></td>
<td>NMNP</td>
<td>0.23</td>
<td>0.18</td>
<td>0.29</td>
<td>–1.19</td>
<td>0.02</td>
</tr>
</tbody>
</table>

*Treatments: GMEP = grazed mixed exotic pasture; GINP = grazed Indian grass native pasture; GMNP = grazed mixed native pasture; NMNP = non-grazed mixed native pasture.
Table 2.3  Summary statistics of stage- and treatment-specific survival ($\phi$) and detection ($p$) probabilities estimated by the JS nest density model.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>State</th>
<th>Treatment$^a$</th>
<th>Mean</th>
<th>SD</th>
<th>Lower</th>
<th>Upper</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Lay to incubation</td>
<td>GMEP</td>
<td>0.06</td>
<td>0.10</td>
<td>0.00</td>
<td>0.34</td>
</tr>
<tr>
<td></td>
<td></td>
<td>GINP</td>
<td>0.13</td>
<td>0.20</td>
<td>0.00</td>
<td>0.77</td>
</tr>
<tr>
<td></td>
<td></td>
<td>GMNP</td>
<td>0.64</td>
<td>0.24</td>
<td>0.16</td>
<td>0.99</td>
</tr>
<tr>
<td></td>
<td></td>
<td>NMNP</td>
<td>0.05</td>
<td>0.08</td>
<td>0.00</td>
<td>0.29</td>
</tr>
<tr>
<td>$\phi$</td>
<td>Lay to nestling</td>
<td>GMEP</td>
<td>0.45</td>
<td>0.17</td>
<td>0.12</td>
<td>0.77</td>
</tr>
<tr>
<td></td>
<td></td>
<td>GINP</td>
<td>0.65</td>
<td>0.21</td>
<td>0.20</td>
<td>1.00</td>
</tr>
<tr>
<td></td>
<td></td>
<td>GMNP</td>
<td>0.66</td>
<td>0.19</td>
<td>0.26</td>
<td>0.99</td>
</tr>
<tr>
<td></td>
<td></td>
<td>NMNP</td>
<td>0.68</td>
<td>0.12</td>
<td>0.43</td>
<td>0.90</td>
</tr>
<tr>
<td></td>
<td>Incubation to nestling</td>
<td>GMEP</td>
<td>0.18</td>
<td>0.05</td>
<td>0.09</td>
<td>0.30</td>
</tr>
<tr>
<td></td>
<td></td>
<td>GINP</td>
<td>0.24</td>
<td>0.07</td>
<td>0.12</td>
<td>0.40</td>
</tr>
<tr>
<td></td>
<td></td>
<td>GMNP</td>
<td>0.20</td>
<td>0.06</td>
<td>0.10</td>
<td>0.32</td>
</tr>
<tr>
<td></td>
<td></td>
<td>NMNP</td>
<td>0.21</td>
<td>0.05</td>
<td>0.12</td>
<td>0.33</td>
</tr>
<tr>
<td></td>
<td>Lay</td>
<td>GMEP</td>
<td>0.58</td>
<td>0.09</td>
<td>0.39</td>
<td>0.76</td>
</tr>
<tr>
<td></td>
<td></td>
<td>GINP</td>
<td>0.39</td>
<td>0.10</td>
<td>0.20</td>
<td>0.61</td>
</tr>
<tr>
<td></td>
<td></td>
<td>GMNP</td>
<td>0.38</td>
<td>0.09</td>
<td>0.22</td>
<td>0.57</td>
</tr>
<tr>
<td></td>
<td></td>
<td>NMNP</td>
<td>0.33</td>
<td>0.07</td>
<td>0.20</td>
<td>0.49</td>
</tr>
<tr>
<td>$p$</td>
<td>Incubation</td>
<td>GMEP</td>
<td>0.79</td>
<td>0.04</td>
<td>0.72</td>
<td>0.86</td>
</tr>
<tr>
<td></td>
<td></td>
<td>GINP</td>
<td>0.72</td>
<td>0.05</td>
<td>0.61</td>
<td>0.82</td>
</tr>
<tr>
<td></td>
<td></td>
<td>GMNP</td>
<td>0.68</td>
<td>0.04</td>
<td>0.60</td>
<td>0.77</td>
</tr>
<tr>
<td></td>
<td></td>
<td>NMNP</td>
<td>0.71</td>
<td>0.03</td>
<td>0.65</td>
<td>0.77</td>
</tr>
<tr>
<td></td>
<td>Nestling</td>
<td>GMEP</td>
<td>0.33</td>
<td>0.05</td>
<td>0.24</td>
<td>0.45</td>
</tr>
<tr>
<td></td>
<td></td>
<td>GINP</td>
<td>0.27</td>
<td>0.05</td>
<td>0.18</td>
<td>0.38</td>
</tr>
<tr>
<td></td>
<td></td>
<td>GMNP</td>
<td>0.24</td>
<td>0.04</td>
<td>0.17</td>
<td>0.32</td>
</tr>
<tr>
<td></td>
<td></td>
<td>NMNP</td>
<td>0.26</td>
<td>0.03</td>
<td>0.20</td>
<td>0.32</td>
</tr>
</tbody>
</table>

$^a$Treatments: GMEP = grazed mixed exotic pasture; GINP = grazed Indian grass native pasture; GMNP = grazed mixed native pasture; NMNP = non-grazed mixed native pasture.
Table 2.4 Summary statistics for stage-specific mean and variance hyper-parameters for entry ($\gamma$) and survival ($\phi$) estimated by the multi-state JS model for Dickcissel nest density, on the probability scale.

<table>
<thead>
<tr>
<th>Hyper-parameter$^a$</th>
<th>Mean</th>
<th>SD</th>
<th>Lower</th>
<th>Upper</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\mu_{\gamma_1}$</td>
<td>0.005</td>
<td>0.002</td>
<td>0.002</td>
<td>0.008</td>
</tr>
<tr>
<td>$\sigma_{\gamma_1}$</td>
<td>0.851</td>
<td>0.369</td>
<td>0.318</td>
<td>1.751</td>
</tr>
<tr>
<td>$\mu_{\gamma_2}$</td>
<td>0.013</td>
<td>0.005</td>
<td>0.006</td>
<td>0.023</td>
</tr>
<tr>
<td>$\sigma_{\gamma_2}$</td>
<td>0.967</td>
<td>0.301</td>
<td>0.528</td>
<td>1.684</td>
</tr>
<tr>
<td>$\mu_{\gamma_3}$</td>
<td>0.001</td>
<td>0.001</td>
<td>0.000</td>
<td>0.002</td>
</tr>
<tr>
<td>$\sigma_{\gamma_3}$</td>
<td>1.917</td>
<td>3.099</td>
<td>0.239</td>
<td>10.184</td>
</tr>
<tr>
<td>$\mu_{\phi_1}$</td>
<td>0.310</td>
<td>0.242</td>
<td>0.014</td>
<td>0.888</td>
</tr>
<tr>
<td>$\sigma_{\phi_1}$</td>
<td>10.841</td>
<td>26.44</td>
<td>0.530</td>
<td>66.526</td>
</tr>
<tr>
<td>$\mu_{\phi_2}$</td>
<td>0.604</td>
<td>0.161</td>
<td>0.257</td>
<td>0.895</td>
</tr>
<tr>
<td>$\sigma_{\phi_2}$</td>
<td>1.265</td>
<td>1.391</td>
<td>0.245</td>
<td>4.588</td>
</tr>
<tr>
<td>$\mu_{\phi_3}$</td>
<td>0.218</td>
<td>0.068</td>
<td>0.117</td>
<td>0.375</td>
</tr>
<tr>
<td>$\sigma_{\phi_3}$</td>
<td>0.550</td>
<td>0.402</td>
<td>0.191</td>
<td>1.531</td>
</tr>
</tbody>
</table>

$^a$Subscripts denote: $\gamma_1$ = lay stage entry; $\gamma_2$ = incubation stage entry; $\gamma_3$ = nestling stage entry; $\phi_1$ = survival from lay to incubation stage; $\phi_2$ = survival from lay to nestling stage; $\phi_3$ = survival from incubation to nestling stage.
Figure 2.1  Relative number of active nests (●) and active nests estimated by the JS nest density model (▲; and 95% CrI) from bi-weekly searches for Dickcissel nests at the Mississippi State University Prairie Research Unit in Prairie, MS, USA.
Figure 2.2  Mean Dickcissel nest density (and 95% CrI) estimated by treatment from relative abundance (●), relative abundance with incidental nests (■), and the JS nest density model (▲).
Figure 2.3  Mean posterior transition probability estimates\textsuperscript{a} (survival) for analysis of simulated datasets from 4 scenarios using the multi-state Jolly-Seber model.

\textsuperscript{a}Transitions included lay to incubation stage ($\phi_1$), lay to nestling stage ($\phi_2$), and incubation to nestling stage ($\phi_3$).
Figure 2.4  Mean posterior nest abundance estimates from analysis of simulated datasets from 4 scenarios using the multi-state Jolly-Seber model, compared with known (true) abundance and observed (relative) abundance for each dataset.
CHAPTER III
TESTING HYPOTHESES ABOUT NEST SITE SELECTION AND BREEDING SUCCESS OF AN OBLIGATE GRASSLAND BIRD IN NATIVE AND EXOTIC GRAZING SYSTEMS

Introduction
Characterizing habitat quality by relating ecological processes and management to demographic measures such as survival and reproduction is essential for conservation (Johnson 2007). For example, predation is a major source of nest failure among grassland birds (Winter 1999, Walk et al. 2004, Rahmig et al. 2009, Klug et al. 2010), and nest site selection may relate to predation risk. According to the total-foliage hypothesis, nest survival should increase with greater vegetation density at nest sites due to concealment from predators (Martin 1993). Conversely, the potential-prey-site hypothesis suggests nest survival is a function of the number of potential nests sites in a given area and the efficiency of predators in locating nests (Chalfoun and Martin 2009). Additional hypotheses and mechanisms are proposed for relating avian nest site selection to demographic parameters (e.g., Chalfoun and Schmidt 2012), yet few studies specifically test these hypotheses in the context of management (Johnson 2007).

Identifying mechanisms for nest site selection and productivity in response to grassland management is important for avian conservation in the Southeastern United States. Exotic grasses such as tall fescue (Schedonorus arundinaceus) and bermudagrass
(Cynodon dactylon) benefited from widespread establishment as livestock forage, but their low vertical height and homogeneous structure is highly unsuitable for most wildlife (Barnes et al. 2013). Heavy and uniform grazing of contemporary livestock management can also reduce reproductive success of grassland obligate birds such as Dickcissels (Spiza americana; With et al. 2008, Rahmig et al. 2009). Native warm-season grasses (NWSG) are promoted as a sustainable alternative to exotic forages because of their lower input requirements and drought tolerance (Harper et al. 2007), but NWSG may also be valuable nesting habitat for grassland birds (Hughes et al. 1999, Giuliano and Daves 2002). Native forages are also not grazed as heavily as exotic grass pasture (Mousel et al. 2003, Chamberlain et al. 2012), and therefore may retain structural complexity for cover and nesting. In Chapter 2, I reported that Dickcissel (Spiza americana) nest density was least among exotic grass pastures, greatest in non-grazed NWSG, and intermediate (albeit not statistically different) in grazed NWSG. This nest distribution pattern may be adaptive, conferring advantages in individual fitness to Dickcissels nesting in NWSG over exotic pastures, and several hypotheses can be posited. For example, greater vegetation density at nest sites in NWSG could reduce predation risk (total-foliage hypothesis). Alternatively, a greater number of potential nest sites in NWSG could increase nest survival by reducing predator foraging efficiency (potential-prey-site hypothesis). Birds may also respond to plant composition through food availability (Rotenberry 1985), as reduced floristic richness and diversity in exotic grass pastures may result in lower avian prey abundance (Fulbright et al. 2013). Arthropods are the primary food source for breeding grassland birds, and their availability has important implications for incubating females, nestlings, and fledglings (Martin 1987). Therefore,
the *food limitation* hypothesis may account for additional differences in grassland bird
distribution and reproductive success between exotic and NWSG pastures.

I therefore evaluated alternative hypotheses relating to vegetation structure and
prey biomass for a breeding population of Dickcissels nesting in beef production systems
in northeastern Mississippi. Specifically, my objectives were to (1) test whether stand
type and management (treatment), vegetation density (*total foliage* hypothesis), and nest
site selection (*potential-prey-site* hypothesis) affected daily nest survival; and (2)
quantify the relationship between nestling body condition, arthropod prey biomass, and
treatment (*food limitation* hypothesis). Additionally, inferences based on individual
fitness may not correspond with population dynamics if reproductive success is
negatively correlated with nest density (Van Horne 1983, Johnson 2007), so I (3)
determined Dickcissel productivity (fledglings ha$^{-1}$) among treatments using estimates of
nest density, brood size, and survivorship.

**Methods**

**Study Area**

The study was conducted at Mississippi State University’s Prairie Research Unit
(PRU) in Monroe Co., Mississippi, USA (lat 33°47'N, long 88°38'W) during May–July,
2011–2012. The PRU is located in the Black Belt Prairie region, one of the southern
extensions of Great Plains grasslands known as the Blackland Prairies. Since the 19$^{th}$
century native prairies in the Black Belt were extensively reduced due to degradation and
conversion to agriculture (Barone 2005). Total growing season precipitation (April–
October) was 711 mm and 808 mm in 2011 and 2012, respectively, and both years mean
daily maximum temperature for July was 33.6°C.
Twelve experimental pastures (range = 6.4–10.5 ha) were assigned to one of four treatments replicated three times (Fig. 3.1), including a grazed mix of bermudagrass and tall fescue (hereafter, grazed mixed exotic pasture, or GMEP), and two grazed native grass treatments: an Indian grass monoculture (*Sorghastrum nutans*; hereafter grazed Indian grass native pasture, or GINP), and grazed mixed native pasture (GMNP) consisting of big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*), and Indian grass. I also studied a non-grazed NWSG treatment (hereafter, non-grazed mixed native pasture, or NMNP). During the 2007 growing season, exotic forages (primarily bermudagrass) were eradicated from paddocks to be planted to NWSG using 3.5 L ha$^{-1}$ Chopper® (imazapyr) and 9.4 L ha$^{-1}$ glyphosate. The following spring (2008), NWSG pastures were prescribed burned and treated with 1.6 L ha$^{-1}$ Journey® (imazapic + glyphosate) and 2.34 L ha$^{-1}$ glyphosate to control annual grasses and residual exotic forage grasses. After fire and herbicide treatment, GINP pastures were planted in May 2008 at 9.0 kg ha$^{-1}$ and GMNP pastures were planted at 13.5 kg ha$^{-1}$ using a no-till drill (Truax company, Inc., New Hope, MN). Exotic pastures received two applications of 75% sulfosulfuron for bermudagrass release. In spring 2011 and 2012, all NWSG treatments were prescribed burned prior to addition of cattle (*Bos taurus*). Grazed pastures were continuously stocked mid-May until September with fall-born steer calves (average initial body weight [BW]: 250 kg) at 2.7 steers ha$^{-1}$. In June 2012, 2,4-D herbicide was applied to all pastures to control broadleaf forb competition, and stocking rates were uniformly reduced in July 2012 due to prolonged drought in May and June.
Vegetation Sampling

I characterized vegetation structure and composition along four transects in each pasture (Fig. 3.1). I used ArcMAP 9.3 (ESRI, Redlands, CA) to establish four concentric buffers 50–100, 100–150, 150–200, and >200 m from each pasture's primary water source, or where water sources would likely have been placed in non-grazed pastures, because water sources could influence distribution of cattle and grazing (Bailey et al. 1996). Within each concentric buffer I randomly established one point > 25 m from the pasture edge and trees and >100 m from the next point to avoid transects overlapping edge and other transects. Transects centers in one pasture were spaced <100m apart due to the pasture’s size and the configuration of trees and edge. Each random point served as the transect center, which consisted of two 50-m lines overlaid perpendicularly North-South and East-West and intersecting at their midpoints (Fig. 3.1). From each transect I sampled vegetation from one point at the center and two points at 10- and 20-m from the center in each cardinal direction, totaling nine points per transect and 36 points per pasture. Transects were sampled twice each year: once in late May–early June (26 May–6 June), and again approximately one month later (24 June–7 July).

At each sampling point I characterized composition within a 0.25-m² frame using a method modified from Daubenmire (1959). I visually estimated percent coverage of live grass, live forb, live shrub, standing dead vegetation, litter, bare ground, tall fescue, and bermudagrass, and assigned each to a coverage class as follows: 0 = 0, 1 = <1%, 2 = 1–5%, 3 = 6–25%, 4 = 26–50%, 5 = 51–75%, 6 = 76–95%, or 7 = >95%. I then used midpoints of assigned cover classes as the measure of percent coverage. At the southwest corner of each frame I measured litter depth to the nearest 0.5 cm, considering litter to be...
any plant matter on the soil surface detached from the ground or another plant. I also took visual obstruction readings (VOR) in four cardinal directions using a Robel pole (Robel et al. 1970) positioned in the center of the frame. I averaged all 36 sampling points to characterize vegetation of the entire pasture during a given sampling event.

**Nest Searching and Monitoring**

Nest searching and monitoring protocol is described in detail in Monroe et al. (2014). I estimated nest age by candling eggs (Lokemoen and Koford 1996) or using voucher photos of nestling development. Nests were considered fledged when at least one nestling fledged and other signs of fledging were evident (Grant et al. 2005). I considered nests as depredated if found empty or their contents damaged before their potential fledge date, and considered nests abandoned when no adults were present during the visit yet nestlings were found recently dead or eggs previously incubated were found cold. Trampled nests exhibited evidence of destruction from cattle or farm equipment, and nests classified as “other” included nests failed due to weather, brood parasitism, or unknown.

