**Converting exotic forages to native warm-season grass can increase avian productivity in
beef production systems**

Adrian P. Monroe,^{a,*} Richard B. Chandler^b, L. Wes Burger, Jr.^a, and James A. Martin^{a,1}

^aDepartment of Wildlife, Fisheries, & Aquaculture, Mississippi State University, Mississippi
State, MS 39762, USA

^bWarnell School of Forestry and Natural Resources, Savannah River Ecology Lab, University of
Georgia, Athens, GA 30602, USA

*Corresponding author. Present address: Natural Resource Ecology Laboratory, Dept. 1499,
Colorado State University, Fort Collins, CO 80523, USA.

Email addresses: apmonr@gmail.com (A.P. Monroe), rbchan@uga.edu (R.B. Chandler),

lwb6@msstate.edu (L.W. Burger), jmart22@uga.edu (J.A. Martin)

¹Present address: Warnell School of Forestry and Natural Resources, University of Georgia,
Athens, GA 30602, USA

ABSTRACT

Grasslands are among the most imperiled ecosystems in the world, and establishment of exotic forage grasses and management for uniform utilization may have contributed to population declines of many obligate grassland bird species in North America. Native warm-season grasses (NWSG) are increasingly promoted as viable alternatives to exotic forages currently in production such as bermudagrass (*Cynodon dactylon*) and tall fescue (*Schedonorus arundinacea*), but structure of native bunchgrasses also may offer nesting habitat for birds such as the dickcissel (*Spiza americana*). Establishing NWSG pastures may thereby create an opportunity for land-sharing, where agriculture incorporates biodiversity-friendly practices. We investigated dickcissel responses to NWSG and grazing at the Prairie Research Unit in Monroe Co., Mississippi (USA), where we established a gradient of management intensity among four treatments in small, operational-scale pastures (6.4–10.5 ha). Treatments included grazed exotic forages, two grazed NWSG treatments including Indian grass (*Sorghastrum nutans*) monoculture and grazed mixed NWSG polyculture of Indian grass, little bluestem (*Schizachyrium scoparium*), and big bluestem (*Andropogon gerardii*), and a non-grazed NWSG polyculture treatment. We applied a multi-state capture-recapture model in a Bayesian framework to estimate dickcissel nest density and productivity while accounting for nest stage-specific variation in survival and detection. Nest density and productivity were consistently greater in non-grazed NWSG than grazed exotic pasture, whereas grazed NWSG productivity was intermediate but declined between years. We also found that variation in survival and density did not always correspond with estimated productivity, and thus solely relying on either parameter may be misleading when making inferences on habitat quality. These results suggest a positive response to NWSG among dickcissels in this system, but grazing may reduce nest site availability, and

consequently productivity. Native warm-season forages may be a viable land-sharing alternative by increasing productivity of tall structure specialists such as dickcissels compared with exotic grass pastures currently in production, but grazing should be managed to ensure availability of tall vegetation structure for nest sites.

Key words: Bayesian analysis, detection error, dickcissel, land-sharing, native warm-season grasses, *Spiza americana*.

1. Introduction

Conservation of biodiversity in agricultural landscapes often operates along a dichotomy of land-sparing and land-sharing (e.g., Phalan et al., 2011; Pimentel et al., 1992). Land-sharing proposes incorporating biodiversity-friendly practices with agriculture, whereas land-sparing advocates maximizing production on current agricultural lands while setting aside natural areas. This land-sparing/land-sharing debate has extended to temperate grasslands (e.g., Brown and McDonald, 1995; Egan and Mortensen, 2012; Hodgson et al., 2010; Wright et al., 2012), which are among the most imperiled ecosystems in the world (Hoekstra et al., 2005) and where livestock production is a widespread form of land-use (Asner et al., 2004). In North America, management for uniform vegetation structure and composition in pastures and rangelands is common and can be detrimental to native biodiversity by limiting opportunities for species that favor structural and floristic heterogeneity (Askins et al., 2007; Fuhlendorf et al., 2012; Toombs and Roberts, 2009). Although land-sparing efforts such as the Conservation Reserve Program (CRP) have been successful in providing habitat for multiple grassland birds (Askins et al., 2007; Vickery and Herkert, 2001), landowner participation may be sensitive to market factors. For example, demand for biofuels may prompt widespread conversion of CRP enrollments to corn and soybeans production (Wright and Wimberly, 2013). Given the projected global human

population growth through 2050 (UN DESA, 2015) and increased demand for meat in the developing world (Steinfeld et al., 2006), novel land-sharing approaches to pasture and rangeland management may be needed to alleviate stressors on biodiversity while also supporting food production (Askins et al., 2007).

In the Southeastern United States, monocultures of exotic forages such as bermudagrass (*Cynodon dactylon*) and tall fescue (*Schedonorus arundinacea*) are established across millions of hectares (Barnes et al., 2013) and can be managed with high stocking rates and large inputs of nitrogen fertilizer (Burns et al., 1984; Phillips and Coleman, 1995). Obligate grassland bird populations in North America have exhibited precipitous declines (Sauer and Link, 2011), and the structural and compositional homogeneity often created by contemporary grazing systems can reduce reproductive success of birds such as dickcissels (*Spiza americana*; Davis et al., 2016; With et al., 2008). Native warm-season grasses (NWSG) are increasingly promoted as a sustainable alternative to exotic forages because of their lower input requirements and drought tolerance (Harper et al., 2007), but NWSG also may create suitable nesting habitat for grassland birds (Giuliano and Daves, 2002; Harper et al., 2015; Hughes et al., 1999). In addition to the greater height and structural complexity of native bunchgrasses, these forages generally are not grazed as heavily as exotic grass pasture (Chamberlain et al., 2012; Harper et al., 2015; Mousel et al., 2003), and thus may retain structure for cover and nesting. Grazed NWSG therefore may be a land-sharing alternative to exotic forages and set aside programs, offering benefits for wildlife while also permitting beef production.

In this study we investigate use of native and exotic grass pastures by nesting passerines in Mississippi. We also surveyed non-grazed NWSG to evaluate effects of grazing on avian habitat quality and to include a land-sparing comparison. We focused on dickcissels because they are an

obligate grassland birds and tall structure specialists (Temple, 2002) and therefore are useful for examining effects of stand-type and grazing for species with similar preferences for tall structure (e.g., Henslow's sparrow [*Ammodramus henslowii*]; Winter, 1999; Zimmerman, 1988). Conservation implications also are relevant for this Neotropical migrant because their populations have declined in Mississippi (Sauer et al., 2014) and availability of tall structure is likely limited in pastures and rangeland currently managed for uniform utilization of forage (Fuhlendorf et al., 2012).

Avian habitat quality is commonly assessed through nest searching and monitoring to estimate nest survival rates (indices 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. Previous grassland bird studies typically evaluated nest densities using relative or apparent indices (e.g., Churchwell et al., 2008; Conover et al., 2011b; Hatchett et al., 2013). However, as with other survey methods, nest detectability is rarely 100%, so apparent indices may confound variation in true abundance with variation in detectability (Royle and Dorazio, 2008). An important advance in nest density estimation was proposed by Péron et al. (2014), who used a capture-recapture model to estimate waterfowl nest density while accounting for variation in nest survival and detectability. Here, we extend their approach to our study by using a multi-state capture-recapture model to account for nest stage-specific variability in survival, recruitment, and detectability. In addition, we use the nest density model to estimate the number of successful nests and compare productivity (fledglings ha⁻¹) among treatments. Because our model incorporates a detection process, these

productivity estimates include both nests observed to have fledged nestlings as well as successful but unobserved nesting attempts. We hypothesized that breeding dickcissels respond to pasture stand type through availability of suitable nest sites, predicting greater nest density and productivity in NWSG relative to exotic grass pastures, whereas grazing may reduce nest site availability for this tall structure specialist.

