AN ABSTRACT OF THE THESIS OF

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 Conservation Reserve Program grasslands

Abstract approved:_

Grassland birds have benefitted from the Conservation Reserve Program (CRP), which creates grassland habitat through restoration of marginal cropland. Grazing by domestic cattle (*Bos taurus*), which is currently restricted in CRP, might improve habitat structure for some bird species. However, changes in habitat structure, and the presence of cattle, might hinder nest concealment from predators, attract brood-parasitic brownheaded cowbirds (*Molothrus ater*), and alter invertebrate food availability for birds. Higher abundance of arthropods, which constitute the diet for most songbird nestlings in grasslands, might allow greater parental provisioning and, consequently, improved nestling condition and survival. During the summers of 2017–2019, I investigated the effects of experimental grazing on nest survival and brood parasitism (where appropriate) of five bird species that utilize grassland habitat in Kansas. Additionally, I examined nestling condition of dickcissels (Spiza americana) in relation to abundance of arthropod prey across sites. Experimental grazing by cattle, which occurred during the first two years of study, had inconsistent effects on nest success and parasitism by cowbirds among the bird species analyzed. Negative consequences of grazing included reduced nest success and increased brood parasitism in dickcissels, as well as reduced nest success in meadowlarks (Sturnella spp.), but some effects varied over years or were

conditional upon conservation practice. Management had no effect on arthropod biomass, and nestling condition showed no clear relationships with field-level variation in food availability. Instead, nestlings in larger broods were generally in poorer condition than those in smaller broods. Thus, parents might be more limited in their capacity to feed nestlings in large broods than limited by the availability of food within CRP fields. Negative consequences of grazing tended to be weak, so short-term grazing, as might be implemented for mid-contract management of CRP fields, might not have long-lasting effects on grassland bird reproduction.

Keywords: brood parasitism, CRP, dickcissel, food limitation, grasshopper sparrow, grassland birds, meadowlark, mourning dove, nest success, nestling condition, passerines

Effects of cattle grazing and food availability on avian reproduction in

Conservation Reserve Program grasslands

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PREFACE

This thesis is divided into two chapters, with the first chapter covering nest success and brood parasitism of birds commonly utilizing grassland habitat and the second chapter covering physiological condition of nestling dickcissels. Chapter one will be submitted to, and follows the format guidelines for, *The Journal of Wildlife Management*. Chapter two will be submitted to and follows the format guidelines for *Ecology*. All animal use was approved by Emporia State University's Animal Care and Use Committee (ESU-ACUC-16-006, ESU-ACUC-18-002, and ESU-ACUC-19-002). Collection and handling of nestlings was done in accordance with a U.S. Fish and Wildlife Service Scientific Collecting permit (MB82561B) and Kansas Department of Wildlife Parks and Tourism Scientific, Education, or Exhibition Wildlife Permits (SC-027-2017, SC-058-2018, and SC-094-2019).

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CHAPTER 1

Nest success and brood parasitism of birds in response to cattle grazing in Conservation Reserve Program grasslands

INTRODUCTION

The Conservation Reserve Program (CRP), a Farm Bill program initiated in 1985, has been instrumental in restoring perennial grasslands throughout the Great Plains (Jones-Farrand et al. 2007). Since its creation, the CRP has become the largest federally supported, private-cropland idling program in the Unites States, with approximately 23.4 million acres voluntarily enrolled nationwide (USDA 2016). Given the substantial loss of native grassland throughout North America (Samson and Knopf 1994), with temperate grasslands considered among the most endangered terrestrial biomes because habitat loss far exceeds habitat protection (Noss et al. 1995, Hoekstra et al. 2005), the CRP is vital for maintaining land as wildlife habitat that would otherwise be in crop production (Hansen 2007).

Over recent decades, grassland birds have experienced steep declines compared to other North American bird groups (Sauer et al. 2014, Soykan et al. 2016), likely the result of habitat loss (Brennan and Kuvlesky 2005). Grassland bird populations respond to changes to the agricultural landscape (Murphy 2003), including positive responses to conservation programs, such as CRP (Veech 2006, Herkert 2009). In multiple cases, regional populations of grassland-obligate bird species, such as Henslow's sparrow (*Centronyx henslowii*; Herkert 1997, 2007a, 2007b) and grasshopper sparrow (*Ammodramus savannarum*; Herkert 1998) have exhibited positive population trends in areas with high local enrollment in the CRP. Furthermore, studies have shown that many declining bird species use CRP fields (Johnson and Schwartz 1993, Best et al. 1997), indicating that CRP has potential to substitute for native prairie and stabilize the continent-wide decline of birds that depend on grasslands.

Compared to row crops, CRP fields provide nesting habitat for a more diverse assemblage of grassland birds (Patterson and Best 1996, Best et al. 1997). However, even though many grassland birds use CRP fields, the diversity of grassland birds in CRP fields remains lower than in remnant native prairie grazed by cattle (Rahmig et al. 2009, Ribic et al. 2009), potentially because CRP does not completely restore plant composition to that of native prairie (Jog et al. 2006). As grassland bird species require specific habitat features for nesting (Whitmore 1981, Hubbard et al. 2006), the vegetative qualities of CRP fields may be optimal for some species and not others. Additionally, the diversity and abundance of plants (Jog et al. 2006) and insects (McIntyre and Thompson 2003) are higher in native prairie compared to CRP, which might affect resource selection and food intake by birds.

Historically, herbivory by large mammals along with climate, drought, and fire shaped the formation, maintenance, and heterogeneity of prairie ecosystems (Knapp et al. 1999, Fuhlendorf and Engle 2001, Anderson 2006). Despite this history of grazing in prairie systems, grazing as a management tool to influence succession and enhance wildlife habitat quality of CRP fields has not been evaluated and is not currently an approved management option for some CRP conservation practices (e.g., CP25; USDA 2010). Given that grazed pastures and native prairie support a more diverse group of grassland bird species than ungrazed CRP fields (Rahmig et al. 2009), cattle grazing has potential to improve habitat quality of CRP fields for grassland birds.

However, grazing also has the potential to negatively alter the quality of nest sites within CRP grasslands. In one study, grassland birds nesting in grazed grasslands had lower nest success and productivity compared to birds nesting in ungrazed grasslands (Temple et al. 1999). As grazed pastures tend to have lower vegetation cover than ungrazed pastures (Sutter and Ritchison 2005), changes to nest-site characteristics might affect nest visibility and vulnerability to predators. Vegetation at nest sites tends to positively affect nest success of a variety of grassland birds (Davis 2005, Frey et al. 2008, Kerns et al. 2010), and birds choose nesting sites with denser, taller vegetation than by random chance (Davis 2005). As nest success in birds is largely determined by evasion of would-be predators of eggs and nestlings (Ricklefs 1969), variation in nest success might be driven by differences in vegetative cover at potential nest sites (Martin 1993). Predation remains the leading cause of nest failure in grasslands, with common predators including mice and ground squirrels (Pietz and Granfors 2000). As such, changes to the vegetation structure resulting from grazing could lead to higher rates of depredation if nests become more detectable by predators.

Additionally, introduction of cattle onto CRP fields may attract brown-headed cowbirds (*Molothrus ater*, cowbirds hereafter), as the presence of cattle tends to increase cowbird density (Goguen and Mathews 1999). Cowbirds are obligate brood parasites, laying their eggs in the nests of other songbirds and usually removing one host egg for each egg they lay (Lowther 1993). With the reduction in host clutch size and raising of cowbird young, host species incur a fitness cost (Lorenzana and Sealy 1999). Although

cowbirds are common throughout the Great Plains, grazing increases rates of parasitism (Patten et al. 2006), which in turn may affect host productivity.

Grazing by cattle in CRP fields is currently limited to certain CRP conservation practices (CPs) and is not typically allowed during avian nesting seasons. Additionally, landowners receive reduced payments from the U.S. Department of Agriculture (USDA) even if grazing is permitted in CRP fields. Grazing during the growing season, coincident with nesting of most bird species, might mimic natural patterns of herbivory in grasslands, could increase diversity of vegetation structure, and could be more profitable for landowners who raise domestic cattle. My objective was to evaluate how grazing during the nesting season (15 April to 15 July in Kansas), as an alternate management strategy for CRP grasslands, influences reproductive indices of common North American grassland birds, specifically dickcissels (Spiza americana), mourning doves (Zenaida macroura), meadowlarks (Sturnella spp.), and grasshopper sparrows (Ammodramus savannarum). Demographic vital rates are key to assessing habitat quality for wildlife, such as grassland birds, beyond density or diversity measures (Van Horne 1983). Abundance may not always be a reliable index of habitat suitability, as patterns of abundance and nest success of grassland birds respond differently to habitat characteristics (Hughes et al. 1999). For instance, dickcissels were found to have higher daily nest survival in prairie hayfields than CRP, even though densities were highest in CRP (Rahmig et al. 2009). By assessing patterns of nest success and brood parasitism between cattle-grazed and ungrazed CRP fields, my research addresses a knowledge gap needed to inform future CRP policy regarding cattle grazing in CRP with regard to its consequences for imperiled grassland bird populations.

STUDY AREA

The study area was located in central Kansas with 36 CRP fields across 10 counties— Ness, Hodgeman, Pawnee, Rush, Barton, Stafford, Reno, Rice, Ellsworth, and McPherson (Figure 1-1). Conservation Reserve Program fields were abundant across the study area (13.3% of landscape), with the largest portion (45.5%) of CRP acreage enrolled in conservation practice 25 (CP25; rare and declining habitat). Fields seeded for CP25 utilize a high diversity seed mixture—containing a minimum of 15 species, with five native grass species and 10 native forbs—compared to other practices, such as conservation practice 2 (CP2; USDA 2012). Conservation practice 2 (CP2; establishment of permanent native grasses) constituted 22.0% of CRP acreage in the area, with enrolled fields planted using a minimum of three species—two native grasses and one forb (USDA 2012). Both CP2 and CP25 fields were included in my study, with fields differing not only in the required seed mixture but also time since establishment. Conservation practice 2 appeared with the 1985 Farm Bill, while CP25 emerged with the 1996 Farm Bill. Consequently, in my study, CP2 fields were established for a mean of 22.22 ± 2.23 (SE) years versus 11.89 ± 0.79 (SE) years for CP25 fields (means \pm SE calculated using 9 fields with known establishment history in each CP; USDA, unpubl. data). In both CPs, vegetation was dominated by little bluestem (Schizachyrium scoparium), big bluestem (Andropogon gerardi), and sideoats grama (Bouteloua *curtipendula*).

The regional climate is humid continental, with mean monthly temperatures ranging from a minimum of -6° C in January to a maximum of 34.2° C in July (1981–

2010 monthly normals at Great Bend, Kansas weather station [Arguez et al. 2010]). Precipitation increases from west to east across the study area from 56–76 cm, with annual precipitation averaging 67.8 cm in the center of the study area, of which almost half falls from May–July (Arguez et. al. 2010). To best encompass the precipitation gradient of central Kansas, the study area, which was centered around Great Bend, was aligned roughly perpendicular to the average angle of precipitation isoclines (1981–2010 average; Arguez et al. 2010), so that it spanned 80.5 km across the precipitation gradient (approximately east/west) and 40.2 km parallel to the gradient (approximately north/south).

METHODS

Experimental Design

My research plots, which were associated with a larger study on the importance of grazing and plant diversity in CRP grasslands to various trophic levels, were in CP2 and CP25 fields (*n* =18 fields each). A grazing treatment was also applied: ungrazed or season-long grazing by domestic cattle (*Bos taurus*) yielding a total of four treatment combinations in a factorial design. Nine of the 18 CP25 fields and eight of the CP2 fields were grazed (the imbalance due to changes in landowner plans regarding cattle grazing). The Natural Resources Conservation Service specified stocking rates designed to remove 50% of biomass during the grazing season based on field size, cattle type (cow-calf or yearling steers), and length of grazing (120 to 180 days from 1 April to 31 October). Grazing occurred during the first two years of the study (2017–2018) to represent an experimental mid-contract management option and was authorized via experimental

allowance from the U.S. Department of Agriculture (USDA). Two years of grazing were implemented rather than a single year due to less-than-expected biomass removal on grazed fields in 2017 (Appendix A). Grazed fields tended to have shorter, sparser vegetation with more bare ground and structural heterogeneity (F. Watson, unpubl. data, Wichita State University). Appendix A only illustrates general vegetative patterns among management treatments and I did not perform statistical hypothesis tests of these data (Johnson 1999). Fields were not grazed in 2019 to allow testing for any residual effects of grazing one year post-disturbance. Burning of fields varied annually, per landowner prerogative, but relatively few fields were burned in any given year. In 2017, 13.9% of fields were burned, whereas 2.8% of fields were burned in 2018 and 5.6% in 2019. Across all years, burning occurred equally on grazed and ungrazed fields. Due to this variation I did not explicitly incorporate fire regime as a covariate.

