The Interactive Effects of Annual Climatic Variability and Rangeland Management on the Reproductive Success of Dickcissels (*Spiza americana*)

Lauren A. Spahr

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Acceptance of Senior Honors Thesis

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____
Norm Reichenbach, Ph.D.
Thesis Chair

____
Gene Sattler, Ph.D.
Committee Member

____
Jillian Ross, Ph.D.
Committee Member

____
David E. Schweitzer, Ph.D.
Assistant Honors Director

____
Date

Abstract

Grassland songbird populations have declined due to poor rangeland management and habitat fragmentation. Few studies have taken into account variation in climatic conditions in tallgrass prairie systems when determining the factors contributing to songbird reproductive success. During a six year study we measured reproductive success in Dickcissels on five rangeland treatments. We estimated daily survival rates (DSRs) and linked estimates of daily survival to rangeland management type and climate data. DSRs were best predicted by the model including mean temperature, winter season precipitation, and interactions, which had 7.5 times more support than the constant model. Mean annual temperature was negatively correlated with daily survival rates. Thus climate conditions play important roles in the health and stability of grassland songbird populations.

Patterns in current populations of grassland songbirds are heavily influenced by the past history of the tallgrass prairie, the rangeland management treatments used in the prairie, and the natural history of the birds themselves.

History of Grassland Songbird Populations and Land Management

The Dickcissel (*Spiza americana*) is a grassland songbird that inhabits tallgrass prairies throughout the Midwest. Dickcissel populations are of interest because of the declines they, along with other grassland songbird species, have experienced over the past century. These declines are linked quite clearly with the tallgrass prairie ecosystem, which has also experienced considerable decreases in size and quality (Vickery et al., 1999). Songbird population declines are due to several factors, including the conversion of prairie to cropland, the fragmentation of the ecosystem, and decreased habitat quality due to poor land management schemes. Thus in order to understand the ecological factors that affect Dickcissel populations, it is necessary to discuss the ecological system they inhabit.

One of the largest factors in reducing grassland songbird populations has been the significant reduction of their habitat. It is estimated that prior to settlement by humans, there were 162 million hectares of prairie throughout the Great Plains region, of which 1.6 - 29.2 million hectares are left (Samson & Knopf, 1994). Much of this land has been converted to cropland, and while some species have adapted to this modified habitat, many have not. Cropland does provide some benefits, such as food sources, but lacks the vegetative structure that most grassland bird species require for nesting.

What little tallgrass prairie remains is highly fragmented and several grassland songbirds have been shown to have area-preference when selecting territory – smaller fragments are avoided in favor of larger ones (Herkert, 1994). This damages the infrastructure of songbird populations, although Dickcissels were the only species found that had no preference for either large or small fragments. Also, Brown-headed Cowbirds (*Molothrus ater*) (hereafter, cowbirds) are obligate brood parasites that have been shown to have negative effects on Dickcissels and other grassland songbirds (Zimmerman, 1983). As a species, cowbirds have thrived near increasing cattle populations in the Great Plains and have become more stationary, rather than moving with roaming bison herds. The combination of concentrating host nests in small fragments, and concentrating cowbird populations has made host species increasingly susceptible to parasitism.

Lastly, much of the prairie grassland has been controlled with different management schemes and used for grazing cattle, which has decreased habitat quality. The most popular of these is known as intensive-early stocking, or annual burning and grazing (ABG). It involves burning the entire pasture early in the spring and then stocking it with cow-calf pairs. This treatment severely decreases the vegetative heterogeneity of the landscape by promoting grasses over shrubs and herbaceous plants (Gibson & Hulbert, 1987). This is helpful for cattle-owners because it increases the amount of nutritious forage available on their land; however it has a negative effect on birds because it decreases the amount of dead leaf litter and forbs available for building nests. In 2001, a new rangeland management scheme, patch-burn grazing (PBG), had been suggested as a method to increase vegetative heterogeneity and still provide cattle with nutritious forage (Fuhlendorf & Engle, 2001). The method proposes dividing a pasture into several ‘patches’ that are burned rotationally, rather than all at once. Not only does this leave some areas of the pasture with the proper materials for nesting, but it also provides areas for cattle to graze and birds to forage. Currently, several studies are underway testing the effectiveness of this method in increasing reproductive success and decreasing parasitism by cowbirds.

Natural History of the Dickcissel

The Dickcissel is a sparrow-sized passerine in the family Cardinalidae. Two particularly unique field marks include the bright yellow breast and belly, as well as the black throat patch in breeding males. The back and wings are chestnut, and the crown and nape are gray with a yellow eyestripe. Females are drabber, with a brown head, diminished yellow on their ventral side, and no black throat patch. Juveniles mimic the coloration of the female until fully grown (Temple, 2002).

Dickcissels can be monogamous within each breeding season although polygamous males have been noted. Mating occurs primarily in the spring, as does nest construction (Temple, 2002). Open-cup nests are typically built 15-20 cm (6-8 inches) above the ground and located in a forb such as leadplant or false-indigo. The nest is usually covered by vegetation, and three to five blue eggs are normally laid; however, there can be between one and nine cowbird eggs also present (differentiated by coloration, which is tan with darker speckles). Eggs are usually incubated for 12-14 days, and after hatching the young remain in the nest for seven to ten days (Sandercock, Hewett, & Kosciuch, 2008). Nestlings are able to open their eyes about five days after hatching, but even prior to this they will beg for food at the slightest disturbance to the nest. Cowbird nestlings are slightly larger than Dickcissel young when first hatched; furthermore, the differential in size increases as they grow. Young of both species can be differentiated by the bill and rictal flanges of the mouth, which are white in cowbirds but yellow in Dickcissels (Temple, 2002). Fledglings of both species remain near the nest and beg for food, and both parents are usually involved in feeding the nestlings and fledglings.