I characterized nest-site vegetation after completion of each nesting attempt, standardized to 11–14 days after anticipated hatch date to avoid biasing measurements for nests that failed at an early nesting stage (M. McConnell, unpublished data). I estimated percent vegetation composition within a 0.25-m² frame at five points, including one at the nest and four in each cardinal direction, 0.5 m from the nest (Winter 1999). I also measured litter depth and VOR with a Robel pole placed adjacent and northeast of the nest cup. I classified nesting substrate (grass, forb, shrub, or ground) and used a 6.5 cm diameter ball placed in the nest cup to visually estimate overhead cover to the nearest 5%.
I used overhead cover as an index of nest exposure to solar radiation, which could affect nest microclimate (Nelson and Martin 1999). I repeated the five vegetation-sampling points (excepting overhead cover) at a random location 30 m from each nest (Walk et al. 2004), constrained within pastures. The minimum territory size for male Dickcissels is reported to be 0.36 ha (Zimmerman 1971), or the equivalent of a 34-m radius circle. Therefore, a random point at 30 m permits comparison with habitat available yet unused by each nesting female.

Finally, proximity of imported fire ant (Solenopsis spp.) mounds may increase probability of nest failure for Dickcissels (Conover et al. 2011b). Imported fire ant territories may encompass as much as 197 m² (Adams 2003), equivalent to a 7.9-m radius circle, so I measured foraging activity of fire ants within an 8-m radius around each nest. I captured imported fire ants in bait cups consisting of glass vials containing crushed Keebler Sandies Pecan Shortbread cookies (Kellogg Co., Battle Creek, MI; J. Hill, personal communication). I placed one bait cup under the nest and one in each cardinal direction, 8 m apart \( (n = 5 \text{ cups nest}^{-1}) \), and capped vials after 30 minutes (Hill et al. 2008). This sampling procedure was repeated at the paired random point. Vial contents were then frozen before determining mean number of ants collected per vial after 30 minutes as an index of imported fire ant abundance around each nest or random point.

**Measuring Nestling Condition**

Nestling body mass may increase with prey availability (Naef-Daenzer and Keller 1999, Brickle et al. 2000; but see Streby et al. 2014a), and there is evidence for a positive relationship between weight and fledgling survival among Dickcissels (Suedkamp Wells et al. 2007, Conover 2009; but see Berkeley et al. 2007). To examine the relationship
between treatment and nestling condition, I measured nestling mass to the nearest 0.25 g with a spring scale and length of the right tarsus to the nearest 0.1 mm with digital calipers when nestlings were age day 5–6 to avoid force-fledging (Berkeley et al. 2007, Monroe et al. 2014). During 2011, I selected every other nest that reached weighing age to compare fledging rates between nests with weighed and non-weighed nestlings. I subsequently determined that measuring nestling condition did not have a major effect on nest success (Monroe et al. 2014), so in 2012 I measured nestlings from all nests that reached weighing age. The Mississippi State University Institutional Animal Care and Use Committee approved these methods (permit #11-020).

**Arthropod Sampling**

I sampled arthropods using a vacuum device (Harper and Guynn 1998) because this method is effective for sampling epigeal invertebrates and invertebrates that cling to vegetation (Standen 2000, Maidens and Carroll 2002). Within 1–2 days after pasture vegetation measurements I sampled transects with a modified leaf blower (Meyer et al. 2002), walking along each transect at a steady pace with the nozzle of the leafblower ~10 cm above ground, high enough to avoid congesting the nozzle with vegetation. I sampled transects between 1000 and 1500 (CST) when vegetation was dry and wind speeds ≤ 20 km h⁻¹. Samples were oven-dried at 60°C for 48 h and weighed (± 0.0001 g; dry weight) to quantify biomass. I restricted analysis to Orthoptera (grasshoppers and crickets) because they account for >90% of prey items delivered to nestling Dickcissels (Mitchell et al. 2012). I averaged samples of Orthoptera from both surveys by pasture and year as an index of prey availability.
Statistical Analysis

Nest and Pasture Vegetation

I used descriptive statistics (mean ± SE) to report pasture-level vegetation measurements for each survey pooled among sampling transects. I also used Constrained Analysis of Principal Coordinates (CAP; Anderson and Willis 2003) with function `capscale` from the package `vegan` (Oksanen et al. 2013) in R (version 3.0.2, R Development Core Team 2014) to discriminate between nest sites and paired random points within treatments. This method begins with an unconstrained ordination by classical (metric) multidimensional scaling (MDS) followed by canonical discriminant analysis (CDA) based on groupings hypothesized *a priori* for sites, thus orienting axes to maximize differences among groups rather than sites. This approach is advantageous because it may reveal patterns that are otherwise lost with unconstrained methods (Anderson and Willis 2003). Variables included VOR, litter depth, and percent coverage of live grass, bermudagrass, tall fescue, live forbs, shrubs, litter, and bare ground, and mean imported fire ant abundance. I square root transformed and standardized variables and used Bray-Curtis dissimilarity for ordination (Bray and Curtis 1957). I modeled constraints for treatment × sample type (nest or random point) and assessed significance by permutation of the full model over 10,000 iterations stratified by pasture. I then evaluated distribution of groups in ordinal space with 95% confidence intervals of dispersion ellipses based on a weighted average of site scores. Finally, I tested whether proportional use of nesting substrates differed by treatment with a chi-square test of independence, using Monte-Carlo resampling to estimate the null distribution with the
*coin* package in program R (Hothorn et al. 2013). Substrates included grass, forb, shrub, and ground, and I tested years separately.

**Nest Survival and Productivity**

I used nest survival models to evaluate *total-foliage* and *potential-prey-site* hypotheses, predicting support for the *total-foliage* hypothesis if VOR measured at nest sites (VOR<sub>n</sub>) had a positive effect on daily survival rates (DSR). Previous tests of the *potential-prey-site* hypothesis involved species that selected nest sites with specific structural attributes, such as shrubs of a certain range in size and dimensions, permitting researchers to effectively estimate the number of available but unused nest sites (Martin 1993, Chalfoun and Martin 2009). However, Dickcissels build nests in a variety of substrates, including grasses, forbs, and shrubs (Temple 2002), so determining the absolute number of potential nest sites in my study was not feasible. Instead, I characterized available nesting habitat along a gradient of suitability based on similarity to used nest sites. I used ordination (without constraints) from non-metric multidimensional scaling (NMDS; Faith et al. 1987, Minchin 1987) with the R package *vegan* to collapse a set of vegetation variables from nest sites and paired random points that previously characterized Dickcissel nest sites and survival (Table 3.1) into several uncorrelated components, one for each ordination axis. Variables were again transformed by square root and Wisconsin double standardization, and ordination was based on Bray-Curtis dissimilarity. I used a Shepard diagram to evaluate goodness of fit, determining that three axes were adequate for ordination (stress = 0.1191). I then computed the absolute difference between site scores of nest sites and paired random points (|ΔNMDS|), yielding an index of similarity for each nest, with values at 0 indicating
perfect similarity to random points, and increasing dissimilarity as $|\Delta \text{NMDS}| > 0$. I predicted support for the potential-prey-site hypothesis if there was a negative relationship between $|\Delta \text{NMDS}|$ and DSR.

I used a Bayesian approach to model DSR (Royle and Dorazio 2008), which estimates survival of nest $i$ at time $t$ as the outcome of independent Bernoulli trials with probability $\phi_{i,t}$, given the nest was active at $t - 1$. I used a logit link to model covariates affecting $\phi_{i,t}$, and I created seven a priori models, including a model for treatment effects (1), a total-foliage model with VOR$_n$ (2), a potential-prey-site model with $|\Delta \text{NMDS}|$ (3), and a model with mean imported fire ant (IFA) abundance at nest sites (4). Vegetation could also function to mediate nest microclimate (With and Webb 1993, Nelson and Martin 1999, Lusk et al. 2003), so I created a model (5) with overhead cover (Covr), daily maximum temperature (Temp) collected from a nearby weather monitoring station (NCDC 2014), and Covr $\times$ Temp interaction. Temperature and date were not highly correlated ($r = 0.47$ and 0.51 for 2011 and 2012, respectively). Vegetation density at the broader pasture scale could also influence nest survival through effects on predator foraging (Mullin et al. 1998), so I modeled DSR with an index (VOR$_p$) from mean pasture VOR measurements for each year (6). Finally I created a null (intercept-only) model (7). I standardized all continuous nest site variables prior to analysis, and I tested for multicollinearity among covariates using variance inflation factors (VIF; Zuur et al. 2009). All VIFs were <1.4, permitting inclusion of the full set of covariates in each model. In all models except the null I included linear and quadratic covariates for nest age and date, and effect of year because these previously accounted for variation in daily survival rates among passerine nests (Grant et al. 2005, Churchwell et al. 2008, Conover
et al. 2011a, 2011b). Additionally, multiple nests were located within each pasture and their survival rates could be correlated due to proximity, so I included a random effect for \( j \) pastures \((\varepsilon_j \sim N[0, \sigma^2])\).

I estimated parameters from the joint posterior distribution of each model by sampling from three Markov chains for 75,000 iterations after burning the first 2,000 and thinning by 5. I assessed convergence by visually examining the chains and with the \( R \) statistic, which compares within- and between-chain variation (Gelman et al. 2014). I used standard vague priors for all parameters, including \( \beta \sim N(0,1000) \) for fixed effects and \( \sigma \sim \text{Unif}(0,20) \) for the random effect standard deviation. I assessed goodness of fit from a Bayesian \( p \)-value, which is a discrepancy measure that compares observed and expected values of nest survival based on the model (Schmidt et al. 2010). I used 95% credible intervals (CrI) to evaluate parameter estimates, and ranked models by Deviance Information Criterion (DIC), which is analogous to Akaike’s Information Criterion (AIC) for maximum likelihood models (Spiegelhalter et al. 2002).

Inferences based solely on survival may be inadequate due to potential correlations with density (Van Horne 1983). I therefore used treatment-specific nest density estimates from Chapter 2 and estimates of nest survivorship and brood size from the nesting study to compute mean no. fledglings ha\(^{-1}\), or productivity. Mean brood size for each treatment was estimated from no. nestlings present in nests on the last visit before fledging (With et al. 2008). Within the treatment nest survival model I exponentiated DSR over a 21-day nesting cycle (Temple 2002) to calculate survivorship for each treatment type, incorporating effects of age and year. Then during each iteration I calculated productivity for each treatment and year as the product of brood size,
survivorship, and nest density. Estimates of brood size and nest density were sampled from a normal distribution with treatment-specific mean and variance.

**Food Limitation Hypothesis**

To test if nestling condition responded to treatment and prey biomass measured from each pasture, I first regressed nestling mass against tarsus length with the package `nlme` in R (Pinheiro et al. 2014) to control for differences in size due to age. Given the nested structure of nestling measurements, I used likelihood ratio tests to compare models with fixed effects only, with a random effect for nest, or with a random effect of nest within pasture. I then used the residuals of the best-supported model to quantify nestling condition (Ardia 2005). I tested response of nestling condition to treatment and to prey biomass measured from each pasture, additionally including fixed effects of year, clutch size, and treatment × clutch or biomass × clutch interactions. I again used likelihood ratio tests to determine whether nest or nest within pasture random effects were supported. I compared the final models to a null (intercept-only) model, and I considered statistical significance at $\alpha = 0.05$.

**Results**

**Pasture Vegetation**

Among grazed treatments, mean VOR was similar among months and years, whereas VOR was 2–3 times greater in NMNP than grazed treatments and increased within years (Fig. 3.2a). Percent coverage of bermudagrass remained constant in GMEP and NMNP treatments (Fig. 3.2c), but approximately doubled between years in both grazed native treatments (GINP and GMNP). Pastures from the GMEP treatment were
characterized by greater coverage of tall fescue (Fig. 3.2d) and tended to have greater and more variable shrub coverage, though in general shrubs were a small (<5%) component of plant coverage (Fig. 3.2f). Within years, live grass increased or remained constant in all treatments from June to July (Fig. 3.2b). Forb coverage was also similar among treatments, except was highest in June 2012 for NMNP (Fig. 3.2e). Bare ground coverage was highest among native grass treatments in June 2011, and then remained lower for the duration of the study (Fig. 3.2h). Litter coverage (Fig. 3.2g) tended to be higher and similar among grazed native pastures than GMEP or NMNP.

**Nest Site Vegetation**

I monitored 85 nests in 2011 and 123 nests in 2012. Permutation indicated constraints of treatment × type on ordination of nest and random points were significant (Pseudo-$F = 12.40$, $P < 0.001$), and the cumulative proportion of constrained eigenvalues explained by the first two axes was 0.933. Factor loadings indicated that axis 1 represented greater VOR, live grass, and bare ground coverage, and less coverage of tall fescue and shrubs (Table 3.2). Axis 2 represented greater VOR and shrub coverage and less coverage of bare ground, litter, and bermudagrass. For each treatment there was broad overlap between nest and random points in ordinal space (Fig. 3.3), though dispersion ellipses showed slightly less overlap along axis 2, with nest points higher along axis 2 (greater VOR and shrub cover) and random points lower (greater bermudagrass and litter). Dispersion ellipses indicated clustering by treatment, with GMEP distinguished primarily by greater coverage of tall fescue, bermudagrass, and shrubs (Table 3.2). Nests from both grazed native treatments (GINP and GMNP) were virtually indistinguishable and lower along axis 2 (greater litter, bermudagrass, bare
ground coverage), whereas NMNP sites tended to be higher along axis 2 (greater VOR). Use of nesting substrates differed by treatment in 2011 ($\chi^2_{9} = 27.13, P < 0.001$) and in 2012 ($\chi^2_{9} = 53.64, P < 0.001$) with GMEP nests built more frequently in shrubs, whereas Dickcissels relied on grass and forb substrates in native grass treatments (Fig. 3.4).

**Nest Survival**

Over two years and among all nests ($n = 208$), apparent fledging rate was 24% ($n = 49$). Causes of failure for unsuccessful nest attempts included 81% from predation ($n = 128$), 11% from abandonment ($n = 17$), 3% from trampling ($n = 5$), and 6% from other ($n = 9$). Four nests were trampled in grazed pastures, and one was crushed by farm equipment in a non-grazed pasture. Thirteen nests (6%) were found with IFA, though I was unable to determine whether ants were the direct source of nest failure. Among all nests, seventeen nests (8%) were parasitized by brown-headed cowbirds (*Molothrus ater*). Mean clutch size and number of fledglings produced per successful nest were similar among treatments (Table 3.3).

Bayesian $p$-values suggested all nest survival models adequately fit the data (range: 0.43–0.48), when $p < 0.05$ or $> 0.95$ typically indicate poor fit (Gelman et al. 2014). All covariate models were better supported than the null model (Table 3.4). The top-ranked model included a negative effect of temperature ($\beta = -0.33, 95\% \text{ CrI} = -0.59, -0.08$) and a positive effect of overhead cover ($\beta = 0.17, 95\% \text{ CrI} = 0.00, 0.35$), though a $\text{Temp} \times \text{Covr}$ interaction was not supported ($\beta = -0.02, 95\% \text{ CrI} = -0.24, 0.19$). The $\text{VOR}_p$ model ranked next, followed by the IFA model and the potential-prey-site model. Survival rates increased with $\text{VOR}_p$, albeit with uncertainty from overlapping credible
intervals ($\beta = 0.22$, $95\% \text{ CrI} = -0.04, 0.46$), whereas effect of IFA was near 0 ($\beta = -0.04$, $95\% \text{ CrI} = -0.22, 0.15$), and credible intervals for $|\Delta \text{NMDS}|$ (potential-prey-site) from each axis also broadly overlapped 0. Models for total-foliage and treatment received still less support. Estimates of DSR were lowest among nests in GMEP (0.91, $95\% \text{ CrI}: 0.85, 0.95$) and highest for NMNP (0.95, $95\% \text{ CrI}: 0.92, 0.97$), though credible intervals overlapped. Posterior DSR estimates for GiNP (0.92, $95\% \text{ CrI}: 0.85, 0.96$) and GMNP (0.93, $95\% \text{ CrI}: 0.88, 0.96$) were intermediate and similar. Effect of VOR$n$ (total-foliage) was not substantiated ($\beta = 0.05$, $95\% \text{ CrI} = -0.16, 0.26$).

Models 1–6 each indicated a negative effect of age (Table 3.5). Mean estimates of year effect were also negative, though credible intervals overlapped zero in all but one model. Credible intervals for all other covariates broadly overlapped zero. Over a 21-d nesting period, while accounting for effects of age and year, the treatment model predicted 0.33 ($95\% \text{ CrI} = 0.14, 0.56$) and 0.22 ($0.08, 0.43$) probabilities of survival for NMNP nests in 2011 and 2012, respectively, whereas survivorship for GMEP nests were correspondingly 0.14 (0.03, 0.32) and 0.07 (0.01, 0.21). Nest survivorship was intermediate and similar for grazed native grass treatments, with estimates of 0.23 (0.07, 0.44) and 0.14 (0.03, 0.32) for GMNP in 2011 and 2012, and 0.18 (0.03, 0.40) and 0.10 (0.01, 0.29) for GiNP. Productivity was least for GMEP with estimates of <1 fledgling ha$^{-1}$, whereas productivity was greatest for NMNP, with credible intervals encompassing >3 fledglings ha$^{-1}$ in 2012 (Fig. 3.5). Productivity estimates among grazed native treatments were intermediate but GiNP tended to be lower than GMNP, particularly in 2012.

46
Nestling Condition

Excluding three nests parasitized by brown-headed cowbirds, I measured condition of 179 nestlings from 18 nests in 2011 and 30 nests in 2012. Regressing nestling mass against tarsus length, likelihood ratio tests suggested support for a random effect of nest over the model with only fixed effects ($L = 20.61, df = 1, P < 0.001$), but random effects of nest within pasture did not improve fit ($L = 0.00, df = 1, P > 0.99$). Nestling condition models with random effects did not approximate the data better than models without random effects, so I restricted inferences to the latter group of models. No covariates in the treatment model were significant, and this model was not better supported than a null (intercept only) model ($L = 10.81, df = 8, P = 0.21$). Conversely, the prey biomass model approximated the data better than the null ($L = 11.38, df = 4, P = 0.023$). This model estimated a negative effect of clutch size ($\beta = -1.238, SE = 0.514, P = 0.017$) and prey biomass ($\beta = -6.679, SE = 3.014, P = 0.028$), but there was also a significant positive biomass × clutch interaction ($\beta = 1.625, SE = 0.769, P = 0.036$). Effect of year was not significant. These models suggest that nestling condition responded to variation in prey availability at the pasture scale but not among treatments. Furthermore, at low levels of Orthoptera biomass, condition was greater for nestlings in small clutches than large clutches, but as Orthoptera biomass increased, differences in condition among clutch sizes decreased.