The study area was divided into three sub-regions (west, central, and east), spanning the range of average precipitation (1981–2010; Arguez et al. 2010), within which approximately a third of the replicates per treatment (n = 3) were established via selection from a randomly-ordered list of fields in a USDA database. Initially, landowners were contacted to discuss the possibility of allowing access to their fields and their implementing cattle grazing. After grazing participants were found, a list of potential ungrazed fields was generated by selecting fields under the same CP within a 8.05-km radius of the grazed site but excluding fields 1-km distant so as to pair similar yet independent fields. The search area around grazed sites was expanded by 8.05-km increments until a landowner with a matching CP field agreed to allow access. All fields included in my study were ≥ 14.2 ha as determined using ArcGIS (version 10.3; ESRI, Redlands, CA) to ensure minimum area requirements for several grassland bird species were met (Winter and Faaborg 1999, Johnson and Igl 2001). Fields were also omitted if the CRP contract was established after 2012 (less than five growing seasons prior to the first growing season of data collection in 2017) or expired before 2019, as vegetation structure differs between newly established and older CRP fields (Millenbah et al. 1996), and we required access to fields through 2019. Within selected fields, a 200-m \times 300-m plot was centered within the largest interior portion of the field and oriented parallel to the longest axis of the field. These plots were used as the focal area for nest searches.

Nest Searching and Monitoring

I conducted nest searches on fields from mid-May to late-July over three breeding seasons (2017–2019). I searched for nests within plots and outside plots, as time allowed. Field sites were routinely visited by three separate field crews of four observers each, with each crew visiting each of 12 sites twice per week. Crews visited four sites per day with nest searching and monitoring occurring on the first two sites visited (starting at 06:00) and only nest monitoring occurring on the remaining two sites visited. When logistically feasible, site visitation order was rotated throughout the seasons to intersperse visitation times.

I located nests of grassland bird species predominately through rope dragging, which induces female birds to flush from nests. A rope (2 cm diameter, 15-m length) was pulled between two people with the rope perpendicular to the path of travel and gliding

atop the vegetative canopy. Starting location for rope dragging was rotated each visit to maximize search area covered. Nests found incidentally via flushing incubating females while walking through sites, or found via parental behavior (carrying building material, food, intense chipping), were also included. Once nests were located, geographic coordinates of nests were obtained using a Global Positioning System unit (GPS; Garmin eTrex, Garmin Ltd., Olathe, KS) and marked with blue vinyl flagging tied to vegetation 5 m from the nest in any direction for open-cup nesters and facing nest openings for dome nesters. Another flag was tied at a 90° arc from the original flagging to form a triangle with the nest forming the right angle. Wooden garden stakes were placed below flagging as a redundant marker in case flagging was removed by cattle. I monitored nests every 3– 4 days until young fledged or the nesting attempt failed. I considered a nesting attempt successful if at least one host nestling fledged. Cues, such as age of brood at last visit, parental activity proximate to the nest, presence of undiscarded fecal sacs, and fledglings observed nearby, were all indicative of successful nests. Signs of disturbance to nest material or removal of nest contents prior to suitable fledging age were considered indicators of nest failure.

Vegetation Measurements

I measured vegetation structure around nests within one week after completion of a nesting attempt to account for potential covariation in nest concealment with nest survival and brood parasitism. For open cup or platform nesters (i.e. dickcissel, mourning dove), vertical structure of vegetation was measured by placing a marked pole graduated in half decimeters directly next to a nest and averaging observed visual obstruction readings

(VOR) taken from the four cardinal directions when observed at a height of 1 m and distance of 4 m (Robel et al. 1970). For species that orient their nest openings (i.e. grasshopper sparrow, meadowlark), I used a modified procedure and averaged four VOR taken at 90° increments with one reading oriented in line with the nest opening. As an estimate of nest concealment, I subtracted nest height, measured as distance from ground to rim of the nest, from average VOR. This measure approximates the degree to which a nest is hidden by surrounding vegetation. For nests that were still active at the end of each season, or if nest material was destroyed by predators, I was unable to obtain VOR and/or nest height measures. When VOR or nest height were missing for such nests, I imputed data for such nests by using the mean VOR or nest height for a given species on the same field during that year of data collection as this provided balanced data sets for nests as was necessary for model selection (Nakagawa and Freckleton 2011).

Statistical Analysis

Daily nest survival rate (DSR) was modeled, separately per species, as an unbiased index of nest success (Mayfield 1975). Eastern (*S. magna*) and western (*S. neglecta*) meadowlarks were pooled as their nests are indistinguishable and both species were present in the study area. All DSR analysis was done in program R version 3.6.1 (R Core Team 2019), using package RMark (Laake 2013), which interfaces with program MARK (Colorado State University, Ft. Collins, Colorado). RMark uses a maximum likelihood approach to estimate DSR and requires, minimally, four pieces of information: (1) day nest discovered, (2) last day nest active, (3) day nest last checked, and (4) fate—either successful (0) or failed (1). For successful nests, last day nest active and day nest last checked must be identical, as the nest survival model assumes fledge date is known, while unsuccessful nests do not require an exact failure date—instead using the interval between last day nest active and day nest last checked to estimate when failure occurred (Dinsmore et al. 2002). In addition, nests with identical dates for day nest discovered, last day nest active, and day nest last checked are invalid as no encounter history can be generated. Instead of assuming successful nests fledge on the day a nest is last seen active, which likely underestimates exposure period of many nests, I estimated fledging to occur on the midpoint between monitoring visits, rounded to the lowest integer. This allowed inclusion of nests found late during the nestling stage, which otherwise would have had no exposure history. Nests that contained only cowbird eggs or young when found were excluded from DSR analysis, as exposure days for host contents could not be determined. However, I included these nests in analysis of brood parasitism (i.e., whether host nests were parasitized by cowbirds) and intensity (i.e., number of cowbird offspring per parasitized host nests). I ran generalized-linear models using the logit-link function for brood parasitism and a log-link function for parasitism intensity within program R. As mourning doves are not suitable hosts for cowbirds, I did not include them in analysis of brood parasitism or intensity.

For all species, initiation dates were calculated through backdating. When a nest was found during the laying period, the nest contents were used to determine date first egg laid. For nests that progressed to the nestling stage, I used estimated nestling age to determine initiation date, assuming a 12, 14, 14, and 12-day incubation period for dickcissels, mourning doves, meadowlarks, and grasshopper sparrows, respectively. For nests that failed during the incubation period, I calculated latest initiation date based on nest contents. When a host species was parasitized by cowbirds, I assumed host eggs were removed on a 1:1 basis (Lowther 1993) unless clutch size exceeded 6, 7, or 6 total eggs for dickcissels, meadowlarks, and grasshopper sparrows, respectively. When nest contents exceeded maximum clutch size, I used the maximum clutch size for that species. Additionally, if nest contents during incubation were below minimum clutch size for a species, I used minimum clutch size when calculating initiation date: 3, 2, 4, and 3 for dickcissels, mourning doves, meadowlarks, and grasshopper sparrows, respectively. For nests found during the nestling period, if nests contents were below modal size: 4, 2, 5, and 4 for dickcissels, mourning doves, meadowlarks, and grasshopper sparrows, respectively, I used modal clutch of each species to calculate initiation date. Otherwise, I estimated initiation date of nests found during the nestling period based on nestling age and nest contents. I used initiation date to determine the age of each nest upon discovery, which I used to calculate the age of the nest at the start of the nesting season. RMark used this information to generate a set of time-dependent covariates for each day of the nesting season (Laake and Rexstad 2017).

I evaluated candidate models, using an information theoretic approach to rank models based on AIC_c values (Burnham and Anderson 2002). For all species, I developed candidate model sets that evaluated three tiers of predictor effects: management practices, nest-site characteristics, and time (Table 1-1). This approach ensured that tests of management practice effects were not overshadowed by other potentially influential predictors. Competitive models ($\Delta AIC_c \le 4$) from each tier that were informative (i.e. differed from the most competitive model by three or more parameters [Burnham and Anderson 2002, Arnold 2010]), were placed into a final pooled model set to determine whether additional predictors explained more variation in the data. Means of continuous predictor variables (VOR and concealment) between two-category predictor variables (grazing, CP, cowbird parasitism—nests containing cowbird offspring or not) were compared using *t* tests (using a less conservative $\alpha = 0.10$) and associated (*P* < 0.10) predictors were not included in the same models to limit multicolinearity. I accounted for model uncertainty by model averaging among competitive models that contained the predictor of interest (Burnham and Anderson 2002), which omitted correlated predictors from model-averaged sets (Cade 2015). The strength of parameter estimates (β) from model-averaged estimates among competitive models was assessed using 85% confidence intervals (CI) and their degree of overlap with 0 (Arnold 2010).

Vegetation structural variables at the field level were not included as covariates as preliminary analyses found correlation with categorical grazing treatment was common (Appendix A). Landscape composition covariates (e.g., % woodland in a defined buffer) were also not included as there were longitudinal landscape patterns (more woodland and fragmentation in the east of the study area) that were apparently correlated with longitudinal patterns in cowbird distribution and parasitism (higher in the west of the study area).

RESULTS

I found 2004 nests of 21 avian species, with nests of dickcissels, mourning doves, meadowlarks, and grasshopper sparrows most frequently detected, respectively. All other species contributed less than 5% to the total number of nests found (Table 1-2). Of the commonly encountered avian species, all four species nested in each treatment type

(Table 1-3). Mourning dove nests were roughly twice as common on CP25 fields as CP2 fields (66.2% of nests). I discovered the majority of dickcissel nests on ungrazed CP2 fields (32.6% of nests found), whereas nests of meadowlarks and grasshopper sparrows were most commonly found on grazed CP25 fields, constituting 32.2 and 54.3% of each species' nests, respectively. The majority of dickcissel (64.57%), mourning dove (62.53%), meadowlark (63.31%), and grasshopper sparrow (57.24%) nests failed, with 84.71, 79.78, 90.45, and 90.80% of nest failures for dickcissels, mourning doves, meadowlarks, and grasshopper sparrows estimated as depredations, respectively. Abandonment of nests was estimated as 9.30, 19.12, 5.73, and 1.15% of nest failures for dickcissels, mourning doves, meadowlarks, and grasshopper sparrows, respectively. Trampling by cattle was estimated to have destroyed 3 dickcissel nests and 1 meadowlark nest in grazed fields. Across all years, I found cowbirds parasitized 45.6, 39.1, and 27.4% of dickcissel, grasshopper sparrow, and meadowlark nests, respectively. Parasitism intensity varied by species, but multiple parasitism (> 1 cowbird egg per parasitized host nest) was common, with 60.4, 67.8, and 67.7% of parasitized dickcissel, grasshopper sparrow, and meadowlark nests containing multiple cowbird eggs, respectively (Figure 1-2).

Daily Survival Rate

I used 1007, 425, 240, and 143 nests of dickcissels, mourning doves, meadowlarks, and grasshopper sparrows for analyses of DSR, because some nest histories did not contain sufficient information for analysis, failure resulted from observer-related causes, or nests did not utilize CRP habitat. Among the management practice model set of DSR, grazing

by cattle varied in its importance to nest success of the focal species (Table 1-4). The best supported model for dickcissels described an interactive effect of grazing treatment with year, having over 5 times more support than the constant model (i.e., without predictors). Daily nest survival of dickcissels related negatively to grazing, but the strength of the effect differed among years, with the largest difference in DSR between grazed and ungrazed sites observed in 2019 (albeit weak as the 85% CI overlapped 0; Table 1-5; Figure 1-3). The stand-alone effect of grazing best explained DSR of meadowlarks within the management practice model set, having 1.6 times more support than the constant model. Although the effect was marginal (85% CI overlaps 0 slightly), grazing negatively affected DSR of meadowlarks among years (Table 1-5; Figure 1-3). The constant model emerged as the most competitive models for mourning dove and grasshopper sparrow DSR; and although CP, grazing, and the additive effects of CP and grazing explained some variation in DSR for these species ($\Delta AIC_c \le 4$; Table 1-4), the 85% CIs for these effects tended toward symmetry around 0, indicating weak effects (Table 1-5).

Among the nest-site characteristics model set of DSR, parasitism (whether nest contained any cowbird offspring), VOR, and the combination between the two varied in importance in predicting nest survival of the four bird species (Table 1-4). The best supported model for DSR of dickcissels, contained the parasitism effect and had over 6 times more support than the constant model and 1.4 times the support of a model including parasitism and VOR. The best supported model for DSR of grasshopper sparrows contained VOR, with 8.4 times more support than the constant model. Nest survival related negatively to parasitism for dickcissel nests and positively to VOR for dickcissel and grasshopper sparrow nests, though negligibly for the former species (β and

85% CI near 0; Table 1-5). No nest-site covariates proved useful for improving predictions of DSR for mourning doves or meadowlarks (Table 1-4).

In the time model set of DSR, day within season, year, and nest age differed among species in importance for nest survival (Table 1-4). For mourning doves and meadowlarks, the only competitive model contained nest age (Table 1-4). Daily nest survival increased as eggs and nestlings aged (Table 1-5). The most parsimonious model ($w_i = 0.72$) for DSR of dickcissels included year and a linear day within season trend (Table 1-4). Model-averaged estimates predicted that DSR decreased throughout the nesting season and was lowest in 2018 and highest in 2019 (Table 1-5). Although my analysis showed multiple plausible models for DSR of grasshopper sparrows within the time model set, the constant model was most plausible and no model was strongly supported (Table 1-4).

Among the pooled model sets of DSR, the best supported model for dickcissels contained an additive combination of day-within-season, year, and parasitism, having 5 times the support of the next best model containing only day-within-season and year (Table 1-6). Nest survival related negatively to parasitism and day within season, with DSR highest in 2019 and lowest in 2018 (Table 1-7; Figure 1-4). Models containing the grazing treatment and nest age best explained DSR of meadowlark nests within the pooled model set (Table 1-6). Survival of meadowlark nests related negatively to grazing, but positively to nest age (Table 1-7). As only one model qualified for inclusion in the pooled model set of DSR for mourning dove and grasshopper sparrow, the results from the pooled model set reflect the competitive model from the time and nest-site characteristics model sets, respectively.