Young Dickcissels are predominantly fed insects, while adult Dickcissels feed on seeds as well (Temple, 2002). One study found that Dickcissel young are primarily fed grasshoppers, along with the occasional spider or caterpillar (Mitchell, Riffell, Burger, & Vilella, 2012). Adults typically forage on the ground, often disappearing into the vegetation, and then reappearing minutes later with provisions. Dickcissels face few unusual predators as adults; however their nests are predated by many different creatures. Garter snakes and yellow-bellied racers have been observed consuming young and eggs, and box turtles are also suspected as predators (Sandercock et al., 2008; Long, Long, Knops, & Matulionis, 1965; Shochat et al., 2005). Omnivorous or carnivorous mammals are also likely predators, particularly raccoons, foxes, and coyotes. Other dangers to nests include being trampled by cattle or bison, being flooded during heavy rains, or being abandoned if too many parasite eggs or young are present.

Another important aspect that affects reproductive output is polygyny. Polygyny is a rare trait in songbirds, and Dickcissels exhibit interesting dynamics, with males seeking extra-pair copulations and females engaging in extra-pair paternity (Sousa &

Westneat, 2012). Males typically only have one nesting female on their territory although there are exceptions to this. Males seek out chances to mate with nearby females, and this is thought to increase the male's fitness. But this is at the cost of mate guarding, which may potentially decrease paternity rates within their own nests. Females also seek chances to mate with other fitter males, thus increasing the genetic variety in their clutch. Studies of Dickcissels have shown that polygynous males actually have higher within-pair paternity, larger numbers of extra-pair young, and increased nest survival (Sousa & Westneat, 2013).

The Natural History of Other Important Tallgrass Prairie Songbirds

Understanding the natural history of the Brown-headed Cowbird is also important to understanding the success of Dickcissel populations. Brown-headed Cowbirds are obligate brood parasites that parasitize most passerine species. Males spend time in large flocks because they do not attend territories and are very gregarious (Sandercock et al., 2008). Females are more solitary and spend their time finding nests to lay inordinate numbers of eggs in. Parasitism rates are above 90% in many parts of the prairie, and intensity is also high (i.e. there are more cowbird eggs than Dickcissel eggs in most nests) (Sandercock, 2014)

Henslow's Sparrows (*Ammodramus henslowii*) and Grasshopper Sparrows (*Ammodramus savannarum*) are two other species we encountered in this study. Both species build covered nests with side entrances. They are small, secretive, and non-descript, and lay clutches of 2-6 small white eggs with brown and reddish speckles (Vickery, 1996; Herkert, Vickery, & Kroodsma, 2002). Cowbird parasitism is particularly devastating to these sparrows because they are so small that even one parasite egg will likely lead to abandonment of the nest. Another species, the Eastern Meadowlark (*Sturnella magna*) also builds a covered nest with a side entrance and has large tan eggs that are speckled with brown. The young are larger than Dickcissels and cowbirds and have ivory bills and rictal flanges (Lanyon, 1995). They consistently reject cowbird eggs and have a very high nest survival rate compared to Dickcissels and other grassland songbirds. Red-winged Blackbirds (*Agelaius phoeniceus*) are another common species of songbird that rejects cowbird eggs and can be found throughout the Great Plains in semi-aquatic habitats (Yasukawa & Searcy, 1995). All of these species were encountered in the fieldwork for this study although Dickcissels were the primary focus.

Prior Work and Hypotheses

Previous studies have analyzed the effects of patch-burn grazing and other rangeland management schemes on Dickcissel reproductive success. In 2013, one project determined that neither male territory size nor female nesting site placement were negatively affected by the edge habitat created by patch-burn grazing (Biodrowski, 2013). It has also been shown that Dickcissel densities are higher in patch-burn grazing units (except in the year-of-burn unit) than in traditionally managed pastures (Sandercock, Winder, Erickson, & McNew, 2014). However, the same study was unable to find a significant difference in nest survival rates between patch-burn grazing treatments and intensive-early stocking units. In Oklahoma, studies have found better nest survival rates, as well as lower cowbird parasitism rates in patch-burn grazing managed pastures, although mean egg and fledgling numbers were not significantly different (Churchwell, Davis, Fuhlendorf, & Engle, 2008). Surprisingly, most of these studies have neglected to consider annual climatic variability in estimating of reproductive success. Tallgrass prairies throughout the Great Plains experience large amounts of fluctuation in both total annual precipitation and mean temperature. In addition, winter season precipitation and growing season precipitation can have independent and potentially antagonistic effects on vegetative structure and insect populations, but such effects have not yet been studied. The three objectives of this study will provide clarity regarding these gaps in the current body of scientific knowledge.

Objective 1: We expect to demonstrate more significant differences in survival rates between patch-burn grazing and annually burned and grazed treatments than prior studies have, due to the length of our study and because we are taking climatic variability into account.

Objective 2: If patch-burn grazing is a significantly better alternative to traditional treatments (annual burning and grazing), then we would hypothesize that patch-burn grazing survival rates in poor climate conditions will be even higher than survival rates from traditional pastures in good climatic conditions.

Objective 3: We also hypothesize that parasitism rates and intensity will drop in patch-burn grazing treatments due to the increased vegetative heterogeneity. The relationship between parasitism rates and climatic conditions can also be analyzed through this study since poorer weather is likely to reduce reproductive output of cowbirds.

Methods and Materials

Field Work

This study took place at the Konza Prairie Biological Station, which encompasses almost 3500 hectares of native tallgrass prairie, as shown in Figure 1. The land is located in the heart of the Flint Hills (39°05’ N, 96°35’ W) and has been preserved since 1971 for conservation purposes, scientific research, and public enjoyment. Konza is divided into units (separated by natural watershed boundaries) which receive a variety of treatments, including prescribed fire and grazing by cattle and bison herds.