2. Methods

2.1. Study area

We conducted our study 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 19th century, native prairies in the Black Belt have been extensively reduced due to degradation and conversion to agriculture (Barone 2005). The landscape context of our experimental units was mostly exotic pastures and row-crop fields, interspersed with woodland corridors and blocks. Total growing season precipitation (April–October) was 712 mm and 808 mm in 2011 and 2012, respectively, and mean daily maximum temperature in July was similar between years (2011: 33.7°C; 2012: 33.4°C; NCDC, 2016).

We conducted nest searches in 12 pastures (range = 6.4–10.5 ha) at the PRU. Pastures were assigned one of four treatments, and each treatment was replicated three times. One treatment consisted of a grazed non-native grass mix of bermudagrass and tall fescue (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 NWSG polyculture 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 (NMNP). As an operation-scale study with pasture sizes within the range of beef production operations typically found in Mississippi and the Southeast (USDA NASS, 2014), each pasture was managed using conventional practices recommended for each treatment (H. Boland, personal communication). Management included prescribed fire for native treatments (grazed and non-grazed) in spring during each study year, and grazed treatments (native and exotic) were stocked continuously with fall-born steers from mid-May until September at 2.7 head ha⁻¹. Following results from soil tests, fertilizer was applied to exotic grass pastures at twice the rate as native grass treatments (67.3 kg ha⁻¹ vs. 33.6 kg ha⁻¹). Other management actions were required to mitigate changes in stand condition, including application of 2,4-D herbicide to all pastures (grazed and non-grazed) in June 2012 to control excessive forb cover. Additionally, although total growing season precipitation (April–October) was somewhat greater in 2012 (808 mm) than in 2011 (712 mm), precipitation before July was less in 2012 (194 mm) than 2011 (368 mm; NCDC, 2016), and as a result stocking rates in grazed treatments (native and exotic) were uniformly reduced by one third in July 2012. Additional details on pasture establishment and management are reported by Monroe (2014). Treatment effects therefore represent both stand-type and the cumulative effect of their respective management regimes.

2.2. Nest searching and monitoring

From mid-May through July each year, we used a rope-drag method (Winter et al., 2003) to search each pasture for nests once every two weeks (five searches in 2011, six in 2012). Beginning at one corner, three observers systematically traversed the entire pasture in parallel swaths, dragging a 30-m rope and noting 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 two observers with a third observer positioned in-between to spot flushing females. We 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 we varied the order in which we searched pastures within a day to reduce potential temporal biases in nest attendance by females (Davis and Holmes, 2012; Winter et al., 2003). We 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).

We 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. We also recorded whether females were present during initial nest discovery and subsequent nest visits. Nest age and stage were estimated by noting whether eggs felt warm (generally indicating incubation), by egg candling (Lokemoen and Koford, 1996), and with voucher photos of nestling development (R. Conover, personal communication). We similarly monitored nests found opportunistically (i.e., outside of search events, hereafter incidental nests).

2.3. Nest density modelling

We used a multi-state formulation of the Jolly-Seber (JS) capture-recapture model (Jolly, 1965; Kéry and Schaub 2012; Seber, 1965) within a Bayesian framework to estimate nest density in our study population. Based on bi-weekly nest search events and concurrent nest monitoring, we developed an encounter history and latent state history for each individual nest to derive treatment-specific estimates of detection (p) and daily survival (s) probabilities. As an open-population model, the JS model permits estimation of a larger (latent) superpopulation of nests

(with abundance N_s) that includes observed nests as well as unobserved nests. Variation in pasture nest abundance by treatment (α) was specified with a log-linear model (Chandler and Clark, 2014; Royle and Converse, 2014), and we modelled linear and quadratic terms (ζ) for seasonal nest initiation probability (Appendix A). The multi-state formulation of JS can account for nest-stage specific variability in detection and survival by estimating transition probabilities (ψ) between nest stages (i.e., from lay to incubation, and incubation to nestling stage). A unique feature of our model is the use of an additional transition probability to distinguish between nests that failed or fledged nestlings (ψ_3), allowing us to estimate the true (observed and unobserved) number of successful nests and, correspondingly, the number of fledglings produced from each nest and treatment (productivity; P). We further elaborate and justify our modelling approach in Appendix A.

Length of the lay stage (1–4 days in our study) was shorter than for other stages, and only one nest each year failed when last observed during the lay stage, suggesting we lacked sufficient data to estimate nestling survival (s_{1j}) for each treatment j . However, predation rates for altricial species are estimated to be higher during the nestling stage than during lay or incubation stages due to greater activity of provisioning adults (Jehle et al., 2004; Stake et al., 2005), so we assumed lay and incubation survival probabilities were equal ($s_{1j} = s_{2j}$). In addition, 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 stage (Giovanni et al., 2011; Powell et al., 2012; Winter et al., 2003). Therefore, we modelled detection conditional on female absence (β_1) or attendance (β_2), and we modelled female nest attendance probability (δ) for each stage and treatment to predict attendance for unobserved nests. We lacked data on female attendance during the lay stage for all treatments, so we

assumed δ was constant for the lay stage. We also did not include nest site vegetation covariates for nest attendance because previous analyses did not indicate that these were more important than treatment in our study system (Monroe, 2014). We lack data on the probability of missing a nest despite flushing a female, so β_2 may be an overestimate. However, with three observers present in each search group this bias was likely to be small. Another potential source of bias is from the search method itself, for example, if females remain on the nest despite use of the rope-drag method (Giovanni et al., 2011). To test if female dickcissels failed to flush from the rope-drag method, we 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 likely effective in our study, given female attendance.

We restricted analyses to nests found during bi-weekly nest search events because many incidental nests were found during visits to other nests, so their inclusion would bias our sample (and likely our estimates of nest density) towards pastures with many nests or higher nest survival. Preliminary analyses indicated treatment interactions with year, so we analyzed each year separately. We fit the nest density model using JAGS (version 3.4.0; Plummer, 2003) and the package *rjags* (Plummer et al., 2015) in R (R Development Core Team, 2015). Priors are reported with model code in Appendix B. We ran each model on three parallel chains, discarding 1,000 iterations for the adaptive phase and 500,000 iterations as burn-in, then saving 100,000 samples. We assessed convergence by visually examining the chains, and with the $\hat{R}$ statistic, which compares within and between variations of parallel chains (Gelman et al., 2014). The $\hat{R}$ statistic indicated that all but one of the structural parameters had achieved approximate convergence ($\hat{R} < 1.1$). The exception was ψ_3 (nestling to fledged transition probability, ψ_3) in

2012 ($\hat{R} = 1.18$), but examination of the traceplot and density plot for the parameter did not suggest that saving additional iterations would substantially affect our posterior estimates or inferences (Fig. C.1, Appendix C). We report mean posterior estimates and 95% Bayesian credible intervals (CI), and compare parameters with posterior predictive checks by computing the proportion of iterations where one parameter is greater than the other (e.g., $s_{3_GMEP} > s_{3_GINP}$). With a Bayesian approach, this yields a probability statement such that, for example, a value of 0.95 indicates a 95% probability that $s_{3_GMEP} > s_{3_GINP}$, and therefore strong support for a difference between the two parameters.

3. Results

We found 208 dickcissel nests over two years ($n = 85$ and 123 in 2011 and 2012, respectively). Clutch size and number of fledglings produced per successful nest were variable but generally similar among treatments (Table 1). Of these nests, 63 in 2011 and 87 in 2012 were found during nest search events and were used in the nest density model (thus excluding $n = 58$ incidentals).