Brood Parasitism

With respect to the management practice model set, the best supported model for probability of parasitism contained an interaction between grazing and CP for dickcissel nests and a grazing and year interaction for Grasshopper Sparrow nests, whereas no models were good predictors of parasitism by cowbirds for meadowlarks (Table 1-8). Dickcissel nests experienced higher parasitism probability by cowbirds on grazed than ungrazed CP2 sites, but there was a reversed pattern among CP25 fields (Table 1-9; Figure 1-5). Cowbird parasitism of grasshopper sparrow nests was higher on ungrazed sites in 2017 but on grazed sites in 2018 and 2019 (Table 1-9; Figure 1-6). Within the nest-site characteristics model set, the constant model was most supported for parasitism probability of dickcissel nests, whereas concealment of nests explained parasitism probability for meadowlarks and grasshopper sparrows (Table 1-8), with parasitism probability of nests negatively related to concealment (Table 1-9). The best supported model of parasitism probability for dickcissels and meadowlarks within the time model set included a quadratic initiation date covariate, whereas for grasshopper sparrows, the best supported model contained year as a covariate (Table 1-8). Parasitism by cowbirds peaked approximately midway through the nesting season for dickcissel nests, whereas meadowlark nests experienced higher probability of parasitism early in the nesting season (Figure 1-7). Parasitism probability of grasshopper sparrow nests was lowest in 2017 and greatest in 2019 (Table 1-9).

In the pooled model set for parasitism probability, the best supported model for dickcissel nests contained an interaction between grazing and CP and a quadratic
initiation date covariate (Table 1-10). For both meadowlarks and grasshopper sparrows, concealment weighed heavily in top models (Table 1-10), with probability of parasitism negatively related to concealment (Table 1-11). Initiation date, although included in top pooled models, had a weak effect on parasitism probability rate of meadowlark nests (85% CI overlapped 0; Table 1-11). Competitive models of grasshopper sparrows predicted probability of parasitism was lowest in 2017 and highest in 2019 (Table 1-11).

Interactions between grazing and CP, and grazing and year, were the best supported models for the intensity with which dickcissel nests were parasitized by cowbirds in the management practice tier (Table 1-12). Parasitism intensity followed a pattern similar to probability of parasitism among dickcissel nests; nests contained more cowbird offspring on grazed CP2 sites than in ungrazed CP2, but within CP25 the pattern was reversed among grazing treatments, with the strength of the effect depending on year in both CP2 and CP25 (Table 1-13, Figure 1-8). In general, dickcissel nests containing more cowbird offspring contained fewer host offspring (glm with Poisson distribution; β = -0.155 ± 0.015 SE), and among successful nests the number of cowbird offspring negatively affected the number of host young fledged (glm with Poisson distribution; $\beta =$ -0.375 ± 0.046 SE); thus, patterns in parasitism intensity of dickcissel nests are relevant to patterns in dickcissel productivity. Among the predictors in the management practice tier, CP best explained the intensity with which meadowlark nests were parasitized by cowbirds, although this model was only slightly better supported than the constant model (Table 1-12). In CP2 meadowlark nests contained more cowbird offspring than in CP25 fields, though the effect was weak given the 85% CI overlapped 0 (Table 1-13). Parasitism intensity of grasshopper sparrows was best explained by the constant model, it having twice the support of the next competing model. Neither nest-site characteristics nor time predictors significantly influenced parasitism intensity by cowbirds for any of the species I investigated (Table 1-12), and thus models were not pooled across model set tiers.

DISCUSSION

Experimental grazing had inconsistent effects on nest success and cowbird parasitism among the bird species analyzed and these patterns also varied over the three years of study, with grazing by cattle occurring only in the first two years. Grazing effects were also variously contingent upon differences between CP2 and CP25 plantings that varied in plant diversity and field age. Although more intense or longer-term grazing by cattle might have had more pronounced effects, my results can be viewed as short-term responses to potential application of grazing as a mid-contract management practice during the nesting season in CRP fields in Kansas and perhaps elsewhere in the Midwestern U.S.

Grazing by cattle varied in its importance for nest success among the study species. Grazing appeared to have little effect on mourning dove and grasshopper sparrow nest success, whereas grazing had weak negative effects on dickcissel (inconsistent across years) and meadowlark nest success. Grazing had delayed negative consequences on nest success in dickcissels. Dickcissel nest success was lower in grazed than ungrazed fields one-year post-grazing, potentially because vegetation—and perhaps predators—respond slowly to removal of grazing pressure. For instance, Ernest et al. (2000) demonstrated rodent populations responded to precipitation and plant cover but

the response lagged by at least one growing season. However, latent effects on nest success were not seen in other study species, which might have been due to their lower sample sizes of nests (dickcissels being two to five times more numerous than the other species analyzed). As dickcissels commonly constructed open-cup nests in clumps of big bluestem in the study sites, another possibility might be that dickcissel nesting substrates were more impacted by grazing than ground-nesting mourning doves and grasshopper sparrows. However, ground-nesting meadowlarks were marginally more successful in ungrazed versus grazed fields overall, resembling patterns of eastern meadowlark survival in grazed versus ungrazed tallgrass prairie (Rohrbaugh et al. 1999). Thus, grazing of CRP might negatively affect reproductive success of meadowlarks, at least temporarily. CRP fields support less floristic diversity, forb cover, and grass cover with more patches of bare ground than native warm-season pastures (Jog et al. 2006, Klute et al. 1997). Cattle may further exacerbate patchiness within CRP habitat through their foraging preferences, favoring consumption of particular grasses, including big bluestem and little bluestem (Tomanek et al. 1958). While native, perennial grasses are thought to respond to removal of aboveground biomass, particularly apical meristems, by increasing rhizome growth and tiller recruitment, this idea is inconsistently substantiated (Briske and Richards 1995). Thus, cattle may have created small clumps of ungrazed vegetation interspersed with numerous patches of shorter grazed vegetation and bare ground. Examination of Appendix A indicated grazed fields tended to be more structurally heterogeneous than ungrazed fields. Short, patchy vegetation might enable predators to easily move throughout fields or reduced number of potential nest sites thereby improving search efficiency of predators (Martin 1993).

Other studies in the northern Great Plains also found no (Lusk and Koper 2013) or species-dependent effects of grazing on nest success of grassland birds. For instance, western meadowlark and gadwall (Mareca strepera) nest survival rates were unaffected by livestock grazing, while grazing appeared detrimental to savannah sparrow (Passerculus sandwichensis) and potentially clay-colored sparrow (Spizella pallida) nest survival (Fondell and Ball 2004, Kerns et al. 2010). However, the species-specific patterns I detected were not always consistent with species-specific patterns found in previous studies. Sutter and Ritchison (2005) found nest success of grasshopper sparrows to be higher in ungrazed grassland mowed yearly than continuously grazed grassland in Kentucky, whereas I found no detrimental effects of grazing on grasshopper sparrow nest success. Though I found grazing by livestock to negatively affect nest success of meadowlarks, Fondell and Ball (2004) found western meadowlarks equally successful in grazed and ungrazed grassland. Inconsistences in the species-specific effect of grazing on nest success between previous studies and my own research might be a result of differences in predator communities among habitats and their responses to grazing.

However, detectability of nests may not limit predation risk, as nest success in my study was not well correlated with vertical density of vegetation except in grasshopper sparrows. Snakes and small mammals commonly prey upon grassland songbird eggs and nestlings, whereas avian predators are uncommon (Klug et al. 2010, Pietz and Granfors 2000). Since snakes and small mammals likely use temperature and olfaction, respectively, to find nests, predation of nests on or near ground level might be unrelated to concealment (Colombelli-Négrel and Kleindorfer 2009). Others have found that vegetation characteristics between successful and failed nest sites of dickcissels were indistinguishable (Walk et al. 2004). Even though a species, such as eastern meadowlark, may choose nest sites with higher visual obstruction, vegetative cover near the nest does not always improve nest success (Frey et al. 2008). Only nest success of grasshopper sparrows responded positively to vertical vegetation structure around nest sites. Grasshopper sparrows build distinctive, domed, ground-level nests, which they frequently enter and leave by running on the ground (Vickery 1996). Of the species studied, grasshopper sparrow nests are the most cryptic, and secretive parental behavior, perhaps concealed by vegetation, might limit the ability of predators to use parental cues to locate nests. While some studies have found similar positive relationships between concealment and nest success in grasshopper sparrows (approximated by litter cover in Frey et al. 2008), others have found no differences in vegetative characteristics between successful and depredated grasshopper sparrow nests (Sutter and Ritchison 2005). Variation in predator communities between studies might again account for inconsistent effects of concealment. If grazing in CRP, perhaps more intense than that implemented in the current study, resulted in reduced vertical vegetation structure, then it might increase predation risks posed to grasshopper sparrow nests.

Cattle grazing activity, or simply the presence of cattle, which attracts cowbirds, had an impact on parasitism probability of dickcissel and grasshopper sparrow nests, but the effect was conditional upon conservation practice for the former and year for the latter species. In grazed CP2 fields, dickcissels experienced not only higher rates of cowbird parasitism but also greater numbers of cowbird offspring (eggs or nestlings) compared to other habitat treatments. The presence of livestock might have increased cowbird densities in grazed CP2 fields due to opportunities for commensalistic foraging by adult cowbirds (Morris and Thompson 1998, Goguen and Mathews 1999). Why was this effect not consistent across CP treatments? As noted earlier, fields in the CP2 practice have generally been established for a longer period of time than CP25. Differences in establishment history of these CPs (earlier for CP2), and perhaps use by cowbirds locally, might have influenced the pattern of cowbird parasitism observed for dickcissels. Irrespective of grazing treatment, parasitism intensity of meadowlark nests was also slightly higher in CP2 fields. Regardless, in CP25 plantings, parasitism probability and intensity of parasitism for dickcissel nests were higher in ungrazed fields, leaving much uncertainty as to the importance of grazing on cowbird parasitism of dickcissels in CRP fields. However, a grazing effect was apparent for parasitism of grasshopper sparrow nests. Given the interaction between grazing and year seen in parasitism probability of grasshopper sparrow nests, parasitism frequency, and presumably cowbird density, appeared to respond slowly to experimental changes of cattle activity in the CRP fields I used.

Except for dickcissels, concealment at the nest site reduced cowbird parasitism probability, though concealment did not impact the number of cowbird offspring per nest in any host species. Support of concealment hindering the ability of cowbirds to find nests has been equivocal thus far. Some studies found a similar negative relationship between concealment and parasitism (Burhans 1997, Saunders et al. 2003), while others detected no pattern (Hauber and Russo 2000, Winter 1999). As female cowbirds rely on visual cues to locate nests (Norman and Robertson 1975), concealment at nest sites may serve as an effective strategy to reduce detectability of nests. For ground-nesting species, dense cover around the nest may especially conceal movements of adult birds. Dickcissels build open cup nests, which are generally more exposed than nests of groundnesting species; thus, concealment might not aid in reducing parasitism to the same extent observed in ground-nesting species. Nonetheless, my results add to the body of evidence that suggests vegetative cover around nests impacts the ability of cowbirds to parasitize nests of grassland birds. As with potential effects on nest predation, grazing-induced reductions in vegetative height might have a negative consequence in increasing cowbird parasitism of some grassland host species.

Parasitism by cowbirds can impact nest success and host productivity (Johnsgard 1997). Although the probabilities of cowbird parasitism I found were high compared to those reported in some locations (e.g., Patten et al. 2006), they were lower than others recorded elsewhere in Kansas (see table in Shaffer et al. 2003, Jensen and Cully 2005). Only on dickcissel nests did cowbird parasitism exert a negative effect on nest success, potentially because cowbirds routinely parasitize their nests and might also be nest predators (Arcese et al. 1996). Cowbirds can parasitize a variety of grassland bird species but prefer dickcissels over other host species (Rivers et al. 2010). Thus, effects of parasitism may be more strongly exhibited in this species than other hosts. Abandonment of nests following parasitism, removal of host offspring by cowbirds, and increased predation of parasitized nests, all might explain reduced nest success of parasitized dickcissels (Johnsgard 1997, Arcese et al. 1996). Parasitism probability and intensity were higher in grazed CP2 fields and clutch sizes and number of offspring fledged were negatively related to the number of cowbird offspring per nest overall; thus, removal of host eggs, and perhaps nestlings (Arcese et al. 1996), by cowbirds might contribute to lower dickcissel productivity in grazed CP2 fields. However, it is noteworthy that even

within the epicenter of cowbirds' geographic range in the Great Plains, cowbird density and parasitism frequency exhibit much local and regional variation (Herkert et al. 2003, Jensen and Cully 2005, Igl and Johnson 2007).

Lastly, although all four focal species nested across all grazing and CP treatments, mourning dove nests were approximately twice as common in CP25 compared to CP2 plantings, irrespective of grazing treatment (mean number of nests \pm SE): 3.50 \pm 0.64 in CP2 grazed vs. 6.08 \pm 0.59 CP25 grazed; 3.26 \pm 0.46 in CP2 ungrazed vs. 7.26 \pm 0.84 in CP25 ungrazed. Although I am unsure why mourning doves apparently nested more frequently in CP25 than CP2 (assuming equal detectability), one obvious difference between the practices is that CP25 requires incorporation of more forb species into seeding mixtures. Alternatively, CP25 fields were established more recently than CP2 fields, younger CRP fields have been found to have less grass cover and more bare ground (Millenbah et al. 1996), and mourning doves nest on bare ground or areas of thin litter in grasslands (HMK, WEJ, pers. observ.). Regardless of the mechanism, this pattern might be of interest to managers of mourning dove populations.