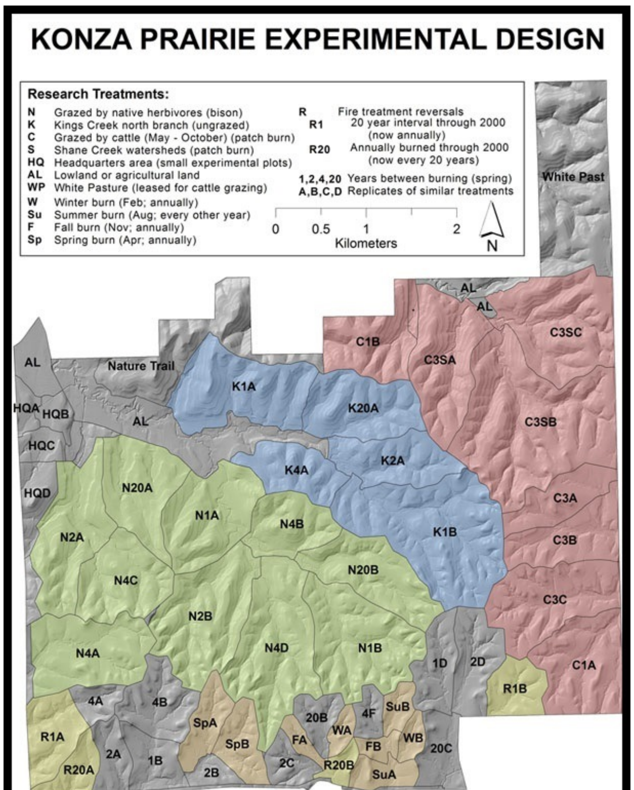

Figure 1. Layout of Konza Prairie Biological Station (KPBS). The map shows the experimental treatments undergone by different watersheds on KPBS. Our study included the watersheds C3A-C3C and C1A and 1D as controls. Retrieved from: *http://lterold.konza.ksu.edu/pages/research/kknzcor.apsx*. Copyright 2016 by the Konza LTER Program. Reproduced by permission.

We studied reproductive success of songbirds in five units, including two control units and three units that received patch-burn grazing (PBG) treatment. The control treatments consisted of watersheds that were either annually burned and grazed or annually burned and ungrazed (ABG and ABN respectively). Three watersheds (PB0, PB1, and PB2) made up the PBG treatment and received yearly grazing by cow-calf pairs and prescribed fire every three years. In any given year, PB0 was the watershed that had been burned that year, PB1 had been burned the year before, and PB2 had been burned two years prior. The cyclical nature of rotational burning resulted in an increase in dead plant matter and vegetative buildup from PB0 to PB2. Nests were located by flushing adults off the nest and other observational methods. Females were observed carrying nesting materials and giving alarm chips, and both sexes were observed bringing food to nestlings. When these behaviors occurred, the observer retreated a short distance to watch the nesting pair until they entered the nest. Nests were marked discreetly using flagging tape on vegetation that was a short distance away. Universal Transverse Mercator (UTM) coordinates were recorded for each nest, and observers were careful to minimize disturbance and scent trails left near the nests to avoid artificially increasing predation.

We returned to nests every two to three days and recorded nest contents with each visit. We noted the numbers of parasite and host eggs or young, the presence or absence of adults, the stage of the nesting cycle, and the date. We also recorded the final nest fate as successful or failed due to predation, abandonment, weather, or unknown causes (but not parasitism). We monitored nests of many different grassland songbird species although the bulk of data was from a few dominant species. Nests were monitored during the field season (mid-May to mid-August) of each year from 2011 to 2016.

For these years, we gathered data on annual temperature and precipitation amounts from regional and national sources. Due to the Konza Long Term Ecological Research Program, an on-site weather station recorded daily, monthly, and yearly weather information for the local area, which was available to the public. We also used data from the National Oceanic and Atmospheric Administration when local Konza data were unavailable. We chose three climate variables to examine in relation to reproductive success: annual mean temperature (AMT), growing season precipitation (GSP), and winter season precipitation (WSP). Growing season precipitation was defined as the rainfall received between March and August, and winter season precipitation as the rainfall received between September and February. For analytical purposes, these continuous variables were converted into categorical variables (i.e., each year was classified as hot or cool and wet or dry relative to the respective 100-year averages of the variables).

Computational Methods

To understand which variables have the greatest effects on reproductive success in grassland songbirds, we took an information theory approach, which compares models that incorporate different variables to see which most closely resembled reality. In particular, we used the Akaike information criterion (AIC) as a measure of model reliability and accuracy (Akaike, 1974). We used R to run basic analyses and the RMark package within R to run analyses from Program MARK through the R interface. RMark was used to run sets of models that incorporate different combinations of variables and generate each model's AIC value, providing a relative comparison of model integrity.

These models also predict daily survival rates (DSRs), which are the chances that a nest will survive on any given day of the nesting cycle. These daily survival rates differ from raw nest survival rates in two ways: they take into account both the bias that occurs due to not finding nests immediately upon initiation (i.e., some nests are found halfway through the nesting cycle) and the fact that failed nests are much less likely to be discovered by observers (which artificially inflates success rates).

We examined the relationships between variables, including weather (AMT, WSP, GSP), treatment (ABN, ABG, PB0, PB1, PB2), nest fate (successful, predated, abandoned, trampled, unknown), and parasitism status (parasitized or unparasitized). We also looked for patterns in the date of nest initiation and duration of the nesting cycle by converting dates into numbers using the Julian calendar. To study objective 1, we looked at models incorporating nest fate and land management treatment. For objective 2, we ran models with nest fate, treatment, and weather variables. Our weather models treated temperature and precipitation separately. Lastly, for objective 3, we looked at parasitism rates in response to weather and the direct effect upon nest fate.

Results

Sample Sizes and Initial Analyses

The majority of nests found in this study were Dickcissel nests (n = 361, 63.3%), followed by the nests of Eastern Meadowlarks (n = 98, 17.1%) and other species (n =

111, 19.6%), including Grasshopper Sparrows and Mourning Doves (*Zenaida macroura*) (see Figure 2). These data were gathered over approximately 3,000 man-hours during the six summers of the project. We chose to include only the Dickcissel and Eastern Meadowlark nests for further analyses due to small sample sizes for the other species. Across all years and treatments, the raw nest survival rates were 32.5% for the Dickcissel and 42.7% for the Eastern Meadowlark, where the nest survival rate is defined as the raw percentage of successful nests (nests that fledged young, either cowbirds or Dickcissels). Examining Dickcissel nest survival rates across the different treatments, we saw that the ABN, PBG, and ABG treatments had nest survival rates of 38.2%, 31.4%, and 28.3%, respectively. For the same treatments, the Eastern Meadowlark had nest survival rates of 77.7%, 38.8%, and 50%. Within the patch-burn grazing treatment, we saw Dickcissel nest survival rates of 37.7%, 33.6% and 21.8% for PB0, PB1, and PB2 patches, respectively. We also saw rates of 22.2%, 43.8%, and 38.6% for the Eastern Meadowlark nest survival rates within those same patches.