3.1. State process

In 2011, there was weak support for greater nest density ($D = e^a$) in non-grazed NWSG than grazed exotic pasture ($\Pr[D_{NMNP} > D_{GMEP}] = 0.82$), whereas densities for grazed NWSG treatments were intermediate and more similar (Fig. 1). Density generally increased from 2011 to 2012 among treatments, except for grazed Indian grass pasture which declined substantially between years ($\Pr > 0.99$ that density was greater in other treatments than Indian grass pasture). Nest initiation probability declined over time during our survey period in 2011, although credible intervals for linear (ζ_1) and quadratic terms (ζ_2) overlapped 0 (Table 2). The following year, there was a negative linear trend and a positive quadratic trend. Transition probability estimates

were similar between years, and transition from the lay to incubation stage was greater than transition from the incubation to nestling stage ($\Pr[\psi_1 > \psi_2] = 1.00$ during both years; Table 2), likely reflecting the longer duration of incubation than the lay stage.

Daily survival probability tended to be higher during lay and incubation stages ($s_{1j} = s_{2j}$) than the nestling stage (s_{3j} ; Fig. 2). Estimates for daily survival probability during lay and incubation stages were similar among treatments during 2011, but in 2012 there was a decline among grazed exotic grass and grazed mixed NWSG nests (Fig. 2a). Incubation survival in 2012 was higher for non-grazed NWSG than grazed mixed NWSG ($\Pr[s_{2_NMNP} > s_{2_GMNP}] = 0.99$) and grazed exotic pasture ($\Pr[s_{2_NMNP} > s_{2_GMEP}] = 1.00$), but not grazed Indian grass pasture ($\Pr[s_{2_NMNP} > s_{2_GINP}] = 0.64$). Incubation survival also tended to be higher for grazed Indian grass pasture than grazed mixed NWSG ($\Pr[s_{2_GINP} > s_{2_GMNP}] = 0.92$) and grazed exotic pasture ($\Pr[s_{2_GINP} > s_{2_GMEP}] = 0.94$). In 2011, there was support for greater nestling stage survival (s_{3j}) between grazed mixed NWSG and grazed exotic pasture ($\Pr[s_{3_GMNP} > s_{3_GMEP}] = 0.93$) and between non-grazed NWSG and grazed exotic pasture ($\Pr[s_{3_NMNP} > s_{3_GMEP}] = 0.96$), whereas survival was intermediate for both grazed NWSG treatments (Fig. 2b). The following year survival in NWSG treatments declined whereas grazed exotic pasture remained mostly constant, and nestling survival probabilities were more similar between NWSG and grazed exotic pasture ($\Pr[s_{3_NWSG} > s_{3_GMEP}] = 0.64\text{--}0.75$).

3.2. Detection process

Most nests found from nest searching were first detected during the incubation stage ($n = 93$), followed by the lay stage ($n = 45$), and the nestling stage ($n = 12$). Probability of detecting a nest was higher when a female was present (β_2) than when absent (β_1 ; Table 3). Female nest attendance varied among nest stages (Table 1.C in Appendix C), generally being highest during

the incubation stage and lowest during lay and nestling stages. In 2011, nest attendance tended to be greater for grazed exotic pasture than NWSG treatments during incubation ($\Pr[\delta_{2_GMEP} > \delta_{2_GINP}] = 0.89$; $\Pr[\delta_{2_GMEP} > \delta_{2_GMNP}] = 0.94$; $\Pr[\delta_{2_GMEP} > \delta_{2_NMNP}] = 0.94$) and nestling stages ($\Pr[\delta_{3_GMEP} > \delta_{3_GINP}] = 0.84$; $\Pr[\delta_{3_GMEP} > \delta_{3_GMNP}] = 0.98$; $\Pr[\delta_{3_GMEP} > \delta_{3_NMNP}] = 0.93$; Table C.1 in Appendix C). Similarly, in 2012 there was support for greater nest attendance for grazed exotic pasture than NWSG treatments during the nestling stage ($\Pr[\delta_{3_GMEP} > \delta_{3_GINP}] = 0.89$; $\Pr[\delta_{3_GMEP} > \delta_{3_GMNP}] = 0.99$; $\Pr[\delta_{3_GMEP} > \delta_{3_NMNP}] = 0.87$), and to a lesser degree during the incubation stage ($\Pr[\delta_{2_GMEP} > \delta_{2_GINP}] = 0.72$; $\Pr[\delta_{2_GMEP} > \delta_{2_GMNP}] = 0.74$; $\Pr[\delta_{2_GMEP} > \delta_{2_NMNP}] = 0.85$).

3.3. Derived parameters

We estimated similar superpopulation sizes in 2011 ($N_s = 332$, 95% CI: 207, 598) and in 2012 ($N_s = 390$, 95% CI: 241, 698). Of the nests found from nest searching, we observed 18 nests each year that reached the fledged stage, lower than the number of fledged nests estimated for 2011 (37, 95% CI: 25, 60) and 2012 (27, 95% CI: 20, 41). In 2011, our density estimates of successful nests increased with decreasing management intensity among treatments (i.e., $GMEP < GINP < GMNP < NMNP$; Fig. 3a). The following year, estimates among grazed treatments were more similar, with declines among native pastures, whereas grazed exotic pasture remained constant between years. Density of successful nests was highest in non-grazed NWSG and did not differ between years, with 1.5 and 2.9 times greater mean density than the next greatest treatment, grazed mixed NWSG, in 2011 and 2012, respectively. A similar pattern was observed for dickcissel productivity (fledglings ha^{-1} ; Fig. 3b). In 2011, productivity in grazed exotic pastures was lower than for grazed mixed NWSG ($\Pr[P_{GMNP} > P_{GMEP}] = 0.97$), for non-grazed NWSG ($\Pr[P_{NMNP} > P_{GMEP}] = 1.00$), and for grazed Indian grass monoculture, but to a lesser

degree of support ($\Pr[P_{\text{GINP}} > P_{\text{GMEP}}] = 0.86$). There was support for differences in productivity between non-grazed NWSG and grazed Indian grass monoculture ($\Pr[P_{\text{NMNP}} > P_{\text{GINP}}] = 0.96$), and less support for differences between other NWSG treatments ($\Pr[P_{\text{GMNP}} > P_{\text{GINP}}] = 0.73$; $\Pr[P_{\text{NMNP}} > P_{\text{GMNP}}] = 0.89$). The following year, productivity declined among grazed NWSG and remained constant in grazed exotic pasture and non-grazed NWSG. There was no support for greater productivity in grazed mixed NWSG than grazed exotic pasture ($\Pr[P_{\text{GMNP}} > P_{\text{GMEP}}] = 0.48$), whereas productivity was lower for grazed Indian grass monoculture than grazed mixed NWSG ($\Pr[P_{\text{GMNP}} > P_{\text{GINP}}] = 0.92$) and grazed exotic pasture ($\Pr[P_{\text{GMEP}} > P_{\text{GINP}}] = 0.94$). There was strong support for greater productivity in non-grazed NWSG than other treatments ($\Pr = 1.00$ for all tests). Mean estimates of dickcissel productivity in non-grazed NWSG were 1.54 and 3.30 times greater than the next greatest treatment, grazed mixed NWSG, in 2012 and 2012, respectively.