MANAGEMENT IMPLICATIONS

Within the CRP early successional habitat is maintained by disturbances, which occur at least once mid-way through 10-15-year CRP contracts. Burning, disking, inter-seeding, and occasionally grazing and haying are options landowners can employ to fulfill requirements of mid-contract management and improve wildlife habitat. However, grazing within the CRP is currently prohibited in CP25, is discouraged though landowner payment reduction in CP2, and can only occur outside of designated avian nesting

seasons (USDA 2011). Before implementing or reducing the restriction of grazing in CRP, policy makers should consider the impacts cattle may cause to nesting grassland birds. Although grazing in CRP across Kansas had few effects on grassland bird abundance (B. Wilson, unpubl. data), my results indicate grazing can be potentially detrimental to reproductive success of some grassland bird species. However, negative consequences of grazing tended to be weak, so short-term, mid-contract grazing, as might be implemented on CRP fields, may not have long-lasting effects on grassland bird reproduction. Variation in patterns I observed between CP2 vs. CP25 fields could have been due to indirect effects of seed mixes or the older ages of CP2 fields on animal communities (e.g., predators and their prey); thus, it is unclear what mechanisms might have driven the observed patterns between these two CRP conservation practices. Further monitoring of bird responses to CP2 vs. CP25 (the latter having been especially targeted toward wildlife habitat improvement [USDA 2010]) is warranted. Consequences to not only grassland birds but also the grassland vegetation, the invertebrate community (e.g., pollinators, insects as wildlife forage), and other aspects of biodiversity should be considered when making policy decisions pertaining to management of CRP fields.

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Table 1-1. List of all candidate models and their notations for models of daily nest survival and brood parasitism.

Covariate of interest	Model notation		
Tier I: Management practice			
Grazing treatment	Grazed		
Conservation practice	СР		
Grazing treatment and conservation practice	Grazed+CP		
Grazing treatment and conservation practice interaction	Grazed*CP		
Grazing treatment and year interaction	Grazed*Year		
Grazing treatment and year interaction with conservation	Grazed*Year + CP		
practice			
Grazing treatment and year interaction with grazing	Grazed*CP + Grazed*Year		
treatment and conservation practice interaction			
Tier II: Nest-site characteristics			
Visual obstruction of vegetation (cm)	VOR		
Concealment (cm) ^a	Conceal		
Parasitism ^{†b,c}	Para		
Visual obstruction of vegetation and parasitism ^{b,c}	VOR+Para		
Tier III: Time			
Day of nesting season ^d	Time		
Quadratic day of nesting season ^d	Time ²		
Year	Year		
Day of nesting season ^d and year	Time+Year		

Nest age⁺

Age

^a Covariate not included in DSR model sets. For Dickcissels concealment is VOR minus

nest height for all other species it is VOR.

^b Not included for models of Mourning Dove daily nest survival.

^c Covariate not included in brood parasitism model sets

^d For DSR analysis date nest found active used. For brood parasitism and intensity

analysis initiation date used.

[†]Whether or not nest contained Brown-headed Cowbird offspring.

⁺ Time dependent covariate calculated based on age of nest on the first day of the nesting season

Table 1-2.	Comprehensiv	ve list of avian	species found	l nesting on	Conservation	Reserve Progr	am grasslands	in central
Kansas, U	SA, 2017–2019	9.						

Species	Scientific name	2017	2018	2019	Total	% Total
Dickcissel	Spiza americana	295	322	413	1030	51.40
Mourning dove	Zenaida macroura	177	129	126	432	21.56
Meadowlark	Sturnella spp.	58	83	107	248	12.38
Grasshopper sparrow	Ammodramus savannarum	36	53	62	151	7.53
Red-winged blackbird	Agelaius phoeniceus	11	22	28	61	3.04
Ring-necked pheasant	Phasianus colchicus	10	10	4	24	1.20
Common nighthawk	Chordeiles minor	8	4	4	16	0.80
Northern bobwhite	Colinus virginianus	3	5	1	9	0.45
Blue-winged teal	Anas discors	0	0	7	7	0.35
Lark sparrow	Chondestes grammacus	0	0	6	6	0.30
Brown thrasher	Toxostoma rufum	3	0	0	3	0.15

Field sparrow	Spizella pusilla	0	0	3	3	0.15
American robin	Turdus migratorius	0	0	1	2	0.10
Eastern kingbird	Tyrannus	0	1	1	2	0.10
Mallard	Anas platyrhynchos	1	1	0	2	0.10
Upland sandpiper	Bartramia longicauda	1	0	1	2	0.10
Wild turkey	Meleagris gallopavo	0	0	2	2	0.10
American goldfinch	Spinus tristis	0	1	0	1	0.05
Common yellowthroat	Geothlypis trichas	0	0	1	1	0.05
Killdeer	Charadrius vociferous	0	1	0	1	0.05
Wilson's phalarope	Phalaropus tricolor	0	0	1	1	0.05

Table 1-3. Number of nests for focal species detected in Conservation Reserve Program treatment types (grazed, Y; ungrazed, N; CP2, CP25) in central Kansas, USA, 2017–2019.

		Species					
Grazed	СР		Mourning		Grasshopper		
Treatment	treatment	Dickcissel	Dove	Meadowlark	Sparrow		
N	2	336	72	50	17		
Ν	25	277	148	55	27		
Y	2	167	74	63	25		
Y	25	250	138	80	82		

Table 1-4. Model selection results for tiered model sets management practice, nest-site characteristics, and time with respect to daily nest survival rate of dickcissel, mourning dove, meadowlark, and grasshopper sparrow nests in CRP fields in central Kansas, USA, 2017–2019. ΔAIC_c = change in Akaike's Information Criterion corrected for small sample size between top ranked model and given model. w_i = probability of a model given the data and compared to other models in model set. Values for models in each tier are given only when $\Delta AIC_c \leq 4$. **Bold** values indicate the best-supported (lowest AIC_c) model from each tier, per species. See Table 1-1 for predictor notation.

Mourning					Grassl	nopper			
		Dick	cissel	Do	ove	Meado	owlark	Spar	row
Model Set	Model predictors	ΔAIC_c	Wi	ΔAIC_c	Wi	ΔAIC_c	Wi	ΔAIC_c	Wi
I. Management	Constant	3.507	0.065	0.000	0.513	0.887	0.199	0.000	0.438
practice	СР			2.000	0.189	2.080	0.110	1.914	0.168
	Grazed			1.959	0.193	0.000	0.311	1.541	0.203
	Grazed + CP			3.966	0.071	1.329	0.160	3.379	0.081
	Grazed * CP					2.964	0.071		
	Grazed * Yr	0.000	0.377			2.398	0.094		

	Grazed $*$ Yr + CP	1.972	0.141						
	Grazed * CP + Grazed * Yr	0.517	0.291						
II. Nest-site	Constant	3.41	0.09	0.000	0.580	0.000	0.446		
characteristics	VOR			0.646	0.420	0.560	0.337	0.000	0.844
	Para ^a	0.000	0.502			1.437	0.217		
	VOR + Para ^{a,b}	0.701	0.354						
III. Time	Constant							0.000	0.274
	Time							1.923	0.105
	Time ²							3.535	0.047
	Year							0.543	0.209
	Time + Yr	0.000	0.718					2.534	0.077
	$Time^2 + Yr$	1.997	0.265						
	Age			0.000	1.000	0.000	0.856	0.109	0.260

^a Mourning Doves are not suitable hosts for Brown-headed Cowbirds, therefore model not included in analysis for this species

^b Parasitism by Brown-headed Cowbirds correlated with VOR for Meadowlark and Grasshopper Sparrows, therefore not included in same model

Table 1-5. Parameter estimates (β) and 85% confidence intervals averaged across competitive daily nest survival models ($\Delta AIC_c \le 4$) within model sets management practice, nest-site characteristics and time for grassland birds in central Kansas, USA, 2017–2019. See Tables 1-1 for notation descriptions. Negative values of β for categorical predictors indicate that daily nest survival in, e.g., grazed (Y), was lower than ungrazed (N) treatment, lower in CP25 vs. CP2, etc. Parameter estimates for years (2018, 2019) are relative to responses in 2017.

Model Set	Parameter	Dickcissel	Mourning Dove	Meadowlark	Grasshopper Sparrow
Management	Grazed (Y vs. N)	-0.074 (-0.354, 0.207)	0.026 (-0.156, 0.209)	-0.352 (-0.716, 0.012)	-0.179 (-0.554, 0.195)
practice	CP (25 vs. 2)	-0.101 (-0.269, 0.068)	-0.006 (-0.199, 0.186)	-0.169 (-0.456, 0.117)	0.089 (-0.283, 0.460)
	Yr: 2018	-0.163 (-0.354, 0.028)		-0.450 (-0.928, 0.027)	
	Yr: 2019	0.224 (0.030, 0.417)		-0.388 (-0.874, 0.097)	
	Grazed * CP	0.318 (0.073, 0.563)		0.210 (-0.286, 0.707)	
	Grazed * Yr: 2018	-0.038 (-0.343, 0.267)		0.238 (-0.419, 0.896)	
	Grazed * Yr: 2019	-0.167 (-0.469, 0.135)		0.639 (-0.012, 1.290)	
Nest-site	Para ^a (Y vs. N)	-0.193 (-0.311, -0.075)		0.143 (-0.133, 0.420)	
characteristics	VOR	0.004 (-0.001, 0.008)	0.008 (-0.002, 0.018)	0.016 (-0.003, 0.035)	0.047 (0.018, 0.076)

Time	Time	-0.009 (-0.020, 0.002)			0.002 (-0.022, 0.027)
	Time ²	0.000 (0.000, 0.000)			0.000 (-0.001, 0.000)
	Yr: 2018	-0.202 (-0.352, -0.053)			-0.233 (-0.663, 0.196)
	Yr: 2019	0.253 (0.099, 0.407)			0.264 (-0.160, 0.688)
	Age		0.046 (0.027, 0.064)	0.034 (0.011, 0.057)	0.030 (-0.001, 0.062)

^a Mourning Doves are not suitable hosts for Brown-headed Cowbirds, therefore parameter not included in analysis for this species

Table 1-6. Model selection results from pooled competitive models for daily nest survival rate of dickcissel, mourning dove, meadowlark, and grasshopper sparrow nests in CRP fields in central Kansas, USA, 2017–2019. ΔAIC_c = change in Akaike's Information Criterion corrected for small sample size between top ranked model and given model. w_i = probability of a model given the data and compared to other models in model set. Only competitive models ($\Delta AIC_c \le 4$) are listed. See Table 1-1 for notation descriptions.

Species	Model predictors	Δ AIC _c	Wi
Dickcissel	Time + Yr + Para	0.000	0.742
	Time + Yr	3.288	0.143
Mourning dove	Age	0.000	1.000
Meadowlark	Grazed + Age	0.000	0.404
	Age	0.237	0.359
	CP + Age	1.603	0.181
Grasshopper sparrow	VOR	0.000	0.892

Table 1-7. Parameter estimates (β) and 85% confidence intervals averaged across competitive daily nest survival models (ΔAIC_c) within pooled competitive models for grassland birds in central Kansas, USA, 2017–2019. See Table 1-1 for notation descriptions. Negative β for categorical predictors indicate that daily nest survival in, e.g., grazed (Y), was lower than ungrazed (N) treatment, lower in CP25 vs. CP2, etc. Parameter estimates for years (2018, 2019) are relative to responses in 2017.

Predictor	Dickcissel	Mourning Dove	Meadowlark	Grasshopper Sparrow	
Time	-0.009 (-0.014, -0.005)				
Yr: 2018	-0.209 (-0.359, -0.060)				
Yr: 2019	0.244 (0.090, 0.398)				
Para (Y vs. N)	-0.189 (-0.307, -0.071)				
Grazed (Y vs. N)			-0.256 (-0.503, -0.009)		
Age		0.046 (0.027, 0.064)	0.033 (0.016, 0.050)		
CP (25 vs. 2)			-0.136 (-0.381, 0.109)		
VOR				0.047 (0.018, 0.076)	

Table 1-8. Model selection results from model sets management practice, nest-site characteristics and time for brown-headed cowbird parasitism probability (whether or not nests contained cowbird offspring) of dickcissel, meadowlark, and grasshopper sparrow nests in Conservation Reserve Program fields in central Kansas, USA, 2017–2019. ΔAIC_c = change in Akaike's Information Criterion corrected for small sample size between top ranked model and given model. w_i = probability of a model given the data and compared to other models in model set. Values for models in each tier are given only when $\Delta AIC_c \leq 4$. **Bold** values indicate the best-supported (lowest AIC_c) model from each tier, per species. See Table 1-1 for notation descriptions.