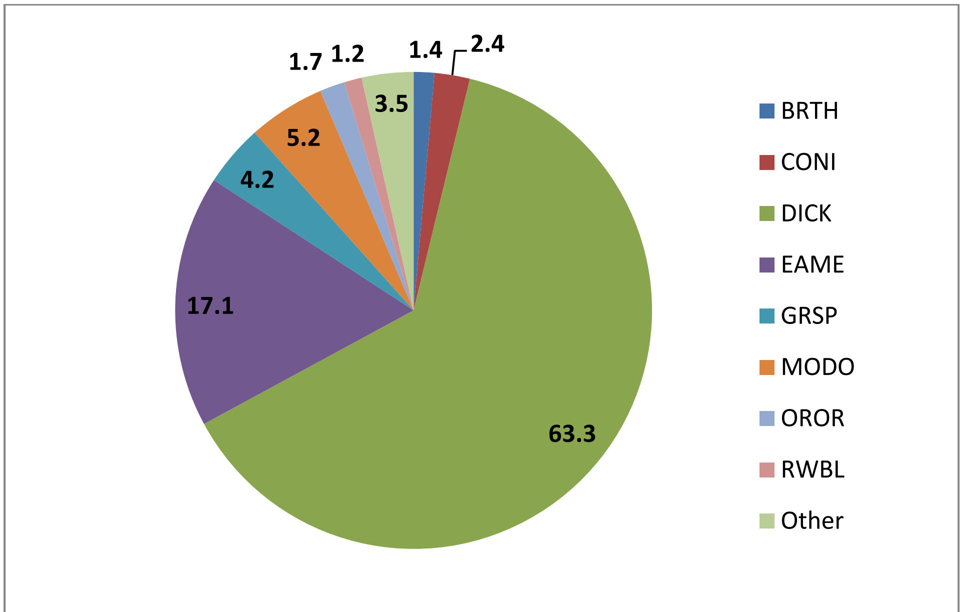

Figure 2. Species composition of sampled nests. The relative percentages for each species that made up our sample included Brown Thrashers (BRTH), Common Nighthawks (CONI), Dickcissels (DICK), Eastern Meadowlarks (EAME), Grasshopper Sparrows (GRSP), Mourning Doves (MODO), Orchard Orioles (OROR), Red-winged Blackbirds (RWBL), and other species (<1%).

Raw Nest Survival Rates in Response to Climate and Land Management

We also examined how nest survival rates differed by weather patterns by considering both Dickcissel and Eastern Meadowlark nest survival rates in comparison with mean temperature (MT), growing season precipitation (GSP), and winter season precipitation (WSP). We found that survival was higher in cool years (37.5%) than in warm years (32.4%). GSP and WSP showed opposite (but insignificant) trends: when GSP was higher, survival was lower (37.1% vs 33.1% for low GSP vs high GSP);

whereas, when WSP was higher, survival was higher (31.6% vs 38.1% for low WSP vs high WSP).

Weather also had interesting effects on the effectiveness of different land treatments in raising reproductive success. For both Dickcissels and Eastern Meadowlarks, we saw that the negative effects of warm weather were best minimized in the PBG and ABN treatments, and were the worst in the ABG treatment. The effects of growing season precipitation on all of the treatments were similar (~5% difference between dry and wet years). Lastly, winter season precipitation showed the highest contrasts between dry and wet years (10-17% difference) for the ABN and ABG treatments; however, the PBG treatment minimized this contrast with a difference of only about 3%.

We examined the raw nest survival rates to see whether there were any interesting correlations when climate variables were used differentially. We found a significant negative correlation (at $\alpha = 0.05$) between mean temperature and nest survival rate, measured over the six years of the study ($r = -0.84$, $t = 3.04$, $p = 0.038$). There was also a significant positive correlation between winter season precipitation and daily survival rate over the study period ($r = 0.84$, $t = 3.08$, $p = 0.037$) (shown in Figures 3 & 4). We looked at the relationships between daily survival rate and parasitism rates, and found a slight positive correlation, although it was not significant ($r = 0.66$, $t = 1.77$, $p = 0.15$). There was also a slight positive correlation ($r = 0.74$, $t = 2.22$, $p = 0.091$) between winter season precipitation and parasitism rates.

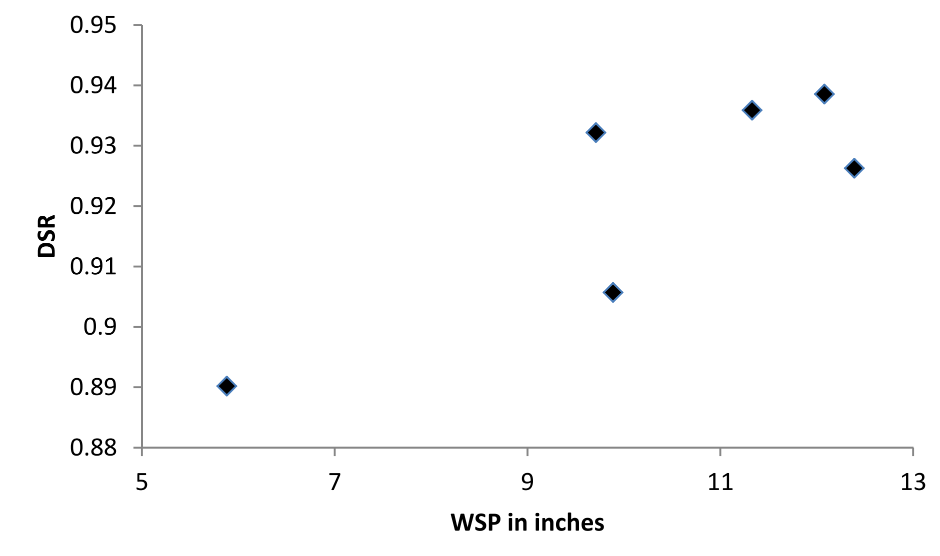

Figure 3. Correlation between WSP and DSR. We determined the relationship between winter season precipitation (WSP) and daily survival rate (DSR). Daily survival rates were obtained from the output of the Year+Treatment model restricted to patch-burn grazing units.