Discussion

This study indicated a positive effect of native grasses on Dickcissel productivity relative to exotic pastures, but this relationship may be countered by a reduction in vegetation density from grazing. However, neither nest site hypothesis was supported in
explaining this pattern. Support for the total-foliage hypothesis was weak because I did not detect a positive effect of \( \text{VOR}_n \) on DSR, despite ordination suggesting that females tended to select nest sites with greater VOR than random in all treatments, and that \( \text{VOR}_n \) was greater for nests in NMNP than grazed treatments. I similarly did not find support for the potential-prey-site hypothesis because increasing similarity of nest sites to random points did not increase DSR, and nest sites generally overlapped random points in ordinal space irrespective of treatment. My results are similar to another study that found higher Dickcissel densities in restored native grass than exotic sites, yet nest survival rates were statistically similar among treatments (Lituma et al. 2012). However, my estimated treatment effects (albeit with uncertainty from overlapping credible intervals) may also suggest the influence of vegetation at the broader pasture scale, supported by a positive effect of pasture-level VOR on DSR. For example, snakes may be an important predator in this system, and dense vegetation in NMNP could hinder foraging movements for snakes more than in other treatments with less VOR (Mullin et al. 1998). Treatment trends also agree with previous studies of Dickcissels, where recent fire and grazing reduced Dickcissel nest success in the Flint Hills of Oklahoma and Kansas (Churchwell et al. 2008, Rahmig et al. 2009), and apparent nest densities were lower in grazed than fallow and non-grazed prairie (Zimmerman 1982, Churchwell et al. 2008, Rahmig et al. 2009).

The food limitation hypothesis was also not well supported, as I did not find a significant relationship between nestling condition and treatment, though there was evidence for effect of pasture-level prey biomass on nestling condition varying with clutch size. Prey abundance in grasslands is typically associated with forb coverage
(Fulbright et al. 2013), but both forb coverage and grasshopper biomass (Chapter 4) tended to be similar among treatments in this study. Forb abundance and diversity may increase with grazing (Hickman et al. 2004), but a lack of response of forbs to treatment in my study may result from (1) the recent establishment of native treatments (following herbicide pre-treatment), (2) the relatively short duration of this study (two years), and (3) herbicide applications in 2012 that reduced forb coverage across all treatments, and hence perhaps Orthoptera abundance.

An alternative mechanism (which I did not test directly) for nest site vegetation affecting DSR is the *thermal-refuge* hypothesis, when adults select nest locations based on their potential to mediate nest microclimate (With and Webb 1993, Nelson and Martin 1999, Lusk et al. 2003). A negative effect of daily maximum temperature on DSR suggests summer heat may have contributed to nest failure. However, although I did not measure nest microclimate with temperature sensors at the nest site, effect of daily maximum temperature did not vary with overhead cover and therefore may be unrelated to shading. For example, high temperatures may correspond with increased nest predation rates, particularly by snakes (Cox et al. 2013). Other factors influencing DSR included a strong negative effect of age, indicating higher failure rates at the nestling stage than for other stages. Effect of age is consistent with another study of Dickcissels (Churchwell et al. 2008) and may be related to predators using cues from activity of attending females (Skutch 1949, Martin et al. 2000, Stake et al. 2005). Unlike previous studies (Allen et al. 2004, Conover et al. 2011b), I did not find support for increased nest failure due to IFA activity. Of the colonies tested in my study sites (Chapter 4), all were either *S. richteri* or *S. richteri × invicta* hybrids, and none showed evidence of the *S. invicta* polygyne
breeding system that exhibits higher mound densities and greater activity (Porter et al. 1991) than their monogyne congeners. Species composition and breeding system of IFA at my study sites may therefore account for fewer predation events than reported in previous studies.

Given the higher nest densities estimated in NMNP (Chapter 2) yet similar DSR among treatments, it is possible that other unmeasured factors may account for this pattern (Chalfoun and Schmidt 2012). Differences in detectability could also bias nest density estimates and confound any meaningful relationships. However, I used a Jolly-Seber capture-recapture model to estimate nests while accounting for variability in survival and detectability (Chapter 2), so detection bias was unlikely to be a factor in this study. Additionally, nesting in this study may have followed ideal free distribution (Fretwell and Lucas 1969, Fretwell 1972), where occupation of suitable nesting sites in preferred habitat increases until nest density decreases survival, whereby occupation of less suitable nest sites becomes an equivalent strategy. Such a pattern was previously noted for Dickcissels in old-field and grassland habitat (Zimmerman 1982). Differences in nest site suitability may be reflected in Dickcissels using shrubs in GMEP more frequently than grass or forbs compared with native treatments (Fig. 3.4). Shrubs were a relatively small component of all treatments, so it is likely that the sod-forming structure of exotic grasses limited nest site suitability for Dickcissels in this study. In contrast, bunchgrasses were readily used for nest sites in native pastures, even in grazed treatments. Finally, lack of relationship between nest density and DSR may be due to females selecting nest sites that maximize survival of fledglings (Streby et al. 2014b), and
higher fledgling survival was reported for Dickcissels in tall and dense vegetation (Berkeley et al. 2007).

**Implications for NWSG Conversion in Grazing Systems**

My results suggest native forages have the potential to provide nesting habitat for declining tall grass specialists in the Southeast and make meaningful contributions to avian productivity on private lands. Dickcissel productivity was not increased by an adaptive advantage from nesting in NWSG, as I hypothesized, but instead through a greater carrying capacity for nesting Dickcissels. However, grazing may have a disproportionate effect on availability of nest sites in NWSG for this species. If reduced stocking rates or resting is recommended for managing and maintaining native warm-season grass pastures (Mousel et al. 2003, Chamberlain et al. 2012), my study indicates that employing such regimes on native grass pastures may increase availability of nesting habitat relative to exotic grass pastures in this region. One important caveat is that I did not consider other members of the avian grassland community such as Grasshopper sparrows (*Ammodramus savannarum*) that may respond positively to low structure in exotic cool-season grass fields (McCoy et al. 1999, McCoy et al. 2001). Incorporating NWSG into current exotic forage operations to foster a mosaic of tall and short structure may be beneficial for the full complement of avian biodiversity in this region (Giuliano and Daves 2002).
Table 3.1  Vegetation parameters measured at nest sites used for pair-wise combinations in nest survival models based on results from previous studies of nesting Dickcissels (Spiza americana).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Citation</th>
</tr>
</thead>
<tbody>
<tr>
<td>VOR, vegetation density</td>
<td>Harmeson 1974; Patterson and Best 1996; Winter 1999;</td>
</tr>
<tr>
<td></td>
<td>Conover 2011b</td>
</tr>
<tr>
<td>% Shrub cover</td>
<td>Klug et al. 2010</td>
</tr>
<tr>
<td>% Dead vegetation cover</td>
<td>Harmeson 1974; Hughes et al. 1999</td>
</tr>
<tr>
<td>% Forb cover</td>
<td>Harmeson 1974; Patterson and Best 1996; Winter 1999</td>
</tr>
<tr>
<td>% Grass cover</td>
<td>Winter 1999; Conover et al. 2011a, 2011b</td>
</tr>
<tr>
<td>% Litter cover</td>
<td>Hughes et al. 1999; Winter 1999</td>
</tr>
</tbody>
</table>
### Table 3.2
Mean (SE) nest site vegetation estimates by treatment\(^a\), and their factor loadings, for the first two dimensions of Canonical Analysis of Principal Coordinates (CAP) ordination for Dickcissel nests and paired random points at the Mississippi State University Prairie Research Unit in Monroe Co., MS, USA, 2011–2012.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>GMEP (n = 43)</th>
<th>GINP (n = 27)</th>
<th>GMNP (n = 42)</th>
<th>NMNP (n = 96)</th>
<th>Factor loadings</th>
</tr>
</thead>
<tbody>
<tr>
<td>VOR (cm)</td>
<td>20.5 (1.3)</td>
<td>20.1 (1.5)</td>
<td>18.7 (1.3)</td>
<td>37.4 (1.6)</td>
<td>1.30 1.63</td>
</tr>
<tr>
<td>Litter depth (cm)</td>
<td>0.4 (0.06)</td>
<td>0.3 (0.06)</td>
<td>0.3 (0.04)</td>
<td>0.2 (0.03)</td>
<td>-0.41 -0.46</td>
</tr>
<tr>
<td>Grasses (%)</td>
<td>54.6 (3.2)</td>
<td>55.6 (3.9)</td>
<td>57.5 (2.7)</td>
<td>57.5 (2.4)</td>
<td>1.03 0.15</td>
</tr>
<tr>
<td>Forbs (%)</td>
<td>21.0 (3.4)</td>
<td>22.9 (4.2)</td>
<td>17.9 (2.0)</td>
<td>19.9 (2.1)</td>
<td>0.22 -0.04</td>
</tr>
<tr>
<td>Shrubs (%)</td>
<td>7.6 (2.1)</td>
<td>0.4 (0.3)</td>
<td>0.5 (0.3)</td>
<td>4.4 (1.2)</td>
<td>-0.48 0.55</td>
</tr>
<tr>
<td>Litter (%)</td>
<td>4.4 (0.6)</td>
<td>6.7 (1.3)</td>
<td>8.9 (0.9)</td>
<td>5.7 (0.8)</td>
<td>0.34 -1.00</td>
</tr>
<tr>
<td>Bare ground (%)</td>
<td>5.3 (0.8)</td>
<td>17.5 (2.4)</td>
<td>18.2 (1.6)</td>
<td>13.9 (1.0)</td>
<td>1.76 -0.70</td>
</tr>
<tr>
<td>Bermudagrass (%)</td>
<td>10.7 (1.7)</td>
<td>18.1 (3.3)</td>
<td>14.8 (3.5)</td>
<td>8.2 (1.1)</td>
<td>-0.28 -0.85</td>
</tr>
<tr>
<td>Tall fescue (%)</td>
<td>39.3 (3.5)</td>
<td>0.0 (0.0)</td>
<td>0.0 (0.0)</td>
<td>0.92 (0.7)</td>
<td>-3.50 0.32</td>
</tr>
<tr>
<td>IFA abundance (ants vial(^{−1}))</td>
<td>32.5 (5.8)</td>
<td>20.7 (4.8)</td>
<td>19.6 (4.8)</td>
<td>20.7 (2.1)</td>
<td>0.03 0.40</td>
</tr>
</tbody>
</table>

\(^a\)Treatments: GMEP = grazed mixed exotic pasture; GINP = grazed Indian grass native pasture; GMNP = grazed mixed native pasture; NMNP = non-grazed mixed native pasture.
Table 3.3  Mean (SE) number of Dickcissel eggs per nest and number of fledglings per successful nest by treatment\textsuperscript{a}.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>GMEP Mean (SE)</th>
<th>GINP Mean (SE)</th>
<th>GMNP Mean (SE)</th>
<th>NMNP Mean (SE)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eggs nest\textsuperscript{−1}</td>
<td>4.35 (0.14)</td>
<td>4.56 (0.16)</td>
<td>4.5 (0.12)</td>
<td>4.22 (0.08)</td>
</tr>
<tr>
<td>Fledglings nest\textsuperscript{−1}</td>
<td>3.00 (0.97)</td>
<td>3.00 (0.55)</td>
<td>3.22 (0.28)</td>
<td>3.17 (0.27)</td>
</tr>
</tbody>
</table>

\textsuperscript{a}Treatments: GMEP = grazed mixed exotic pasture; GINP = grazed Indian grass native pasture; GMNP = grazed mixed native pasture; NMNP = non-grazed mixed native pasture.

Table 3.4  A priori candidate set of nest survival models for Dickcissels ranked by Deviance Information Criterion (DIC).

<table>
<thead>
<tr>
<th>Model\textsuperscript{a}</th>
<th>ΔDIC\textsuperscript{b}</th>
<th>pD\textsuperscript{c}</th>
<th>K\textsuperscript{d}</th>
</tr>
</thead>
<tbody>
<tr>
<td>Temp × Covr + Age + Age\textsuperscript{2} + Date + Date\textsuperscript{2} + Year</td>
<td>0.0</td>
<td>409.4</td>
<td>9</td>
</tr>
<tr>
<td>VOR\textsubscript{p} + Age + Age\textsuperscript{2} + Date + Date\textsuperscript{2} + Year</td>
<td>6.9</td>
<td>407.8</td>
<td>7</td>
</tr>
<tr>
<td></td>
<td>ΔNMDS\textsubscript{1}</td>
<td>+</td>
<td>ΔNMDS\textsubscript{2}</td>
</tr>
<tr>
<td>IFA + Age + Age\textsuperscript{2} + Date + Date\textsuperscript{2} + Year</td>
<td>9.4</td>
<td>410.0</td>
<td>7</td>
</tr>
<tr>
<td>VOR\textsubscript{a} + Age + Age\textsuperscript{2} + Date + Date\textsuperscript{2} + Year</td>
<td>11.4</td>
<td>411.6</td>
<td>7</td>
</tr>
<tr>
<td>Treatment + Age + Age\textsuperscript{2} + Date + Date\textsuperscript{2} + Year</td>
<td>11.4</td>
<td>412.5</td>
<td>9</td>
</tr>
<tr>
<td>Null (intercept-only)</td>
<td>17.0</td>
<td>411.2</td>
<td>1</td>
</tr>
</tbody>
</table>

\textsuperscript{a}All models included a random effect for pasture.
\textsuperscript{b}Distance from the top model (min. DIC = 944.8).
\textsuperscript{c}Effective number of parameters.
\textsuperscript{d}No. fixed effects.
Table 3.5  Mean, standard deviation, and 95% credible intervals (CrI) of parameter estimates for six models for Dickcissel nest survival.

<table>
<thead>
<tr>
<th>Covariate</th>
<th>Mean</th>
<th>SD</th>
<th>Lower</th>
<th>Upper</th>
<th>Mean</th>
<th>SD</th>
<th>Lower</th>
<th>Upper</th>
<th>Mean</th>
<th>SD</th>
<th>Lower</th>
<th>Upper</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Age</td>
<td>-0.34</td>
<td>0.10</td>
<td>-0.54</td>
<td>-0.14</td>
<td>-0.32</td>
<td>0.10</td>
<td>-0.52</td>
<td>-0.13</td>
<td>-0.32</td>
<td>0.10</td>
<td>-0.52</td>
<td>-0.13</td>
</tr>
<tr>
<td>Age²</td>
<td>-0.07</td>
<td>0.10</td>
<td>-0.26</td>
<td>0.13</td>
<td>-0.06</td>
<td>0.09</td>
<td>-0.23</td>
<td>0.12</td>
<td>-0.06</td>
<td>0.09</td>
<td>-0.24</td>
<td>0.12</td>
</tr>
<tr>
<td>Day</td>
<td>-0.09</td>
<td>0.12</td>
<td>-0.32</td>
<td>0.15</td>
<td>-0.04</td>
<td>0.12</td>
<td>-0.27</td>
<td>0.20</td>
<td>-0.04</td>
<td>0.12</td>
<td>-0.28</td>
<td>0.20</td>
</tr>
<tr>
<td>Day²</td>
<td>-0.06</td>
<td>0.13</td>
<td>-0.30</td>
<td>0.19</td>
<td>-0.04</td>
<td>0.12</td>
<td>-0.29</td>
<td>0.20</td>
<td>-0.05</td>
<td>0.13</td>
<td>-0.30</td>
<td>0.20</td>
</tr>
<tr>
<td>Year</td>
<td>-0.33</td>
<td>0.19</td>
<td>-0.70</td>
<td>0.03</td>
<td>-0.26</td>
<td>0.19</td>
<td>-0.64</td>
<td>0.11</td>
<td>-0.28</td>
<td>0.19</td>
<td>-0.64</td>
<td>0.09</td>
</tr>
<tr>
<td>σ²</td>
<td>0.10</td>
<td>0.21</td>
<td>0.00</td>
<td>0.57</td>
<td>0.08</td>
<td>0.12</td>
<td>0.00</td>
<td>0.37</td>
<td>0.10</td>
<td>0.13</td>
<td>0.00</td>
<td>0.43</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Age</td>
<td>-0.33</td>
<td>0.10</td>
<td>-0.53</td>
<td>-0.13</td>
<td>-0.30</td>
<td>0.10</td>
<td>-0.51</td>
<td>-0.11</td>
<td>-0.32</td>
<td>0.10</td>
<td>-0.52</td>
<td>-0.13</td>
</tr>
<tr>
<td>Age²</td>
<td>-0.07</td>
<td>0.09</td>
<td>-0.24</td>
<td>0.12</td>
<td>-0.08</td>
<td>0.09</td>
<td>-0.25</td>
<td>0.11</td>
<td>-0.06</td>
<td>0.09</td>
<td>-0.24</td>
<td>0.12</td>
</tr>
<tr>
<td>Day</td>
<td>-0.01</td>
<td>0.12</td>
<td>-0.26</td>
<td>0.23</td>
<td>0.10</td>
<td>0.13</td>
<td>-0.15</td>
<td>0.36</td>
<td>-0.08</td>
<td>0.12</td>
<td>-0.31</td>
<td>0.16</td>
</tr>
<tr>
<td>Day²</td>
<td>-0.06</td>
<td>0.12</td>
<td>-0.29</td>
<td>0.19</td>
<td>-0.13</td>
<td>0.13</td>
<td>-0.38</td>
<td>0.13</td>
<td>-0.05</td>
<td>0.12</td>
<td>-0.29</td>
<td>0.19</td>
</tr>
<tr>
<td>Year</td>
<td>-0.26</td>
<td>0.19</td>
<td>-0.64</td>
<td>0.11</td>
<td>-0.27</td>
<td>0.18</td>
<td>-0.64</td>
<td>0.08</td>
<td>-0.43</td>
<td>0.20</td>
<td>-0.83</td>
<td>-0.04</td>
</tr>
<tr>
<td>σ²</td>
<td>0.08</td>
<td>0.12</td>
<td>0.00</td>
<td>0.38</td>
<td>0.07</td>
<td>0.11</td>
<td>0.00</td>
<td>0.35</td>
<td>0.05</td>
<td>0.09</td>
<td>0.00</td>
<td>0.27</td>
</tr>
</tbody>
</table>
Figure 3.1  Distribution of treatments\(^a\) and vegetation sampling transects at the Mississippi State University Prairie Research Unit in Monroe Co., MS, USA, 2011–2012.