4. Discussion

Widespread establishment of exotic forages for beef production in the Southeastern United States has likely limited nesting opportunities for grassland bird species (Barnes et al., 2013), necessitating evaluation of potential land-sharing opportunities such as NWSG as part of efforts to stem further declines of avian population. We used a capture-recapture model to compare dickcissel nest density and productivity in native and exotic grass pastures while accounting for nest stage-specific variability in survival and detection. Dickcissel productivity was consistently greater in non-grazed NWSG than grazed exotic pasture, whereas productivity was intermediate in grazed native pastures but declined between years. Dickcissels construct nests in tall and dense vegetation (Frey et al., 2008; Hatchett et al., 2013; Winter, 1999; Zimmerman, 1971), and nest density and rates of polygyny increase with nest site availability (Zimmerman, 1971;

Zimmerman, 1982). Bermudagrass forms low rhizomatous mats (Ball et al., 2007) and is unlikely to provide a suitable nesting substrate for dickcissels, whereas birds will readily nest in native bunchgrasses (Giuliano and Davies, 2002; Hughes et al., 1999). Vegetation structure (height and density) was greatest for non-grazed NWSG pastures and tended to be lower and more similar among grazed treatments (exotic and native grass; Monroe, 2014), suggesting the observed trends in dickcissel productivity reflect the availability of suitable nest sites in each treatment due to a combination of stand-type and management, rather a response to plant species or origin *per se*. Importance of structure for dickcissels also is supported in previous studies that observed similar densities of this species in cool- and warm-season grass fields (Jacobs et al., 2012; Jaster et al., 2014), whereas dickcissels responded positively to tall fescue-dominated pastures when livestock management increased biomass of native warm-season grasses (Johnson and Sandercock, 2010). Densities of dickcissels also did not differ significantly between grazed bermudagrass and restored native grass pastures in Blackland Prairie of Texas (Lituma et al., 2012).

Our productivity estimates generally corresponded with trends in nest density estimates, yet there was stronger support for variation in productivity among treatments than variation in nest density. Imprecise nest density estimates may have resulted from our nest searching protocol, and given a 21-day nesting period it is likely that many nests were initiated and failed between our two-week survey intervals and thus were never available for detection. Nest searching effort of each study may be constrained by logistics (as in our case) or concern for disrupting vegetation (e.g., Conover et al., 2011a), yet the necessary effort should be considered with respect to a species' ecology (e.g., nest survivorship) and desired precision of nest density estimates. Nevertheless, we posit that our systematic nest searching protocol detected nests that

were representative of the larger population, so our estimates were not likely to be biased by nests missed between search events. We also were able to obtain useful assessments of habitat quality and treatment by combining information on survival, fecundity, and density. Another factor that could influence nest density is landscape context and adjacent land cover types (Ribic et al., 2009). Previous studies have found declines in the number of dickcissel nests with greater proximity to tree cover (Adams et al., 2013; Jensen and Finck, 2004; Walk et al., 2010) while others did not (Conover et al., 2011b; Winter and Faaborg, 1999). Tree cover (woodlands) adjacent to pastures was variable among pastures within each treatment but not among treatments (A.P. Monroe, unpublished data), and thus was unlikely to disproportionately affect a given treatment but may have increased variability of our nest density estimates. Adjacent tree cover also may increase rates of brood parasitism by brown-headed cowbirds (*Melothrus ater*; Benson et al., 2013), but few nests in our study were parasitized (8% including incidentals; Monroe, 2014). Given the extent of grassland fragmentation grasslands in the Black Belt region (Barone, 2005) and across the Eastern US (Askins et al., 2007), our estimates may offer a conservative prediction of dickcissel nest density and productivity in NWSG pastures with varying amounts of adjacent tree cover.

Vegetation structure at or around nest sites can have a positive effect on dickcissel nest survival (Frey et al, 2008; Winter, 1999), and tall structure offered by NWSG bunchgrasses could affect nest survival by concealing nests from predators (*total foliage* hypothesis; Martin, 1993) and by moderating nest microclimate (*thermal-refuge* hypothesis; Hovick et al., 2015; Lusk et al., 2003; With and Webb, 1993). Replacing exotic forages with NWSG bunchgrasses also could increase availability of potential nest sites, thereby reducing foraging efficiency of predators (*potential prey-site* hypothesis; Chalfoun and Martin, 2009). Although nestling

survival was greater among NWSG treatments than exotic grass pastures in 2011, this was not consistent between years or nestling stage (Fig. 2). Interannual variability in survival could reflect differences in weather and its effects on prey availability (Martin, 1987) and predator distribution (Cox et al., 2013). Mean maximum temperature in July was similar between years, but was somewhat lower in June of 2012 than in 2011. However, the real difference in weather was likely from precipitation. Although total precipitation was somewhat greater in 2012 than in 2011, precipitation before July was lower in 2012 than in 2011. The combined effects of low precipitation and grazing could have limited growth of native forages compared with the previous year, which may reduce vegetation cover at nest sites. Greater replication (temporal and spatial) and studies of nest site vegetation may be required to determine the mechanisms behind treatment effects on survival.

Interestingly, in certain cases our estimates of nest density and survival did not correspond with trends in dickcissel productivity, demonstrating the value in jointly modelling density and survival data when estimating productivity because inferences restricted to a single metric may not correspond with habitat quality (Van Horne, 1983). For example, nest density in the grazed mixed NWSG increased from 2011 to 2012 (Fig. 1) but productivity decreased, likely due to declines in incubation and nestling stage survival (Fig. 2a, b). Similarly, productivity in grazed exotic grass pastures remained unchanged despite an increase in nest density and a decrease in incubation survival. The decline in productivity for grazed Indian grass pastures was likely driven by a sharp decrease in nest density because survival parameters remained largely similar between years. The mechanism for this decline in nest density is unclear. Distribution of grazing may be less spatially and temporally heterogeneous in monocultures than polycultures (Bailey, 2005), which could leave less tall structure for nest sites. Different responses to grazing between

monocultures and polycultures could be compounded during periods of drought (Tilman et al., 2006). Dickcissels also will readily nest in forbs (Temple, 2002), and in 2012 all pastures were treated with herbicide to control excessive forb coverage. However, overall forb coverage in each treatment was similar between years (Monroe, 2014), whereas nest density declined between years in Indian grass pastures but increased in other treatments (Fig. 1). In addition, coverage of bermudagrass approximately doubled across grazed native grass pastures during our study (but not in non-grazed native pastures; Monroe, 2014), so it is possible that selective grazing released bermudagrass and limited nest site availability. The potential for re-establishment from bermudagrass and implications for wildlife use of NWSG pastures indicates the importance of adequately controlling exotic grasses when establishing NWSG (Harper et al., 2007).

Although the positive response of dickcissels to non-grazed NWSG suggests an interaction between NWSG and grazing, we could not fully evaluate this interaction without a non-grazed exotic grass treatment. However, the grasses in our study differed fundamentally in potential structure (in the absence of grazing), with bermudagrass growing at most to 0.61 m in height, whereas Indian grass and big bluestem are bunchgrasses that can reach 1.83 m (Ball et al., 2007). Therefore, even without grazing it is unlikely that our exotic grass treatment would have supported the levels of dickcissel productivity that we estimated in non-grazed NWSG. In addition, prescribed fire in NWSG treatments likely had an important influence on the observed vegetation structure, and consequently on dickcissel productivity. In the absence of grazing, fire can stimulate greater vegetation productivity during the growing season than in unburned prairie (Knapp and Seastedt, 1986). Without fire, ungrazed prairie can support greater densities of dickcissel nests (Robel et al., 1998) and correspond with greater nest survival (Rahmig et al.,

2009; Robel et al., 1998) than spring-burned areas. However, periodic fire is necessary to maintain perennial grasslands regardless of grazing regime. Without spring fires, grazing the following growing season also could produce a different response than that which we observed for NWSG such as somewhat greater vegetation density and standing dead vegetation (Rahmig et al., 2009). Finally, high inputs of fertilizer are applied to bermudagrass to increase forage production (Burns et al., 1984; Phillips and Coleman, 1995), and it is possible that lower rates of fertilizer application would have reduced suitability of grazed exotic grass pastures for tall structure specialists like dickcissels.