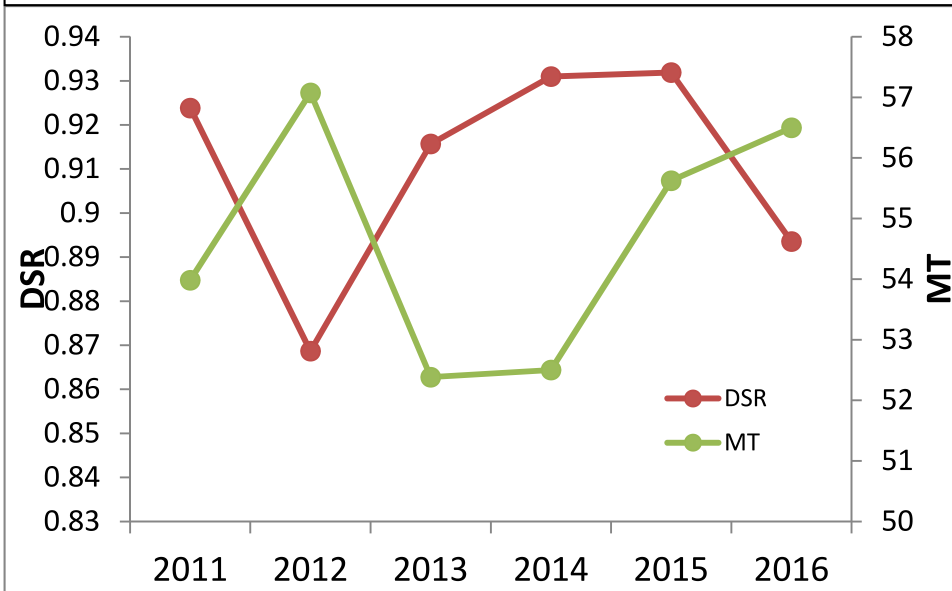

Figure 4. Trends in daily survival rate (DSR) and mean temperature (MT) across six years. We calculated daily survival rates and compared them against mean temperature for the years 2011-2016. This illustrates the mirrored relationship between extreme variability in temperature from year to year and the corresponding daily survival

Parasitism Rates and Their Effects on Survival

Parasitism rates over all six years were calculated at 85.7% and 44.8% for Dickcissels and Eastern Meadowlarks, respectively. When nests were parasitized, the nest survival rate increased from 32.4% from 42.3%. Parasitism rates did differ between treatments, with the highest parasitism rate in the ABG treatment (87.1%) and lower rates (70.4% and 77.1%) in the ABN and PBG treatments. Specifically within the PBG treatment, parasitism rates were highest in the year of burn (PB0) and decreased as time since burn increased (83.3%, 81.3% and 67.7% in PB0, PB1 and PB2, respectively).
We also checked to see whether parasitism rates of Dickcissel nests varied with annual fluctuations in temperature and precipitation. Temperature, growing season precipitation, and winter season precipitation all seemed to have mild effects with hotter, wetter conditions increasing parasitism, as shown in Figure 5. For mean temperature, parasitism increased from 83.8% in cool years to 87.2% in warm years. Similarly, growing season precipitation and winter season precipitation caused parasitism rates to increase from 83.5% and 82.5% in dry years to 87.1% and 88.8% in wet years.

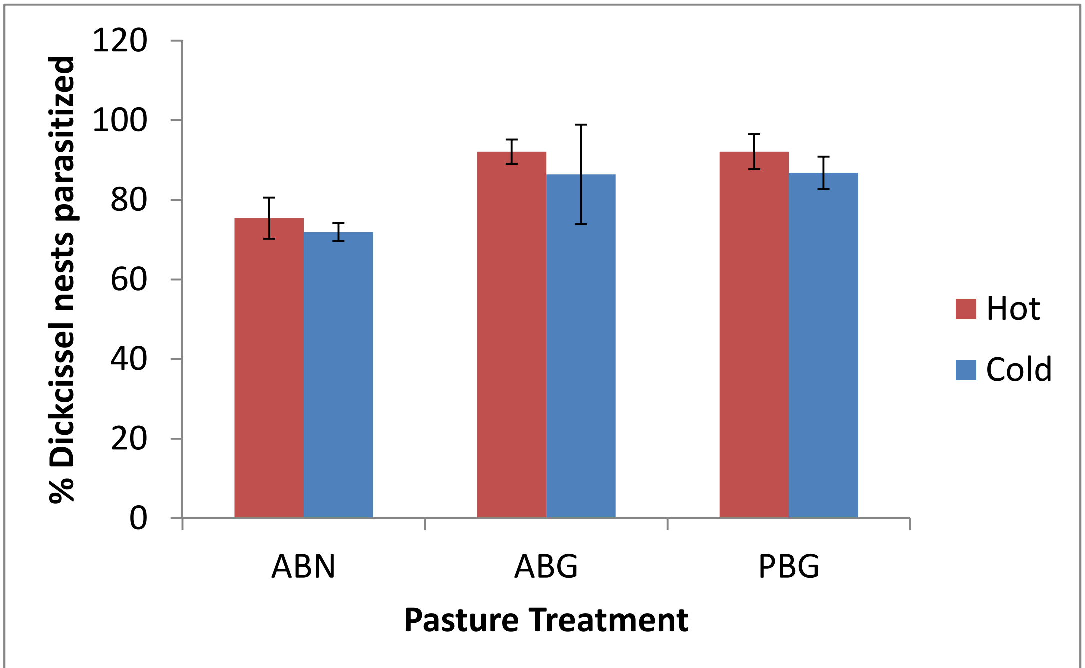

Figure 5. Comparison of parasitism rates across treatments and years varying in temperature. We measured parasitism rates in each of three treatments: annually burned and ungrazed land (ABN), annually burned and grazed land (ABG), and the patch-burn grazing treatment (PBG). These values were compared across warm and cool years, and we saw that warm years increased parasitism rates in all treatments.

Modeling Results and Predicted Daily Survival Rates

To determine which factors play the most important roles in determining reproductive success in Dickcissels and Eastern Meadowlarks, we used the RMark package to calculate daily survival rates of nests under different conditions. The models and their respective predicted daily survival rates were compared with each other using the Akaike information criterion to determine which were most reliable and accurate. We considered models that incorporated species, treatment, mean temperature, growing season precipitation and winter season precipitation as factors, as well as their interactions (shown in Table 1).