\(^a\)Treatments included grazed mixed exotic pasture (GMEP), grazed Indian grass native pasture (GINP), grazed mixed native pasture (GMNP), and non-grazed mixed native pasture (NMNP)
Figure 3.2  Treatment\textsuperscript{a} mean estimates (± SE) of pasture vegetation structure and composition\textsuperscript{b}, from June to July in 2011 (○) and 2012 (▲).

\textsuperscript{a}Treatments included grazed mixed exotic pasture (GMEP), grazed Indian grass native pasture (GINP), grazed mixed native pasture (GMNP), and non-grazed mixed native pasture (NMNP).

\textsuperscript{b}Variables included VOR (a), live grass (b), bermudagrass (c), tall fescue (d), live forb (e), shrub (f), litter (g), and bare ground (h).
Figure 3.3  Treatment-specific\(^a\) dispersion ellipses from Canonical Analysis of Principal Coordinates (CAP) ordination of Dickcissel nest sites (solid line) and paired random points (dashed line) based on vegetation and fire ant covariates\(^b\).

\(^a\)Treatments included grazed mixed exotic pasture (GMEP), grazed Indian grass native pasture (GINP), grazed mixed native pasture (GMNP), and non-grazed mixed native pasture (NMNP).

\(^b\)Covariate codes: Bagr = bare ground; Bgrs = bermudagrass; Forb = live forbs; Grass = live grass; IFA = imported fire ants; LD = litter depth; Ltrr = litter; Shr = live shrubs; TF = tall fescue; VOR = visual obstruction reading (Robel).
Proportional use of nesting substrates by treatment for Dickcissels at the Mississippi State University Prairie Research Unit in Monroe Co., MS, USA, 2011–2012.

Treatments included grazed mixed exotic pasture (GMEP), grazed Indian grass native pasture (GINP), grazed mixed native pasture (GMNP), and non-grazed mixed native pasture (NMNP).
Figure 3.5  Mean Dickcissel productivity (and 95% CrI) by treatment\textsuperscript{a} in 2011 and 2012.

\textsuperscript{a}Treatments included grazed mixed exotic pasture (GMEP), grazed Indian grass native pasture (GINP), grazed mixed native pasture (GMNP), and non-grazed mixed native pasture (NMNP).
CHAPTER IV

ARTHROPOD COMMUNITY RESPONSE TO IMPORTED FIRE ANTS AND
CONVERSION OF EXOTIC GRASS PASTURE TO
NATIVE WARM-SEASON GRASS

Introduction

Arthropod community structure can be driven by plant diversity and structure (bottom-up control; e.g., Kruess and Tscharntke 2002), by species at upper trophic levels such as predators (top-down control; e.g., Moran et al. 1996), or by a combination of bottom-up and top-down factors and their interactions (Hunter and Price 1992, Moran and Scheidler 2002). In North America, introduction and establishment of exotic grasses has driven a structural and compositional simplification of grasslands through competition with native flora and by altering ecosystem processes (D'Antonio and Vitousek 1992). Decreases in arthropod diversity and abundance often follow (Fulbright et al. 2013) because abundance, richness, and diversity of insects are positively related to plant richness and diversity (e.g., Murdoch et al. 1972, Southwood et al. 1979, Siemann et al. 1998, Woodcock et al. 2009). In the Southeastern United States, exotic forages such as bermudagrass (*Cynodon dactylon*) and tall fescue (*Schedonorus arundinaceus*) were planted on millions of hectares for forage (Barnes et al. 2013), and these forages may be exerting bottom-up influence on local arthropod communities.
Presence of another exotic species in the Southeast, the imported fire ant
(Solenopsis invicta Buren, S. richteri Forel, and S. invicta × richteri hybrid; collectively
hereafter, IFA), may simultaneously exert top-down control of arthropod communities.
Since their introduction during the 1930’s, IFA have spread across 11 states in the
Southern United States (Callcott and Collins 1996) and are reported to reduce abundance
and richness of native ants and other arthropods through competition or predation (Porter
and Savignano 1990, Lubertazzi and Tschinkel 2003, Stuble et al. 2009, Epperson and
Allen 2010), thereby exerting top-down control of arthropod communities. IFA are also
implicated in effects cascading to primary trophic levels (Stiles and Jones 2001).

In recent years native warm-season grasses (NWSG) are increasingly promoted
for replacing exotic grasses as forage for livestock and habitat for wildlife (Taylor 2000,
Giuliano and Daves 2002, Harper et al. 2007). However, replacing exotic forage with
NWSG also has the potential to restore local arthropod communities through bottom-up
processes (Gratton and Denno 2006). For example, individual native grass species may
vary in growth and phenology (Ball et al. 2007, Harper et al. 2007), so planting native
polycultures may provide a greater diversity of niches for arthropods throughout the
growing season than exotic monocultures (plant diversity hypothesis; e.g., Hutchinson
1959). An alternative (though not mutually exclusive) hypothesis is that increased
vegetation growth provides more complex architecture and thus can support a greater
abundance and diversity of invertebrates (resource productivity hypothesis; e.g.,
Murdoch et al. 1972, Southwood et al. 1979, Kruess and Tscharntke 2002). For example,
arthropod richness and biomass are often greatest in extensively grazed or non-grazed
pastures (e.g., Gibson et al. 1992a, Dennis et al. 1998, Kruess and Tscharntke 2002,
Dennis et al. 2008). Pastures converted to NWSG could provide structural complexity to support more abundant and diverse arthropod communities because resting and reduced stocking rates are recommended for managing NWSG pasture (Mousel et al. 2003, Chamberlain et al. 2012).

However, testing arthropod response to NWSG conversion may be complicated because predation and competition from IFA may counter any potential bottom-up processes. Alternatively, IFA and native arthropods may covary independently with factors that determine community diversity (Levine and D'Antonio 1999). For example, unlike many arthropods, IFA respond positively to frequency and intensity of disturbance such as grazing and reductions in vegetation (Tschinkel 1988, Stiles and Jones 1998, King and Tschinkel 2008, Stuble et al. 2009, Tucker et al. 2010). IFA were also more abundant in grazed exotic pastures than undisturbed remnant native prairie (Hill et al. 2008), suggesting they may respond to NWSG reconstruction and restoration. Monitoring IFA in conjunction with arthropod community sampling may thus reveal potential top-down and bottom-up interactions and test the restoration potential of NWSG conversion through reduced disturbance and increased floristic and structural diversity in pastures already invaded by IFA.

In this study I assess the relative influence of bottom-up and top-down factors from exotic species in shaping arthropod communities in exotic grass pastures and pastures recently converted to NWSG in Mississippi. Specifically I measured arthropod biomass among treatments including exotic grass forages, NWSG monoculture and polycultures, and non-grazed NWSG, to assess support for plant diversity and resource productivity hypotheses. I predicted a positive effect of stand diversity but a negative
effect of grazing on arthropod community composition and biomass. I also tested response of IFA to NWSG conversion, and evaluated whether arthropod taxa covaried with IFA.

Methods

Study Area

I conducted this study at Mississippi State University’s Prairie Research Unit (PRU) in Monroe Co., Mississippi, USA (lat 33°47'N, long 88°38'W), during 2011 and 2012. The station is located in the Black Belt Prairie region, which extends from northeast Mississippi through central Alabama and underwent extensive conversion to agriculture (Peacock and Schauwecker 2003). Total growing season precipitation (April–October) was 711 mm in 2011 and 808 mm in 2012, and mean maximum daily temperature in July both years was 33.6°C. We assigned one of four treatments to experimental pastures (range = 6.4–10.5 ha), and each treatment was replicated three times. Treatments included a grazed mixed native pasture with a mix of big bluestem (*Andropogon gerardii* Vitman), little bluestem (*Schizachyrium scoparium* [Michx.] Nash), and Indian grass (GMNP); Indian grass monoculture to test effects of NWSG diversity (*Sorghastrum nutans* [L.] Nash; hereafter, grazed Indian grass native pasture, or GINP); and a non-grazed NWSG treatment to test effects of grazing (hereafter, non-grazed mixed native pasture, or NMNP). After pre-treatment herbicide applications and prescribed fire (Chapter 3), native treatments were planted in May 2008 at 9.0 kg ha\(^{-1}\) and 13.5 kg ha\(^{-1}\) for GINP and GMNP, respectively. For reference I included a grazed mix of bermudagrass and tall fescue (hereafter, grazed mixed exotic pasture, or GMEP)
that was already established at PRU. This treatment only received herbicide applications for bermudagrass release prior to the study’s initiation.

In spring 2011 and 2012, all native grass treatments were prescribed burned prior to the addition of cattle. Grazed pastures were continuously stocked mid-May through September with fall-born steer calves (average initial body weight: 250 kg) allotted to pastures at 2.7 steers ha\(^{-1}\). In June 2012, all pastures received 2,4-D herbicide application in June to control excessive forb cover. The following month, prolonged drought prompted a uniform reduction in stocking rates among grazed treatments by one third.

**Vegetation Sampling**

I quantified vegetation structure and composition along four transects in each pasture (see Chapter 3). From each transect I sampled vegetation from one point at the center, and two points at 10 m and 20 m from the center in each cardinal direction, totaling 9 points per transect \((n = 36 \text{ points per pasture})\). I sampled transects each year once in late May–early June (26 May–6 June) and again approximately one month later (24 June–7 July). I characterized composition at each sampling point within a 0.25-m\(^2\) frame using a method modified from Daubenmire (1959). I estimated percent coverage of live grass (natives and exotics), live forbs, standing dead vegetation, litter, bare ground, tall fescue, and bermudagrass. I assigned each a coverage class of either 0 = 0, 1 = < 1%, 2 = 1–5%, 3 = 6–25%, 4 = 26–50%, 5 = 51–75%, 6 = 76–95%, or 7 = > 95%, and used the midpoint as the measure of percent coverage. I also measured litter depth to the nearest 0.5 cm at the southwest corner of each frame and recorded visual obstruction readings (VOR) in four cardinal directions using a Robel pole (Robel et al. 1970) positioned in the center of the frame. I used the mean of all 36 sampling points to
characterize vegetation of the entire pasture during each sampling event.

**Arthropod Sampling**

I sampled arthropods with a modified leaf blower (Meyer et al. 2002), which is effective for sampling invertebrates that cling to vegetation and those on the ground (Cooper and Whitmore 1990, Harper and Guynn 1998). Sampling occurred within 1–2 days after vegetation measurements, between 1000 and 1500 (CST) when vegetation was dry and wind speeds ≤ 20 km h\(^{-1}\) (Doxon et al. 2011). I walked along each transect at a steady pace with the leafblower nozzle ~10 cm above ground, high enough to avoid congesting the nozzle with vegetation. At the end of each transect I removed the collection net while the vacuum was activated and transferred the closed bag to a container with ethyl acetate until samples were stored by freezing. Individuals ≥ 5 mm (McIntyre and Thompson 2003) were then sorted by Order, oven-dried at 60°C for 48 h, and weighed (± 0.0001 g; dry weight) to quantify biomass. I averaged arthropod biomass from the four transects to characterize pastures during each survey.

**Fire Ant Surveys**

Fire ants are typically surveyed with baits and mound counts (Killion and Grant 1993), though each may reflect different aspects of this species' presence and activities. For example, occurrence at baits is an index of discovery rate and scouting efficiency, whereas abundance indicates recruitment efficiency after the bait is discovered (Porter and Tschinkel 1987). Additionally, fire ant activity may be influenced by multiple factors such as microclimate and habitat (Porter and Tschinkel 1987, Vogt et al. 2003) and may not correlate with mound density (Killion and Grant 1993), suggesting the need for
multiple indices to characterize IFA presence and activity. I therefore measured fire ant activity by placing 9 bait vials at 10-m intervals along each transect ($n = 36$ vials per pasture) on days without precipitation and with temperatures between 20 and 40°C (Porter and Tschinkel 1987, Vogt et al. 2003). Transects were surveyed twice each year: once in mid- to late-April before the addition of cattle to grazing units, and once in September after cattle were removed. For bait cups I used glass capsule vials containing a piece of Keebler Sandies Pecan Shortbread cookies (Kellogg Co., Battle Creek, MI; J. Hill, personal communication) and capped vials after 30 minutes (Hill et al. 2008). Vials were then frozen to determine occurrence and abundance of IFA in each vial. Concurrent with bait sampling, I estimated mound density using distance sampling to account for imperfect detectability (Forbes et al. 2000). I walked along transects at a slow pace (~1 km h$^{-1}$), recording distance and angle of each mound that occurred within the $50 \times 50$ m survey area (maximum strip width $= 25$ m). I determined if mounds were active by lightly disturbing the mound with a stick. I also recorded heights of active mounds (cm), as tall mounds may be more detectable. Differences in vertical vegetation structure could affect detectability of fire ant mounds (Forbes et al. 2000, Tucker et al. 2010), so after each survey I recorded VOR in four cardinal directions at five points along each transect (one at the center and one in each cardinal direction at 15 m from the center) using a Robel pole. I averaged all Robel measurements to characterize VOR of each transect during a given survey.

My study sites were located along the hybrid zone between $S. invicta$ and black imported fire ant ($S. richteri$ Forel) (Shoemaker et al. 1994, Streett et al. 2006), and two breeding systems are found among $S. invicta$ including monogyne colonies with one
fertile queen per colony and a polygyne system with multiple queens per colony. Polygynous mounds are often more numerous and closely spaced (Porter et al. 1991, Vogt et al. 2009), and ants from these colonies forage farther than their monogynous congeners (Martin et al. 1998). Identifying species and breeding system of mounds can account for mound distribution, response to management, and impacts on other arthropods and breeding birds (Forbes et al. 2002, Hale et al. 2011). In mid-April 2013, I randomly selected one mound from each transect for ant identification ($n = 4$ mounds per pasture). At each mound, I removed the top portion of the mound with a shovel and placed it in a bucket. A sample of 100 ants was then extracted using an aspirator and placed in a vial with 5 mL of hexane. Individuals from each mound were then identified to species or hybrid by analyzing their cuticular hydrocarbons and venom alkaloids with gas chromatography/mass spectrometry (Vander Meer et al. 1985, Ross et al. 1987). Samples were analyzed at the USDA Agricultural Research Service in Stoneville, Mississippi, following Menzel et al. (2008). I collected an additional 20 workers from each mound to distinguish among monogyne, polygyne, and hybrid colonies, preserving them in 70% isopropanol for polymerase chain reaction (PCR). Polygyne ants possess both alleles for the $Gp$-9 gene ($B$ and $b$) whereas ants from monogyne colonies possess only the $B$ allele, so PCR offers an accurate and cost-effective method for discriminating between the two breeding systems (Valles and Porter 2003). DNA was amplified with PCR following the protocol of Valles and Porter (2003), except we used TaKaRa Taq (hot start version) for DNA polymerase, and 65–125 ng genomic DNA per 23.8 µL reaction (D. Cross, personal communication). We also used a MyCycler™ thermal cycler (Bio-Rad Laboratories, Inc., Hercules, CA, USA), and electrophoresed 3 µL of amplified
DNA on agarose gel with GelRed (Biotium) to detect and photograph DNA under UV light.

**Statistical Analysis**

I used descriptive statistics (mean ± SE) to summarize treatment-level vegetation structure and composition. Grazing may facilitate the spread of exotic grasses (Smith and Knapp 1999, Bock et al. 2007), which could then influence the arthropod community through structural and compositional simplification, so I formally tested this among my treatments using linear mixed models and the package *nlme* (Pinheiro et al. 2014) in R (version 3.0.2, R Development Core Team 2014). Tall fescue was seldom detected in native grass pastures, so I restricted this analysis to bermudagrass. I modeled mean bermudagrass coverage from each pasture as the response, fixed effects of treatment, month, and year, and a random effect for pasture. Beginning with the most complex model (treatment × season × year), I used likelihood ratio tests to assess support for sequentially more parsimonious fixed effects models until further simplification did not improve model fit (Zuur et al. 2009). I visually examined the residuals and square root transformed the response to meet assumptions of normality. I considered statistical significance at $\alpha = 0.05$.

**Arthropod Community**

I used non-metric multidimensional scaling (NMDS; Faith et al. 1987, Minchin 1987) with the package *vegan* in R (Oksanen et al. 2013) to discriminate among treatments based on biomass of arthropod Orders, including Orthoptera, Hemiptera, Mantodae, Hymenoptera, Lepidoptera, Neuroptera, Coleoptera, Diptera, Odonata,
Ephemoptera, and Araneae. Biomass of each Order was centered and scaled, and ordination was based on Bray-Curtis dissimilarity (Bray and Curtis 1957). Upon examining the data, one transect sample from NMNP contained an unusually large sample of Hemiptera (nearly four times the mass than the next largest sample), so I excluded it as an outlier. I used a Shepard diagram to assess number of dimensions needed for adequate interpretation and to judge goodness of fit. NMDS ordination reached solution with two dimensions, and a stress plot confirmed goodness-of-fit (stress = 0.0572). I then tested whether ordination was correlated with pasture vegetation, month, and year with the function `envfit` in the package `vegan`, with significance determined from 10,000 permutations. I also tested for correlations between arthropod ordination and IFA by including covariates for mound abundance and mean occurrence and abundance captured with bait vials from each pasture in the spring and fall, 2011–2012. Finally, I used dispersion ellipses (based on 95% confidence intervals) to group site scores by treatment and month.