		Dic	Dickcissel		Meadowlark		Grasshopper Sparrow	
Model Set	Parasitism Probability	ΔAIC_{c}	Wi	ΔAICc	Wi	ΔAIC_{c}	Wi	
	Model							
I. Management	Constant	3.93	0.098	0.00	0.348	1.05	0.207	
practice	СР			0.72	0.243	2.29	0.111	
	Grazed			1.38	0.174	2.45	0.103	
	Grazed + CP			2.05	0.125	3.91	0.050	
	Grazed * CP	0.00	0.697	2.71	0.090			
	Grazed * Yr					0.00	0.350	

	Grazed * Yr + CP					2.12	0.122
	Grazed * CP + Grazed * Yr						
II. Nest-site	Constant	0.00	0.630				
characteristics	Conceal	1.06	0.370	0.00	0.999	0.00	0.903
III. Time	Constant					1.51	0.210
	Time			0.04	0.375	3.56	0.075
	Time ²	0.00	0.773	0.00	0.382		
	Year					0.00	0.447
	Time + Yr			2.37	0.117	2.05	0.160
	$Time^2 + Yr$	3.31	0.147	2.24	0.125	3.94	0.062

Table 1-9. Parameter estimates (β) and 85% confidence intervals averaged across competitive brown-headed cowbird parasitism probability models ($\Delta AIC_c \le 4$) within model sets management practice, nest-site characteristics and time for grassland birds in central Kansas, USA, 2017–2019. See Table 1-1 for notation descriptions. Negative β for categorical predictors indicate that probability of parasitism in, e.g., grazed (Y), was lower than ungrazed (N) treatment, lower in CP25 vs. CP2, etc. Parameter estimates for years (2018, 2019) are relative to responses in 2017.

Model Set	Parameter	Dickcissel	Meadowlark	Grasshopper Sparrow
Management	Grazed (Y vs. N)	0.383 (0.109, 0.657)	0.322 (-0.197, 0.842)	-0.926 (-2.363, 0.512)
practice	CP (25 vs 2)	0.215 (-0.019, 0.450)	-0.250 (-0.775, 0.274)	0.238 (-0.349, 0.825)
	Yr: 2018			-1.140 (-2.479, 0.199)
	Yr: 2019			-0.152 (-1.185, 0.882)
	Grazed * CP	-0.786 (-1.160, -0.412)	-0.691 (-1.537, 0.154)	
	Grazed * Yr: 2018			2.328 (0.644, 4.012)
	Grazed * Yr: 2019			1.995 (0.552, 3.439)
Nest-site characteristics	Conceal	0.006 (-0.003, 0.014)	-0.096 (-0.149, -0.046)	-0.071 (-0.116, -0.030)
Time	Time	0.249 (0.131, 0.367)	0.078 (-0.141, 0.295)	0.021 (-0.117, 0.159)

Time	e^2 -0.001 (-0	.001, 0.000) -0.001	(-0.001, 0.000)	0.000 (-0.001, 0.001)
Yr: 2	-0.098 (-0	0.333, 0.137) -0.494	(-1.068, 0.079)	0.297 (-0.388, 0.982)
Yr: 2	-0.133 (-0		(-0.654, 0.411)	0.958 (0.302, 1.614)

Table 1-10. Model selection results from pooled competitive models for parasitism probability of dickcissel, meadowlark, and grasshopper sparrow nests by brown-headed cowbirds in Conservation Reserve Program fields in central Kansas, USA, 2017-2019. $\Delta AIC_c =$ change in Akaike's Information Criterion corrected for small sample size between top ranked model and given model. $w_i =$ probability of a model given the data and compared to other models in model set. Only competitive models ($\Delta AIC_c \leq 4$) are listed. See Table 1-1 for notation descriptions.

Species	Parasitism Probability Model	ΔAIC_{c}	Wi
Dickcissel	Grazed * CP + Time ²	0.00	0.842
Meadowlark	Conceal + Time	0.00	0.546
	$Conceal + Time^2$	0.42	0.442
Grasshopper Sparrow	Conceal + Yr	0.00	0.340
	Conceal	0.37	0.283
	Conceal + Time	2.35	0.105
	Yr	3.32	0.065
	Grazed * Yr	3.78	0.051
Table 1-11. Parameter estimates (β) and 85% confidence intervals averaged across competitive parasitism probability models (Δ AIC_c \leq 4) within pooled competitive models for grassland birds in central Kansas, USA, 2017-2019. See Table 1-1 for notation descriptions. Negative values of β for categorical predictors indicate that probability of parasitism in, e.g., grazed (Y), was lower than ungrazed (N) treatment, lower in CP25 vs. CP2, etc. Parameter estimates for years (2018, 2019) are relative to responses in 2017.

Parameter	Dickcissel	Meadowlark	Grasshopper Sparrow	
Grazed (Y vs. N)	0.448 (0.173, 0.725)		-1.317 (-2.474, -0.161)	
CP (25 vs. 2)	0.205 (-0.031, 0.442)			
Grazed * CP	-0.806 (-1.182, -0.430)			
Time	0.250 (0.133, 0.370)	0.057 (-0.145, 0.259)	0.003 (-0.011, 0.017)	
Time ²	-0.001 (-0.001, 0.000)	-0.001 (-0.001, 0.000)		
Conceal		-0.087 (-0.125, -0.049)	-0.069 (-0.113, -0.025)	
Yr: 2018			0.099 (-0.920, 1.117)	
Yr: 2019			0.767 (-0.090, 1.623)	
Grazed * Yr: 2018			2.336 (0.654, 4.018)	
Grazed * Yr: 2019			2.002 (0.560, 3.444)	

Table 1-12. Model selection results from model set management practice, nest-site characteristics and time for brown-headed cowbird parasitism intensity (number of cowbird offspring per parasitized nest) of dickcissel, meadowlark, and grasshopper sparrow nests in Conservation Reserve Program fields in central Kansas, USA, 2017–2019. $\Delta AIC_c =$ change in Akaike's Information Criterion corrected for small sample size between top ranked model and given model. $w_i =$ probability of a model given the data and compared to other models in model set. Values for models in each tier are given only when $\Delta AIC_c \leq 4$. **Bold** values indicate the best-supported (lowest AIC_c) model from each tier, per species. See Table 1-1 for notation descriptions.

		Dickcissel		Meadowlark		Grasshopper Sparrow	
Model Set	Parasitism Intensity Model	ΔAIC_c	Wi	ΔAIC_c	Wi	ΔAIC_{c}	Wi
I. Management	Constant			0.04	0.334	0.00	0.488
practice	СР			0.00	0.341	2.14	0.167
	Grazed			1.91	.0131	1.45	0.236
	Grazed + CP			2.05	0.122	3.66	0.078
	Grazed * CP	0.09	0.488	3.55	0.058		
	Grazed * Yr						
	Grazed $*$ Yr + CP						

	Grazed * CP + Grazed * Yr	0.00	0.509				
II. Nest-site	Constant	0.00	0.732	0.00	0.735	0.00	0.743
characteristics	Conceal	2.01	0.268	2.04	0.265	2.12	0.257
III. Time	Constant	0.00	0.562	0.00	0.592	0.00	0.577
	Time	2.02	0.205	2.08	0.210	1.97	0.216
	Time ²	4.00	0.076			3.86	0.084
	Year	3.40	0.130	3.84	0.087	3.84	0.084
	Time + Yr						
	Time 2 + Yr						

Table 1-13. Parameter estimates (β) and 85% confidence intervals averaged across competitive brown-headed cowbird parasitism intensity models ($\Delta AIC_c \le 4$) within model sets management practice, nest-site characteristics and time for grassland birds in central Kansas, USA, 2017–2019. See Table 1-1 for notation descriptions. Negative values of β for categorical predictors indicate that parasitism intensity in, e.g., grazed (Y), was lower than ungrazed (N) treatment, lower in CP25 vs. CP2, etc. Parameter estimates for years (2018, 2019) are relative to responses in 2017.

Model Set	Parameter	Dickcissel	Meadowlark	Grasshopper Sparrow
Management	Grazed (Y vs. N)	0.504 (0.247, 0.760)	0.096 (-0.175, 0.367)	-0.172 (-0.470, 0.125)
practice	CP (25 vs. 2)	0.018 (-0.101, 0.137)	-0.214 (-0.484, 0.056)	0.008 (-0.309, 0.325)
	Yr: 2018	0.180 (0.026, 0.334)		
	Yr: 2019	0.160 (0.010, 0.309)		
	Grazed * CP	-0.479 (-0.663, -0.296)	-0.292 (-0.783, 0.198)	
	Grazed * Yr: 2018	-0.444 (-0.682, -0.206)		
	Grazed * Yr: 2019	-0.347 (-0.565, -0.130)		
Nest-site characteristics	Conceal	0.000 (-0.003, 0.004)	-0.004 (-0.024, 0.016)	0.003 (-0.025, 0.031)
Time	Time	0.002 (-0.030, 0.035)	-0.001 (-0.009, 0.006)	-0.015 (-0.108, 0.077)

Time ²	0.000 (0.000, 0.000)		0.000 (0.000, 0.001)
Yr: 2018	0.018 (-0.135, 0.098)	-0.147 (-0.462, 0.167)	-0.168 (-0.560, 0.224)
Yr: 2019	0.039 (-0.069, 0.148)	-0.088 (-0.365, 0.190)	-0.173 (-0.530, 0.185)

Figure 1-1. Study area in central Kansas, with Great Bend at the approximate center, which spans 12 counties: Ness, Hodgeman, Pawnee, Rush, Ellis, Russell, Barton, Stafford, Reno, Rice, Ellsworth, and McPherson.



Figure 1-2. Cowbird parasitism intensity (i.e., number of cowbird offspring per parasitized host nests) of dickcissel (light gray), grasshopper sparrow (black), and meadowlark (dark gray) nests, in central Kansas, USA, 2017–2019. Numbers above bars represent total number of nests at each intensity for a given species.



Figure 1-3. Predicted daily nest survival rate in relation to covariates from the top-ranked model within model set management practice for (A) dickcissels and (B) meadowlarks in central, Kansas, USA, 2017–2019. Open circles represent ungrazed and closed circles represent grazed fields.



Figure 1-4. Predicted daily nest survival rate in relation to covariates (A) day of nesting season, year, and (B) parasitism (i.e. whether host nests were parasitized by cowbirds) from the top-ranked model within the pooled competitive model set for dickcissels in central, Kansas, USA, 2017–2019. In B, open circles represent unparasitized and closed circles represent parasitized daily nest survival on day 35 of the nesting season.



Figure 1-5. Predicted brown-headed cowbird parasitism probability (i.e. whether host nests were parasitized by cowbirds) in relation to grazing and conservation practice (CP) from the top-ranked model within model set management practice for dickcissels in central, Kansas, USA, 2017–2019. Open circles indicate ungrazed and closed circles indicate grazed fields.



Figure 1-6. Predicted brown-headed cowbird parasitism probability (i.e. whether host nests were parasitized by cowbirds) in relation to grazing and year from the top-ranked model within model set management practice for grasshopper sparrows in central, Kansas, USA, 2017–2019. Open circles indicate ungrazed and closed circles indicate grazed fields.



Figure 1-7. Predicted probability of parasitism (i.e. whether host nests were parasitized by brown-headed cowbirds) in relation to initiation date from the top-ranked model within model set time for (A) dickcissel and (B) meadowlark nests in central Kansas, USA, 2017–2019.



Figure 1-8. Predicted parasitism intensity by brown-headed cowbirds (i.e., number of cowbird offspring per parasitized host nests) in relation to grazing regime across years in (A) conservation practice (CP) 2 and (B) CP25 from top-ranked model within model set management practice for dickcissel nests in central Kansas, USA, 2017–2019. Open circles indicate ungrazed and closed circles indicate grazed fields.



CHAPTER 2

Nestling condition of a grassland bird not associated with food availability in restored grasslands

INTRODUCTION

Food availability is generally thought to contribute substantially to reproductive investment by birds during the breeding season (Martin 1987). Within the nesting period, food can be limiting at any stage: egg formation, incubation, nestling, and/or postfledgling; however, in altricial species the greatest demand for food generally occurs during the nestling and fledgling stage, when parents must meet the food requirements of their offspring as well as themselves (Martin 1987). Manipulative food experiments, both supplementation and reduction, have shown food can limit both present and future reproductive output, through consequences to nestling survival, post-fledgling survival, and second nesting attempts by parents (Simons and Martin 1990, Rodenhouse and Holmes 1992).

Although food is limiting for breeding birds in many ecosystems (Kalinski et al. 2017, Perez et al. 2016), some authors have argued that food is superabundant for birds in grasslands, at least during the breeding season, and food does not restrict avifaunal community composition (Wiens 1974, Wiens 1977, Wiens and Rotenberry 1979). While competition-mediated food limitation might not explain low avifaunal diversity within grasslands, food may still limit reproductive output in some years. Grasslands are dynamic environments, in which climatic instability (mainly periodic drought), fire, and herbivory by large mammals interact to shape and maintain these ecosystems (Anderson

2006). Precipitation can be highly variable within grasslands, especially during the summer months (Borchert 1950). Coincident with inter-annual fluctuations in precipitation is variation in aboveground net primary production in grasslands (Yang et al. 2008). As vegetation provides habitat and food for arthropods, overall primary production can influence the diversity and abundance of arthropods (Joern and Laws 2013), which represent the main food source of most grassland birds during the breeding season. Thus, variation in arthropod food availability may be an important factor impacting survival and reproductive success in grassland birds, whose populations have experienced declines in recent decades (Brennan and Kuvlesky 2005, Sauer et al. 2014).