Table 1
Model arrangements for computation of daily survival rate.

Model Name	Species	Treatment	MT	GSP	WSP
Constant (~)					
Species					
Treatment					
WSP					
WSP+Treatment					
WSP*Treatment					
GSP					
GSP+Treatment					
GSP*Treatment					
GSP+WSP					
GSP*WSP					
MT					
MT+Treatment					
MT*Treatment					
MT+GSP+Treatment					
MT+WSP+Treatment					
MT*GSP*Treatment					
MT*WSP*Treatment					

Daily survival rate (DSR) was predicted from variables such as species, treatment, mean temperature (MT), growing season precipitation (GSP) and winter season precipitation (WSP). A model accounting for two variables is denoted ‘+’ and lightly shaded, while one also accounting for their interactions is denoted ‘*’ and shaded more darkly.

When this analysis focused on both Dickcissels and Eastern Meadowlarks, we found the best model to be MT*WSP, which accounted for temperature and winter season precipitation, as well as the interactions between these two variables. This model had over ten times more support than the constant model. When restricted to only Dickcissels, the same model was found to be the best, with more than 7.5 times the support of the constant model. Another highly weighted model that included both species was the Species*Treatment model which had 9 times more support than the constant model.

The daily survival rates predicted by our Treatment model were not significantly different: 0.92 for ABN treatment, 0.89 for ABG treatment, and 0.92 for the PBG treatment. However, once weather was factored in, a slight pattern developed, although again, it was not significant. For hot and cool years respectively, the ABN DSRs were 0.918 and 0.927, the ABG DSRs were 0.894 and 0.905 respectively, and the PBG DSRs were 0.921 and 0.93 respectively. When we looked at low and high winter season precipitation amounts, the ABN DSRs were 0.912 and 0.928, the ABG DSRs were 0.887 and 0.907, and the PBG DSRs were 0.918 and 0.933, respectively (see Figures 6 & 7).

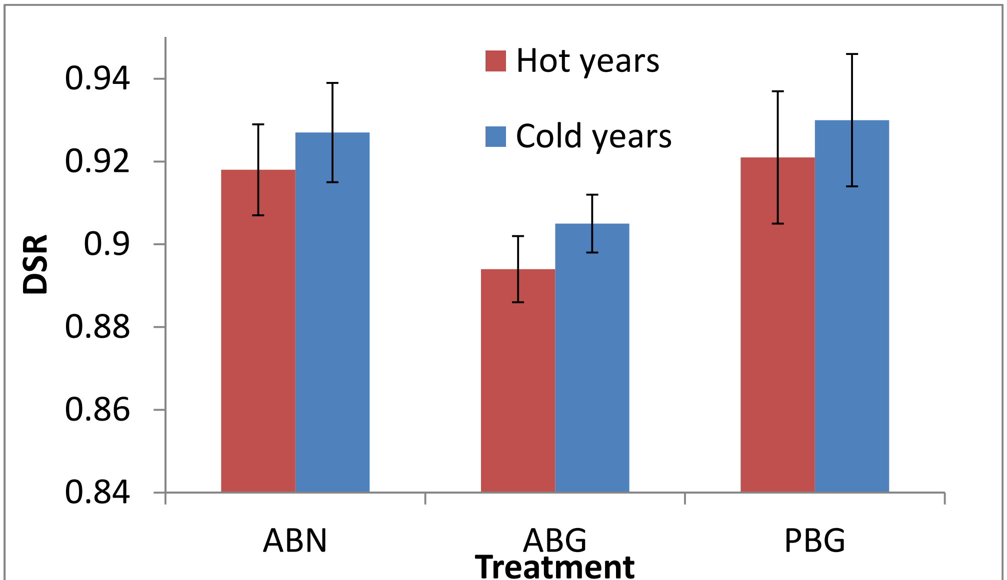

Figure 6. Comparison of daily survival rate (DSR) across treatments and temperature variance. Daily survival rates were calculated using the MTTreatmentAdd model and values from warm and cool years were contrasted. We saw that the patch-burn grazing treatment (PBG) had a higher daily survival rate in warm years than the annually burned and grazed treatment (ABG) had in cool years.

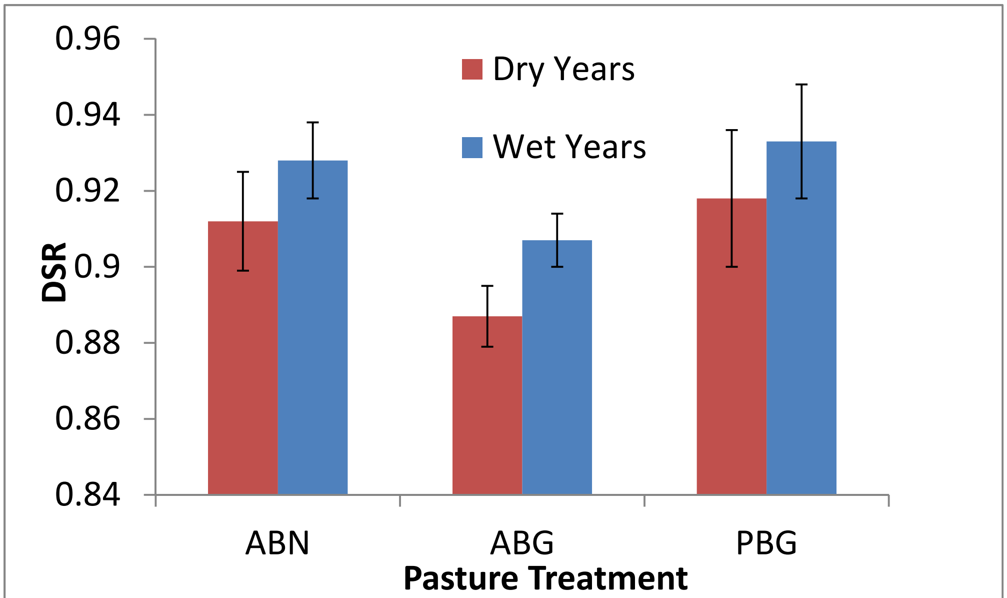

Figure 7. Comparison of daily survival rate (DSR) across treatments and precipitation variance. Daily survival rates were calculated using the WSPTreatmentAdd model and values from dry and wet years were contrasted. We saw that the patch-burn grazing treatment (PBG) also had a higher daily survival rate in dry years than the annually burned and grazed treatment (ABG) had in wet years.