I conducted univariate analyses to test for differences in biomass among treatments. I restricted analysis to the four most represented Orders in my samples: Orthoptera (86.6%), Hemiptera (7.4%), Araneae (2.6%), and Coleoptera (1.2%). I constructed linear mixed models using package `nlme` in R with mean arthropod biomass sampled from pastures by month and year as the response, fixed effects of treatment, year, season, and a random effect for pasture. Beginning with the full model (treatment × season × year), I again used likelihood ratio tests to assess support for sequentially more parsimonious fixed effects models (Zuur et al. 2009). If model residuals exhibited substantial non-normality I applied a square root root transformation to the response variable.
to ensure model assumptions were met. I also regressed biomass against covariates that correlated ($P < 0.05$) with arthropod ordination and against each IFA covariate, and reported marginal $R^2$ as a statistic for variance explained by fixed effects (Nakagawa and Schielzeth 2013).

**Imported Fire Ants**

I modeled IFA occurrence in each vial using logistic regression with the package `lme4` in R (Bates et al. 2014). Fixed effects included treatment, year, and season, and I included a random effect for transect nested within pasture to account for non-independence of repeated surveys of transect subsamples. I used likelihood ratio tests to compare increasingly simpler models beginning with the most complex model (Zuur et al. 2009). Modeling abundance of IFA recruited to individual vials proved more difficult, likely due to great variability in abundance among samples (range: 1–433 individuals), and I could not meet model assumptions using linear mixed models. Furthermore, modeling with a Poisson distribution resulted in substantial overdispersion ($\hat{\epsilon} >> 15.0$). I therefore log-transformed mean IFA abundance from each pasture during a given survey, and used linear mixed models in the R package `nlme` to test effects of treatment, season, and year, and a random effect for pasture. I again sequentially tested increasingly parsimonious models with likelihood ratio tests beginning with the most complex model until the best-fitting model was identified.

I used a Bayesian hierarchical modeling approach to estimate mound densities (active mounds ha$^{-1}$) while incorporating random effects and individual covariates for mound height (Royle and Dorazio 2008). I analyzed this model using JAGS (version 3.3.0, Plummer 2003) and the package `R2jags` (Su and Yajima 2013) in program R. This
approach uses a half-normal function to model variability in detection of individuals with
distance to transect, and data augmentation is used to estimate the number of individuals
that occurred in the population but were missed, and thus the true population in our study
(Royle and Dorazio 2012). I appended to my sample of \( n \) observed mounds a sample (\( M \)) of
potential unobserved mounds for each transect during each survey. The sample of \( M \) was
sufficiently large to avoid influencing posterior estimates of mound abundance.

Detection of an individual mound during a survey (\( Y_i = 1 \)) is modeled from independent
Bernoulli trials and individual inclusion probability (\( \psi_i \)) from \( n + M \) individuals in the
augmented dataset conditional on individual detection probability (\( p_i \)), or \( Y_i \sim \text{Bern}(\psi_i \cdot
p_i) \). I modeled \( \psi_i \) on the logit scale as a function of treatment, year, season, and treatment
\( \times \) year and treatment \( \times \) season interactions. I initially attempted to specify transect-level
random effects nested within pasture-level random effects to account for non-
independence of repeated surveys. However the model fit the data poorly, likely due to
the small number of replicate transects in each pasture (\( n = 4 \)). So instead I specified a
random effect for pasture \( j \) as \( \varepsilon_j \sim \text{N}(0, \tau_j) \) where \( \tau_j = 1/\sigma_j^2 \):

\[
\logit(\psi_i) = \alpha_1 \text{GMEP}_j + \alpha_2 \text{GINP}_j + \alpha_3 \text{GMNP}_j + \alpha_4 \text{NMNP}_j + \alpha_5 \text{Year}_t + \alpha_6 \text{GINP}_j \times \text{Year}_t + \alpha_7 \text{GMNP}_j \times \text{Year}_t + \alpha_8 \text{NMNP}_j \times \text{Year}_t + \alpha_9 \text{Season}_k + \alpha_{10} \text{GINP}_j \times \text{Season}_k + \alpha_{11} \text{GMNP}_j \times \text{Season}_k + \alpha_{12} \text{NMNP}_j \times \text{Season}_k + \varepsilon_j
\]

(4.1)

To account for effects on individual detectability from vegetation volume
measured from transect \( l \) during season \( k \) of year \( t \) (\( \text{VOR}_{tkl} \)) and mound height (\( \text{Height}_i \)), I
modeled \( \sigma_i \) from the detection function on the log-scale:

\[
\log(\sigma_i) = \beta_1 + \beta_2 \text{VOR}_{tkl} + \beta_3 \text{Height}_i
\]

(4.2)
Detectability was then computed with the half-normal function:

\[
\log(p_i) = -\frac{x_i^2}{\sigma_i^2}
\]  

(4.3)

To account for detection distances and mound heights for undetected ant mounds, I specified a uniform prior for distance \(x_i\) from 0 to 25 m (the maximum strip width), and assigned a normal distribution for mound height: \(\text{Height}_i \sim N(\mu_m, \tau_m)\) (Royle 2009). Mound height may vary with disturbance (Stiles and Jones 1998) so I specified treatment-specific hyper-parameters for the mean \((\mu_m \sim N[0,1000])\) and precision \((\tau_m \sim \text{Gamma}[0.001,0.001])\). Therefore, mounds from treatment \(m\) informed hyper-parameters for mound height, and height measurements for the unobserved mounds in each treatment were drawn from their respective hyper-parameter distributions. Treatment-specific mound densities for each season and year were then computed as derived parameters, dividing abundance by total area covered by 12 transects in each treatment (3 ha). I used a standard uninformative prior of \(N(0,1000)\) for detection covariates and effects of year and season, and a weakly-informative prior of \(\logit(\alpha) \sim U(0,1)\) for treatment effects. I also tested whether mound abundance in each pasture was correlated with fire ant occurrence and abundance (log-transformed) using Pearson's correlation coefficient. Correlation was computed during each MCMC iteration, thus providing mean estimates and 95% credible intervals (CrI) from the posterior distribution. I used estimates from the posterior distribution of 25,000 iterations from each of three parallel chains after discarding the first 10,000 as burn-in and thinning by 5. I assessed convergence using the \(\hat{R}\) statistic (Gelman et al. 2014), and by visually examining the chains.
Results

In general I found greater VOR and live forb coverage in NMNP and lesser and similar VOR in grazed treatments (Table 4.1). Bare ground coverage was greater in the two grazed native treatments, intermediate in NMNP, and lowest in GMEP. Only GMEP pastures contained substantial coverage of tall fescue, whereas coverage of bermudagrass was estimated in all treatments. Coverage of dead vegetation was also greater in GMEP than other treatments. However, treatment averages belie intra- and interannual changes in certain variables, as VOR in NMNP tended to increase from June to July, whereas VOR remained constant or decreased over time in grazed treatments (Chapter 3). Bare ground coverage among all treatments decreased from June to July the first year and remained constant or increased the second year. The best-supported model for bermudagrass coverage included fixed effects for treatment, month, year, and treatment × year interactions. Across treatments and years bermudagrass coverage (square root-scale) increased from June to July ($\beta = 0.492$, SE = 0.121, $P < 0.001$). There was also a significant positive treatment × year interaction for GMNP ($\beta = 2.127$, SE = 0.342, $P < 0.001$) and for GINP ($\beta = 1.284$, SE = 0.342, $P < 0.001$), whereas effects of year and NMNP × year interaction were not supported ($P > 0.15$). This is reflected in increased bermudagrass coverage among grazed native grass pastures from 2011 to 2012 (averaged across months), whereas coverage remained relatively constant between NMNP and GMEP across years (Fig. 4.1).
**Arthropod Community Response to NWSG Conversion and IFA**

There was significant ($P \leq 0.05$) correlation between arthropod community site scores and four covariates, including a positive correlation of both axes with VOR and shrub coverage, and a negative correlation with coverage of standing dead vegetation and bermudagrass (Table 4.2). Significant correlations were evident with month ($r^2 = 0.23$, $P < 0.001$) but not year ($r^2 = 0.01$, $P = 0.47$) in the distribution of site scores, with June samples associated positively with axes 1 and 2, and July samples negatively associated with these axes (Fig. 4.2a). Covariates for IFA activity and mound abundance were not significantly correlated with arthropod ordination. Grouping sites by treatment with dispersion ellipses revealed considerable overlap among treatments in June, though spread tended to be greater for GINP and NMNP than GMEP and GMNP (Fig. 4.2b). However, in July spread among grazed treatments (native and exotic) was reduced and distributed similarly, whereas spread was greater for NMNP (Fig. 4.2c).

For Orthoptera biomass (square root-scale), effects from treatment were not supported, and the final model ($R^2 = 0.26$) included positive effects from year ($\beta = 0.121$, $SE = 0.052$, $P = 0.028$) and July ($\beta = 0.249$, $SE = 0.052$, $P < 0.001$), but a negative year × month interaction ($\beta = -0.159$, $SE = 0.074$, $P = 0.039$). This suggests an increase in Orthoptera biomass from June to July the first year, but less so the second year. Inclusion of treatment and treatment × month interactions were supported in the final model for Hemiptera (square root-scale, $R^2 = 0.44$), indicating a negative effect of July ($\beta = -0.137$, $SE = 0.063$, $P = 0.016$), and a positive NMNP × month interaction ($\beta = 0.159$, $SE = 0.041$, $P = 0.034$), whereas other effects were not significant. Final model for Araneae ($R^2 = 0.28$) suggested a positive effect from NMNP ($\beta = 0.013$, $SE = 0.005$, $P = 0.038$).
and July ($\beta = 0.007$, SE = 0.003, $P = 0.020$), but no significant interactions. Only effect of month was significant in explaining variation of Coleoptera ($R^2 = 0.09$), with a decrease in biomass (square root-scale) from June to July ($\beta = -0.028$, SE = 0.012, $P = 0.022$).

Orthoptera biomass was positively associated with dead vegetation and negatively associated with shrubs (Fig. 4.3), whereas only a negative effect of dead vegetation was supported for Coleoptera biomass ($P = 0.020$; Fig. 4.4). Hemiptera (Fig. 4.5) and Araneae (Fig. 4.6) suggested a positive response to VOR, but response to dead vegetation differed between the two Orders, with a negative effect on Hemiptera and a positive effect on Araneae. Response to bermudagrass coverage was generally weak among Orders, though all but Orthoptera suggested a negative effect of the grass, particularly for Hemiptera ($P = 0.047$; Fig. 4.5). None of the arthropod taxa varied with indices of IFA ($P > 0.3$, $R^2 < 0.03$ for each regression).

**Fire Ant Response to NWSG Conversion**

*Activity*

I captured 27,163 IFA individuals over four sampling events. Native ants also captured included *Monomorium minimum* Buckley ($n = 13,045$), *Solenopsis molesta* Say ($n = 119$), and *Nylanderia vividula* Nylander ($n = 4$), which is similar to ant richness reported in other exotic pastures in the Black Belt (Hill et al. 2008). Of the 48 mounds sampled in 2013, amplification from PCR indicated that all belonged to the monogyne breeding system, none possessing the polygene $Gp-9^b$ allele. I also determined that 8 mounds were *S. richteri* (Alkaloid index $[I] < 0.06$, where $0.06 < I < 0.85$ suggests the
colony is hybrid; Ross et al. 1987), whereas the rest ($n = 40$) were $S. \text{invicta} \times r. \text{richteri}$ hybrids ($I$ range: 0.06–0.54).

Beginning with the three-way interaction model, the most parsimonious model for fire ant occurrence contained fixed effects for treatment, season, and year, and treatment × season and treatment × year interactions. This model also approximated the data better than a null (intercept-only) model ($L = 119.14, df = 11, P < 0.001$). The model suggested significant positive interactions for GINP × year ($\beta = 1.136, SE = 0.321, P < 0.001$) and NMNP × year ($\beta = 1.307, SE = 0.333, P < 0.001$), whereas the overall effect of year was negative ($\beta = –1.664, SE = 0.248, P < 0.001$). There was also a significant negative interaction for GINP × season ($\beta = –0.807, SE = 0.311, P = 0.010$), whereas the effect of season alone was positive ($\beta = 0.648, SE = 0.235, P = 0.006$). This is best illustrated with interaction plots (Fig. 4.7), where occurrence of IFA at vials among all treatments generally decreased from 2011 to 2012, though to a lesser degree for GINP and NMNP, and where occurrence was greater in Fall than in Spring for all treatments except GINP.

**Abundance**

The best-supported model contained only additive effects of season and year, and this approximated my data better than the null model ($L = 14.11, df = 2, P < 0.001$).

Inclusion of treatment effects did not improve fit ($L = 6.17, df = 3, P = 0.10$). The model suggested overall mean abundance (log-scale) of IFA captured in each pasture increased from spring to fall ($\beta = 0.534, SE = 0.218, P = 0.020$) and decreased from 2011 to 2012 ($\beta = –0.689 SE = 0.218, P = 0.003$).
Mound density

Over two years and four surveys I detected 1,351 IFA mounds across all study sites. The detection process of the model revealed a negative effect of VOR ($\beta_2$) and a positive effect of mound height ($\beta_3$; Table 4.3), and I estimated 4,064 mounds in the superpopulation (95% CrI: 3,801–4,340). These estimates indicate that ignoring variation in detectability would have substantially underestimated and biased mound density at my study sites. For the process part of the model, mean estimates for effects of year ($\alpha_5$) and of season ($\omega_9$) were positive and negative, respectively, though credible intervals of both parameters overlapped zero (Table 4.3). Credible intervals from all interaction terms also overlapped zero ($\alpha_{6-8}, \alpha_{10-12}$). Mean parameter estimate for treatment was higher for GINP than NMNP whereas GMEP and GMNP were more similar, though there was broad overlap among credible intervals. These parameter estimates are reflected in derived treatment estimates of mound density (Fig. 4.8), with slight intra-annual decreases and inter-annual increases in mound density, but overlapping credible intervals among treatments. Mound abundance was negatively correlated with IFA occurrence ($r = -0.15, 95\% \text{ CrI} = -0.26, -0.02$) and, to a lesser degree, abundance ($r = -0.09, 95\% \text{ CrI} = -0.22, 0.04$), illustrating the importance of monitoring multiple IFA indices to adequately characterize processes in this species.

Discussion

In this study, ordination of arthropod community suggested a bottom-up response to NWSG conversion and a negative effect from grazing. However, the majority of biomass in our samples consisted of Orthoptera that did not respond to treatment, and there was overlap among treatments in ordinal space. Still, two of the four most common
taxa responded positively to VOR in non-grazed NWSG. In addition, ordination did not correlate with any index of IFA, and therefore patterns in arthropod biomass were not likely confounded by top-down control from IFA. Numerous studies indicate a positive relationship between arthropod and floristic diversity (e.g., Murdoch et al. 1972, Southwood et al. 1979, Siemann et al. 1998, Woodcock et al. 2009), though disturbance from grazing may also depress arthropod numbers (e.g., Gibson et al. 1992a, Dennis et al. 1998, Kruess and Tscharntke 2002, Dennis et al. 2008). My study of NWSG conversion reflects the latter, with greater ordinal richness in non-grazed NWSG and a simplified arthropod community in grazed treatments irrespective of stand type, consistent with the resource productivity hypothesis.

Lack of support for the plant diversity hypothesis, reflected in similar ordinal response to stand type among grazed treatments, may be attributed to several factors. First, restricting analyses to higher taxonomic levels (Orders) ≥ 5 mm in length prevented me from measuring responses at lower levels. For example, Orthoptera density may respond positively to grazing (Holmes et al. 1979, Joern 2004) and recent fire (Swengel 2001, Joern 2004), but response to disturbance and plant composition often occurs at the guild and species level (Holmes et al. 1979, McIntyre and Thompson 2003, Meyer et al. 2002, Jonas and Joern 2007). In central Kansas, Orthoptera richness increased with plant richness, but overall abundance was similar between native and exotic stands (Jonas et al. 2002). Alternatively, all native pastures in my study were burned each spring, which likely reduced if not eliminated many species and required dispersal from nearby habitat to reconstitute arthropod communities (Swengel 2001). In the Black Belt prairie, few native prairies remain and thus colonists likely consisted of generalists from adjacent
cropland and exotic grass pastures rather than native grass specialists (Tscharntke and Brandl 2004). Arthropod communities consisting of generalists may then be less likely to respond to NWSG conversion. For example, diversity of Hemiptera communities was not correlated with plant richness when composed of zoophagous and polyphagous species (Di Giulio et al. 2001).

Interestingly, spread of site scores appeared greater in June for GINP than GMNP, the opposite of what is predicted by the plant diversity hypothesis. However, one month later spread remained greatest for NMNP and reduced but similar among grazed pastures, illustrating the effect of grazing on the observed community. Furthermore, a positive effect of stand type from GINP is unlikely because Indian grass does not reach peak productivity until later in the season than for big and little bluestems (Keyser et al. 2011). Instead, some other unmeasured factor may be influencing the initial June arthropod community, prior to being shaped by grazing. For example, land-use histories of individual pastures may influence the observed community (Debinski et al. 2011), and one pasture each of GINP and NMNP were converted to wildlife areas three years before NWSG conversion (W. Burger, personal communication), whereas all other pastures in this study were converted directly from exotic forages. Patterns of arthropod communities among treatments and within seasons further illustrate the importance of grazing rather than stand type in influencing arthropod communities at my study sites.