Despite using management regimes typically employed for each treatment, continuous season-long grazing by livestock may have had an important influence on vegetation structure, and our results do not preclude the use of other grazing regimes that also could benefit wildlife in NWSG pastures. For example, varying the application of fire in space and time within pastures (e.g., patch-burn management) could focus grazing to recently-burned patches and relieve pressure from unburned patches, thereby increasing overall structural heterogeneity of a pasture (Fuhlendorf et al., 2012). Such heterogeneity-based management has been shown to benefit birds that favor tall structure (dickcissels) and short structure (grasshopper sparrows; *Ammodramus savannarum*) compared with annually-burned, season-long grazing (Hovick et al., 2012; Davis et al., 2016) without losses in production (Limb et al., 2011). Increasing pasture size (Bailey, 2005) and incorporating NWSG into current exotic forage operations (Giuliano and Daves, 2002) also may increase heterogeneity of vegetation structure in beef production systems.

We could not estimate the size of the female dickcissel population based on nest abundance because females can re-nest up to three times in a season (Temple, 2002) and we did not ring 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 our study were constructed by new females. Additionally, we did not monitor survival of fledglings until independence, so caution is warranted when interpreting our productivity estimates as measures of habitat quality (Streby et al., 2014). Still, a previous telemetry study of fledgling dickcissels found survival increased in tall and dense vegetation (Berkeley et al., 2007), suggesting fledglings also may have benefited from vegetation structure in non-grazed NWSG pastures.

Female nest attendance increased the probability of detecting nests using the rope-drag method, and we found that attendance varied among nest stages. Reduced female nest attendance during the nestling stage relative to the incubation stage is consistent with other studies (Giovanni et al., 2011; Powell et al., 2012; Smith et al., 2009), as females typically spend more time off the nest foraging. We also found support for variation in nest attendance by treatment, with attendance tending to be higher for grazed exotic pasture than NWSG treatments during incubation and nestling stages, and several potential mechanisms may be posited for this pattern. Greater food availability may increase adult attendance, improving survival through more frequent antipredator behaviors (Duncan Rastogi et al., 2006). However, we did not estimate differences in prey availability among treatments (Monroe, 2014), nor did greater nest attendance among nests in grazed exotic pasture correspond with survival estimates for this treatment. Furthermore, activities of adults at the nest site also may alert predators (Martin et al., 2000). Another mechanism for patterns in nest attendance and survival is microclimate. Exotic grasses such as bermudagrass may trap heat (Martin et al., 2015), and a combination of reduced vegetation cover and elevated temperatures could increase nest attendance and reduce feeding rates (Lloyd and Martin, 2004). Regardless of the mechanism, greater nest attendance probability

increased the probability of detecting nests, and therefore inferences from apparent nest density indices could be confounded if nests with greater female attendance are more represented in samples due to greater detectability.

Although our modelling approach is conceptually similar to that proposed by Péron et al. (2014), there are notable differences. For example, estimating nest age for our approach is helpful for back-dating nests and parameter estimation, but this is not strictly necessary due to the use of stage transition probabilities. In addition, our modelling approach included an additional stage for nests that fledged nestlings, thereby permitting estimation of the true number of successful nest attempts in our study population. Use of the fledged state is an improvement over the conventional approach for estimating nest survivorship, which is typically based on exponentiating daily survival estimates over a fixed nesting period length. Conventional survivorship and productivity estimates also typically do not include variation in temporal or nest-site covariates, but these can be accommodated in this model.

5. Conclusions

Our results suggest that native forages have the potential to provide nesting habitat for a declining grassland specialist and increase avian productivity on private lands in the Southeastern United States. However, season-long continuous grazing also may have had a strong effect on availability of nest sites for dickcissels in NWSG, and by the second year dickcissel productivity was similar to (GMNP) or less than (GINP) that of our grazed exotic grass treatment. As a result a greater area of grazed NWSG may be necessary to achieve the same level of dickcissel productivity as non-grazed NWSG. Nevertheless, producers also would forego most economic opportunities with land-sparing. If NWSG pastures are managed with reduced stocking rates, deferment, or resting (Chamberlain et al., 2012; Harper et al., 2015;

Mousel et al., 2003), our study indicates that employing such management in a land-sharing regime may increase availability of dickcissel nesting habitat relative to exotic grass pastures. An important caveat is that we did not consider other members of the avian grassland community such as grasshopper sparrows that may respond positively to pastures and fields with lower vegetation structure (Johnson and Sandercock, 2010; Hovick et al., 2012; McCoy et al., 1999). Establishing NWSG while managing livestock and fire in a way that fosters a mosaic of varying structure may be beneficial for the full complement of avian biodiversity in this region.

Acknowledgements

We are indebted to our friend and colleague Sam Riffell for his conceptual and financial support of the larger grazing and bird study. We are also grateful to W. Batton, C. Bogan, J. Burger, A. Clark, K. Drey, S. Easley, K. Fleming, T. Guthrie, L. Latino, M. McConnell, B. McKinley, E. O'Donnell, M. Thornton, and A. Tisdale for their assistance with nest-searching and monitoring. K. Evans, K. Newcomb, and S. Riffell offered helpful comments that improved earlier versions of this manuscript. R. Conover provided guidance on ageing dickcissel eggs and nestlings. H. Boland, T. Best, and the Mississippi State University Prairie Research Unit managed livestock for our study. 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 College of Forest Resources at Mississippi State University provided additional support. This material is based upon work that was supported by the National Institute of Food and Agriculture, U.S. Department of Agriculture, Hatch project under accession number 206903.

References

495 Adams, H.L., Burger, Jr., L.W., Riffell, S., 2013. Disturbance and landscape effects on avian
 496 nests in agricultural conservation buffers. *J. Wildl. Manage.* 77, 1213–1220.

497 Askins, R.A., Chávez-Ramírez, F., Dale, B.C., Haas, C.A., Herkert, J.R., Knopf, F.L., Vickery,
 498 P.D., 2007. Conservation of grassland birds in North America: understanding ecological
 499 processes in different regions. *Ornithol. Monogr.* 64, 1–46.

500 Asner, G.P., Elmore, A.J., Olander, L.P., Martin, R.E., Harris, A.T., 2004. Grazing systems,
 501 ecosystem responses, and global change. *Annu. Rev. Env. Resour.* 29, 261–299.

502 Bailey, D.W., 2005. Identification and creation of optimum habitat conditions for livestock.
 503 *Rangeland Ecol. Manag.* 58, 109–118.

504 Ball, D.M., Hoveland, C.S., Lacefield, G.D., 2007. Southern forages: modern concepts for forage
 505 crop management. International Plant Nutrition Institute, Norcross, Georgia.

506 Barnes, T.G., DeMaso, S.J., Bahm, M.A., 2013. The impact of 3 exotic, invasive grasses in the
 507 Southeastern United States on Wildlife. *Wildl. Soc. Bull.* 37, 497–502.

508 Barone, J.A., 2005. Historical presence and distribution of prairies in the Black Belt of
 509 Mississippi and Alabama. *Castanea* 70, 170–183.

510 Benson, T.J., Chiavacci, S.J., Ward, M.P., 2013. Patch size and edge proximity are useful
 511 predictors of brood parasitism but not nest survival of grassland birds. *Ecol. Appl.* 23,
 512 879–887.