Summary of Results

With few exceptions, our results showed the expected patterns, though few trends were significant. We saw that the annually burned and grazed treatment resulted in slightly lower survival rates than the patch-burn grazed treatment, both for the raw percent survival values (28.3% vs. 31.4%) and the daily survival rate outputs (0.89 vs. 0.92) of the models. Parasitism did have negative effects on reproductive success although the results did not have quite the influence expected. Parasitism rates decreased as vegetative material in the landscape increased. Cool temperatures and heavy winter season precipitation had a positive effect on reproductive success, and we also found that the reproductive success was higher in patch-burn grazing treatments during hot, dry conditions (0.92) than annually burned and grazed treatments under favorable conditions (0.91). The model that was most highly weighted for Dickcissels and Eastern Meadowlarks was the model that accounted for mean temperature, winter season precipitation, and their interactions. Lastly, we found a significant positive correlation between winter season precipitation and daily survival rate, and a significant negative correlation between mean temperature and daily survival rate.

Discussion

General Conclusions

Overall, our samples sizes were large enough to draw reasonable conclusions about population stability, size, and long-term success in the Flint Hills region. The difference in raw nest survival rates between Dickcissels and Eastern Meadowlarks (32.5% vs. 42.7%) could be due to several factors. Eastern Meadowlarks are much more likely to reject parasitic cowbird eggs, as demonstrated by parasitism rates that are half the parasitism rates of Dickcissels (45% compared with 86%). This has been found to be the case in other studies, and may be related to their larger body and nest size relative to Dickcissels (Peer, Robinson, & Herkert, 2000, Peer & Sealy, 2004).

The differences seen in raw nest survival rates between treatments do follow the expected trends, although both their significance and reliability are somewhat questionable. As mentioned above, nest survival rates that are calculated directly as a percentage of successful nests fail to account for bias that results because failed nests are less likely to be discovered than successful ones. They also do not account for nests that are found partially through the nesting cycle, and because of these two issues, raw nest survival tends to severely overestimate success rates (Rotella, 2016). Nonetheless, they still present a general picture of what is happening with the population.

The fact that we found significant positive and negative correlations between winter season precipitation, mean temperature and nest success using raw nest survival rates and daily survival rates respectively, strengthens the argument that these factors are critical to understanding nest success. When we treated climate as a categorical variable, we saw slight trends, which were strengthened and showed significance when climate was treated as a continuous variable. However, there were no significant correlations between climate and parasitism rates. This prompts an interesting question: why is it that climate plays a more important role in the reproductive output of Dickcissels than cowbirds. The answer may be related to the fact that parasitism rates only measure the initial reproductive output of cowbirds, while success rates include a time factor across the breeding season. Thus harsh climatic conditions may not reduce egg laying capacities for females, but they instead have their impact on the ability of adults to care for young (i.e., creating the right incubation temperatures and proper amounts of food).

The Effects of Treatment on Survival

We saw that the annually burned and ungrazed treatments consistently produced the highest survival rates. This makes sense because ungrazed land is likely to have a lower cowbird presence and fewer disturbances due to cattle and ranchers. Land that is managed this way also has higher amounts of grass in it because grass is selectively chosen as forage by grazing cattle over woody or herbaceous forbs (Allred, Fuhlendorf, Engle, & Elmore, 2011). The nest success in patch-burn grazing treatments over the annually burned and grazed pastures may be due to the increased vegetative heterogeneity caused by patches being in different states of re-growth after burning. Specifically within the patches, though, we observed an unexpected trend: reproductive success decreased with time since burning, and thus decreased as vegetative buildup increased. An opposite trend would be expected since grassland songbirds are known to prefer dead plant material buildup, which is used as nesting and cover (Sandercock et al., 2014). Also, since studies have shown that cattle spend 75% of their time in the most recently burned patch (PB0), it would seem that cowbird parasitism and trampling/disturbances would be highest there (Fuhlendorf & Engle, 2004). It is possible that insect communities and abundances are more favorable in areas with cattle, and this could influence adults to build nests in the area, but no studies have shown this to be the case. Due to the fact that nest densities tend to be much lower in the PB0 patch, there may also be some bias introduced by smaller sample sizes.

The Effects of Climate on Nest Survival

The interesting patterns observed with climate were unsurprising, and yet their importance in determining nest fate has been strongly underestimated until now. It is clear that cool temperatures are beneficial to nest success and this makes sense for two reasons. First, excessively high temperatures reduce moisture content in prairie environments and affect the speed of nutrient and vegetation cycling, which can have a detrimental effect on plant life (Johnson, Werner, & Guntenspergen, 2016). Change in host plant forage quality affects insect populations, which may reduce food sources for both adults and fledglings (Jonas, Wolesensky, & Joern, 2015). Second, although low temperatures could potentially be mediated by increased egg incubation times, if it is unusually warm (i.e. at lethal temperatures for the embryos), adults might not be able to reduce egg temperature below the ambient temperature and could lose their nest.

Splitting annual precipitation amounts into winter season and growing season precipitation was somewhat unconventional; however, we gained several insights by using this metric. Precipitation that falls during the winter in the Flint Hills primarily ends up in deeper soil and/or groundwater, while precipitation during the summer typically stays in the uppermost layers of soil (Chimner & Welker, 2005). This means that two entirely different categories of plants benefit, depending on when precipitation falls. Grasses and other warm-season plants benefit from growing season precipitation, while forbs and herbaceous plants, which have deeper roots, are benefited by winter rains (“Example Root,” n.d.). Winter season precipitation had the expected effect of increasing nest success (32% to 38%). What was surprising was that growing season precipitation actually had negative effects (survival decreased from 37% to 33% when GSP increased). The reasons for this remain unknown, although it is possible that large increases in rainfall during the nesting season cause nests and eggs to rot.