I observed a doubling in bermudagrass coverage between years in grazed native grass pastures, but not in non-grazed NWSG, suggesting that the incomplete eradication of bermudagrass during NWSG conversion may have been exacerbated by disturbance from grazing. Bermudagrass has a highly rhizomatous and stoloniferous growth form and
will readily spread following grazing (Newman et al. 2003). Bermudagrass spread likely further simplified vegetation structure and composition in grazed NWSG, precluding detection of any response to native grass diversity from arthropods. In Germany, introduced bermudagrass outcompeted native grasses and corresponded with declines in leafhoppers (Biedermann et al. 2005). In my study, bermudagrass was negatively associated with ordinal distribution of most taxa, and regressing bermudagrass coverage against arthropod biomass indicated a negative response among three of the four taxa examined, though the effect was weak and only statistically significant for Hemiptera.

Correlation between habitat variables and ordination suggested the positive response to NMNP was driven by vegetation volume and recent fire (less standing dead vegetation). Fire may increase productivity of native grasses (Knapp and Seastedt 1986, Harper et al. 2007), and in subsequent months common arthropod species can recolonize quickly (Swengel 2001). Orthoptera responded positively to standing dead vegetation, suggesting a negative response to fire. Previous studies generally report a positive response of Orthoptera to fire (with a few exceptions), and it is possible that effect of fire depends on the scale at which it is applied (Swengel 2001). For Araneae, abundance and diversity may be negatively affected by grazing (Gibson et al. 1992a, 1992b, Dennis et al. 2008), though they may also be less responsive to plant diversity because at a higher trophic level this group is limited more by abundance rather than diversity of prey items (Gibson et al. 1992b, Dennis et al. 1998). In contrast, diversity of Hemiptera can be attributed to both structural and species diversity of plants in grasslands (Murdoch et al. 1972, Southwood et al. 1979, Gibson et al. 1992a, Kőrösi et al. 2012), and Hemiptera are increasingly promoted as indicators of disturbance and habitat quality (e.g., Biedermann...
et al. 2005). Greater size and complexity of plants increase diversity and availability of substrates for Hemiptera to complete their lifecycles (Biedermann et al. 2005), and abundance and diversity of Hemiptera may be reduced with haying and grazing (e.g., Morris and Lakhani 1979, Dennis et al. 1998, Di Giulio et al. 2001, Dennis et al. 2008). Such ecological differences between Hemiptera and Araneae are reflected in similar positive responses to VOR yet opposite responses to dead vegetation.

I did not detect a relationship between IFA activity and arthropod community in ordinal space, nor when regressing biomass of specific taxa against IFA indices, although my study is admittedly correlational because I did not directly alter IFA abundance. Furthermore, fire ant activity and density may vary seasonally, so testing a direct relationship was not possible because IFA surveys did not coincide with arthropod sampling. Nevertheless, genetic analysis of mounds indicated mounds were all hybrids between S. invicta and competitively inferior black imported fire ants (S. richteri; Streett et al. 2006), and none showed evidence of the polygyne breeding system that is reported to reduce abundance of arthropods and native ants (Porter and Savignano 1990). The lack of relationship between arthropod community and IFA may also relate to equivalence of IFA among treatments. Whereas initial IFA invasion may reduce arthropod abundance and diversity (Porter and Savignano 1990), arthropods can recover to pre-invasion levels (Morrison 2002). Given IFA were first detected in Monroe Co., MS > 50 years ago (Callcott and Collins 1996), a similar recovery to pre-invasion community may be evident at my sites, though I lack data on pre-invasion arthropod communities.

I also did not detect a response in IFA abundance or occurrence to NWSG conversion, though there was seasonal and annual variation unrelated to treatment. This
may reflect seasonal fluctuations in fire ant populations, which often decline from spring until mid-summer due to allocation of resources toward production of sexuals rather than workers, then recover in the fall through winter (Tschinkel 1993). Similarly, mound density decreased from February–August in nearby Clay Co., MS, before increasing again in the fall (Vogt et al. 2004). Additionally, soil temperature and insolation that may affect mound density and foraging activity of IFA (Porter and Tschinkel 1987, Vogt et al. 2003, Vogt et al. 2009), and disturbance may facilitate establishment and maintenance of IFA colonies while reducing richness and diversity of native ants (Stiles and Jones 1998, King and Tschinkel 2008, Stuble et al. 2011). Disturbance from recent NWSG establishment, and grazing in two of the native treatments, may have precluded observing conditions similar to other native prairie in the region.

Together, these results suggest that isolated conversion of exotic grass pastures to NWSG is unlikely to have a strong impact on arthropod communities, at least in the short-term. This is consistent with other studies of restored and reconstructed grasslands that fell short of the diversity found in remnant prairie (e.g., Brand and Dunn 1998, McIntyre and Thompson 2003, Shepherd and Debinski 2005). Arthropod diversity in reconstructed prairie may also be influenced by source populations in adjacent patches (Burger et al. 2003, Shepherd and Debinski 2005), so research is needed on the role of the broader landscape in structuring arthropod communities following NWSG conversion, as well as the long-term effects of conversion on grazing lands in the Southeast. Still, the positive response of several taxonomic groups to non-grazed NWSG suggests the potential for increasing arthropod diversity through bottom-up processes when coupled with resting or reduced stocking rates.
Table 4.1  Treatment\textsuperscript{a} mean estimates (SE) for vegetation measurements at Mississippi State University Prairie Research Unit, 2011-2012.

<table>
<thead>
<tr>
<th>Variable</th>
<th>GMEP</th>
<th>GINP</th>
<th>GMNP</th>
<th>NMNP</th>
</tr>
</thead>
<tbody>
<tr>
<td>VOR\textsuperscript{b} (cm)</td>
<td>15.09 (1.23)</td>
<td>17.29 (1.59)</td>
<td>15.77 (0.84)</td>
<td>33.22 (2.46)</td>
</tr>
<tr>
<td>Litter depth (cm)</td>
<td>0.30 (0.04)</td>
<td>0.31 (0.04)</td>
<td>0.23 (0.02)</td>
<td>0.20 (0.03)</td>
</tr>
<tr>
<td>Live grass (%)</td>
<td>60.11 (2.66)</td>
<td>53.92 (2.27)</td>
<td>57.53 (2.17)</td>
<td>55.82 (4.34)</td>
</tr>
<tr>
<td>Live forb (%)</td>
<td>21.86 (2.88)</td>
<td>22.46 (3.30)</td>
<td>17.99 (1.94)</td>
<td>31.34 (5.02)</td>
</tr>
<tr>
<td>Bermudagrass (%)</td>
<td>14.78 (2.08)</td>
<td>16.35 (3.45)</td>
<td>15.84 (2.60)</td>
<td>7.28 (2.11)</td>
</tr>
<tr>
<td>Tall fescue (%)</td>
<td>38.33 (5.38)</td>
<td>0.04 (0.04)</td>
<td>0</td>
<td>0.07 (0.05)</td>
</tr>
<tr>
<td>Dead vegetation (%)</td>
<td>16.11 (1.44)</td>
<td>8.42 (1.36)</td>
<td>9.63 (1.43)</td>
<td>6.57 (1.10)</td>
</tr>
<tr>
<td>Shrub (%)</td>
<td>1.03 (0.47)</td>
<td>0.88 (0.40)</td>
<td>0.17 (0.09)</td>
<td>0.63 (0.29)</td>
</tr>
<tr>
<td>Litter (%)</td>
<td>6.03 (0.76)</td>
<td>10.46 (1.51)</td>
<td>9.89 (0.67)</td>
<td>5.18 (0.91)</td>
</tr>
<tr>
<td>Bare ground (%)</td>
<td>10.24 (1.40)</td>
<td>18.17 (1.79)</td>
<td>21.88 (1.28)</td>
<td>14.47 (1.73)</td>
</tr>
</tbody>
</table>

\textsuperscript{a}Treatments included grazed mixed exotic pasture (GMEP), grazed Indian grass native pasture (GINP), grazed mixed native pasture (GMNP), and non-grazed mixed native pasture (NMNP).

\textsuperscript{b}Visual obstruction reading, measured by Robel pole (Robel et al. 1970).
Table 4.2  Correlation ($r^2$) of vegetation, imported fire ant (IFA) indices, and survey month and year with arthropod ordination axes from nonmetric multidimensional scaling (NMDS).

<table>
<thead>
<tr>
<th></th>
<th>NMDS1</th>
<th>NMDS2</th>
<th>$r^2$</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Visual obstruction reading (VOR)</td>
<td>0.23</td>
<td>0.97</td>
<td>0.20</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Litter depth</td>
<td>0.45</td>
<td>-0.89</td>
<td>&lt;0.01</td>
<td>0.99</td>
</tr>
<tr>
<td>Live grass</td>
<td>-0.87</td>
<td>-0.50</td>
<td>&lt;0.01</td>
<td>0.82</td>
</tr>
<tr>
<td>Live forb</td>
<td>0.11</td>
<td>0.99</td>
<td>0.06</td>
<td>0.22</td>
</tr>
<tr>
<td>Live shrub</td>
<td>0.81</td>
<td>0.58</td>
<td>0.13</td>
<td>0.05</td>
</tr>
<tr>
<td>Dead vegetation</td>
<td>-0.51</td>
<td>-0.86</td>
<td>0.27</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Litter</td>
<td>0.38</td>
<td>-0.92</td>
<td>0.02</td>
<td>0.63</td>
</tr>
<tr>
<td>Bare ground</td>
<td>0.08</td>
<td>-1.00</td>
<td>0.06</td>
<td>0.28</td>
</tr>
<tr>
<td>Bermudagrass</td>
<td>-0.31</td>
<td>-0.95</td>
<td>0.19</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Tall fescue</td>
<td>-0.73</td>
<td>-0.68</td>
<td>0.05</td>
<td>0.30</td>
</tr>
<tr>
<td>IFA occurrence (spring)</td>
<td>-0.18</td>
<td>-0.98</td>
<td>0.04</td>
<td>0.45</td>
</tr>
<tr>
<td>IFA occurrence (fall)</td>
<td>0.30</td>
<td>0.95</td>
<td>0.02</td>
<td>0.64</td>
</tr>
<tr>
<td>IFA abundance (spring)</td>
<td>0.34</td>
<td>-0.94</td>
<td>0.03</td>
<td>0.51</td>
</tr>
<tr>
<td>IFA abundance (fall)</td>
<td>-0.99</td>
<td>-0.15</td>
<td>0.03</td>
<td>0.55</td>
</tr>
<tr>
<td>IFA mound density (spring)</td>
<td>0.58</td>
<td>-0.82</td>
<td>0.05</td>
<td>0.35</td>
</tr>
<tr>
<td>IFA mound density (fall)</td>
<td>0.88</td>
<td>-0.48</td>
<td>0.02</td>
<td>0.68</td>
</tr>
<tr>
<td>Month (June)</td>
<td>0.21</td>
<td>0.03</td>
<td>0.23</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Month (July)</td>
<td>-0.21</td>
<td>-0.03</td>
<td>0.23</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Year (2011)</td>
<td>0.05</td>
<td>0.02</td>
<td>0.01</td>
<td>0.47</td>
</tr>
<tr>
<td>Year (2012)</td>
<td>-0.05</td>
<td>-0.02</td>
<td>0.01</td>
<td>0.47</td>
</tr>
</tbody>
</table>
Table 4.3  Mean, standard deviation, and 95% credible intervals (CrI) for parameter estimates from distance sampling model of IFA mound density.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Mean</th>
<th>SD</th>
<th>Lower</th>
<th>Upper</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\alpha_1$ GMEP$^a$</td>
<td>0.28</td>
<td>0.36</td>
<td>-0.45</td>
<td>0.96</td>
</tr>
<tr>
<td>$\alpha_2$ GINP$^a$</td>
<td>0.63</td>
<td>0.36</td>
<td>-0.07</td>
<td>1.36</td>
</tr>
<tr>
<td>$\alpha_3$ GMNP$^a$</td>
<td>0.03</td>
<td>0.33</td>
<td>-0.61</td>
<td>0.71</td>
</tr>
<tr>
<td>$\alpha_4$ NMNP$^a$</td>
<td>-0.09</td>
<td>0.34</td>
<td>-0.74</td>
<td>0.57</td>
</tr>
<tr>
<td>$\alpha_5$ Year</td>
<td>0.37</td>
<td>0.26</td>
<td>-0.12</td>
<td>0.90</td>
</tr>
<tr>
<td>$\alpha_6$ GINP$^a \times$ Year</td>
<td>0.00</td>
<td>0.38</td>
<td>-0.75</td>
<td>0.74</td>
</tr>
<tr>
<td>$\alpha_7$ GMNP$^a \times$ Year</td>
<td>-0.10</td>
<td>0.33</td>
<td>-0.76</td>
<td>0.54</td>
</tr>
<tr>
<td>$\alpha_8$ NMNP$^a \times$ Year</td>
<td>0.38</td>
<td>0.37</td>
<td>-0.35</td>
<td>1.08</td>
</tr>
<tr>
<td>$\alpha_9$ Season</td>
<td>-0.22</td>
<td>0.23</td>
<td>-0.67</td>
<td>0.23</td>
</tr>
<tr>
<td>$\alpha_{10}$ GINP$^a \times$ Season</td>
<td>-0.15</td>
<td>0.36</td>
<td>-0.85</td>
<td>0.57</td>
</tr>
<tr>
<td>$\alpha_{11}$ GMNP$^a \times$ Season</td>
<td>-0.26</td>
<td>0.31</td>
<td>-0.89</td>
<td>0.35</td>
</tr>
<tr>
<td>$\alpha_{12}$ NMNP$^a \times$ Season</td>
<td>0.11</td>
<td>0.40</td>
<td>-0.64</td>
<td>0.93</td>
</tr>
<tr>
<td>$\sigma$ Pasture random effect</td>
<td>0.45</td>
<td>0.19</td>
<td>0.19</td>
<td>0.90</td>
</tr>
<tr>
<td>$\beta_1$ Intercept (Detectability)</td>
<td>1.88</td>
<td>0.02</td>
<td>1.84</td>
<td>1.92</td>
</tr>
<tr>
<td>$\beta_2$ VOR$^b$ (Detectability)</td>
<td>-0.39</td>
<td>0.02</td>
<td>-0.43</td>
<td>-0.35</td>
</tr>
<tr>
<td>$\beta_3$ Mound height (Detectability)</td>
<td>0.27</td>
<td>0.03</td>
<td>0.22</td>
<td>0.33</td>
</tr>
</tbody>
</table>

$^a$Treatments included grazed mixed exotic pasture (GMEP), grazed Indian grass native pasture (GINP), grazed mixed native pasture (GMNP), and non-grazed mixed native pasture (NMNP).

Figure 4.1  Mean bermudagrass (*Cynodon dactylon*) coverage (and 95% CI)\textsuperscript{a} by treatment\textsuperscript{b} and year, measured at the MSU Prairie Research Unit in Prairie, MS, USA, 2011–2012.

\[\text{Estimates were averaged across June and July sampling each year.}\]

\[\text{Treatments included grazed mixed exotic pasture (GMEP), grazed Indian grass native pasture (GINP), grazed mixed native pasture (GMNP), and non-grazed mixed native pasture (NMNP).}\]
Figure 4.2 Ordination plot\textsuperscript{a} from non-metric multidimensional scaling (NMDS) of eight Orders (a), and dispersion ellipses (95\% CI) for arthropod Orders grouped by treatment in June (b) and in July (c).

\textsuperscript{a}Arrows represent species correlations with vegetation variables measured at each site (only variables significant at $P \leq 0.05$ shown), including visual obstruction reading (VOR), and coverage of shrubs (Shrb), dead vegetation (Dveg), and bermudagrass (Bgrs).
Figure 4.3  Mixed effects regression\textsuperscript{a} of Orthoptera biomass against four vegetation parameters correlated with arthropod community ordination.

\textsuperscript{a}I report marginal $R^2$, representing the proportion of variance explained by fixed effects (Nakagawa and Schielzeth 2013).
Figure 4.4  Mixed effects regression$^a$ of Coleoptera biomass against four vegetation parameters correlated with arthropod community ordination.

$^a$I report marginal $R^2$, representing the proportion of variance explained by fixed effects (Nakagawa and Schielzeth 2013).
Figure 4.5  Mixed effects regression\textsuperscript{a} of Hemiptera biomass against four vegetation parameters correlated with arthropod community ordination.

\textsuperscript{a}I report marginal $R^2$, representing the proportion of variance explained by fixed effects (Nakagawa and Schielzeth 2013).
Figure 4.6  Mixed effects regression\textsuperscript{a} of Araneae biomass against four vegetation parameters correlated with arthropod community ordination.

\textsuperscript{a}I report marginal $R^2$, representing the proportion of variance explained by fixed effects (Nakagawa and Schielzeth 2013).
Figure 4.7  Interaction plots for mean IFA occurrence (± SE) by treatmenta measured from 36 vials per pasture.

aTreatments included grazed mixed exotic pasture (GMEP), grazed Indian grass native pasture (GINP), grazed mixed native pasture (GMNP), and non-grazed mixed native pasture (NMNP).
Figure 4.8  Mean IFA mound density (and 95% CrI) by treatment\textsuperscript{a} estimated from pastures.

\textsuperscript{a}Treatments included grazed mixed exotic pasture (GMEP), grazed Indian grass native pasture (GINP), grazed mixed native pasture (GMNP), and non-grazed mixed native pasture (NMNP).
CHAPTER V

ECONOMIC AND CONSERVATION IMPLICATIONS OF CONVERTING EXOTIC FORAGES TO NATIVE WARM-SEASON GRASS

Introduction

Agricultural intensification supplies food to a growing human population by increasing productivity per unit of area through greater inputs of fertilizers and pesticides (Tilman et al. 2001). However, intensive agriculture also reduces the compositional and structural diversity of local vegetation, negatively impacting biodiversity including native plants, birds, and insects (e.g., Donald et al. 2001, Fuhlendorf and Engle 2001, Benton et al. 2002, Kleijn et al. 2009). Developing agricultural practices that can meet future increases in food demand without incurring additional environmental costs is critical to avoiding further biodiversity loss (Tilman et al. 2001).