513 Berkeley, L.I., McCarty, J.P., Wolfenbarger, L.L., 2007. Postfledging survival and movement in
 514 dickcissels (*Spiza americana*): implications for habitat management and conservation.
 515 *Auk* 124, 396–409.

516 Brown, J.H., McDonald, W., 1995. Livestock grazing and conservation on southwestern
 517 rangelands. *Conserv. Biol.* 9, 1644–1647.

518 Burns, J.C., Mochrie, R.D., Timothy, D.H., 1984. Steer performance from two perennial
 519 *Pennisetum* species, switchgrass and a fescue–‘Coastal’ bermudagrass system. *Agron. J.*
 520 76, 795–800.

521 Chalfoun, A.D., Martin, T.E., 2009. Habitat structure mediates predation risk for sedentary prey:
 522 experimental tests of alternative hypotheses. *J. Anim. Ecol.* 78, 497–503.

523 Chamberlain, S.K., Paine, L.K., Harrison, J.L., Jackson, R.D., 2012. Tradeoffs in performance of
 524 native warm-season grass cultivars and locally harvested seed managed for wildlife
 525 habitat or livestock production. *Agron. J.* 104, 1383–1391.

526 Chandler, R.B., Clark, J.D., 2014. Spatially explicit integrated population models. *Methods Ecol.*
 527 *Evol.* 5, 1351–1360.

528 Churchwell, R.T., Davis, C.A., Fuhlendorf, S.D., Engle, D.M., 2008. Effects of patch-burn
 529 management on dickcissel nest success in a tallgrass prairie. *J. Wildl. Manage.* 72, 1596–
 530 1604.

531 Conover, R.R., Burger Jr., L.W., Linder, E.T., 2011a. Grassland bird nest ecology and survival in
 532 upland habitat buffers near wooded edges. *Wildl. Soc. Bull.* 35, 353–361.

533 Conover, R.R., Dinsmore, S.J., Burger Jr., L.W., 2011b. Effects of conservation practices on bird
 534 nest density and survival in intensive agriculture. *Agric. Ecosyst. Environ.* 141, 126–132.

535 Cox, W.A., Thompson III, F.R., Reidy, J.L., 2013. The effects of temperature on nest predation
 536 by mammals, birds, and snakes. *Auk* 130, 784–790.

537 Davis, C.A., Churchwell, R.T., Fuhlendorf, S.D., Engle, D.M., Hovick, T.J., 2016. Effect of
 538 pyric herbivory on source-sink dynamics in grassland birds. *J. Appl. Ecol.* (In Press
 539 doi:10.1111/1365-2664.12641).

540 Davis, S.K., Holmes, T.G., 2012. Sprague's pipit incubation behavior. *Stud. Avian Biolog.* 43,

541 67–76.

542 Duncan Rastogi, A., Zanette, L., Clinchy, M., 2006. Food availability affects diurnal nest
543 predation and adult antipredator behaviour in song sparrows, *Melospiza melodia*. Anim.
544 Behav. 72, 933–940.

545 Egan, J.F., Mortensen, D.A., 2012. A comparison of land-sharing and land-sparing strategies for
546 plant richness conservation in agricultural landscapes. Ecol. Appl. 22, 459–471.

547 Fretwell, S.D., 1972. Populations in a Seasonal Environment. Princeton University Press,
548 Princeton, New Jersey.

549 Frey, C.M., Jensen, W.E., With, K.A., 2008. Topographic patterns of nest placement and habitat
550 quality for grassland birds in tallgrass prairie. Am. Midl. Nat. 160, 220–234.

551 Fuhlendorf, S.D., Engle, D.M., Elmore, R.D., Limb, R.F., Bidwell, T.G., 2012. Conservation of
552 pattern and process: developing an alternative paradigm of rangeland management.
553 Rangeland Ecol. Manag. 65, 579–589.

554 Gelman, A., Carlin, J.B., Stern, H.S., Dunson, D.B., Vehtari, A., Rubin, D.B., 2014. Bayesian
555 Data Analysis, third ed. CRC Press, Boca Raton, Florida.

556 Giovanni, M.D., Post Van Der Burg, M., Anderson, L.C., Powell, L.A., Schacht, W.H., Tyre,
557 A.J., 2011. Estimating nest density when detectability is incomplete: variation in nest
558 attendance and response to disturbance by western meadowlarks. Condor 113, 223–232.

559 Giuliano, W.M., Daves, S.E., 2002. Avian response to warm-season grass use in pasture and
560 hayfield management. Biolog. Conserv. 106, 1–9.

561 Harper, C.A., Bates, G.E., Hansbrough, M.P., Gudlin, M.J., Gruchy, J.P., Keyser, P.D., 2007.
562 Native Warm-Season Grasses: Identification, Establishment, and Management for
563 Wildlife and Forage Production in the Mid-South. University of Tennessee Extension,

564 Knoxville, Tennessee.

565 Harper, C.A., Birckhead, J.L., Keyser, P.D., Waller, J.C., Backus, M.M., Bates, G.E., Holcomb,
566 E.D., Brooke, J.M., 2015. Avian habitat following grazing native warm-season forages in
567 the Mid-South United States. *Rangeland Ecol. Manag.* 68, 166–172.

568 Hatchett, E.S., Hale, A.M., Bennett, V.J., Karsten, K.B., 2013. Wind turbines do not negatively
569 affect nest success in the dickcissel (*Spiza americana*). *Auk* 130, 520–528.

570 Hodgson, J.A., Kunin, W.E., Thomas, C.D., Benton, T.G., Gabriel, D., 2010. Comparing organic
571 farming and land sparing: optimizing yield and butterfly populations at a landscape scale.
572 *Ecol. Lett.* 13:1358–1367.

573 Hoekstra, J.M., Boucher, T.M., Ricketts, T. H., Roberts, C., 2005. Confronting a biome crisis:
574 global disparities of habitat loss and protection. *Ecol. Lett.* 8, 23–29.

575 Hovick, T.J., Miller, J.R., Dinsmore, S.J., Engle, D.M., Debinski, D.M., Fuhlendorf, S.D., 2012.
576 Effects of fire and grazing on grasshopper sparrow nest survival. *J. Wildl. Manage.* 76,
577 19–27.

578 Hovick, T.J., Elmore, R.D., Fuhlendorf, S.D., Dahlgren, D.K., 2015. Weather constrains the
579 influence of fire and grazing on nesting greater prairie-chickens. *Rangeland Ecol. Manag.*
580 68, 186–193.

581 Hughes, J.P., Robel, R.J., Kemp, K.E., Zimmerman, J.L., 1999. Effects of habitat on dickcissel
582 abundance and nest success in Conservation Reserve Program fields in Kansas. *J. Wildl.*
583 *Manage.* 63, 523–529.

584 Jacobs, R.B., Thompson III, F.R., Koford, R.R., La Sorte, F.A., Woodward, H.D., Fitzgerald,
585 J.A., 2012. Habitat and landscape effects on abundance of Missouri’s grassland birds. *J.*
586 *Wildl. Manage.* 76, 372–381.

587 Jaster, L., Jensen, W.E., Forbes, A.R., 2014. Nest survival of grassland birds in warm- and cool-
 588 season grassland restorations. *Am. Midl. Nat.* 171, 246–257.

589 Jehle, G., Yackel Adams, A.A., Savidge, J.A., Skagen, S.K., 2004. Nest survival estimation: a
 590 review of alternatives to the Mayfield estimator. *Condor* 106, 472–484.

591 Jensen, W.E., Finck, E.J., 2004. Edge effects on nesting dickcissels (*Spiza americana*) in relation
 592 to edge type of remnant tallgrass prairie in Kansas. *Am. Midl. Nat.* 151, 192–199.