The ability of altricial birds to produce high quality offspring of physiological condition sufficient for survival depends to a large extent on parental care, specifically the amount and quality of food provided by parents (Balshine 2012). Thus, higher arthropod abundance might allow greater parental provisioning of nestlings in insectivorous birds and, consequently, improved physiological condition of nestlings that translates into improved survival. Young fed more often and/or with larger food resources tend to weigh more (Simons and Martin 1990), have higher nestling growth rates (Blancher and Robertson 1987), and be in better condition at fledging (Wilkin et al. 2009). Generally, young that fledge in good condition have higher post-fledgling survival (Vitz and Rodewald 2011, Jones et al. 2017), especially in relation to condition late in the nesting season (Naef-Daenzer et al. 2001), which suggests that conditions during development carry over to later life stages and affect survival. Consequently, food availability might affect habitat selection in birds (Johnson and Sherry 2001) and nestlings have been found to be in better condition when in habitats with more food

resources (Bańbura et al 2011, Herring et al. 2011, but see Adams et al. 1994, Zalik and Strong 2008).

Few studies have tested the effects of variable food availability on nestling condition in grassland birds and some grassland habitats may be of higher quality than others. For instance, the diversity and abundance of plants (Jog et al. 2006) and insects (McIntyre and Thompson 2003) are higher in native prairie compared to grasslands restored through the Conservation Reserve Program (CRP), a federally subsidized habitat restoration program. Nonetheless, CRP serves as important habitat for grassland birds, with many species exhibiting positive population trends in areas with high acreages of enrollment in the program (Herkert 1997, 1998, 2007). Although studies have investigated reproductive success within CRP (Granfors et al. 1996, McCoy et al. 1999), none have investigated variability in nestling condition of grassland birds in relation to availability of arthropods as food, which undoubtedly varies among CRP fields, perhaps in relation to CRP management or time since planting. Thus, I investigated nestling condition in the dickcissel (Spiza americana), a common grassland bird species in the central Great Plains of North America, with respect to food availability within CRP grasslands. I predicted that CRP fields with higher arthropod biomass should support nestlings that are in better condition (i.e., higher mass, structural growth metrics, and plasma triglycerides).

METHODS

Study Area

The study area was in central Kansas in 36 CRP fields across 10 counties—Ness, Hodgeman, Pawnee, Rush, Barton, Stafford, Reno, Rice, Ellsworth, and McPherson (Fig. 1-1). Conservation Reserve Program fields are abundant across the study area (13.3% of landscape), with a majority (45.5%) of CRP acreage enrolled in conservation practice 25 (CP25; rare and declining habitat). Fields within CP25 contain a high diversity seed mixture—containing a minimum of 15 species, with five native grass species and 10 native forbs—compared to other practices, such as conservation practice 2 (CP2; USDA 2012). Conservation practice 2 (CP2; establishment of permanent native grasses) constitutes 22.0% of CRP acreage in the area, with enrolled fields planted using a minimum of three species—two native grasses and one forb (USDA 2012). Both CP2 and CP25 fields were included in my study and it is important to note that the fields differed in time since establishment as well as the required seed mixture. Conservation practice 2 appeared with the 1985 Farm Bill, while CP25 was first authorized by the 1996 Farm Bill. In my study, CP2 fields were established for a mean of 22.22 ± 2.23 (SE) years versus 11.89 ± 0.79 (SE) years for CP25 fields (means \pm SE calculated using 9 fields with known establishment history in each CP; USDA, unpubl. data). Among both CPs, vegetation was dominated by little bluestem (Schizachyrium scoparium), big bluestem (Andropogon gerardi), and sideoats grama (Bouteloua curtipendula). The regional climate is humid continental, with mean monthly temperatures ranging from a minimum of -6° C in January to a maximum of 34.2° C in July (1981-2010 monthly normals at Great Bend, Kansas weather station [Arguez et al. 2010]). Precipitation increases from west to east across the study area from 56 - 76 cm, with annual precipitation averaging 67.8 cm in the center of the study area, of which almost half falls from May-July (Arguez

et. al. 2010). To best encompass the precipitation gradient of central Kansas, the study area, which was centered around Great Bend, was aligned roughly perpendicular to the average angle of precipitation isoclines (1981-2010 average; Arguez et al. 2010), so that it spanned 80.5 km across the precipitation gradient (approximately east/west) and 40.2 km parallel to the gradient (approximately north/south).

Experimental Design

My research plots, which overlapped with a larger study on the importance of grazing and plant diversity in CRP grasslands to various trophic levels, were within CP2 and CP25 fields (n = 18 fields each). A grazing treatment was applied: ungrazed or season-long grazing by domestic cattle (Bos taurus) for a total of four treatments in a factorial design. Nine of the 18 CP25 fields and eight of the CP2 fields were grazed (the imbalance due to changes in landowner planning regarding cattle grazing). The Natural Resources Conservation Service specified stocking rates designed to remove 50% of biomass during the grazing season based on field size, cattle type (cow-calf or yearling steers), and length of grazing (120 to 180 days from 1 April to 31 October). Grazing occurred during the first two years of the study (2017-18) to represent an experimental mid-contract management option and was authorized via experimental allowance from the U.S. Department of Agriculture (USDA). Two years of grazing were implemented versus a single year due to less-than-expected biomass removal on grazed fields in 2017 (Appendix A). Grazed fields tended to have shorter, sparser vegetation with more bare ground and structural heterogeneity (F. Watson, unpubl. data, Wichita State University); although, I only show general vegetative patterns among management treatments and did not perform statistical hypothesis tests, as statistical significance does not always coincide with biological significance (Johnson 1999). Fields were not grazed in 2019 to test for any residual effects of grazing one-year post-disturbance. Burning of fields varied annually, per landowner prerogative, but few fields were burned in any year. In 2017 13.9% fields were burned, whereas 2.8% fields were burned in 2018 and 5.6% in 2019. Therefore, I did not explicitly incorporate fire regime as a covariate.

The study area was divided into three sub-regions (west, central, and east), spanning the range of average precipitation (1981-2010; Arguez et al. 2010), within which approximately a third of the replicates per treatment (n = 3) were established via selection from a randomly-ordered list of fields from a USDA database. Initially, landowners were contacted to discuss the possibility of allowing access to their fields and their implementing cattle grazing. After grazing participants were found, a list of potential ungrazed fields was generated by selecting fields under the same CP within a 8.05-km radius of the grazed site but excluding fields 1-km distant for pairing similar yet independent fields. The search area around grazed sites was expanded by 8.05-km increments until a landowner with a matching CP field agreed to allow access.

All fields included in my study were ≥ 14.2 ha as determined using ArcGIS (version 10.3; ESRI, Redlands, CA) to ensure minimum area requirements for several grassland bird species were met (Winter and Faaborg 1999, Johnson and Igl 2001). Fields were also omitted if the CRP contract was established after 2012 (less than five growing seasons prior to the first growing season of data collection in 2017) or expired before 2019, as vegetation structure differs between newly established and older CRP fields (Millenbah et al. 1996), and we required access to fields through 2019. Within selected

fields, a 200-m x 300-m plot was centered within the largest interior portion of the field and oriented parallel to the longest axis of the field (Fig. 2-1). These plots were used as the focal areas for nest searches.

Nest Searching and Monitoring

I conducted nest searches on fields from mid-May to late-July over three breeding seasons (2017-2019). I searched for nests within plots and outside plots, as time allowed. Field sites were routinely visited by three separate field crews of four observers each, with each crew visiting each of 12 sites twice per week. Crews visited four sites per day with nest searching and monitoring occurring on the first two sites visited (starting at 06:00) and only nest monitoring occurring on the latter two sites visited. When logistically feasible, site visitation order was rotated throughout the seasons to intersperse visitation times.

I located nests of grassland bird species predominately through rope dragging, which induces female birds to flush from nests. A rope (2 cm diameter, 15-m length) was pulled between two people with the rope perpendicular to the path of travel and gliding atop the vegetative canopy. Starting location for rope dragging was rotated each visit to maximize search area covered. Nests found incidentally via flushing incubating females while walking through sites, or found via parental behavior (carrying building material, food, intense chipping), were also included. Once nests were located, geographic coordinates of nests were obtained using a Global Positioning System unit (GPS; Garmin eTrex, Garmin Ltd., Olathe, KS) and marked with blue vinyl flagging tied to vegetation 5 m from the nest in any direction for open-cup nesters and facing nest openings for dome nesters. Another flag was tied at a 90° arc from the original flagging to form a triangle with the nest forming the right angle. Wooden garden stakes were placed below flagging as a redundant marker in case flagging was removed by cattle. I monitored nests every 3-4 days until young fledged or the nesting attempt failed. I considered a nesting attempt successful if at least one host nestling fledged. Cues, such as age of brood at last visit, parental activity proximate to the nest, presence of undiscarded fecal sacs, and fledglings observed nearby, were all indicative of successful nests. Signs of disturbance to nest material or removal of nest contents prior to suitable fledging age were considered indicators of nest failure.

Nestling condition indices

I determined nestling age from nest visitation history and nestling characteristics (e.g. feather tract development, eyes open/closed). Between 4- and 6-days post-hatch, I measured nestling mass (g) using a digital scale (0.01g) and tarsus (mm) and wing chord (mm) lengths using dial calipers. From these measurements I calculated three morphological indicators of nutritional condition in nestling dickcissels. Use of morphological measures to indicate condition are well established in the literature (for review see Labocha and Hays 2012). One measure was simply nestling mass corrected to a standardized age, which allowed comparison between nestlings weighted at different ages. The standardized mass was calculated using a regression equation (mass = 1.83*age + 2.32, generated from my data) of nestling mass (dependent variable) against age for all nestlings weighed during the study. To correct the observed values for individual nestlings, I determined the difference between the observed and predicted mass on the day of measurement and added (or subtracted) the difference to (or subtracted from) the predicted mass at day 6 post-hatch (13.32 g).

The second condition index I used was the residuals of nesting mass vs. tarsus length, with nestlings heavier relative to their size at any age assumed to be in better condition. Data from nestling at all ages were used to develop the regression equation (mass = 0.74*tarsus – 1.81). From the regression model I determined the difference between the observed and expected mass at a given tarsus length, with a residual > 0 representing a mass above that predicted for body size (i.e., good condition) and a residual < 0 signifying a mass below that expected for its body size (i.e., poor condition).

The final morphological condition index I used was variation in tarsus length within broods. Greater variation in this metric might be expected under greater nutritional stress (i.e., lower prey availability, parasitism; Merino and Potti 1995). To do this, I calculated the standard deviation of tarsus lengths among nestlings in each nest. Nests with only one nestling were excluded from this index.

Blood sampling and processing

Metabolites, specifically triglycerides, increase in the plasma during food adsorption and transport fat through the bloodstream to adipose tissue and working organs (Jenni-Eiermann and Jenni 1994). Thus, triglycerides represent a measure of fat deposition and were sampled accordingly as an additional proxy of condition. I collected blood samples from a maximum of 2 dickcissel nestlings per nest. Samples were collected from the brachial vein of nestlings in heparinized capillary tubes (70 µl). Following blood collection, I stored samples on ice until they could be centrifuged later the same day. Plasma was stored in microcentrifuge tubes at -20°C until it could be transferred to a -80 °C unit to await metabolite analysis.

Plasma triglycerides (TRIG) were assayed on an Eon microplate spectrophotometer (Biotek Instruments, Inc., Winooski, VT). TRIG concentration (total triglyceride – free triglyceride) was measured in duplicate in 400 μ l flat-bottom, 96-well polystyrene microplates using colorimetric endpoint assays. I diluted plasma 1:1 with saline. In 2017, some samples had insufficient plasma to run in duplicate. When this occurred, I combined samples from nestlings on the same field to obtain the average TRIG (n = 2). To each 5 µl sample I added 240 µl free glycerol reagent (Sigma F6428, MilliporeSigma, Darmstadt, Germany), which reacts with glycerol in plasma, and warmed samples for 10 min at 37°C, after which absorbance was measured at 540 and 750 nm. Then I added 60 µl triglyceride reagent (Sigma T2449, MilliporeSigma, Darmstadt, Germany), which breaks apart ester bonds in triglycerides, and incubated samples for 10 min at 37°C, and measured absorbance at 540 and 750 nm. I calculated TRIG concentration based on standard curves obtained from a serial dilution of glycerol standard (Sigma G7793, MilliporeSigma, Darmstadt, Germany). I averaged TRIG concentration from across wells and calculated CV. Any TRIG concentrations with CV \geq 25% were removed from analysis because of excessive variability in readings. When TRIG values exceeded 5.64mM, I further diluted samples when enough sample remained and re-ran TRIG. Otherwise, readings were removed from analysis because calculated TRIG exceeded the standard curve. Plasma metabolites are a relatively new technique to investigate condition in birds (Kalinski et al. 2017), especially in nestlings. To my

knowledge, no study has investigated plasma metabolites of passerine nestlings in relation to prey abundance in grassland birds.

Prey abundance surveys

Abundance of insect prey was measured at each field using four, 10 m sweep-net transects, with individual transects oriented 50 m from the center of each 200×300 m plot in the direction of plot corners and separated by 90° (Fig. 2-1). Observers sampled each field twice during the field season, with the first sampling period from 23 May -22June 2017–2019 and second sampling period from 24 June – 25 July 2017–2019. Between 07:30 and 18:30, observers used 38 cm diameter canvas sweep-nets to target the top 25% of vegetation in an 180° arc. All sweep-netting was done into the wind, with maximum wind speed not exceeding 36 kmh. Generally, sweep-netting occurred on clear to mostly clear days, but given logistical constraints some sweep-netting occurred on mostly cloudy (14.35%) and overcast (23.61%) days. Sweeping was synchronized with observer's walking pace, so that one sweep was taken with each step. Contents of sweeps were emptied into containers and kept on ice in the field. I stored samples in a freezer until they could be sorted, identified, and weighted. I did not sort prey into size classes to represent potential prey with varying energy supplies (Mitchell et al. 2012), but assume that overall biomass per field is proportionate to prey available to dickcissels.