In the United States, intensive management is often recommended for livestock production, including high stocking rates and uniform distribution of grazers (Fuhlendorf and Engle 2001, Toombs and Roberts 2009). Exotic forages are also widely established (Barnes et al. 2013, Fulbright et al. 2013), and these forages can support high grazer densities with large inputs of fertilizer (Monson and Burton 1982, Burns et al. 1984, Phillips and Coleman 1995). However, price of nitrogen-based fertilizers can be highly volatile (Huang et al. 2009), and high fertilizer costs may negate any additional revenue generated by greater forage yield from additional nutrient inputs (Coleman et al. 2001,
Deak et al. 2010). High stocking rates and fertilizer use may also increase environmental costs via nonpoint source water and air pollution (Stout et al. 2000, Tilman et al. 2002, Eickhout et al. 2006) and emissions of N$_2$O, a greenhouse gas (Snyder et al. 2009, Liebig et al. 2010).

Native warm-season grasses (NWSG) are increasingly promoted as a sustainable alternative to exotic grass forages (Taylor 2000, Harper et al. 2007). Varieties of NWSG can be adapted to local growing conditions, can tolerate poor soil conditions (Jung et al. 1988), and do not require heavy nutrient inputs (Brejda et al. 1995). Fertilizer applications are discouraged because they may reduce native grass establishment success (Doll et al. 2011) and encourage growth of weeds (Berg 1995). Establishing native grasses as a polyculture also has the potential to increase grassland productivity and nutrient retention (Tilman et al. 1996, Sanderson et al. 2005, Deak et al. 2010). Species of NWSG differ in their growth and phenology (Ball et al. 2007), so polycultures can provide extended forage production within a season while tolerating drought and extreme temperatures (Sanderson et al. 2005, Harper et al. 2007, Deak et al. 2010). In addition, native forages are managed less intensively than exotic forages, resulting in higher average daily gain (ADG) for cattle grazing NWSG at lower stocking rates (Phillips and Coleman 1995, Burns and Fisher 2013). NWSG may also be more profitable due to higher production costs of more intensively-managed exotic forages (Phillips and Coleman 1995, Coleman et al. 2001, Gillen and Berg 2001).

Native forages may also offer benefits to wildlife such as grassland birds, whose populations exhibited steep declines during the 20$^{th}$ century (Sauer and Link 2011). Exotic forages are highly unsuitable for most wildlife due to low structure of sod-forming
grasses (Barnes et al. 2013, Fulbright et al. 2013), and contemporary management typically limits availability of nesting habitat for tall structure specialists (Fuhlendorf and Engle 2001, With et al. 2008). In contrast, native grasses have a bunched growth form that certain grassland birds will readily use for nesting (Hughes et al. 1999, Chapter 3), and reduced grazing intensity of native grass forages may benefit species such as the Dickcissel (*Spiza americana*; With et al. 2008), a tall grass specialist and neotropical migrant (Temple 2002).

In the Southeastern United States, bermudagrass (*Cynodon dactylon*) and tall fescue (*Schedonorus arudinaceus*) are the two most common exotic forages, established on >100 million ha (Barnes et al. 2013). Incorporating NWSG in cattle production therefore has potential to substantially improve sustainability and wildlife conservation on private lands in this region. However, NWSG conversion incurs costs from establishment and loss of revenue while pastures are taken out of production for 2–3 years. The possibility of not recovering these losses due to establishment failure, variation in market conditions, or weather therefore presents substantial risks for producers. Despite potential economic and environmental benefits of NWSG, uncertainty regarding establishment and risk remains a significant barrier to incorporating these grasses in livestock operations (Taylor 2000, Doll and Jackson 2009). Information is also needed on the costs and returns from NWSG conversion to assist in distributing cost-share incentives to producers (Claassen et al. 2008). I therefore conducted a partial budget analysis to compare the relative net benefit in converting exotic grass pastures to NWSG using production costs and cattle gains from a study in northeast Mississippi during 2011–2012. I also conducted sensitivity analyses to evaluate the contribution of
factors to marginal rate of return. Finally, I used estimates of avian productivity from my study sites for Dickcissels (Chapter 3) to determine the net benefit to grassland avifauna from investment in NWSG conversion.

Methods and Analysis

Study Site and Experiment

We assigned 9 pastures (range = 6.4–10.5 ha) to one of three treatments replicated in three blocks at Mississippi State University’s Prairie Research Unit (PRU) in Monroe Co., Mississippi, USA. Treatments included a grazed mix of bermudagrass and tall fescue (hereafter, grazed mixed exotic pasture, or GMEP); Indian grass monoculture (Sorghastrum nutans, “Kentucky ecotype”; hereafter, grazed Indian grass native pasture, or GINP); and grazed mixed native pasture (GMNP) planted with big bluestem (Andropogon gerardii, “Kaw”), little bluestem (Schizachyrium scoparium, “Aldous”), and Indian grass. During fall 2007, bermudagrass and tall fescue in native grass pastures were treated with imazapyr (Chopper™) and glyphosate (Table 5.1). The following spring (2008), native pastures were prescribed burned and treated with Journey™ (imazapic + glyphosate) and glyphosate to control annual grasses and residual exotic forage grasses. Native pastures were then planted in May using a no-till drill (Truax Company, Inc., New Hope, MN). During production years (2011 and 2012), we used management regimes typically recommended for exotic or native pastures, respectively. For example, each spring all native pastures were prescribed burned prior to the addition of cattle (Bos taurus). Pastures were continuously stocked mid-May through September with fall-born Angus × Hereford steer calves (average initial body weight [BW]: 237±1.5 kg in 2011 and 262±2.2 kg in 2012) allotted to treatments and pastures by BW at a rate of
2.7 steer ha\(^{-1}\). Following soil tests conducted each spring, fertilizer was applied at 33.6 kg ha\(^{-1}\) for native grass pastures and 67.3 kg ha\(^{-1}\) for GMEP. In June 2012, we applied 2,4-D herbicide to all pastures at a rate of 2.56 L ha\(^{-1}\) to control competition from broadleaf forbs.

Total growing precipitation (April–October, recorded by a weather monitoring station in Aberdeen, MS; NCDC 2014) was 711.7 mm in 2011 and 808.4 mm in 2012, whereas the 30-y average (1983–2012) was 744.7 mm. Total precipitation in 2011 was unusually low in May (35.6 mm) and July (33.2 mm), but increased in June (100.4 mm) and August (92.3 mm). In 2012 total precipitation in May (66.4 mm) and June (59.0 mm) were well below the 30-y averages (129.4 and 114.4 mm for May and June, respectively). Precipitation subsequently increased in July (129.6 mm) and August (277.5 mm). Nevertheless, the prolonged drought earlier in the season necessitated uniform reductions in stocking rate by one third 10–11 July 2012.

**Average Daily Gain Analysis**

I used linear mixed models from the package *nlme* (Pinheiro et al. 2014) in R (version 3.0.2, R Development Core Team 2014) to test effects of treatment and year on ADG (kg d\(^{-1}\)). I computed ADG for each animal by subtracting starting weights in May from end weights measured when steers were removed in September, then dividing by the number of days grazed in each season (111 and 113 days in 2011 and 2012, respectively). Following Zuur et al. (2009), I began by fitting the most complex model, which included fixed effects of treatment, year, and treatment × year interaction, and a random effect of pasture. Then I used likelihood ratio tests to first test for support for the
random effect, and then for sequentially more parsimonious models until dropping additional covariates did not improve fit. I report mean and SE of treatment estimates, and use 95% confidence intervals (CI) to compare treatments.

**Relative Profitability Analysis**

I constructed partial enterprise budgets for each treatment by only including costs that varied among treatments, thus permitting calculation of the marginal rate of return (MRR) for converting GMEP to native grass pasture (CIMMYT 1988). For each treatment and year, I calculated total marginal cost, net benefit, and marginal net benefit for the two native treatments relative to GMEP. Budgets excluded costs for pasture rental, fertilizer application, procurement and marketing costs, and fixed costs such as depreciation, insurance, and taxes, because these should be identical across treatments. All costs and revenue were converted to per ha basis, given a stocking rate of 2.7 steers ha$^{-1}$, and I used the United States Consumer Price Index to adjust prices for inflation to 2011 dollars (Bureau of Labor Statistics 2013).

For NWSG treatments, establishment costs included herbicide purchase and costs associated with two applications for bermudagrass and tall fescue eradication in fall 2007. In spring 2008, costs included fire lane establishment, prescribed fire, pure live seed purchase, no-till planting, and one at-plant herbicide application of glyphosate + imazapic (Table 5.1). Seeding rate for GMNP was higher than GINP due to lower germination rate of little bluestem (Steinberg 2002). Establishment also included real discount rate on operating capital over 6 months. I calculated discount rates by averaging annual interest rates for 2003-2012 (2.5%; U.S. Department of Labor 2013) and subtracted this from a nominal rate reported by a University of Tennessee beef enterprise
budget (8%; Rhea et al. 2007). Establishment costs ($P$) were then prorated using an annuity formula: $A = P \frac{r(1+r)^t}{(1+r)^t-1}$, with an $r = 5.5\%$ annual interest rate prorated over $t = 10$ years (Doxon et al. 2012). Additionally, converting exotic forages to NWSG incurs opportunity cost of taking pastures out of production. Therefore, I summed cash rent reported by NASS (2013b) for pastureland in Monroe Co., Mississippi, during 2009–2010, adjusting for inflation, and included this value among establishment costs for each NWSG treatment. Instead of establishment costs, GMEP pastures incurred maintenance costs from two applications of 75% sulfosulfuron (Outrider™) at 0.14 kg ha$^{-1}$ for bermudagrass release in spring 2009 and 6-month operating capital, the total of which was then prorated over 10 years.

During operation years (2011, 2012), native grass pastures incurred maintenance costs I used price and rates for prescribed fire from my study at the PRU, adjusting fire lane costs for mean pasture size and perimeter length. Fertilizer rates were based on actual use during the study, and I used annual prices of ammonium nitrate reported by NASS (2013a) for East South Central United States. Interest on operating capital was also included. Inputs of lime and phosphorous may incur additional costs to a grazing enterprise, though in my study application rates for lime and phosphorous related to individual pasture condition rather than stand type. As such, these inputs were equivalent to other pasture maintenance items that did not vary by treatment, such as fencing, and therefore were not included in the partial budget analysis. I calculated cost from steer purchase by multiplying treatment-specific mean starting weights by stocking rate and price paid for steers and heifers in May ($\text{kg}^{-1}$) reported by NASS (2013a). After the summer grazing period, I assumed all steers were finished on shelled corn and soybean
meal for 130 days, yielding an ADG of 1.32 kg day$^{-1}$ (Rhea et al. 2007). Cost of capitalization of steer and other operation costs were calculated over the length of the grazing season and finishing period each year. I also included costs from death loss during operation (2%), and death loss (3%) and shrink (2%) during procurement (Rhea et al. 2007). I estimated final weights using treatment- and year-specific ADG estimates multiplied by number of summer grazing days in a season, adding the May starting weights and weight from finishing. I then computed annual gross income as the product of final weight, price received for steers the following January reported by NASS (2013a), and the stocking rate. To account for the mid-season uniform reduction of stocking rates in 2012 (see Study Site and Experiment), I repeated the procedure for modeling ADG, this time with cattle weights from July, and calculated the revenue from selling one third of the herd with price received reported for July 2012 (NASS 2013a). The revenue received from selling the rest of the herd the following January was correspondingly adjusted to two-thirds the initial stocking rate.

I calculated MRR for NWSG conversion (GINP or GMNP) by dividing the marginal net benefit (difference in net benefit between NWSG treatment and GMEP) by the total marginal cost (difference in total cost between NWSG treatment and GMEP) and multiplied the result by 100% to convert to percentage. The resulting value is interpreted as the additional benefit (after investment in NWSG conversion) that the enterprise would receive relative to GMEP (CIMMYT 1988). I also conducted sensitivity analyses by varying individual parameters in each partial budget by ±20% and monitoring changes in MRR for GINP and GMNP, thus evaluating the relative importance of each parameter. I used prices and rates from 2011 as a baseline scenario,
and parameters to vary included January selling price, ADG, fertilizer price, seed prices, prescribed fire, and interest rates. I also tested the response of MRR to total establishment costs of GINP and GMNP (before being prorated) because variation in establishment success determines the final price paid for establishment.

Finally, cattle prices may have a large influence on profitability of a grazing enterprise (Manley et al. 1997), and it is useful to examine how changes in price would affect MRR beyond the two years of my study. Therefore, I calculated MRR from NWSG conversion for the previous 15 years using my 2011 partial budget as a baseline, and with May price paid (1999–2013) and January price received (2000–2014; NASS 2013a). I then examined the number of years that NWSG conversion yielded a positive rate of return, and calculated the breakeven value for price received.

**Wildlife Response**

During May–August in 2011 and 2012, I intensively searched each pasture every two weeks for Dickcissel nests (Chapter 3). Nest status was checked every 1–4 days to determine nest fate and estimate daily survival rates (DSR) for each treatment. I used estimates of nest density, brood size, and nest survivorship to compute productivity estimates (no. fledglings ha\(^{-1}\)) for each treatment and year (Chapter 3). Using Dickcissel productivity is useful for comparing wildlife benefits because my results can then be interpreted as the relative price per additional fledgling for converting GMEP to either NWSG treatment (Musters et al. 2001). However, previous attempts at relating management practices to nest density assumed perfect detection of nests (Musters et al. 2001, Oosterveld et al. 2011), but this assumption is unlikely due to variation in vegetation structure and female nest attendance (Chapter 2, Giovanni et al. 2011, Powell
et al. 2012). My analysis differs because I used the encounter history of nest search events to estimate nest density while accounting for detection probability (Chapter 2), thus providing an unbiased estimate of wildlife response to conservation-oriented management. I used a partial budget approach to calculate MRR from investment in terms of Dickcissel productivity. In this case, I replaced net benefit with treatment-specific productivity estimates, and divided the marginal net benefit (difference in productivity between NWSG and GMEP) by the marginal cost to yield a marginal rate of return in productivity. I interpreted this value as the change in productivity for every $100 invested in NWSG conversion.

Results

Average Daily Gain Analysis

For May–September ADG, likelihood ratio tests indicated support for inclusion of a random effect for pasture ($L = 20.19, df = 1, P < 0.001$). Inclusion of a Treatment × Year interaction was not supported ($L = 3.60, df = 2, P = 0.17$), but dropping treatment ($L = 13.07, df = 2, P = 0.002$) or year ($L = 51.58, df = 1, P < 0.001$) effects did not improve fit. Overall, ADG was lower in 2012 than 2011 ($\beta = -0.291, SE = 0.039, t_{350} = 7.418, P < 0.001$), and ADG for GMEP was 33% and 31% lower than GINP and GMNP in 2011, respectively, and 42% and 40% lower in 2012 (Table 5.2). Confidence intervals for ADG overlapped broadly between GINP and GMNP. Analysis of ADG for May–July supported inclusion of a pasture random effect ($L = 3.28, df = 1, P = 0.035$), but not Treatment × Year interaction ($L = 3.08, df = 2, P = 0.21$) or Year ($L = 2.48, df = 1, P = 0.12$). Average daily gain was again similar between both native grass treatments,
whereas ADG for GMEP was 34% and 25% lower than GINP and GMNP, respectively (Table 5.2).

**Partial Budget Analysis**

Establishment cost was 10.5% greater for GMNP ($880.12 ha\(^{-1}\)) than GINP ($796.13 ha\(^{-1}\)), driven by higher cost of pure live seed for the native grass mix (Table 5.1). When prorated over ten years, establishment cost per annum was $116.76 ha\(^{-1}\) for GMNP and $105.62 ha\(^{-1}\) for GINP. In contrast, initial maintenance cost for GMEP incurred a prorated annual cost of $12.75 ha\(^{-1}\). Both years, all treatments received positive net revenue from operations, though net revenue declined by $>75\%$ from 2011 to 2012 (Table 5.3). However, higher net benefits in native treatments relative to GMEP compensated for higher total marginal costs, with 35.9\% and 28.5\% MRR for GINP in 2011 and 2012, respectively. Marginal rate of return was also positive for GMNP in 2011 (12.8\%), but not in 2012 (–2.0\%). The disparity between the two years was likely driven by a combination of lower ADG (Table 5.2), heavier starting weights, and 18\% higher spring purchase price for cattle in 2012 but only a 5\% increase in price received in the fall (Fig. 1a). Price of ammonium nitrate was also 5\% higher in 2012 than 2011.

Sensitivity analyses indicated that ADG and selling price contributed greatly to changes in MRR for GMNP, with $>150\%$ change in MRR from 20\% change in gain or selling price (Table 5.4). GINP responded similarly, but to a lesser degree. Decreasing cost of prescribed fire and establishment had a positive effect on MRR, particularly for GMNP with $>50\%$ increase in MRR from each parameter. Fertilizer, seed, and interest rates had comparatively smaller effects on MRR.
During 2000–2014, price received in January for steers (adjusted for inflation) ranged from $2.11 kg\(^{-1}\) in 2000 to $3.32 kg\(^{-1}\) in 2013 (Fig. 5.1a) and was consistently lower than price paid the previous May except for 2013–2014. Assuming all other values were constant from the 2011 partial enterprise budget, GINP would yield a positive MRR for 11 of 15 years under consideration (Fig. 5.1b), with a breakeven selling price of 2.06 kg\(^{-1}\) (or $93.53 cwt\(^{-1}\)). Marginal rate of return would be positive for cattle grazing GINP each year that selling price was at or above this value, though for 1999–2000 MRR was near 0. By comparison, MRR from GMNP was positive for 4 of 15 years under consideration (Fig. 5.1c). The breakeven selling price for this treatment was $2.48 kg\(^{-1}\) (or $112.68 cwt\(^{-1}\)).

Dickcissel productivity decreased in all treatments from 2011 to 2012, though mean estimate of productivity was consistently greater in GMNP than GMEP and GINP (Fig. 5.2). Mean productivity estimates in GINP tended to be greater than in GMEP in 2011 but not 2012. In 2011, GINP increased productivity by 0.14 fledglings ha\(^{-1}\) relative to GMEP for every $100 invested, whereas productivity in GMNP increased by 0.31 for the same investment. In 2012, decreases in productivity for GINP lead to slightly negative MRR for every $100 investment (−0.02), whereas GMNP yielded a 0.27 increase in productivity. This suggests that a greater investment in GINP (such as by converting a larger area) would be required to achieve increases in productivity equivalent to GMNP.