593 Johnson, M.D., 2007. Measuring habitat quality: a review. *Condor* 109, 489–504.

594 Jolly, G.M., 1965. Explicit estimates from capture-recapture data with both death and
 595 immigration-stochastic model. *Biometrika* 52, 225–247.

596 Kéry, M., Schaub, M., 2012. Bayesian Population Analysis using WinBUGS. Elsevier Inc,
 597 Oxford, United Kingdom.

598 Knapp, A.K., Seastedt, T.R., 1986. Detritus accumulation limits productivity of tallgrass prairie.
 599 *BioScience* 36, 662–668.

600 Limb, R.F., Fuhlendorf, S.D., Engle, D.M., Weir, J.R., Elmore, R.D., Bidwell, T.G., 2011. Pyric-
 601 herbivory and cattle performance in grassland ecosystems. *Rangeland Ecol. Manag.* 64,
 602 659–663.

603 Lituma, C.M., Morrison, M.L., Whiteside, J.D., 2012. Restoration of grasslands and nesting
 604 success of dickcissels (*Spiza Americana*). *Southwest. Nat.* 57, 138–143.

605 Lloyd, J.D., Martin, T.E., 2004. Nest-site preference and maternal effects on offspring growth.
 606 *Behav. Ecol.* 15, 816–823.

607 Lokemoen, J.T., Koford, R.R., 1996. Using candlers to determine the incubation stage of
 608 passerine eggs. *J. Field Ornithol.* 67, 660–668.

609 Lusk, J.J., Suedkamp Wells, K., Guthery, F.S., Fuhlendorf, S.D., 2003. Lark sparrow

610 (*Chondestes grammacus*) nest-site selection and success in a mixed-grass prairie. Auk
611 120, 120–129.

612 Martin, J.A., Burkhart, J.K., Thackston, R.E., Carroll, J.P., 2015. Exotic grass alters micro-
613 climate and mobility for northern bobwhite chicks. Wildl. Soc. Bull. 39, 834–839.

614 Martin, T.E., 1987. Food as a limit on breeding birds: a life-history perspective. Annu. Rev.
615 Ecol. Syst. 18, 453–487.

616 Martin, T.E., 1993. Nest predation among vegetation layers and habitat types: revising the
617 dogmas. Am. Nat. 141, 897–913.

618 Martin, T.E., Scott, J., Menge, C., 2000. Nest predation increases with parental activity:
619 separating nest site and parental activity effects. Proc. R. Soc. London B 267, 2287–2293.

620 McCoy, T.D., Ryan, M.R., Kurzejeski, E.W., Burger Jr., L.W., 1999. Conservation Reserve
621 Program: source or sink habitat for grassland birds in Missouri? J. Wildl. Manage. 63,
622 530–538.

623 Monroe, A.P., 2014. Ecological and economic implications of plant diversity and grazing in
624 pasture systems. Dissertation. Mississippi State University, Mississippi State,
625 Mississippi.

626 Mousel, E.M., Schacht, W.H., Moser, L.E., 2003. Summer grazing strategies following early-
627 season grazing of big bluestem. Agron. J. 95, 1240–1245.

628 National Climatic Data Center [NCDC], 2016. NOAA National Climatic Data Center: climate
629 data online search. <http://www.ncdc.noaa.gov/cdo-web/search> (last accessed 6.6.16)

630 Péron, G., Walker, J., Rotella, J., Hines, J.E., Nichols, J.D., 2014. Estimating nest abundance
631 while accounting for time-to-event processes and imperfect detection. Ecology 95, 2548–
632 2557.

633 Phalan, B., Onial, M., Balmford, A., Green, R.E. 2011. Reconciling food production and
634 biodiversity conservation: land sharing and land sparing compared. *Science* 333, 1289–
635 1291.

636 Phillips, W.A., Coleman, S.W., 1995. Productivity and economic return of three warm season
637 grass stocker systems for the Southern Great Plains. *J. Prod. Agric.* 8, 334–339.

638 Pimentel, D., Stachow, U., Takacks, D.A., Brubaker, H.W., Dumas, A.R., Meaney, J.J., O’Neil,
639 J.A.S., Onsi, D.E., Corzilius, D.B., 1992. Conserving biological diversity in
640 agricultural/forestry systems. *BioScience* 42, 354–362.

641 Plummer, M., 2003. JAGS: A Program for Analysis of Bayesian Graphical Models Using Gibbs
642 Sampling, in: Hornik, K., Leisch, F., Zeileis, A. (Eds.), *Proceedings of the 3rd*
643 *International Workshop on Distributed Statistical Computing (DSC 2003)*. Vienna,
644 Austria. pp. 1–10.

645 Plummer, M., Stukalov, A., Denwood, M., 2015. *rjags*: Bayesian graphical models using
646 MCMC. R package version 3–15. <http://cran.r-project.org/web/packages/rjags/index.html>
647 (last accessed 10.8.15).

648 Powell, L.A., Giovanni, M.D., Groepper, S., Reineke, M.L., Schacht, W.H., 2012. Attendance
649 patterns and survival of Western Meadowlark nests. *Stud. Avian Biol.-Ser.* 43, 61–66.

650 R Development Core Team, 2015. R: A Language and Environment for Statistical Computing.
651 Version 3.2.0. R Foundation for Statistical Computing, Vienna, Austria. [http://www.R-](http://www.R-project.org)
652 [project.org](http://www.R-project.org) (last accessed 7.7.15).

653 Rahmig, C.J., Jensen, W.E., With, K.A., 2009. Grassland bird responses to land management in
654 the largest remaining tallgrass prairie. *Conserv. Biolog.* 23, 420–432.

655 Robel, R.J., Hughes, J.P., Hull, S.D., Kemp, K.E., Klute, D.S., 1998. Spring burning: resulting

656 avian abundance and nesting in Kansas CRP. *J. Range Manage.* 51, 132–138.
 657 Royle, J.A., Converse, S.J., 2014. Hierarchical spatial capture-recapture models: modelling
 658 population density in stratified populations. *Methods Ecol. Evol.* 5, 37–43.
 659 Royle, J.A., Dorazio, R.M., 2008. *Hierarchical Modeling and Inference in Ecology: the Analysis*
 660 *of Data from Populations, Metapopulations and communities.* Elsevier Ltd., Oxford,
 661 United Kingdom.
 662 Sauer, J.R., Hines, J.E., Fallon, J.E., Pardieck, K.L., Ziolkowski, D.J., Link, W.A., 2014. The
 663 North American Breeding Bird Survey, Results and Analysis 1966-2012. Version
 664 02.19.2014, USGS Patuxent Wildlife Research Center, Laurel, Maryland.
 665 Sauer, J.R., Link, W.A., 2011. Analysis of the North American Breeding Bird Survey using
 666 hierarchical models. *Auk* 128, 87–98.
 667 Seber, G.A.F., 1965. A note of the multiple-recapture census. *Biometrika* 52, 249–259.
 668 Smith, P.A., Bart, J., Lanctot, R.B., McCaffery, B.J., Brown, S., 2009. Probability of detection of
 669 nests and implications for survey design. *Condor* 111, 414–423.
 670 Stake, M.M., Thompson III, F.R., Faaborg, J., Burhans, D.E., 2005. Patterns of snake predation
 671 at songbird nests in Missouri and Texas. *J. Herpetol.* 39, 215–222.
 672 Steinfeld, H., Gerber, P., Wassenaar, T., Castel, V., Rosales, M., De Haan, C., 2006. *Livestock's*
 673 *long shadow: environmental issues and options.* Food and Agriculture Organization of
 674 the United Nations, Rome, p. 414.
 675 Streby, H.M., Refsnider, J.M., Andersen, D.E., 2014. Redefining reproductive success in
 676 songbirds: moving beyond the nest success paradigm. *Auk: Ornithol. Adv.* 131, 718–726.
 677 Temple, S.A., 2002. Dickcissel (*Spiza americana*), In: Poole, A., Gill, F. (Eds.), *The Birds of*
 678 *North America*, no. 703. Cornell Lab of Ornithology, Ithaca, New York.