Observers separated arthropods from debris and identified arthropods to order. Observers oven-dried each sample for 72 hrs. at 60°C and weighed the dried biomass (0.001g). As orthopterans are the preferred food provision for dickcissel nestlings (Mitchell et al. 2012), I used orthopteran biomass summed across sweep transects from both sampling periods as a measure of food availability for each field. As an additional measure of prey availability, we used total arthropod biomass summed for all arthropod taxa across sweep transects from both sampling periods.

Statistical analysis

I performed all analyses in the statistical program R (ver. 3.6.1; R Core Team 2019) using package lme4 (Bates et al. 2015). Using an information theoretic approach (Burnham and Anderson 2002), I evaluated and ranked models using AIC_c. Among competitive models (Δ AIC_c \leq 4; Burnham and Anderson 2011), I accounted for model uncertainty by using model averaging among models containing the focal parameter (Burnham and Anderson 2002) and assessed parameter effects using 85% confidence intervals (Arnold 2010). To determine whether management practice impacted arthropod biomass, I ran generalized-linear mixed models with CP, grazing, and year as fixed effects and field as a random effect. In addition to stand-alone fixed effects and constant (intercept-only) models, I considered the potential interaction between grazing and CP, grazing and year, and grazing and year with CP as an additive effect.

Nestling condition was assessed in two ways: (1) via averages per field in relation to field-level arthropod biomass and (2) at the level of each nestling while accounting for nest-level covariates. For the first approach, I obtained average condition measures for a field by calculating the mean of each condition index (age-corrected mass, mass/tarsus residuals, TRIG, and variation in tarsus length) for a given year. Field level condition indices were evaluated in relation to orthopteran biomass, arthropod biomass, and the interaction between measures of arthropod biomass and year (to account for effects of inter-annual variation in arthropod abundance), with field includes as a random effect to account for sampling on the same field multiple years.

To assess condition indices at the nestling level, I ran generalized-linear mixed models, using all possible additive combinations of food availability and brood characteristics, as in addition to food availability, brood size can affect nestling condition though intra-brood competition (Ricklefs 1982). For brood characteristics, I included brood size at time of sampling, including nestling brown-headed cowbirds (*Molothrus ater*, cowbird hereafter), maximum brood size during the nestling period, parasitism by cowbirds (containing cowbird nestlings or not), and maximum number of cowbird nestlings as covariates. For any models containing measures of arthropod biomass, I created an additional model with an interaction between measures of arthropod biomass and year. I included nest within fields as random effects for age-corrected mass, mass/tarsus residuals and TRIG. For variation in tarsus, I included field as a random effect.

As preliminary analysis revealed some response variables were not normally distributed (using Shapiro-Wilk test), I transformed variables using package rcompanion (Mangiafico 2019), which used Tukey's Ladder of Powers to determine the best transformation to obtain normality (Tukey 1977). Subsequently, arthropod biomass and orthopteran biomass were log transformed. Field-level means of age-corrected mass, TRIG, and standard deviation of tarsus were transformed using $-1/x^{1.5}$, log*x*, and $x^{0.5}$, respectively. Individual condition indices of age-corrected mass, TRIG, and standard deviation of tarsus were transformed using $x^{1.5}$, log*x*, and $x^{0.5}$, respectively.

RESULTS

I found 1030 dickcissel nests, of which offspring in 288 nests survived to the nestling stage allowing measurements of nestling condition. From 6 June – 27 July 2017–2019, I collected morphometrics from 756 nestlings and collected blood samples from 407 nestlings. Among-field variation in orthopteran and arthropod biomass ranged from 0.007 - 3.405 g and 0.086 - 3.601 g, respectively. Orthopterans accounted for 38.5, 37.1, and 29.3% of all arthropod biomass in 2017, 2018, and 2019 respectively.

Effect of management practice on arthropod biomass

The constant model best explained variation in orthopteran biomass and arthropod biomass (Table 2-1). Grazing and CP explained some variation in orthopteran and arthropod biomass ($\Delta AIC_c \leq 4$; Table 2-1), but the 85% CIs for these predictors tended toward symmetry around 0, indicating weak effects (Table 2-2). Overall arthropod biomass was slightly lower in grazed compared to ungrazed fields, but the grazing model had nearly 5 times less support (w_i) than the constant model and could be considered uninformative (Arnold 2010). Orthopteran biomass varied slightly (85% CIs overlapped zero) among years, being higher in 2017 than 2018 or 2019 (Table 2-2). As orthopteran biomass and total arthropod biomass did not differ among management practices, I did not include management practices in analyses of nestling condition indices.

Field-level nestling condition

I found neither orthopteran biomass nor arthropod biomass to be important predictors of field-level means of age-corrected mass, mass/tarsus residuals, TRIG, and standard deviation of tarsus, as the constant model was the most competitive model for these condition indices (Table 2-3). Orthopteran biomass and arthropod biomass were competitive ($\Delta AIC_c \le 4$) in explaining average mass/tarsus residuals of nestlings on fields, although models containing arthropod measures had approximately half the support of the constant model, with predictor estimates close to or overlapping zero (Table 2-4). Additionally, little variation in mass/tarsus residuals was explained by orthopteran biomass ($r^2 = 0.039$) or arthropod biomass ($r^2 = 0.020$).

Nestling-level condition

A combination of brood size, cowbird parasitism, and arthropod biomass interacting with year best explained age-corrected nestling mass; however, the fixedeffects (marginal $r^2 = 0.026$) and entire model (conditional $r^2 = 0.249$) explained little variation in age-corrected nestling mass. No model was strongly competitive given the most competitive model had only 1.4 times more support than that of the second-best model (Table 2-5). Although multiple predictors explained some variation in agecorrected mass of nestlings, only brood size and maximum brood size had a strong effect (Table 2-6). Nestlings in larger broods tended to have lower age-corrected mass than nestlings in smaller broods (Table 2-6). The best supported model for mass/tarsus residuals of nestlings, contained brood size and had 4.8 times the support of a less parsimonious model including brood size and cowbird parasitism (Table 2-5). Brood size alone explained little variation in mass/tarsus residuals (marginal $r^2 = 0.045$); however, brood size along with random effects explained more variation in mass/tarsus residuals (conditional $r^2 = 0.454$). Mass/tarsus residuals related negatively to brood size and
positively to parasitism for dickcissel nestlings, though the effect of the latter was weak given the 85% CI overlapped zero (Table 2-6). No models proved any better than the constant model at explaining TRIG of dickcissel nestlings, although an interaction between overall arthropod biomass and year was included in the competitive model set (Table 2-5). The latter model had 3 times less support than the constant model and all 85% CI of parameter effects overlapped zero (Table 2-6), indicating weak effects. Within-brood variation in tarsus length was best explained by brood size (Table 2-5), with nestlings within a nest having more variation in tarsus length in larger broods (Table 2-6). In general, however, brood size and the entire model did not strongly explain within-brood variation in tarsus length (marginal $r^2 = 0.089$ and conditional $r^2 = 0.175$, respectively).

DISCUSSION

As orthopteran biomass and total arthropod biomass did not differ between management practices, I inferred that potential food for dickcissel nestlings was not affected by grazing or conservation practice. Despite among-field variation in orthopteran and arthropod biomass, average condition indices of nestlings showed no significant patterns with my metric of prey availability. The apparent competitive environment within individual nests (brood size) was the only significant predictor of nestling condition measures. Larger broods tended to have lower age-corrected mass, lower mass/tarsus residuals, and greater variation in structural size. Thus, my results indicated nestling condition did not respond to prey availability, but instead to characteristics of broods. Although bison (*Bos bison*) grazing has been found to increase orthopteran densities in tallgrass prairie (Joern 2004), I found no such effect of grazing on orthopterans, or arthropods overall, in CRP fields. However, Joern's (2004) study found the positive response of grasshoppers to over a decade of bison grazing, considerably longer than the grazing regime implemented in my study. It could also be that low densities of arthropods or orthopterans overall were unable to respond to short-term effects of grazing in my study (Branson and Sword 2010). In any case, there appeared to be no short-term response of arthropod biomass to cattle grazing in CRP fields or to the longer-term CRP planting practices. Despite any differences in initial floristic diversity in the seeding mixes for CP25 fields, this apparently did not affect arthropod biomass.

Contrary to my prediction, I found food availability had no effect on nestling condition, as examined at the field or individual level. However, food supplementation experiments in a variety of habitats have demonstrated positive changes to nestling body condition in the presence of additional food (Bańbura et al. 2011, Haley and Rosenberg 2013, Simons and Martin 1990). Similarly, declines in growth rates of black-throated blue warblers (*Setophaga caerulescens*) coincided with natural decline in caterpillar abundance (Rodenhouse and Holmes 1992). The influence of food availability on nutritional state of nestlings can also be seen in other un-manipulated breeding populations of wild birds. Nestling condition indices, such as TRIG and body mass, have been found to be higher in habitats with greater prey abundance (Kaliński et al 2017, Teglhoj 2017). However, food might not be a limiting resource to reproduction in some habitats, such as grasslands. Ruffino et al. (2014) found that the positive effects of food supplementation on reproductive responses was less noticeable when natural availably of food resources started off high in the environment. In grasslands, reduction of grasshopper densities around nests of vesper sparrow (*Pooecetes gramineus*) did not affect nestling growth rate or mass before fledging but induced longer flights by provisioning parents during foraging bouts (Adams et al. 1994). As birds are highly mobile and able to fly far distances to forage, they can potentially compensate for variability in food abundance by adjusting their foraging behavior.

Alternatively, lack of a detectable pattern between food availability and reproduction may be a result of sampling deficiencies. I collected arthropod biomass on a limited area within larger sample plots for nests within fields, and arthropods were sampled only twice during the breeding season. Prey abundance on large tracts of land may fluctuate across space and time, thus my measures of prey availability might not have adequately represented those at individual nests during the nestling stage. However, Van Vliet (2017) collected prey around individual nests of savannah sparrow (*Passerculus sandwichensis*) nesting in agricultural and non-agricultural fields and similarly found no correlation between arthropod biomass and nestling condition. Nonetheless, frequent collection of arthropod prey throughout the nesting season and near individual nests may reveal within-field variability that could better explain condition indices of dickcissel nestlings and perhaps other grassland birds.

As sibling competition is thought to be a dominant force shaping growth rates in birds (Ricklefs 1982), competition among nest-mates for limited food resources delivered by parents likely explains the observed negative pattern detected between brood size and condition indices of nestlings. For example, studies carrying out brood size manipulations have consistently demonstrated detrimental effects on nestling condition in enlarged broods, with nestlings in experimentally enlarged broods having lower body mass and mass/tarsus residuals (Bańbura et al. 2008, Bourgeon et al. 2011, Losdat et al. 2010, Neuenschwander et al. 2003), even though parents can adjust food delivery rates to accommodate larger or smaller broods (Neuenschwander et al. 2003). Additionally, enlarged broods tended (albeit not significantly) to have greater variation in body mass within nests (Losdat et al 2010), which resembles the greater variation in tarsus length I observed in larger broods. These results seem to suggest that parents may be more limited in their capacity to adequately provide all nestlings in large broods with similar quantities of food rather than limited by the availability of food on the landscape.

Overall, my research suggests site-level food availability is not limiting to dickcissel nestlings in CRP fields during the breeding season and provides support for the hypothesis that food is superabundant during the breeding season for grassland birds (Wiens 1974). However, longer-term research might reveal that food is indeed limiting in some years under different environmental conditions. As the food superabundance hypothesis argues, harsh years, generally as a result of drought, might negatively impact bird populations (Wiens 1974, Zimmerman 1992), perhaps due to suppressed food availability. Thus, under drought conditions, food may limit reproduction in grassland birds as parents must increase time searching and compete for scarce food resources. Species richness in grassland bird communities has been found to correlate positively with grasshopper species richness (Hamer et al. 2006), suggesting some food limitation to grassland bird community structure. Given concerns regarding global insect declines (Sánchez-Bayo and Wyckhuys 2019), further study is warranted on potential limitation of invertebrate food to consumers, such as grassland birds.

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Table 2-1. Model selection results for measures of orthopteran and overall arthropod biomass in relation to management practices (grazed vs. ungrazed by cattle; CP2 vs. CP25) in Conservation Reserve Program fields in central Kansas, USA, 2017-2019. **Bold** indicates top model (lowest AIC_c) for each condition index.

	Orthoptera	n biomass	Arthropod biomas		
Model	ΔAIC_c	Wi	ΔAIC_c	Wi	
Constant	0.00	0.501	0.00	0.669	
Grazed	2.84	0.121	3.09	0.143	
СР	2.29	0.160	3.47	0.118	
Year	2.38	0.152	5.76	0.038	
Grazed + CP	5.17	.038	6.53	0.025	
Grazed * CP	6.28	0.022	8.95	0.008	
Grazed * Year	9.55	0.004	15.47	0.000	
Grazed * Year + CP	12.07	0.001	19.10	0.000	
Grazed * CP + Grazed * Year	13.37	0.001	21.70	0.000	

Table 2-2. Parameter estimates (β) and 85% confidence intervals averaged across competitive models ($\Delta AIC_c \le 4$) for measures of orthopteran and overall arthropod biomass in relation to management practices (grazed vs. ungrazed by cattle ; CP2 vs. CP25) in Conservation Reserve Program fields in central Kansas, USA, 2017-2019. Negative β for categorical predictors indicate that measures of arthropod biomass in, e.g., grazed (Y), was lower than ungrazed (N), lower in CP25 vs. CP2, etc. Parameter estimates for years (2018, 2019) are relative to responses in 2017.