It appears that patch-burn grazing minimizes the effects of negative climatic conditions compared to other treatments. Particularly with respect to winter season precipitation, there was a 10-17% difference in survival between dry and wet years for the other treatments, but patch-burn grazing was able to minimize the difference to about

3%. This seems to imply that vegetative heterogeneity increases the environment's ability to withstand droughts by giving both cool-season and warm-season plants the ability to flourish in burned and unburned areas. Moreover, these changes in plant community are reflected in the cover and food availability that increase success in grassland songbirds.

The Effects of Parasitism on Survival

It is encouraging that nest survival rates only drop slightly in response to cowbird parasitism; it seems that Dickcissels and other grassland songbirds are able to cope with increased parasitism rates and intensities in areas that are grazed or burned. Other studies have found similar results. Cowbird parasitism is known to decrease throughout the breeding season, have little effect on clutch size, and not decrease success rates (Sandercock et al., 2008). The lack of a decrease in success rates may be due to the fact that we define successful nests as nests that fledge young, either host young or cowbird young. However, clutch size is generally limited to the maximum young that the adults can raise, so it is odd that Dickcissels do not lower the number of eggs laid when large numbers of cowbird eggs are laid in their nest. Rejection of cowbird eggs is rare among small grassland songbirds for two reasons. The costs of raising parasitic young appear to be minimal, and cowbirds can retaliate by destroying nests, eggs or young (Hoover & Robinson, 2007).

As expected, parasitism rates did differ between treatments, with the annually burned and grazed treatments having the highest rates. This makes sense because cattle presence and thus cowbird presence is most concentrated in grazed units, in contrast to the patch-burn grazing units, in which one patch has the worst rates, but the others that were burned longer ago have lower cattle presence and thus lower parasitism rates (68% compared to 83%). The annually burned and ungrazed treatments had the least amount of parasitism due to lack of cattle, but this is not a viable strategy for reducing cowbird parasitism because the bulk of remnant tallgrass prairie is private property of landowners who use it for feeding cattle. Parasitism rates did not vary as much with annual climatic fluctuations as expected, and warm temperatures actually seem to favor cowbird parasitism, despite having negative effects on Dickcissel reproductive success.

Discussion of Modeling Results

The results of our information theory approach to modeling reproductive success are exciting because they indicate strong climatic influences in reproductive success, even when using the unbiased daily survival rate metric. The fact that winter season precipitation is much more important than growing season precipitation seems to imply that plants with deeper root structures play a more important role in the Dickcissel life cycle than shorter rooted grasses. Since studies have shown that grasshoppers are an important food source for nestlings and fledglings, it is possible that winter season precipitation encourages growth of the plants that are food sources for desirable arthropod species (Mitchell et al., 2012).

Treatment and patch variables did not significantly factor into the top models, and this could be interpreted in two ways. First, it could be argued that treatment differences are not significant and that the induced vegetative heterogeneity only plays minor roles in affecting reproductive success. This is validated by the nearly identical daily survival rate values predicted by the treatment models (0.92, 0.89 and 0.92 for ABN, ABG and PBG treatments). Another interpretation is that climatic conditions have such a great effect that they mask treatment effects when both variables are examined at the same time. Either way, landowners and conservation scientists cannot control climatic variation, so the only positive option is to manage land in the best way possible.

The patterns surrounding treatment and climate, although again masked by the strong influences of climate, still showed the expected trends. Furthermore, we saw that even in poor climatic conditions, patch-burn grazing still produced higher daily survival rates than annual burning and grazing in good climatic conditions. The constraints of the models used did not allow for temperature and precipitation to be treated as continuous variables but rather categorical ones. It is possible that using models that incorporate climate as a continuous variable would help show these trends more strongly. This is one of the reasons that we also looked at correlations between variables, something that is not usually done in a study of this type.

Conclusions

Summary

We saw marginal differences between both raw nesting survival rates and daily survival rates in each treatment where patch-burn grazing resulted in higher success than annual burning and grazing. The heavy influences of climate may be minimizing differences between treatments. We found that winter season precipitation and mean temperature had strong positive and negative effects on daily survival rate. This was seen both in correlations among the variables and in the most highly weighted models. These models had 10 times more support than the constant model when focusing on Dickcissels, and 7.5 times more support when Eastern Meadowlarks were included. When the interactions between treatment and climate were considered, we saw the expected patterns; however, they lacked significance. Lastly, we saw that cowbird parasitism has a slightly detrimental effect on reproductive success, but it was not as serious as expected, and it appears that grassland songbirds have adapted well to the increased pressures of parasitism as cowbird populations have grown and been concentrated.

Overall, it is surprising that, given their extremely low survival rates, Dickcissels and other tallgrass prairie songbirds haven't been extirpated yet. Despite poor land management strategies, brutal parasitism rates, and adverse, highly variable climatic conditions, these Flint Hills populations continue to maintain relatively stable numbers, in contrast to national declines. However, further work is needed to better understand the factors that contribute to reproductive success.

Future Work

Specifically, a modeling system that accounts for climate as a continuous variable would probably enable us to tease apart and determine significant differences between survival rates produced by temperature and precipitation. It could potentially also make the differences between treatments under climatic conditions significant.

Also, it would be insightful to set up patch-burn grazing treatments with more patches than the traditional three to see if songbirds exhibit preferences for a certain number of years since burning. The cattle's response to this would also need to be measured, since any solution that improves Dickcissel reproductive success must also hold some reward for the landowners that implement it.

It would be helpful to have a better understanding of the food sources that Dickcissels rely on both as adults and as nestlings. Some dietary mapping between arthropods and prairie plant species has already been done in this area, but a careful observational study of provisioning behavior would elucidate differences between provisioning in Missouri and Kansas (Joern, 2005; Jonas & Joern, 2008). This could lead to better explanations for why winter season precipitation is so beneficial to nest success but growing season precipitation is not.

Finally, using different definitions of nesting success that allow both cowbird parasite success and host success to be measured and compared could help clarify the true impacts of parasitism. Traditionally, successful nests are defined as fledging at least one cowbird or host chick, but it seems likely that counting fledged cowbird young as 'successful nesting' would bias results and mask the true impact that cowbirds are having on nest productivity (Sandercock et al., 2008). Introducing an equivalent variable such as 'parasite success' that could be analyzed against treatment and climate variables might give a clearer picture of whether cowbirds and grassland songbirds respond to environmental stimuli such as climate or land quality in the same way.

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