679 Tilman, D., Reich, P.B., Knops, J.M.H., 2006. Biodiversity and ecosystem stability in a decade-
680 long grassland experiment. *Nature* 441:629–632.

681 Toombs, T.P., Roberts, M.G., 2009. Are Natural Resources Conservation Service range
682 management investments working at cross-purposes with wildlife habitat goals on
683 Western United States rangelands? *Rangeland Ecol. Manag.* 62, 351–355.

684 United Nations, Department of Economic and Social Affairs [UN DESA], Population Division,
685 2015. World Population Prospects: the 2015 Revision, Key Findings and Advance
686 Tables. Working paper no. ESA/P/WP.241. <http://esa.un.org/wpp/Publications> (last
687 accessed 7.12.16).

688 United States Department of Agriculture National Agricultural Statistics Service [USDA NASS],
689 2014. 2012 Census of Agriculture. <https://www.agcensus.usda.gov/Publications/2012/>
690 (last accessed 28.6.16).

691 Van Horne, B. 1983. Density as a misleading indicator of habitat quality. *J. Wildl. Manage.* 47,
692 893–901.

693 Vickery, P.D., Herkert, J.R., 2001. Recent advances in grassland bird research: where do we go
694 from here? *Auk* 118, 11–15.

695 Walk, J.W., Wentworth, K.W., Kershner, E.L., Bollinger, E.K., Warner, R.E., 2004. Renesting
696 decisions and annual fecundity of female dickcissels (*Spiza americana*) in Illinois. *Auk*
697 121, 1250–1261.

698 Winter, M., 1999. Nesting biology of dickcissels and Henslow's sparrows in southwestern
699 Missouri prairie fragments. *Wilson Bull.* 111, 515–527.

700 Winter, M., Faaborg, J., 1999. Patterns of area sensitivity in grassland-nesting birds. *Conserv.*
701 *Biol.* 13, 1424–1436.

702 Winter, M., Hawks, S.E., Shaffer, J.A., Johnson, D.H., 2003. Guidelines for finding nests of
 703 Passerine birds in tallgrass prairie. *Prairie Nat.* 35, 197–211.
 704 With, K.A., King, A.W., Jensen, W.E., 2008. Remaining large grasslands may not be sufficient
 705 to prevent grassland bird declines. *Biolog. Conserv.* 141, 3152–3167.
 706 Wright, C.K., Wimberly, M.C., 2013. Recent land use change in the Western Corn Belt threatens
 707 grasslands and wetlands. *Proc. Natl. Aca. Sci. USA.* 110, 4134–4139.
 708 Wright, H.L., Lake, I.R., Dolman, P.M., 2012. Agriculture—a key element for conservation in
 709 the developing world. *Conserv. Lett.* 5, 11–19.
 710 Zimmerman, J.L., 1971. The territory and its density dependent effect in *Spiza americana*. *Auk*
 711 88, 591–612.
 712 Zimmerman, J.L., 1982. Nesting success of dickcissels (*Spiza americana*) in preferred and less
 713 preferred habitats. *Auk* 99, 292–298.
 714 Zimmerman, J.L., 1988. Breeding season habitat selection by the Henslow’s sparrow
 715 (*Ammodramus henslowii*) in Kansas. *Wilson Bull.* 100, 17–24.

Figure Captions

Fig. 1. Mean treatment nest density (and 95% CI) for dickcissels nesting at the Mississippi State University Prairie Research Unit in Prairie, Mississippi, 2011–2012. Treatment acronyms: GMEP = grazed mixed exotic pasture; GINP = grazed Indian grass native pasture; GMNP = grazed mixed native pasture; NMNP = non-grazed mixed native pasture. Differing letters above error bars denote >95% probability that one parameter was greater than another in 2011 (lower case) and 2012 (upper case) based on posterior predictive checks.

Fig. 2. Mean posterior estimates of daily nest survival for lay/incubation stage (s_2 ; a) and nestling stage (s_3 ; b) by treatment and year for dickcissels nesting at the Mississippi State University Prairie Research Unit in Prairie, Mississippi, 2011–2012. Differing letters above error bars denote >95% probability that one parameter was greater than another in 2011 (lower case) and 2012 (upper case) based on posterior predictive checks. Treatment acronyms are defined in Fig. 1.

Fig. 3. Mean posterior estimates of a) successful nest density (≥ 1 fledglings produced) and b) productivity (fledglings ha^{-1} , with 95% CI) by treatment and year for dickcissels nesting at the Mississippi State University Prairie Research Unit in Prairie, Mississippi, 2011–2012. Differing letters above error bars denote >95% probability that one parameter was greater than another in 2011 (lower case) and 2012 (upper case) based on posterior predictive checks. Treatment acronyms are defined in Fig. 1.

Fig. 1

Fig. 2

Fig. 3

Table 1. Mean number of eggs per nest ($n = 208$) and number of fledglings per successful nest ($n = 48$) by treatment^a of dickcissels at the Mississippi State University Prairie Research Unit, Prairie, Mississippi, 2011–2012. Samples included nests found from nest searching and incidental nests.

Parameter	GMEP		GINP		GMNP		NMNP	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Eggs nest ⁻¹	4.37	0.90	4.66	0.48	4.52	0.74	4.26	0.76
Fledglings nest ⁻¹	4.20	0.84	3.00	1.22	3.22	0.83	3.55	0.99

^aTreatment acronyms: GMEP = grazed mixed exotic pasture; GINP = grazed Indian grass native pasture; GMNP = grazed mixed native pasture; NMNP = non-grazed mixed native pasture.

Table 2. Summary statistics of nest initiation date (ζ) and state transition probability (ψ) parameters estimated by the nest density model for dickcissels at the Mississippi State University Prairie Research Unit, Prairie, Mississippi, 2011–2012.

					95% Credible Interval	
Parameter	Definition	Year	Mean	SD	Lower	Upper
Initiation Date Process						
ζ_1	Linear	2011	−0.06	0.04	−0.14	0.01
ζ_1	Linear	2012	−0.07	0.03	−0.14	0.00
ζ_2	Quadratic	2011	−0.04	0.04	−0.13	0.04
ζ_2	Quadratic	2012	0.08	0.04	0.00	0.15
State Transition						
ψ_1	Lay to Inc.	2011	0.40	0.04	0.32	0.48
ψ_1	Lay to Inc.	2012	0.37	0.03	0.30	0.44
ψ_2	Inc. to Nes.	2011	0.10	0.01	0.07	0.13
ψ_2	Inc. to Nes.	2012	0.08	0.01	0.06	0.11
ψ_3	Nes. to Flg.	2011	0.06	0.01	0.03	0.08
ψ_3	Nes. to Flg.	2012	0.05	0.01	0.03	0.07

Table 3. Summary statistics for parameters modelling effects of female attendance on the detection process of the nest density model for dickcissels at the Mississippi State University Prairie Research Unit, Prairie, Mississippi, 2011–2012.

Parameter	Definition	Year	Mean	SD	95% Credible Interval	
					Lower	Upper
β_1	Absent	2011	0.05	0.03	0.01	0.12
β_1	Absent	2012	0.19	0.07	0.08	0.34
β_2	Present	2011	0.81	0.16	0.44	0.99
β_2	Present	2012	0.75	0.17	0.39	0.99