Parameter	Orthopteran Biomass	Arthropod biomass
Grazed (Y vs. N)	0.060 (-0.345, 0.466)	-0.149 (-0.397, 0.099)
CP (25 vs. 2)	0.215 (-0.186, 0.616)	0.106 (-0.143, 0.355)
Year 2018	-0.280 (-0.596, 0.036)	
Year 2019	-0.471 (-0.787, -0.155)	

Table 2-3. Model selection results for field level condition indices in relation to measures of orthopteran and overall arthropod biomass in Conservation Reserve Program fields in central Kansas, USA, 2017-2019. **Bold** indicates top model (lowest AIC_c) for each condition index.

	Age-correc	cted Mass	Mass/tarsus	s residuals	TRIG ^a Con	centration	Variation	in Tarsus
Model	ΔAIC_c	Wi	ΔAIC_c	Wi	ΔAIC_c	Wi	ΔAIC_c	Wi
Constant	0.00	0.995	0	0.514	0.00	0.891	0.00	0.842
Orthopteran biomass	11.92	0.003	1.27	0.272	6.47	0.035	5.66	0.050
Arthropod biomass	12.15	0.002	1.87	0.201	5.01	0.073	4.13	0.107
Orthopteran biomass * Year	69.24	0.000	8.97	0.006	17.01	0.001	21.00	0.000
Arthropod biomass * Year	68.18	0.000	8.41	0.008	13.89	0.001	12.91	0.001

^aPlasma triglycerides.

Table 2-4. Parameter estimates (β) and 85% confidence intervals averaged across competitive models (ΔAIC_c) for field-level mass/tarsus residuals in relation to measures of orthopteran and overall arthropod biomass in Conservation Reserve Program fields in central Kansas, USA, 2017-2019.

Parameter		β (85% CI)
Orthopteran biomass	-0.238	(-0.433, -0.043)
Arthropod biomass	-0.273	(-0.592, 0.046)

Table 2-5. Competitive models ($\Delta AIC_c \le 4$) for individual nestling condition indices in relation to measures of orthopteran and overall arthropod biomass and brood size in Conservation Reserve Program fields in central Kansas, USA, 2017-2019.

Model	ΔAIC_c	Wi
Age-corrected mass		
Brood size + parasitism + arthropod biomass * year	0.00	0.165
Max brood size + parasitism + arthropod biomass * year	0.70	0.116
Brood size + max cowbirds + arthropod biomass * year	1.02	0.099
Brood size + arthropod biomass * year	1.28	0.087
Max brood size + arthropod biomass * year	1.54	0.076
Max brood size + max cowbird + arthropod biomass * year	1.69	0.071
Brood size + parasitism + orthopteran biomass * year	3.08	0.035
Brood size + parasitism	3.46	0.026
Max brood size + parasitism + orthopteran biomass * year	3.61	0.027
Brood size + parasitism + arthropod biomass	3.88	0.024
Mass/tarsus residuals		
Brood size	0	0.558
Brood size + Parasitism	3.12	0.117
TRIG ^a		
Constant	0	0.525
Arthropod biomass * Year	2.2	0.174
Variation in tarsus		

0 0.752

Brood size

^aPlasma triglycerides.

Table 2-6. Parameter estimates (β) and 85% confidence intervals averaged across competitive models ($\Delta AIC_c \leq 4$) for individual condition indices in relation measures of orthopteran and overall arthropod biomass and brood size in Conservation Reserve Program fields in central Kansas, USA, 2017-2019. Negative β for categorical predictors indicate that nestling condition in parasitized nests (Y) was lower than un-parasitized nests (N). Parameter estimates for years (2018, 2019) are relative to responses in 2017.

Parameter		β (85% CI)			
Age-corrected mass					
Arthropod biomass	-0.520	(-2.563, 1.523)			
Year: 2018	1.790	(-1.098, 4.677)			
Year: 2019	1.288	(-1.174, 3.750)			
Brood size	-1.644	(-2.315, -0.974)			
Parasitism (Y vs. N)	-1.175	(-2.964, 0.614)			
Arthropod biomass * Year: 2018	0.504	(-2.390, 3.398)			
Arthropod biomass * Year: 2019	0.468	(-2.624, 3.560)			
Max brood size	-1.700	(-2.410, -0.989)			
Max cowbirds	-0.677	(-1.885, 0.530)			
Orthopteran biomass	-0.002	(-1.311, 1.307)			
Orthopteran biomass * Year: 2018	0.094	(-1.927, 2.116)			
Orthopteran biomass * Year: 2019	-0.109	(-1.837, 1.619)			
Mass/tarsus residuals					

Brood size	-0.343	(-0.449, -0.238)
Parasitism (Y vs. N)	0.118	(-0.161, 0.396)
TRIG ^a		
Arthropod biomass	-0.061	(-0.202, 0.081)
Year: 2018	0.01	(-0.182, 0.202)
Year: 2019	0.409	(0.249, 0.569)
Arthropod biomass * Year: 2018	0.059	(-0.134, 0.253)
Arthropod biomass * Year: 2019	0.224	(0.018,0.429)
Variation in tarsus		
Brood size	0.134	(0.093, 0.175)
^a Plasma triglycerides.		

Fig. 2-1. Example of a focal plot (200-m x 300-m) oriented along the longest axis of the CRP field with yellow points representing perimeter points used for navigation during nest searching. Red points represent approximate starting locations for sweep-net transects.





Appendix A. Habitat characteristics (mean \pm SE) in and surrounding Conservation Reserve Program fields at 36 study sites in central Kansas, 2017–2019. An equal number of sites were established in one of two conservation practices, CP2 or CP25. Within each practice, sites were either grazed by cattle (n = 8 CP2; n = 9 CP25) or ungrazed (n = 10 CP2; n = 9 CP25).

		Ung	razed	Grazed		
Habitat variable	Year	CP2	CP25	CP2	CP25	
Grass cover ^a	2017	64.431 ± 4.358	72.646 ± 5.287	54.272 ± 5.419	59.449 ± 3.715	
	2018	72.935 ± 5.241	80.147 ± 3.465	68.998 ± 5.379	69.432 ± 5.315	
	2019	66.770 ± 2.337	66.378 ± 4.969	66.407 ± 5.147	71.863 ± 2.935	
Forb cover ^b	2017	9.907 ± 1.972	11.38 ± 3.170	10.673 ± 3.719	8.592 ± 1.330	
	2018	15.092 ± 3.130	12.201 ± 3.686	12.65 ± 2.034	13.749 ± 2.485	
	2019	14.077 ± 2.767	14.003 ± 3.597	14.994 ± 4.012	14.911 ± 3.098	
Shrub cover ^c	2017	0.635 ± 0.303	0.262 ± 0.179	0.197 ± 0.128	0.122 ± 0.098	
	2018	0.510 ± 0.411	0.534 ± 0.47	0.073 ± 0.049	0.099 ± 0.099	
	2019	0.297 ± 0.230	0.998 ± 0.915	0.076 ± 0.053	0.079 ± 0.079	
Grass height ^d	2017	48.493 ± 1.915	42.763 ± 2.009	38.74 ± 2.174	40.331 ± 2.737	

	2018	44.191 ± 2.805	41.509 ± 1.966	34.195 ± 2.420	33.081 ± 1.984
	2019	50.304 ± 2.419	44.525 ± 2.718	39.349 ± 1.842	37.190 ± 1.830
Forb height ^e	2017	18.363 ± 1.713	13.858 ± 1.166	13.97 ± 1.422	15.613 ± 1.514
	2018	19.364 ± 1.506	15.666 ± 1.571	15.253 ± 1.046	16.329 ± 1.858
	2019	21.715 ± 1.625	15.84 ± 1.779	17.540 ± 1.644	18.556 ± 1.544
Shrub height ^f	2017	5.056 ± 2.167	1.667 ± 1.059	1.250 ± 0.735	2.099 ± 1.208
	2018	2.278 ± 1.838	1.296 ± 0.953	0.903 ± 0.506	0.926 ± 0.926
	2019	2.194 ± 1.757	2.099 ± 1.334	1.111 ± 0.757	1.076 ± 1.076
Vegetation structure ^g	2017	0.342 ± 0.024	0.356 ± 0.018	0.246 ± 0.026	0.244 ± 0.016
	2018	0.389 ± 0.034	0.343 ± 0.027	0.240 ± 0.0240	0.240 ± 0.023
	2019	0.445 ± 0.028	0.384 ± 0.021	0.334 ± 0.0220	0.288 ± 0.027
Site heterogeneity ^h	2017	0.286 ± 0.025	0.253 ± 0.028	0.413 ± 0.038	0.438 ± 0.030
	2018	0.330 ± 0.046	0.293 ± 0.027	0.437 ± 0.036	0.463 ± 0.032
	2019	0.287 ± 0.029	0.353 ± 0.043	0.402 ± 0.043	0.398 ± 0.045
Bare ground ⁱ	2017	0.561 ± 0.278	0.321 ± 0.161	2.052 ± 0.810	3.341 ± 1.601

	2018	3.388 ± 1.809	0.544 ± 0.299	2.444 ± 0.599	3.622 ± 1.226
	2019	1.137 ± 0.517	3.316 ± 1.969	2.591 ± 0.805	2.897 ± 0.942
Litter depth ^j	2017	5.130 ± 0.338	3.011 ± 0.636	1.623 ± 0.391	3.108 ± 1.007
	2018	3.846 ± 0.714	3.399 ± 0.479	2.207 ± 0.452	2.136 ± 0.256
	2019	5.848 ± 0.747	4.492 ± 1.400	3.818 ± 0.587	3.629 ± 0.531
Summer biomass ^k	2017	234.169 ± 24.279	259.832 ± 23.578	170.668 ± 21.937	198.988 ± 22.960
	2018	226.296 ± 22.974	212.040 ± 21.489	169.507 ± 20.735	157.530 ± 14.300
	2019	239.173 ± 15.545	202.962 ± 16.060	188.764 ± 13.056	167.736 ± 15.993
CV of summer biomass ¹	2017	0.358 ± 0.048	0.341 ± 0.032	0.323 ± 0.077	0.402 ± 0.045
	2018	0.364 ± 0.061	0.362 ± 0.029	0.366 ± 0.063	0.434 ± 0.068
	2019	0.430 ± 0.057	0.377 ± 0.082	0.402 ± 0.064	0.297 ± 0.052
Late summer biomass ^m	2018	219.960 ± 15.883	224.642 ± 16.217	172.012 ± 13.016	203.149 ± 19.334
CV of late summer biomass ⁿ	2018	0.267 ± 0.042	0.258 ± 0.032	0.311 ± 0.035	0.479 ± 0.071
Woodland in landscape ^o	2017	0.014 ± 0.004	0.031 ± 0.018	0.020 ± 0.009	0.028 ± 0.012
Grassland in landscape ^p	2017	0.568 ± 0.051	0.469 ± 0.051	0.493 ± 0.034	0.652 ± 0.064

^aMean percent cover of grasses (adjusted for observer height; 0s included) (F. Watson, unpubl. data, Wichita State University).

^bMean percent cover of forbs adjusted for observer height, 0s included (F. Watson, unpubl. data, Wichita State University). ^cMean percent cover of shrubs adjusted for observer height, 0s included (F. Watson, unpubl. data, Wichita State University). ^dMean estimated height (cm) of grasses, 0s included; values binned to nearest 5 (F. Watson, unpubl. data, Wichita State University). ^eMean estimated height (cm) of forbs, 0s included; values binned to nearest 5 (F. Watson, unpubl. data, Wichita State University). ^fMean estimated height (cm) of shrubs, 0s included; values binned to nearest 5 (F. Watson, unpubl. data, Wichita State University). ^gMean proportion of space occupied by vegetation in two photos of a 1 × 0.5 m² backstop to create an image of the vegetation of the nine 1 m² sampling areas per field (F. Watson, unpubl. data, Wichita State University).

^hMean coefficient of variation (CV) of space occupied by vegetation in two photos of a 1x0.5m² backstop to create an image of the vegetation of the nine 1 m² sampling areas per field (F. Watson, unpubl. data, Wichita State University).

ⁱMean percent cover of bare ground adjusted for observer height (F. Watson, unpubl. data, Wichita State University). ^jMean depth of vegetation litter (cm; F. Watson, unpubl. data, Wichita State University).

^kMean total biomass (g; live and dead) collected from five $1 \times 0.5 \text{ m}^2$ quadrats in each field (F. Watson, unpubl. data, Wichita State University).

¹Mean coefficient of variance (CV) of total biomass (g; live and dead) collected from five $1 \times 0.5 \text{ m}^2$ quadrats in each field (F. Watson, unpubl. data, Wichita State University).

^mMean total late season (collected in August and September 2018) biomass (g; live and dead) collected from five 1×0.5 m² quadrats in each field (F. Watson, unpubl. data, Wichita State University).

ⁿMean coefficient of variance (CV) of total late season (collected in August and September 2018) biomass (g; live and dead) collected from five 1×0.5 m² quadrats in each field (F. Watson, unpubl. data, Wichita State University).

^oMean percent woodland within 1 km of the survey plot border. Measured from remote sensing imagery and quantified using ArcGIS 10.6 (ESRI, Redlands, CA).

^pMean percent grassland within 1 km of the survey plot border. Measured from remote sensing imagery and quantified using ArcGIS 10.6 (ESRI, Redlands, CA).

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