**Discussion**

Given an enterprise that purchases steer in May, grazes continuously through summer, and sells the following January, NWSG conversion has clear potential to
produce positive MRR on investment relative to exotic grass pastures currently used for livestock production, even when including prorated costs from establishment. The comparative advantage of NWSG pastures over GMEP was primarily from higher ADG. Nutritional analysis of forages among my pastures indicated crude protein and digestibility were highest among GMEP pastures, likely a response to greater fertilizer application rates (Oloyede 2013). However, dry matter yield was higher among native grass pastures, especially for GINP during peak production (July), and therefore forage availability rather than quality may explain observed differences in ADG among treatments. Average daily gain estimated for GMEP in 2011 was comparable with gains reported previously for bermudagrass with higher stocking rates but also with greater nutrient inputs (Utley et al. 1976, Burns et al. 1984, Burns and Fisher 2008, Burns et al. 2009, Burns and Fisher 2013). Higher ADG for NWSG is also consistent with previous studies (Coleman et al. 2001, Gillen and Berg 2001, Burns and Fisher 2013), although increased stocking rates in exotic grass treatments often produced total gain ha⁻¹ equivalent to native grass pasture. However, higher stocking rates in these intensive systems also incurred higher production costs, making native grass systems more profitable overall (Phillips and Coleman 1995, Coleman et al. 2001, Gillen and Berg 2001). Higher stocking rates also exposes producers to greater risk from variability in weather (Parsch et al. 1997) and cattle price (Manley et al. 1997).

Importance of forage availability is also illustrated by the reduction in ADG that coincided with drought in 2012. Drought reduces profitability of grazing enterprises (Dunn et al. 2010), and all treatments yielded lower net revenues in 2012 than in 2011. Drought resistance is touted as a potential benefit for native warm-season grasses due to
their deep root growth (Harper et al. 2007), and for polycultures over monocultures (Sanderson et al. 2005, Deak et al. 2010). However, in my study the response to drought from NWSG and GMEP was similar because a Treatment × Year interaction for ADG was not supported. This trend may reflect the recent establishment of the NWSG pastures, but may also be due to the fairly dry conditions of both years of my study, preventing me from quantifying the response of forages to the full range of precipitation experienced in this region.

**Economic Implications**

Price of nitrogen fertilizer may affect rates of return for NWSG conversion (Doxon et al. 2012), and I found a positive effect of nitrogen prices on MRR. GMEP required twice the amount of fertilizer than native pastures, and as fertilizer prices increase, the difference in cost between GMEP and native pastures also increases, resulting in a higher MRR for native pastures. However, sensitivity analysis indicated that the response to fertilizer prices was relatively small, indicating that benefits from increased ADG due to NWSG conversion surpassed potential savings from reduced fertilizer costs. One study of fescue-bermudagrass pastures demonstrated that higher gains (max. 0.66 kg d⁻¹) could be achieved at higher stocking rates with annual fertilizer applications up to 4.6 times greater than in my study (Franzluebbers et al. 2012). Applying fertilizer at such rates would increase fertilizer costs for GMEP from $36–38 ha⁻¹ to $164–173 ha⁻¹, which approaches the $182–194 ha⁻¹ from maintenance and prorated establishment costs of NWSG pastures. However, intensive management of exotic forages is also accompanied with other costs and risks beyond the price of
fertilizer, such as greater nonpoint source pollution and financial risk from fluctuations in fertilizer prices and drought.

Importance of ADG and selling price also suggests that the advantage of NWSG conversion over current production from exotic forages may depend on external factors such as beef markets and weather. January price received for steer surpassed the breakeven price in MRR ($2.48 kg\(^{-1}\)) for GMNP during the last three years under consideration (2012–2014), so if these trends persist there is a high likelihood that conversion to either GINP and GMNP would yield a positive MRR. Marginal rate of return was also sensitive to establishment costs and price of seeds. Establishment success may vary due to precipitation (Bakker et al. 2003) and control of exotic warm-season grasses (Barnes 2004), and in my study the incomplete eradication of bermudagrass followed by disturbance from grazing likely encouraged the spread of this grass in native pastures (see Chapter 4). Continuation of this study in subsequent years may therefore have incurred additional costs for herbicide treatment and removing NWSG pastures from production for recovery. These results illustrate several important potential sources of risk that producers should consider when investing in NWSG conversion.

**Wildlife Response**

Whereas lower establishment costs and slightly higher ADG for GINP led to a higher financial MRR for this treatment, MRR on Dickcissel productivity was consistently higher for GMNP. The difference in productivity between the grazed native grass treatments was a function of higher nest densities in GMNP (Chapter 2) because daily survival rates and brood size were similar to GINP (Chapter 3), suggesting a greater availability of nest sites in the polyculture than in the NWSG monoculture. Sensitivity
analysis suggests that subsidies aimed at promoting wildlife should seek to offset higher seed and establishment costs of GMNP, and reduce the comparative advantage of higher ADG with GINP given variable livestock prices.

Higher MRR in Dickcissel productivity for GMNP also indicates fledglings are relatively more expensive to produce with GINP. Interpreted from this perspective presents a shift from payment for actions toward payment for results. Instead of mandating a specific management regime, result-oriented payments are offered to producers for specific outcomes such as for number of nests found and protected (Musters et al. 2001). Benefits of result-oriented schemes over payment for actions (reviewed by Burton and Schwarz 2013) include greater cost-efficiency of conservation subsidies, increased flexibility for landowners in making management decisions, and stronger ties between landowners and biodiversity by treating environmental outcomes as another source of revenue in their enterprise. For example, if producers managing NWSG grazing are compensated for each Dickcissel nest in their pasture, they may be further motivated to reduce stocking rates during drought to maintain tall cover and nest site availability. However, ability of landowners or monitoring agencies to effectively and efficiently estimate nest density remains a significant challenge in using such an index as a biodiversity indicator for result-oriented payments (Matzdorf et al. 2008, Matzdorf and Lorenz 2010, Burton and Schwarz 2013).

Conclusions

The ecological value of low-intensity agriculture is widely recognized, though focus of conservation policy is typically directed toward compensating producers for loss in productivity (e.g., Bignal and McCracken 1996, Musters et al. 2001). Proponents of
land-sparing (maximizing productivity on agricultural lands to avoid further cultivation of natural areas) also assumed that biodiversity benefits from land-sharing required decreased agricultural intensity, and thus productivity (e.g., Green et al. 2005, Phalan et al. 2011). However, my study suggests that at equivalent stocking rates NWSG pastures may yield greater livestock gain than exotic forages despite lower intensity (reduced fertilizer inputs), and the additional net benefit for wildlife suggests a win-win scenario for producers and conservationists. Furthermore, the economic benefit of intensive grazing is increasingly questioned given the higher production costs due to heavy fertilizer inputs, which then reduce the return on investment from each animal in production (Coleman et al. 2001, Fuhlendorf and Engle 2001, Gillen and Berg 2001, Burns and Fisher 2013). Currently the majority of Natural Resources Conservation Service (NRCS) assistance and funding promotes intensive livestock management on private lands, such as through increased fencing and water source distribution (Toombs and Roberts 2009). Diverting efforts instead toward promoting NWSG conversion and less intensive management may increase the sustainability and wildlife value of private pastureland in the United States.

My analysis shows that reduction in costs from establishment and management of NWSG can reduce risk from NWSG conversion through substantial increases in MRR. This indicates several potential avenues for subsidies and cost-share to encourage participation. For example, working-land programs such as the Environmental Quality Incentives Program (EQIP) offer payments for a variety of environmentally-beneficial structural and management practices, and >60% of funds are appropriated for livestock producers (Claassen et al. 2008). Surveys indicate a general interest in conservation and
the environment among cattlemen (Jacobson et al. 2003, Doll and Jackson 2009, Willcox et al. 2012), which suggests that they may be receptive to NWSG. Furthermore, successful programs such as the Conservation Reserve Program may have unwittingly discouraged enrollment by excluding grazing and haying from contracts (Esseks and Kraft 1986), so the ability of cattlemen to keep land in production will likely encourage participation in programs that promote NWSG conversion. Many landowners are unaware of the availability and their eligibility for conservation programs, and this is consistently a major factor limiting landowner participation (Esseks and Kraft 1986, Jacobson et al. 2003, Doll and Jackson 2009, Lubell et al. 2013). Active outreach is therefore needed to promote the different cost-share programs available for NWSG conversion while ensuring that both landowners and funding agencies can make informed decisions.
Table 5.1  Rate and cost of items for establishment of GINP and GMNP at the Mississippi State University Prairie Research Unit in Prairie, MS, USA.

<table>
<thead>
<tr>
<th>Item</th>
<th>Function</th>
<th>Rate (ha⁻¹)</th>
<th>Costa ($ ha⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Imazapyr</td>
<td>Pre-plant bermudagrass eradication</td>
<td>3.51 L</td>
<td>139.84</td>
</tr>
<tr>
<td>Glyphosate</td>
<td>Pre-plant tall fescue eradication</td>
<td>9.37 L</td>
<td>82.61</td>
</tr>
<tr>
<td>Imazapic + Glyphosate</td>
<td>At-plant herbicide</td>
<td>1.61 L</td>
<td>46.58</td>
</tr>
<tr>
<td>Glyphosate</td>
<td>At-plant herbicide</td>
<td>2.34 L</td>
<td>20.66</td>
</tr>
<tr>
<td>Spray</td>
<td>Herbicide application</td>
<td>3</td>
<td>77.47</td>
</tr>
<tr>
<td>Fire lane</td>
<td>Prescribed fire</td>
<td>43.24 m</td>
<td>4.08</td>
</tr>
<tr>
<td>Fire</td>
<td>Prescribed fire</td>
<td>1</td>
<td>51.64</td>
</tr>
<tr>
<td>Seed and no-till planting</td>
<td>GMNP establishment</td>
<td>13.45 kg PLS</td>
<td>349.98</td>
</tr>
<tr>
<td>Seed and no-till planting</td>
<td>GINP establishment</td>
<td>8.97 kg PLS</td>
<td>268.23</td>
</tr>
<tr>
<td>Pastureland rent</td>
<td>Opportunity cost</td>
<td>2 years</td>
<td>86.01</td>
</tr>
</tbody>
</table>

aCosts were converted to 2011 prices, accounting for inflation.
Table 5.2  Mean average daily gain (kg d⁻¹, and 95% CI) for steer estimated from linear mixed models by year, removal month, and treatmentᵃ.

<table>
<thead>
<tr>
<th>Year</th>
<th>Month</th>
<th>GMEP</th>
<th>GINP</th>
<th>GMNP</th>
</tr>
</thead>
<tbody>
<tr>
<td>2011</td>
<td>September</td>
<td>0.42 (0.32−0.51)</td>
<td>0.63 (0.54−0.73)</td>
<td>0.61 (0.52−0.70)</td>
</tr>
<tr>
<td>2012</td>
<td>September</td>
<td>0.29 (0.19−0.38)</td>
<td>0.50 (0.40−0.60)</td>
<td>0.48 (0.38−0.57)</td>
</tr>
<tr>
<td>Pooledᵇ</td>
<td>July</td>
<td>0.57 (0.51−0.63)</td>
<td>0.87 (0.70−1.03)</td>
<td>0.76 (0.59−0.93)</td>
</tr>
</tbody>
</table>

ᵃTreatments include grazed mixed exotic pasture (GMEP), grazed Indian grass pasture (GINP), and grazed mixed native pasture (GMNP).
ᵇEffect of year was not supported for July ADG models, so estimates were pooled across years.

Table 5.3  Costs and revenue ($ ha⁻¹) from partial enterprise budgets used to calculate marginal rate of return for conversion of GMEP to GINP or GMNP.

<table>
<thead>
<tr>
<th>Treatmentᵃ</th>
<th>2011</th>
<th>2012</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Total cost</td>
<td>Total revenue</td>
</tr>
<tr>
<td>GMEP</td>
<td>2043.02</td>
<td>3444.20</td>
</tr>
<tr>
<td>GINP</td>
<td>2176.32</td>
<td>3625.36</td>
</tr>
<tr>
<td>GMNP</td>
<td>2188.98</td>
<td>3607.98</td>
</tr>
</tbody>
</table>

ᵃTreatments include grazed mixed exotic pasture (GMEP), grazed Indian grass native pasture (GINP), and grazed mixed native pasture (GMNP).

Table 5.4  Sensitivity analysisᵃ of marginal rate of return from conversion of GMEP to GINP and GMNP.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Baseline value</th>
<th>20% decrease GINP</th>
<th>20% decrease GMNP</th>
<th>20% increase GINP</th>
<th>20% increase GMNP</th>
</tr>
</thead>
<tbody>
<tr>
<td>Selling Price</td>
<td>2.93 ($ kg⁻¹)</td>
<td>−77.2</td>
<td>−166.1</td>
<td>72.6</td>
<td>184.6</td>
</tr>
<tr>
<td>ADGᵇ</td>
<td>0.63, 0.61 (kg day⁻¹)</td>
<td>−75.3</td>
<td>−173.5</td>
<td>73.9</td>
<td>170.0</td>
</tr>
<tr>
<td>Seedᵇ</td>
<td>164.60, 248.19 ($ ha⁻¹)</td>
<td>15.2</td>
<td>45.5</td>
<td>−10.6</td>
<td>−36.8</td>
</tr>
<tr>
<td>Prescribed fire</td>
<td>51.64 ($ ha⁻¹)</td>
<td>38.2</td>
<td>80.6</td>
<td>−31.8</td>
<td>−53.2</td>
</tr>
<tr>
<td>Fertilizer</td>
<td>0.480 ($ kg⁻¹)</td>
<td>−10.3</td>
<td>−21.9</td>
<td>10.9</td>
<td>23.1</td>
</tr>
<tr>
<td>Interest</td>
<td>5.5%</td>
<td>15.1</td>
<td>39.3</td>
<td>−14.3</td>
<td>−37.1</td>
</tr>
<tr>
<td>Establishmentᵇ</td>
<td>796.13, 880.12 ($ ha⁻¹)</td>
<td>71.4</td>
<td>168.4</td>
<td>−51.8</td>
<td>−121.3</td>
</tr>
</tbody>
</table>

ᵃI conducted sensitivity analysis by varying 2011 partial budget parameters (±20%) and quantifying the percent change in marginal rate of return.
ᵇBaseline values are reported for GINP and GMNP, respectively.
Figure 5.1  Price paid in May (1999–2013) and price received in January (2000–2014) for steers reported by NASS (a), and corresponding marginal rate of return for converting GMEP to GINP (b) and GMNP (c), given 2011 partial budget values at the Mississippi State University Research Unit in Monroe Co., MS, USA, 2011–2012.
Figure 5.2  Mean estimates of Dickcissel productivity (and 95% CrI) by treatment (Chapter 3).
CHAPTER VI
GENERAL CONCLUSIONS

The results of my study suggest a positive response from Dickcissels and certain arthropod taxa to NWSG conversion and a negative effect of grazing. Nest site availability, as indicated by my unbiased estimates of nest density, was the primary driver of higher Dickcissel productivity in non-grazed NWSG because estimates of DSR and brood size were largely similar among treatments. Importance of structure is also illustrated by the apparent equivalence of arthropod biomass among grazed native and exotic polycultures and native monocultures, at least in the short-term. One important caveat is that I lacked a non-grazed exotic grass treatment, and therefore I could not test response of wildlife to grazing in exotic forages. However, management for bermudagrass typically requires close grazing and haying (Ball et al. 2007), so it is unlikely that stands of bermudagrass would be left idled or would attain the height of non-grazed NWSG in this region. Tall fescue is also grazed and hayed, but substantial coverage of this grass may be idled through the Conservation Reserve Program (CRP; Carmichael 1997). One comparison between idled tall fescue and NWSG fields found similar total density and biomass of invertebrates (Fettinger et al. 2002), suggesting further support for the role of disturbance in shaping arthropod communities in the Southeast, though further study is needed.
Conservationists that wish to promote NWSG conversion should consider the importance of disturbance and structure in achieving their objectives. Heavy grazing may be detrimental to native grass stands over time, reducing coverage of perennial C₄ grasses (Hickman et al. 2004, Bouressa et al. 2010). Interestingly, the two native grazed treatments exhibited large inter-annual increases in bermudagrass coverage. Disturbance from grazing increased invasion of exotic grasses in other systems (Bock et al. 2007), and preferential grazing for NWSG over bermudagrass (Burns et al. 1991) may have reduced coverage of native grasses and released remnant bermudagrass patches to spread. My study therefore suggests NWSG conversion is sensitive to success of exotic grass eradication and the degree of disturbance following establishment. However, management of native forages typically precludes heavy stocking rates and may require resting (Mousel et al. 2003, Chamberlain et al. 2012). Furthermore, results from this study (Chapter 5) and others (Phillips and Coleman 1995, Coleman et al. 2001, Gillen and Berg 2001) suggest producers will not bear a financial cost for reduced management intensity on NWSG.

Given the extent of exotic forages in the Southeast (Barnes et al. 2013), even converting a subset of pastures to NWSG could increase native grass coverage by millions of hectares, illustrating the importance of private lands for conservation. My results indicate that native grasses are competitive with livestock production on exotic forages at equivalent stocking rates, and may be a viable alternative to current summer grazing enterprises. Incorporating NWSG in livestock production may also benefit declining tall grass birds in this region. Additional study is needed on the long-term viability of NWSG conversion for producers, and on the appropriate grazing regime that
promotes cattle gain without reducing nest site availability or encouraging bermudagrass spread.
LITERATURE CITED


Oloyede, B. 2013. Nutritional profile of native warm-season grass grown as a mono- or multi-species pasture. Thesis, Mississippi State University, Mississippi State, Mississippi, USA.


Skutch, A. F. 1949. Do tropical birds rear as many young as they can nourish? Ibis 91:430–455.


